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# Multilevel selection on social network traits differs between sexes in experimental populations of forked fungus beetles

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## Abstract

Both individual and group behavior can influence individual fitness, but multilevel selection is rarely quantified on social behaviors. Social networks provide a unique opportunity to study multilevel selection on social behaviors, as they describe complex social traits and patterns of interaction at both the individual and group levels. In this study, we used contextual analysis to measure the consequences of both individual network position and group network structure on individual fitness in experimental populations of forked fungus beetles (*Bolitotherus cornutus*) with two different resource distributions. We found that males with high individual connectivity (strength) and centrality (betweenness) had higher mating success. However, group network structure did not influence their mating success. Conversely, we found that individual network position had no effect on female reproductive success but that females in populations with many social interactions experienced lower reproductive success. The strength of individual-level selection in males and group-level selection in females intensified when resources were clumped together, showing that habitat structure influences multilevel selection. Individual and emergent group social behavior both influence variation in components of individual fitness, but impact the male mating success and female reproductive success differently, setting up intersexual conflicts over patterns of social interactions at multiple levels.

**Keywords:** *Bolitotherus cornutus*, contextual analysis, multilevel selection, resource distribution, sexual conflict, social behavior

Populations of organisms are often subdivided into groups, and this subdivision alters how evolution proceeds (Goodnight & Wade, 2000; Wade & Goodnight, 1998). Instead of acting solely on differences among individuals, selection can act on differences among subpopulations (Heisler & Damuth, 1987). When both individual and group phenotypes influence individual fitness, multilevel selection occurs (Goodnight et al., 1992; Heisler & Damuth, 1987; Okasha, 2006). Note that multilevel selection can also be understood as the effect of group phenotypes on group fitness, but here we consider the effect of group phenotypes on individual fitness (Damuth & Heisler, 1988; Okasha, 2005). Most studies of selection ignore group-level effects on individual fitness (Kingsolver et al., 2001; Siepielski et al., 2009, 2013), limiting our understanding of how group level variation impacts adaptation and evolutionary processes.

Growing empirical evidence demonstrates that individual and group traits concurrently influence individual fitness (Aspi et al., 2003; Björklund & Gustafsson, 2013; Bouwhuis et al., 2015; Donohue, 2004; Eldakar et al., 2010; Fisher et al., 2017; Laiolo & Obeso, 2012; Royle et al., 2012; Stevens et al., 1995; Tsuji, 1995; Weinig et al., 2007). These empirical studies provide important insights into how selection operates at multiple levels. We now know that patterns of multilevel selection can vary between sexes and across ecological contexts (Aspi et al., 2003; Bouwhuis et al., 2015; Fisher et

al., 2017). For example, the strength of group selection often intensifies in high-density groups (Donohue, 2004; Weinig et al., 2007). Past work also demonstrates that selection at the group level often opposes individual-level selection, likely generating constant yields in plants and sexual conflict in animals (Eldakar et al., 2010; Laiolo & Obeso, 2012; Stevens et al., 1995; Tsuji, 1995; Weinig et al., 2007).

Despite this growing interest in multilevel selection, surprisingly little research investigates multilevel selection acting on social behaviors (but see Eldakar et al. (2010), Laiolo and Obeso (2012), and Royle et al. (2012)). Social behaviors are often considered individual phenotypes, but they inherently involve interactions among individuals that generate group phenotypes (Moore et al., 1997). In many cases, social behaviors can be described as emergent properties of the group, including schooling in fish, nest building in ants, and pack hunting in wolves. With the potential for both individual and group features of social behaviors to impact variation in fitness, multilevel selection may be a powerful force shaping the evolution of social behavior. Furthermore, environmental contexts that influence how individuals share space and interact, such as the distribution of resources (He et al., 2019), are likely to modulate selection at both group and individual levels.

Social networks provide an ideal opportunity to quantify multilevel selection on social behaviors. Social networks

comprehensively describe both individual and group social behaviors that emerge from simple dyadic interactions among individuals (Croft et al., 2008). For example, social connectivity can be measured at both the individual and group levels. Highly connected groups contain maximal interactions among individuals, whereas individuals that are highly connected in their social network interact often and with many conspecifics. Group and individual social networks affect ecological and evolutionary processes differentially (Croft et al., 2016). Group-level network traits influence how information and diseases spread within groups, where individual positions within networks affect how likely an individual is to contract diseases, receive information, gain mass, secure mates, and successfully reproduce (Allen et al., 2013; Aplin et al., 2015; Oh & Badyaev, 2010; Philson et al., 2022; Solomon-Lane et al., 2015; VanderWaal et al., 2014; Webster et al., 2013). Therefore, both group-level and individual-level social network traits are expected to influence individual survival and reproductive success. Indeed, a growing number of studies demonstrate that the position that an individual occupies within a social network influences individual fitness (Bar Ziv et al., 2016; Brent et al., 2013; Cheney et al., 2016; Formica et al., 2012, 2021; Gilby et al., 2013; Lehmann et al., 2016; McDonald, 2007; Oh and Badyaev, 2010; Ryder et al., 2008; Silk et al., 2003, 2009; Wey & Blumstein, 2012; Wey et al., 2013). However, selection on group social network traits has rarely been quantified (but see Royle et al. (2012)). Contextual analysis enables the distinct evaluation of group and individual contributions of social networks to fitness by using partial regression to partition selection among levels (Goodnight et al., 1992; Heisler & Damuth, 1987).

Social networks further allow us to look at emergent group traits that cannot be reduced to the individual level. Most empirical estimates of multilevel selection measure selection on group averages of individual traits, not emergent group traits (Aspi et al., 2003; Björklund & Gustafsson, 2013; Bouwhuis et al., 2015; Donohue, 2004; Eldakar et al., 2010; Fisher et al., 2017; Laiolo & Obseo, 2012; Royle et al., 2012; Stevens et al., 1995; Tsuji, 1995; Weinig et al., 2007). The absence of emergent group traits in multilevel selection analyses has been viewed as a weakness of multilevel selection studies (reviewed in Okasha (2006)). Social network analysis describes both individual social behaviors and group social phenotypes that are more complex than simple averages of individual values. As such, social networks are ideal for performing multilevel selection analyses on emergent group traits and their individual analogs, thereby filling a critical gap in the multilevel selection literature.

In this study, we quantified multilevel selection on individual-level social network traits (individual network positions) and group-level social network traits (network structures) in experimental populations of forked fungus beetles (*Bolitotherus cornutus*). Forked fungus beetles are tenebrionid beetles that live on wood-rotting polypore bracket fungi in the forests of eastern North America (*Ganoderma applanatum*, *Ganoderma tsugae*, and *Fomes fomentarius*; Liles, 1956). Beetles consume fungus tissue, females oviposit eggs singly on fungus surfaces, larvae develop inside fungus brackets, and social interactions take place on or near fungus brackets (Liles, 1956; Pace, 1967; Wood et al., 2018). The strong association with wood-rotting bracket fungi spatially subdivides wild metapopulations of forked fungus beetles into subpopulations that live on decaying logs. Within a

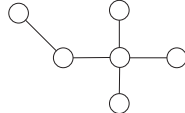
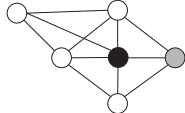
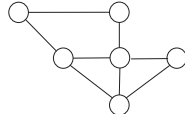
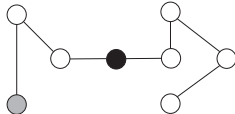
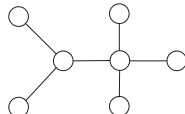
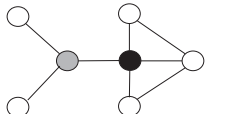
breeding season, most adult beetles remain on a single log, although gene flow is sufficient to maintain genetic homogeneity among logs (Heatwole & Heatwole, 1968; Ludwig, 2008; Wood et al., 2013).

Beetles living on the same log repeatedly interact throughout a breeding season. Social interactions include mating interactions between males and females, agonistic interactions between males competing for access to mates, and proximity interactions among neighboring beetles (Brown & Bartalon, 1986; Conner, 1988; Formica et al., 2012, 2021; Mitchem et al., 2019; Pace, 1967). Forked fungus beetles likely interact through chemical communication when in close proximity, as evidenced by beetles reorienting and waving their antennae when within a few body lengths and by females distinguishing among chemical cues of different males (Formica et al., 2017, 2021; Vilella-Pacheco et al., 2021).

Social networks built from proximity interactions among beetles within a log form non-random structures, and the positions individuals hold within these networks influence male fitness in natural populations (Formica et al., 2012, 2021). Specifically, individual connectivity (formally network strength) and individual centrality (betweenness) are repeatable traits and covary with male mating success, whereas individual cliquishness (local clustering coefficient) is not repeatable and does not consistently influence male fitness (Table 1; Formica et al., 2012, 2017, 2021). Although we know that individual male network position influences male fitness, we do not currently know the patterns of selection on female network positions in wild populations. Furthermore, partitioning selection into individual and group components of social networks in wild populations is challenging because populations vary widely in size, and both emergent social network structure and average individual fitness closely covary with population size (Formica et al., 2021).

To address the limitations of field studies and to disentangle naturally covarying influences on individual fitness, we constructed experimental populations that allowed us to control many variables that naturally differ among wild populations, such as population size, and simultaneously manipulate a key difference among natural logs in the field, the distribution of fungus resources. Previous analyses show that fungus distribution alters beetle space use behavior; when fungus brackets are clumped together, beetles concentrate their activity around resource clumps (Costello, 2020). We expect this change in space use behavior may create different selective environments and impact patterns of selection on individual and group behaviors. Specifically, theory expects intrasexual competition and the strength of selection to intensify when resources and beetles are concentrated in space (Emlen & Oring, 1977; Shuster & Wade, 2003). Applying this theory to a multilevel selection framework, we expect sexual selection in males and fecundity selection in females on both individual-level and group-level social network characteristics to intensify when fungus resources are clumped together due to increased competition for mates and egg-laying sites. We also expect individual-level and group-level selection to act in opposite directions when resources are clumped. In environments with increased intrasexual competition, we expect selection to favor individuals with competitively advantageous positions in social networks but to work against individuals in groups composed of competitive individuals due to increased aggression and decreased mating opportunities in those groups.

**Table 1.** Visual and written descriptions of the three pairs of analogous individual and group social network metrics used in the multilevel selection analyses.

Individual network position	Group network structure	Group with low network structure	Group with high network structure
<b>Strength:</b> Number of social interactions of a focal individual	<b>Network density:</b> Number of social interactions in a network out of all possible social connections		
<b>Betweenness:</b> Number of shortest paths connecting pairs of individuals that pass through a focal individual	<b>Average shortest path length:</b> Average of the shortest path lengths that connect all pairs of individuals in a network		
<b>Local clustering coefficient:</b> Proportion of social partners of a focal individual that interact with each other	<b>Global clustering coefficient:</b> Proportion of all social partners in a network that interact with each other		

*Note.* Visualizations of social networks include circles (nodes) that representing individuals and lines (edges) between circles representing social interactions between individuals. Gray nodes denote individuals with low values of each individual network metric and black nodes denote individuals with high values of each individual network metric. All measures, other than network density, are weighted by social interactions (Opsahl, 2009).

In this study, we used experimental populations of forked fungus beetles to quantify multilevel selection on individual-level and group-level social network characteristics in both sexes and in different resource distribution environments. We estimated multilevel selection on three different pairs of analogous individual-level and group-level social network metrics (Table 1). Our analyses allowed us to quantify the independent contributions to individual fitness of qualitatively similar traits at different levels of organization to individual fitness.

## Material and methods

### Experimental populations

We established 12 experimental populations of forked fungus beetles in 2.44 m x 2.44 m x 1.22 m screen enclosures at Mountain Lake Biological Station (Giles County, Virginia) (as in Cook et al., 2022; Costello et al., 2022). Each experimental population contained a 2.34 m x 0.52 m wooden shelving unit that acted as an artificial log, holding 54 polypropylene filter bags (SacO<sub>2</sub>) filled with hardwood sawdust (see Cook et al. (2022) Supplemental Material for photographs). Eighteen of these bags were inoculated with a cultivated strain of the host fungus, *Ganoderma tsugae* (Sharondale Mushroom Farm). Our cultivated *G. tsugae* produced fungus brackets of identical genotypes and minimal variation in age and bracket size.

To test whether resource distribution influences patterns of multilevel selection on social network metrics, we manipulated the distribution of fungus brackets in the experimental populations (see Costello et al. (2022) for details and photographs). Eighteen bags with fungus brackets were aggregated into three discrete clumps in each of six experimental populations (“clumped”). In the other six populations, the fungus brackets were evenly dispersed across the artificial log (“dispersed”). After 21 days of observation, we switched the resource distribution treatment for each population of beetles. At this time, we replaced the fungus brackets with newly inoculated bags, limiting fungus deterioration between experimental periods. Exposing each

experimental population to both resource distribution treatments allowed us to account for fundamental differences among our populations.

We stocked each experimental enclosure with 36 beetles. Beetles were collected from 126 different logs within a single metapopulation in Giles County, Virginia. To minimize previous social experience among beetles, we placed a maximum of three beetles collected from the same log in the same experimental population. We ensured that each population had the same sex ratio (18 males and 18 females) and similar body size distributions (average elytra length: 6.93 mm;  $F_{11,420} = 0.114$ ,  $p = .9998$ ) using structured sampling from size quantiles (see Cook et al. (2022) Supplemental Material for details). Body size was measured as the length of the elytra from an image taken on a flatbed scanner (Epson Perfection V600 Photo) using ImageJ (Abramoff et al., 2003). Five beetles died within the first three days of the experiment and were replaced with beetles of the same sex and size. Experimental population densities (one male per fungus bracket), population size, and sex ratio all fell within the ranges observed in the field (Conner, 1989; Formica et al., 2011, 2021).

We observed beetle behavior three times per day (0630 to 0930, 1430 to 1630, and 2130 to 0030) for two 3-week periods (June 27–July 17, 2018 and July 27–August 16, 2018). We acclimated beetles to their experimental enclosures for 36 hr before beginning observations. During observations, we systematically searched each population for beetles and performed scan sampling to obtain snapshots of the interactions among beetles within a population. The order in which populations were observed and the researchers performing the observations rotated to avoid temporal and observer bias. Each beetle was labeled with a unique identification tag printed on florescent paper and affixed to its elytra with UV-cured acrylic (Tuffleye Wet-A-Hook Technologies). We used ultraviolet light to easily detect the fluorescent identification tags, although not all beetles were active and able to be seen during every observation.

During observations, we noted fitness-related behaviors (male mate guarding and female egg laying) and social partners

of all identifiable beetles. We defined social partners as beetles within 5 cm, several body lengths, of each other (as in [Formica et al. \(2021\)](#)). At this distance, beetles reorient towards one another, which often leads to mating or antagonistic behaviors ([Formica et al., 2012, 2017, 2021](#)). Male mating success was measured as the number of observed mate guarding events ([Formica et al., 2012, 2021](#)). Mate guarding is a stereotyped mating behavior of forked fungus beetles. After a successful copulation, male forked fungus beetles remain on the dorsum of the female, oriented in the same direction as the female for up to 5 hr ([Conner, 1989](#)). Mate guarding reliably indicates spermatophore transfer and insemination success in male forked fungus beetles ([Conner, 1988, 1989](#)). Female reproductive success was estimated as the number of observed eggs laid. We measured female reproductive success instead of female mating success because female reproductive success is likely a larger component of overall lifetime fitness than female mating success. We were further interested in measuring female egg laying because we expected females to compete over egg laying sites, not over mates, when fungus resources were clumped together.

### Social networks

We used interactions between proximal social partners to construct social networks. Proximity interactions are often used to construct social networks in studies of animal behavior ([Aplin et al., 2015](#); [Leu et al., 2016](#); [Snijders et al., 2017](#); [Wey et al., 2013](#)), and the positions individuals hold within proximity social networks have been shown to influence fitness in forked fungus beetles ([Formica et al., 2012, 2021](#)). We did not include courtship, mating, or mate guarding interactions when constructing our social networks to avoid non-independence between network variables and the fitness metrics in our multilevel selection analyses (see Multilevel selection analyses; [Formica et al., 2021](#)). Many networks are built by assuming that all members in a group interact with all other members in the group ([Croft et al., 2011](#)). Instead of group membership, we used scan sampling of dyadic interactions to identify social connections, an important distinction when testing hypotheses in animal social networks (see Hypothesis testing and permutations; [Croft et al., 2011](#)).

We converted dyadic proximity interactions into undirected, weighted social networks using the simple ratio index. The simple ratio index describes the association between social partners as weighted network edges, ranging from 0 for individuals that were never observed interacting together to 1 for individuals observed interacting together in every behavioral survey period ([Croft et al., 2008](#); [Ginsberg & Young, 1992](#)). We did not include interactions in which one beetle was unidentifiable because a label could not be seen clearly (constituting 2.96% of all interactions) in network construction. The 32 beetles that died during the experimental periods were included in network construction but were excluded from selection analyses because their individual-level social network traits could not be established over the same time period as the beetles that survived. We built three types of social networks: both-sex networks describing interactions among all beetles, male–male networks describing interactions only among males, and female–female networks describing interactions only among females. The male–male and female–female networks contain sex-specific subsets of the interactions in the both-sex networks. We built separate networks for each population during each of the two experimental periods. To reset social networks between experimental periods, we

isolated individuals for four days before beginning the second experimental period ([Formica et al., 2017](#)). [Formica et al. \(2017\)](#) found that four days of isolation were sufficient to return individual- and group-level social network traits of populations of forked fungus beetles to the values observed in the first time period.

We calculated three social network metrics that described the position of individuals within their networks and three metrics that described the overall structure of the networks ([Table 1](#)). *Individual strength* describes how connected an individual is to others in the network by summarizing how often an individual interacts. Individual strength is a weighted measure with repeated interactions between beetles only increasing individual strength by 0.5 (with an alpha weighting parameter of 0.5; [Opsahl, 2009](#)). *Individual betweenness* describes an individual's centrality in the network and requires knowledge of the full social network. Individual betweenness is calculated as the number of shortest paths connecting two individuals that pass through the focal individual ([Opsahl, 2009](#)). *Local clustering coefficient* describes individual cliquishness and requires knowledge of the immediate social environment. Local clustering coefficient measures how often the social partners of an individual interact with each other ([Croft et al., 2008](#)). Beetles with one or no partners have undefined local clustering coefficients and were not included in models analyzing local clustering coefficient (see Multilevel Selection Analyses). Past work in wild populations of forked fungus beetles has detected selection on each of these individual-level social network metrics in males ([Formica et al., 2012, 2021](#)).

We also calculated metrics that describe network level properties that are analogous to the individual properties above. *Network density* is analogous to individual strength and measures how connected a network is by quantifying the number of network edges observed out of all possible edges that the network could have ([Wasserman & Faust, 1994](#)). *Average shortest path length* describes how connected a network is by calculating the average of the shortest path lengths that connect every pair of individuals ([Opsahl, 2009](#)). Average shortest path length is similar to individual betweenness in describing connectedness within the context of the existing network structure. *Global clustering coefficient* describes how modular a network is by calculating the proportion of all social partners that interact with each other ([Opsahl, 2009](#)). Strength, betweenness, local clustering coefficient, average shortest path length, and global clustering coefficient were all calculated as weighted metrics in the `tnet` package in R ([Opsahl, 2009](#)). Formulas for all weighted metrics can be found in [Opsahl 2009](#). Network density was calculated in the `sna` package in R ([Butts, 2016](#)). In total, we calculated network metrics in 24 both-sex, male–male, and female–female social networks. Replication in animal network studies is rarely accomplished or limited in scope due to practical difficulties and financial constraints ([Smith et al., 2019](#)). Network replication, however, is integral for statistical analyses and hypothesis testing.

### Multilevel selection analyses

We used contextual analysis to quantify multilevel selection on individual- and group-level social network metrics. Contextual analysis partitions selection into individual and group components using partial regression, an extension of

the Lande–Arnold selection analysis (Goodnight et al., 1992; Heisler & Damuth, 1987; Lande & Arnold, 1983). Our contextual analyses separately examined three distinct pairs of individual and group traits: individual strength and network density; individual betweenness and average shortest path length; and local and global clustering coefficient. Each pair of traits described analogous network properties at different levels of organization. For example, individual strength quantifies how often an individual interacts whereas network density measures how interactive a network is. In each combination, the group social network metric was not simply a group average of the individual metric but instead described an emergent property of the social network. We chose to analyze analogous pairs to quantify the independent contributions of the individual and group levels of similar traits. Because the limited number of replicated networks available precluded a single selection model that included all individual-level and group-level social network traits, we cannot compare independent contributions of different social network traits on individual fitness.

In addition to the individual-level and group-level social network metrics, each contextual analysis model included resource distribution treatment, trial period, individual elytra length, number of observations (a measure included to control for individual differences in overall activity), and the interactions between resource distribution treatment and social network metrics as fixed effects and beetle identification nested within experimental population as random effects. We ran separate models for males and females, measuring sexual selection in males and fecundity selection in females ( $N = 200$  males,  $N = 200$  females). In total, we ran six different contextual analyses using social network metrics calculated from both-sex networks. We ran an analysis for each fitness proxy (male mating success and female reproductive success) and for each of the three pairs of traits. In our analyses of selection on clustering, we did not include individuals with fewer than two social partners (13 males and 4 females) because local clustering coefficients are undefined. As posthoc analyses, we ran two additional contextual models to explore multilevel selection on individual strength and network density in male–male only and female–female only social networks. Selection analyses on sex-specific networks allowed us to investigate whether selection patterns observed in both-sex networks were driven by interactions among individuals of the same sex.

The scale of standardization in selection analyses requires explicit justification and should depend on the biological and ecological processes that generate selection (De Lisle & Svensson, 2017). We mean-variance standardized individual-level social network metrics at the scale of each replicate experimental population, as selection on individual-level social network position in wild populations has been shown to operate within subpopulations (Formica et al., 2021). We likewise standardized the other individual phenotypes, elytra and number of observations, at the local population level. As group-level selection inherently operates across groups, we standardized group social network metrics at the global level across all experimental populations. Similarly, measuring multilevel selection necessitated relativizing fitness at the global scale; local relativization would eliminate the group differences that are the focus of such an analysis. We performed all standardizations within each experimental period.

Models were built in the R package `glmmTMB` (Brooks et al., 2017). The R package `emmeans` was used to calculate

marginal means (Lenth, 2018). Figures were built in the R package `ggeffect` (Lüdtke, 2018). All analyses were conducted in R version 3.6.2 (R Core Team, 2019).

## Hypothesis testing and permutations

The position an individual holds within their social network is the product of the behavior of both the individual and all of their social partners. Individual-level social network metrics are thereby inherently non-independent and violate fundamental assumptions of parametric tests (Croft et al., 2011; Farine, 2017; Farine & Whitehead, 2015). We used node permutations to address this issue of non-independence. Node permutations shuffle characteristics of individuals, or nodes, across nodes within a social network (Croft et al., 2011). We chose to use node permutations instead of datastream permutations, as datastream permutations produce high false-positive error rates when testing null hypotheses in social networks (Puga-Gonzalez et al., 2020; Weiss et al., 2021). Although datastream permutation methods account for observation biases common to animal social networks, our direct observations of dyadic interactions in uniform experimental enclosures between easily identified individuals avoided common observation biases and made node permutations an appropriate choice for our analyses (Croft et al., 2011; Farine & Carter, 2022; Puga-Gonzalez et al., 2020).

Our node permutations randomly shuffled all variables used in the multilevel selection models without replacement among all individuals of the same sex to create 2,000 permuted datasets. For each permuted dataset, we then ran the multilevel selection analyses described above (see Multilevel Selection Analyses) and extracted  $F$ -statistics for each fixed effect in each model, ultimately creating null distributions of 2,000  $F$ -statistics. We extracted  $F$ -statistics instead of model estimates because interactions between variables have multiple different model estimates.  $p$ -Values were calculated as the proportion of permuted model  $F$ -statistics that were greater than the observed model  $F$ -statistic. Because our permutation method broke apart the covariance between individual-level and group-level social network metrics in the permuted datasets, we were able to test how often variance in fitness is partitioned between levels of social network organization by chance.

## Results

In total, we observed 7,865 dyadic social interactions. A total of 852 interactions occurred between males, 2,765 interactions occurred between females, and 4,248 intersexual interactions occurred. We constructed 24 both-sex social networks from an average of  $655.42 \pm 99.61$  social interactions per experimental population (mean  $\pm$  standard deviation). For our posthoc analyses, we constructed male–male social networks from  $71.00 \pm 22.67$  social interactions and female–female social networks from  $230.42 \pm 44.28$  social interactions per population (mean  $\pm$  standard deviation).

Table 2 lists the individual-level and group-level social network metrics of the both-sex, male–male, and female–female networks. Females have higher individual strength and individual betweenness than males in both sex-networks (Table 2). Group-level network structures differ between male–male and female–female networks. Female–female networks have higher network density and global clustering coefficient but lower average shortest path length than male–male networks

**Table 2.** Means  $\pm$  standard deviations of individual and group social network metrics of both-sex and sex-specific networks in environments with clumped and dispersed resources.

Males			Individual metrics				Group metrics			
	Network type	Treatment	Individual strength	Individual betweenness	Local clustering coefficient	Network density	Average shortest path length	Global clustering coefficient		
Both-Sex	Clumped		1.60 $\pm$ 0.76	9.17 $\pm$ 14.95	0.49 $\pm$ 0.15	0.34 $\pm$ 0.04	1.65 $\pm$ 0.16	0.48 $\pm$ 0.04		
Both-Sex	Dispersed		1.62 $\pm$ 0.76	10.53 $\pm$ 20.04	0.47 $\pm$ 0.16	0.34 $\pm$ 0.05	1.60 $\pm$ 0.13	0.46 $\pm$ 0.04		
Male–Male	Clumped		0.51 $\pm$ 0.28	9.56 $\pm$ 11.77	0.27 $\pm$ 0.27	0.20 $\pm$ 0.05	2.34 $\pm$ 0.33	0.27 $\pm$ 0.09		
Male–Male	Dispersed		0.52 $\pm$ 0.29	9.69 $\pm$ 11.85	0.29 $\pm$ 0.29	0.21 $\pm$ 0.06	2.37 $\pm$ 0.40	0.27 $\pm$ 0.11		
Females			Individual metrics				Group metrics			
Network type	Treatment		Individual strength	Individual betweenness	Local clustering coefficient	Network density	Average shortest path length	Global clustering coefficient		
Both-Sex	Clumped		2.48 $\pm$ 0.83	29.01 $\pm$ 28.12	0.46 $\pm$ 0.09	0.34 $\pm$ 0.04	1.65 $\pm$ 0.16	0.48 $\pm$ 0.04		
Both-Sex	Dispersed		2.34 $\pm$ 0.82	30.23 $\pm$ 35.09	0.47 $\pm$ 0.09	0.34 $\pm$ 0.05	1.60 $\pm$ 0.13	0.46 $\pm$ 0.04		
Female–Female	Clumped		1.39 $\pm$ 0.52	7.08 $\pm$ 7.85	0.55 $\pm$ 0.16	0.45 $\pm$ 0.07	1.52 $\pm$ 0.17	0.55 $\pm$ 0.06		
Female–Female	Dispersed		1.26 $\pm$ 0.47	8.81 $\pm$ 11.44	0.54 $\pm$ 0.16	0.43 $\pm$ 0.07	1.65 $\pm$ 0.21	0.52 $\pm$ 0.05		

Note. Both-sex group network metrics are the same for males and females.

(Table 2). All the networks formed single isolates, where all individuals were connected. Figure 1 visualizes both-sex networks with high and low network densities.

We found selection acted on different levels of social network organization in males and females. In both-sex social networks, individual fitness was influenced by individual strength and individual betweenness in males but group network density in females (Table 3; Figures 2 and 3). Male beetles with higher individual strength and higher individual betweenness had higher mating success, but no measure of group network structure affected male mating success (Table 3; Figures 2 and 3). Conversely, female individual network position did not influence reproductive success, but group network density did (Table 3; Figures 2 and 3). Female beetles in networks with higher network density laid fewer eggs (Table 3; Figure 2). In single-sex networks, although the same patterns of selection on individual strength held for males in male–male networks, network density of female–female networks did not affect reproductive success (Table 4; Figure 4). No selection on local or global clustering coefficient was detected for either males or females (Table 3; Supplementary Figure S1).

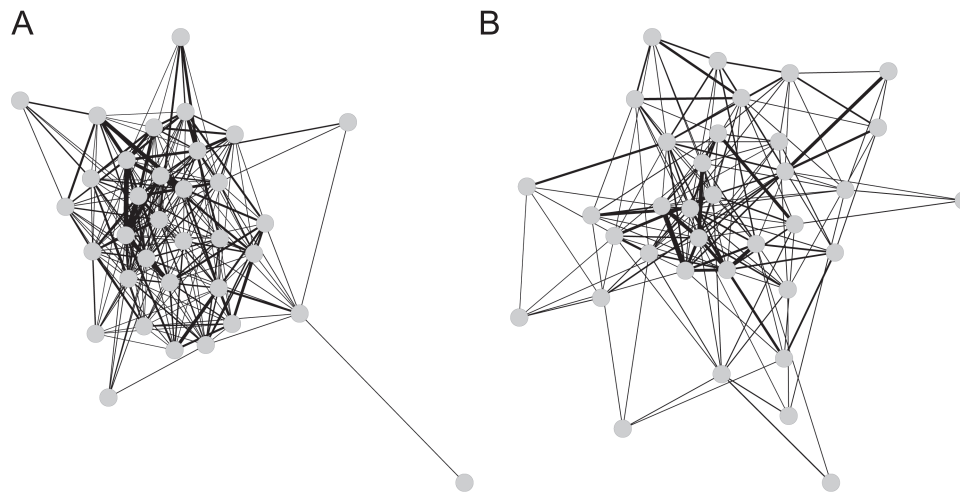
Although resource distribution did not generate differences in fitness for either sex (Tables 3 and 4; Supplementary Figures S2 and S3), resource distribution did impact the relationship between network traits and fitness. The strength of selection on network density for females varied between resource distribution treatments (Table 3; Figure 2). Females in both-sex networks with higher network density laid fewer eggs when fungus resources were clumped together but not when fungus brackets were evenly dispersed (Figure 2). Resource distribution similarly impacted the strength of selection on individual betweenness for males (Table 3; Figure 3). Males with high betweenness experienced higher mating success when fungus resources were clumped together but not when fungus brackets were evenly dispersed (Figure 3). The distribution of fungus resources did not otherwise alter patterns of selection on individual-level and group-level social network characteristics (Tables 3 and 4; Figures 2–4; Supplementary Figure S1).

Males with longer elytra, a measure of body size, had higher mating success, whereas female elytra length did not influence the number of eggs females laid (Tables 3 and 4). Experimental period did not affect male mating success but accounted for variance in the number of eggs laid by females in the linear mixed model including individual strength and network density of both-sex networks (Tables 3 and 4). Beetles observed more often had higher mating and reproductive success (Tables 3 and 4), a typical result for selection analyses of this species (Formica et al., 2012, 2021).

## Discussion

Our results suggest that multilevel selection plays an important and complex role in the evolution of social behaviors in this species. In experimental populations, male and female forked fungus beetles experienced fundamentally different levels of selection acting on social network traits: although individual-level social network positions contributed to male mating success, female reproductive success was explained by an emergent network trait and not by an analogous individual-level network character. The distribution of fungus resources impacted the strength of these patterns but did not change the level of selection experienced in each sex. By





**Figure 1.** Visualizations of both-sex networks with (A) high network density and (B) low network density. Line thickness is proportional to the simple index ratio, and individual nodes are plotted using an algorithm that places highly connected nodes close together.

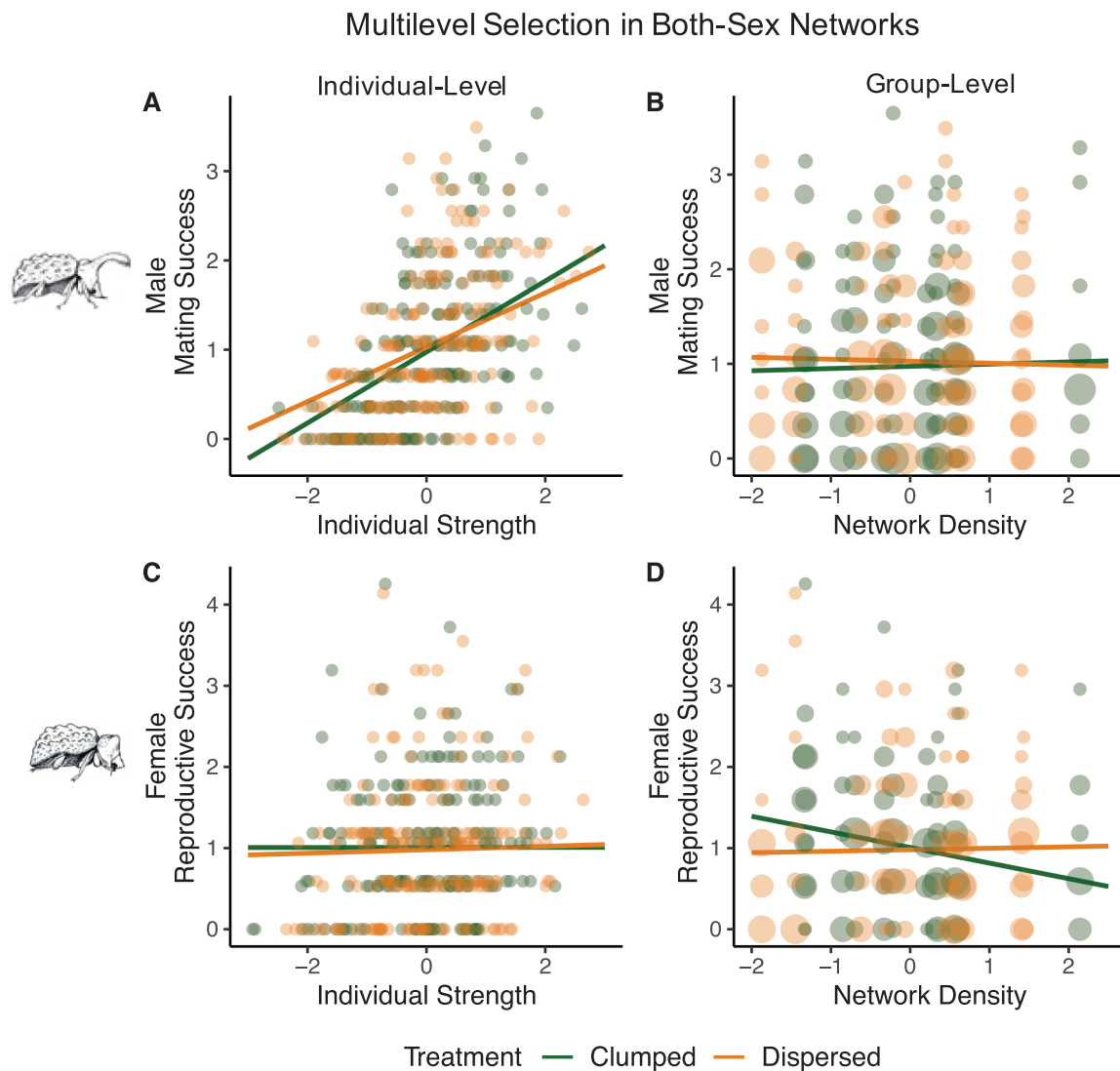
**Table 3.** Multilevel selection on three different pairs of individual network positions and group network traits in both-sex networks.

Males	Individual strength, network density		Individual betweenness, average shortest path		Local clustering, global clustering	
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
Individual network position	0.351	<b>&lt;.001</b>	0.142	<b>&lt;.001</b>	0.031	.42
Group network trait	0.001	.97	-0.002	.97	-0.021	.60
Treatment	Clumped: 0.974 Dispersed: 1.028	.38	Clumped: 0.977 Dispersed: 1.031	.42	Clumped: 0.977 Dispersed: 1.023	.49
Elytra length	0.113	<b>.002</b>	0.147	<b>.001</b>	0.175	<b>&lt;.001</b>
Number of observations	0.162	<b>&lt;.001</b>	0.247	<b>&lt;.001</b>	0.260	<b>&lt;.001</b>
Experimental period	Period 1: 0.995 Period 2: 1.006	.67	Period 1: 1.000 Period 2: 1.010	.86	Period 1: 1.004 Period 2: 0.996	.75
Individual network position × treatment	Clumped: 0.398 Dispersed: 0.304	.16	Clumped: 0.213 Dispersed: 0.071	.05	Clumped: -0.016 Dispersed: 0.077	.22
Group network trait × treatment	Clumped: 0.023 Dispersed: -0.021	.57	Clumped: -0.026 Dispersed: 0.023	.56	Clumped: -0.032 Dispersed: -0.009	.77

Females	Individual strength, network density		Individual betweenness, average shortest path		Local clustering, global clustering	
	Estimate	<i>p</i> -Value	Estimate	<i>p</i> -Value	Estimate	<i>p</i> -Value
Individual network position	0.011	.81	-0.007	.88	-0.050	.22
Group network trait	-0.087	<b>.031</b>	0.054	.25	-0.039	.38
Treatment	Clumped: 1.008 Dispersed: 0.979	.69	Clumped: 0.999 Dispersed: 0.979	.82	Clumped: 1.027 Dispersed: 0.965	.42
Elytra length	-0.033	.47	-0.036	.42	-0.024	.57
Number of observations	0.225	<b>&lt;.001</b>	0.233	<b>&lt;.001</b>	0.202	<b>&lt;.001</b>
Experimental period	Period 1: 1.023 Period 2: 0.964	<b>&lt;.001</b>	Period 1: 0.996 Period 2: 0.981	.29	Period 1: 0.990 Period 2: 1.000	.39
Individual network position × treatment	Clumped: 0.000 Dispersed: 0.021	.80	Clumped: -0.017 Dispersed: 0.003	.80	Clumped: -0.053 Dispersed: -0.047	.94
Group network trait × treatment	Clumped: -0.192 Dispersed: 0.018	<b>.019</b>	Clumped: 0.116 Dispersed: -0.007	.23	Clumped: -0.020 Dispersed: -0.058	.74

*Note.* Linear mixed model estimates are reported for continuous variables and marginal means are reported for categorical variables. All continuous variables are mean-variance standardized, and fitness metrics are relativized to mean fitness. *p*-Values are calculated as the proportion of permuted model *F*-statistics that were greater than the observed model *F*-statistic. Significant *p*-values at the  $\alpha = 0.05$  level are bolded.



**Figure 2.** Marginal effects of individual strength and density on male mating success and female reproductive success in both-sex networks. (A) Male individual strength positively predicts male mating success. (B) Both-sex network density does not affect male mating success. (C) Female individual strength does not affect the number of eggs laid. (D) Both-sex network density negatively predicts the number of eggs laid in the clumped treatment only. The color of the points and gradients represent fungus resource distribution in the experimental populations. Green denotes clumped fungus resources, and orange denotes dispersed fungus resources. The size of the points is scaled by the number of individuals with that value. Note that points are arranged in columns in panels (B) and (D) because all individuals within a population share the same network density. Confidence intervals are not included as permutation testing was used to assess significance. Individual and group social network metrics are mean-variance standardized, and fitness metrics are relativized to mean fitness.

measuring multilevel selection, we uncovered a fitness relationship in females that would have been missed by traditional selection analyses that consider only individual traits. We further found opposing patterns of selection operating across levels and between sexes, suggesting the potential for multilevel sexual conflict to shape the evolution sex-specific social behavior at both the individual and group levels.

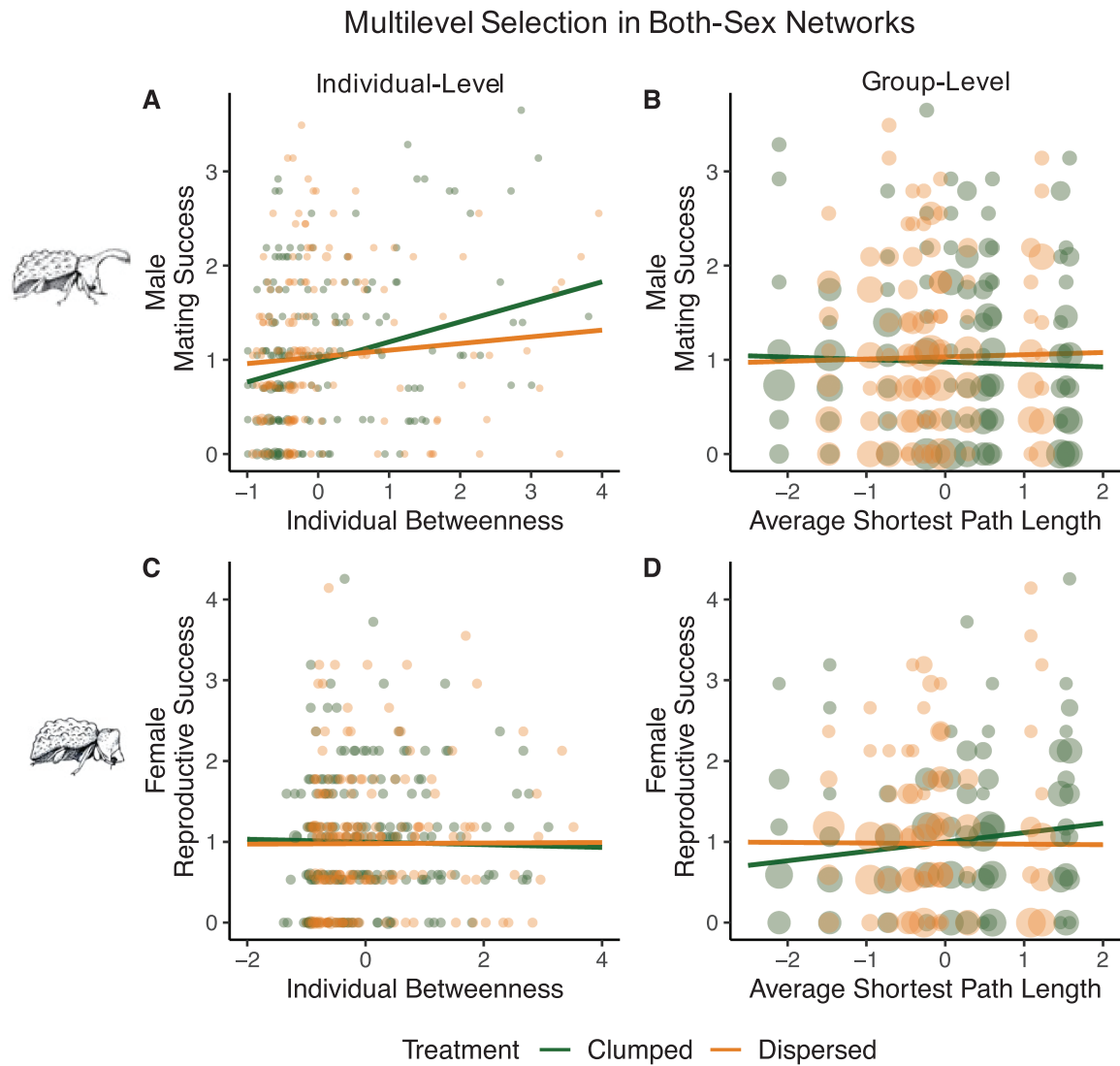
### Social network metrics

Comparisons of individual-level and group-level social network metrics in both-sex, male–male, and female–female social networks paint a picture of social interactions in forked fungus beetles: females interact broadly with both males and females, whereas males primarily interact with females and avoid interactions with males. This generalization of social interactions is evidenced by the lower individual strength and individual betweenness held by males compared to females

in both-sex networks, the lower individual strength in male–male networks compared to female–female networks, the lower network density and global clustering coefficient in male–male networks compared to female–female networks, and the higher average path length in male–male networks compared to female–female networks. This understanding of social interactions in forked fungus beetles informs our interpretation of the patterns of multilevel selection that we observed.

### Individual-level selection

At the individual level, our selection analyses on individual network position in experimental populations of forked fungus beetles generally recapitulated patterns of sexual selection previously observed in wild populations (Formica et al., 2012, 2021). Consistent with recent analyses in wild



**Figure 3.** Marginal effects of individual betweenness and average shortest path length on male mating success and female reproductive success in both-sex networks. (A) Male individual betweenness positively predicts male mating success. This relationship is stronger when resources are clumped. (B) Both-sex average shortest path length does not affect male mating success. (C) Female individual betweenness does not affect the number of eggs laid. (D) Both-sex average shortest path length does not influence the number of eggs laid in either treatment. The color of the points and gradients represent fungus resource distribution in the experimental populations. Green denotes clumped fungus resources, and orange denotes dispersed fungus resources. The size of the points is scaled by the number of individuals with that value. Note that points are arranged in columns in panels (B) and (D) because all individuals within a population share the same average shortest path length. Confidence intervals are not included as permutation testing was used to assess significance. Individual and group social network metrics are mean-variance standardized, and fitness metrics are relativized to mean fitness.

populations, we found selection acted on male strength and betweenness but not local clustering coefficient in our experimental populations (Formica et al., 2021). Under natural conditions, the direction of selection on male social network position varied across wild populations that likewise varied in demography and ecology (Formica et al., 2021). However, in our controlled experimental populations, male strength and betweenness experienced positive selection. Sexual selection on strength did not vary between the two resource distribution treatments but the magnitude of selection on betweenness increased when resources were clumped together. Emlen and Oring (1977) predicted stronger sexual selection in environments with clumped resources that are more easily controlled in intrasexual competition. Our results are only partially consistent with this ecological theory of sexual selection and suggest, alongside behavioral

observations in the field, that male forked fungus beetles may not defend resources in a manner that matches classical assumptions (see also Kamath and Wesner (2020)). More studies are required to understand the mechanisms of selection on social networks in male forked fungus beetles. The fitness consequences of female individual social network position have not been explored in wild populations, and we found no relationship between female network position and female reproductive success in our experimental populations. We found no evidence of competition among females for oviposition sites and greater reproductive success for females with competitive social network positions, not even in environments with clumped fungus resources wherein we expected increased competition for oviposition sites.

Although individual-level selection on male social network position has been well documented in forked fungus beetles

**Table 4.** Multilevel selection on individual strength and network density in males in male–male networks and females in female–female networks.

Males			Females		
Fixed effect	Estimate	<i>p</i> -Value	Fixed effect	Estimate	<i>p</i> -Value
Individual strength	0.207	<b>&lt;.001</b>	Individual strength	-0.013	.78
Network density	-0.016	.67	Network density	-0.001	.97
Treatment	Clumped: 0.097 Dispersed: 1.027	.37	Treatment	Clumped: 1.017 Dispersed: 0.976	.60
Elytra length	0.172	<b>&lt;.001</b>	Elytra length	-0.035	.42
Number of observations	0.226	<b>&lt;.001</b>	Number of observations	0.236	<b>&lt;.001</b>
Experimental period	Period 1: 1.002 Period 2: 0.997	.88	Experimental period	Period 1: 0.996 Period 2: 0.997	.99
Individual strength × treatment	Clumped: 0.204 Dispersed: 0.210	.93	Individual strength × treatment	Clumped: -0.012 Dispersed: -0.013	.98
Network density × treatment	Clumped: -0.027 Dispersed: -0.005	.79	Network density × treatment	Clumped: 0.013 Dispersed: -0.016	.78

*Note.* Model estimates are reported for continuous variables and marginal means are reported for categorical variables. All continuous variables are mean-variance standardized, and fitness metrics are relativized to mean fitness.

*p*-Values are calculated as the proportion of permuted model *F*-statistics that were greater than the observed model *F*-statistic. Significant *p*-values at the  $\alpha = 0.05$  level are bolded. *p*-Values that are qualitatively different than the *p*-values from the both-sex network analyses are italicized.

(Formica et al., 2012, 2021), the biological phenomena that generate this covariance between social network position and male mating success remain unclear. One potential factor is the availability of mates. Males that are more connected and more central in two-sex networks may interact more often with females and thereby experience more mating opportunities. If intersexual interactions drive variance in male mating success, we do not expect to find the same pattern of selection on male social network position in male–male networks. However, posthoc analyses on male–male networks likewise revealed positive selection on male social network traits, providing indirect evidence that it is interactions among males that more strongly impacted male mating success than interactions between males and females. Perhaps males who are highly connected and central within their network increase their mating success because they have more opportunities to court proximal females and to interrupt the mating attempts of proximal males. An alternative explanation is that highly connected males are positioned to receive more information about male competitors. The position an individual holds within a social network can impact their likelihood of receiving and transmitting information (Webster et al., 2013). Female forked fungus beetles use chemical cues to discriminate between winning and losing males (Vilella-Pacheco et al., 2021). Similar chemical cues may be more available to males holding central positions within their social network, providing connected males better evaluation of neighboring male competitors.

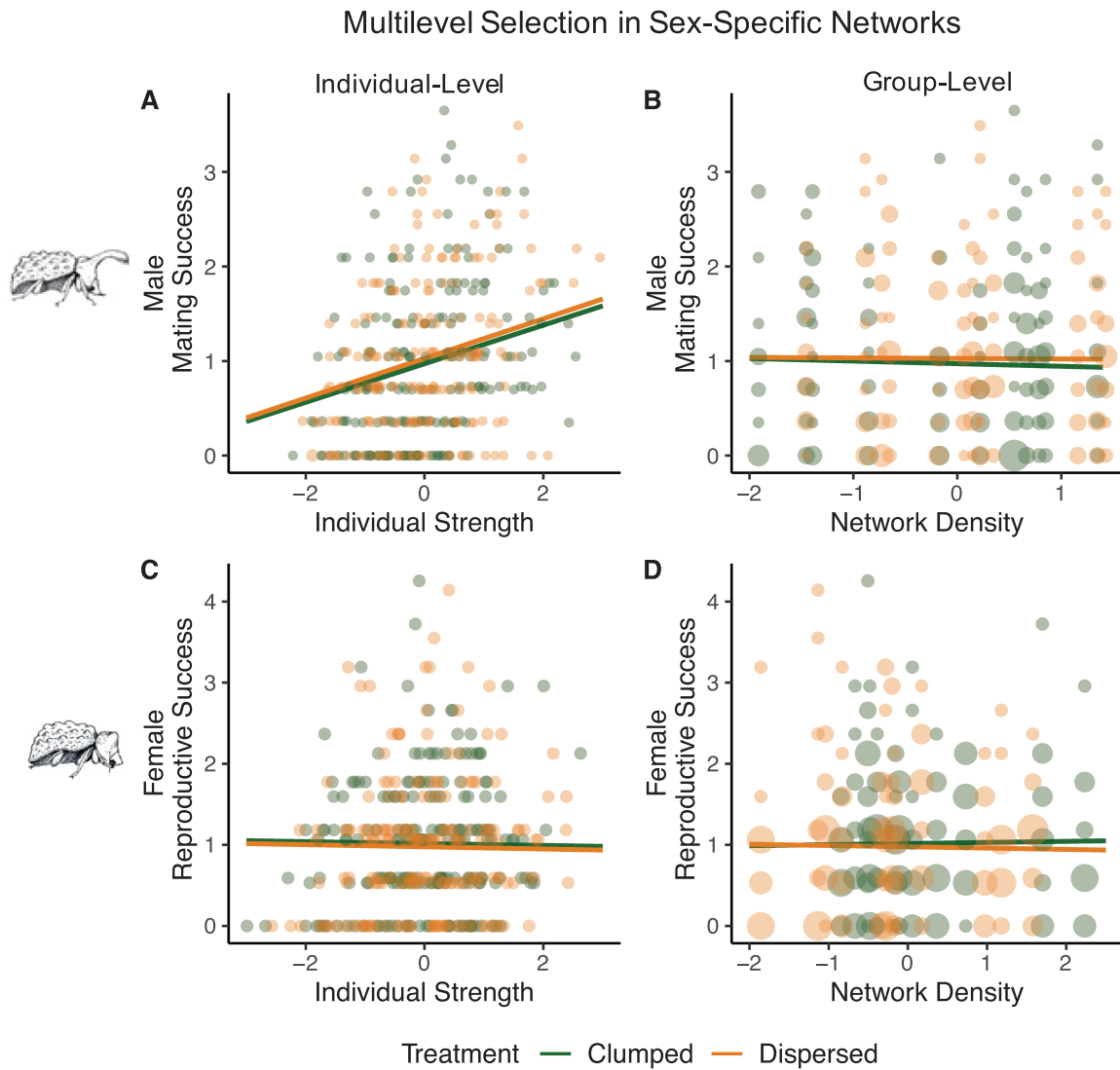
### Group-level selection

Group network structure only influenced variance in individual fitness among females. This contextual effect on female fitness could be due to group dynamics either among females or between females and males. However, posthoc analyses on female-only networks revealed no group-level selection, providing indirect evidence that intersexual interactions drive group-level selection in females. Interlocus sexual conflict over mating interactions often reduces female fitness (Arnqvist & Rowe, 2005; Eldakar et al., 2010; Stutt & Siva-Jothy, 2001). In forked fungus beetles, males grapple with females before

mating, a behavior characteristic of aggressive interactions between males (Mitchem et al., 2019). During courtship, males mount females for many hours, even as females lay eggs and traverse fungus brackets (Formica et al., 2016). These observations cumulatively suggest that increased interactions with males may be costly to female forked fungus beetles and cause females to lay fewer eggs.

Although male interactions may be costly to females, females with highly connected individual network positions did not experience fitness costs. This difference between impacts of individual-level and group-level measures of connectedness suggests that the intersexual interactions that reduce female fitness are complex. One possibility is that more densely connected networks may promote more male aggression. Males in more connected networks occupy closer proximity to females and have more opportunities to act aggressively towards females. Consistent with this hypothesis, group-level selection occurred only in environments with clumped resources, wherein male–male competition and male aggression is expected to be strongest as clumped resources force individuals into close proximity and create more opportunities for aggression (Emlen & Oring, 1977; Shuster & Wade, 2003). Females in populations with more aggressive males may collectively experience more aggressive and costly interactions with males. Alternatively, females in populations with more aggressive males may be sperm limited if competition among males distracts from mate acquisition. Similar male–male interference has been suggested to explain weaker sexual selection on horn size and body size in higher density populations of forked fungus beetles (Conner, 1989; Formica et al., 2011). Whatever the mechanism, females in densely connected networks experienced reduced reproductive output, irrespective of their own individual connectedness within the network. This result showcases that group-level selection on network structures can act independently of selection on individual-level network analogs and underscores the importance of group-level fitness effects through social behavior.

An ongoing debate about multilevel selection is whether group-level selection is merely acting on group averages of individual traits or reflecting emergent group traits (Gardner, 2015;



**Figure 4.** Marginal effects from posthoc analyses of individual strength and male–male network density on male mating success and of individual strength and female–female network density on female reproductive success. (A) Male individual strength (from male–male networks) still positively predicts male mating success. (B) Male–male network density does not affect male mating success. (C) Female individual strength (from female–female networks) does not affect the number of eggs laid. (D) Unlike both-sex network density, female–female network density does not affect the number of eggs laid. The color of the points and gradients represent fungus resource distribution in the experimental populations. Green denotes clumped fungus resources, and orange denotes dispersed fungus resources. The size of the points is scaled by the number of individuals with that value. Note that points are arranged in columns in panels (B) and (D) because all individuals within a population share the same network density. Confidence intervals are not included as permutation testing was used to assess significance. Individual and group social network metrics are mean-variance standardized, and fitness metrics are relativized to mean fitness.

Goodnight, 2015). When group-level selection acts on group averages of individual traits, some researchers argue that evolutionary response to group-level selection will be inconsequential compared to individual-level selection, while others assert that the distinction between types of group traits is irrelevant (reviewed in Okasha (2006) and Eldakar and Wilson (2011)). Our results provide empirical evidence of group-level selection acting on an emergent group trait without fitness consequences for an analogous individual-level trait. In such cases, there can be no argument that group-level selection is somehow a less important selective force. However, the evolutionary response to selection on an emergent trait remains unclear.

### Sex-specific patterns of multilevel selection

Considering sex-specific selection at multiple levels of social network organization in forked fungus beetles revealed

sexually antagonistic selection across levels. Males experienced positive individual-level sexual selection on connectedness traits, whereas negative group-level fecundity selection for group connectivity operated in females. Few other studies have investigated how multilevel selection differs between the sexes or conflicts across levels. Fisher et al. (2017) found that female red squirrels (*Tamiasciurus hudsonicus*) experienced strong selection on growth rate within litters while males experienced no within-litter selection. A contextual analysis that only focused on fitness of one sex (males) found antagonistic selection between individual and group levels. Individual male water striders (*Aquarius remigis*) had higher mating success if they were more aggressive, but lower mating success if they belonged to groups with higher average levels of aggression (Eldakar et al., 2010). The conflicting directions of individual and group selection in water striders resulted from

female dispersal away from groups of more aggressive males. The results of our study show similarly antagonistic multi-level selection operating between sexes: group-level selection in females opposed individual-level selection in males. This multilevel sexual conflict is likely due to sex differences in optimal social strategies—males benefit from increased interactions with females, but females experience fitness costs in groups with more interactions with males—and may shape sex-specific social behavior and dispersal among groups. It is also important to emphasize that our results are based on different fitness components for males and females, and a complete understanding of sex-specific multilevel selection requires measuring lifetime fitness in both sexes.

### Effect of resource distribution on patterns of multilevel selection

Resource distribution altered patterns of multilevel selection, with stronger individual- (males) and network-level (females) selection detected when fungus resources were distributed in more discrete clumps. Variation in the strength of multilevel selection across environments aligns with patterns observed in multilevel selection analyses across a wide range of taxa (Aspi et al., 2003; Bouwhuis et al., 2015; Donohue, 2004; Fisher et al., 2017; Weinig et al., 2007). The magnitude of group-level selection typically increases in more densely populated groups in both plants and animals (Aspi et al., 2003; Donohue, 2004; Fisher et al., 2017; Weinig et al., 2007; but see Bouwhuis et al. (2015)). Multilevel selection across contexts other than conspecific density, however, has rarely been investigated (but see Aspi et al. (2003) and Bouwhuis et al. (2015)). Bouwhuis et al. (2015) creatively used multilevel selection to identify ecological agents of selection in great tits (*Parus major*). Food availability modulated higher-level selection, whereas predation and conspecific density affected individual-level selection.

Our experimental manipulations revealed that another environmental axis, resource distribution, modulated multilevel selection. Previous analyses established that forked fungus beetles concentrated their space use around resource patches but further found that resource distribution had little or no impact on social network positions or group social network structures (Costello, 2020; Costello et al., 2022). Despite minimal changes to social networks (Costello et al., 2022), resource distribution still modulated the strength of selection on social network traits in both sexes: individual betweenness in males and network density in females. In other words, although resource distribution did not alter network phenotypes, resource distribution impacted the relationship between network phenotypes and individual fitness. This effect of resource distribution may contribute to the variable patterns of selection on individual network position seen in wild beetle populations (Formica et al., 2021). If resource distribution drives patterns of multilevel selection in wild beetle populations, the cycle of proliferation, and decay of fungi along logs in the temperate forests of eastern North America will structure an ever-changing fitness landscape. In wild populations, unlike in our experimental populations, beetles can move among subpopulations to parts of the fitness landscape with more favorable fitness effects. For example, we would expect female beetles to move away from subpopulations with highly connected social network structures to shelter from negative group-level effects on individual reproductive success, similar to female movement away from groups of

aggressive males seen in water striders (Eldakar et al., 2010). This type of movement among subpopulations may dampen or obscure the magnitude of multilevel selection in wild populations.

Resource distribution is one of many potential factors driving patterns of selection in wild forked fungus beetle populations. To isolate the effect of resource distribution in our experimental design, we controlled for many of these other factors, including population size, density, and sex ratio. However, we expect population size to play an outsized role in shaping patterns of multilevel selection on social network characteristics in wild populations. Population size varies dramatically among wild populations and covaries with both social network structure and individual fitness; larger populations form more connected networks and experience more mating events (Formica et al., 2021). Population size may thereby modulate the impact of resource distribution on multilevel selection by exaggerating the strength of individual-level selection in large subpopulations with more mating events and of group-level selection in metapopulations with high variance in subpopulation sizes. Future work in forked fungus beetles and other systems should investigate how resource distribution, subpopulation size, and movement among subpopulations interact to shape patterns of multilevel selection.

### Evolution of social networks

Social networks describe properties of interacting individuals, and understanding how social networks evolve thereby requires a multilevel selection framework (Fisher & McAdam, 2017). Although individual-level selection on network position has been well documented in a wide range of organisms (Bar Ziv et al., 2016; Brent et al., 2013; Cheney et al., 2016; Formica et al., 2012, 2021; Gilby et al., 2013; Lehmann et al., 2016; McDonald, 2007; Oh and Badyaev, 2010; Ryder et al., 2008; Silk et al., 2003, 2009; Wey & Blumstein, 2012; Wey et al., 2013), the effect of overall network structure on individual fitness rarely has been quantified (but see Royle et al. (2012), Solomon-Lane et al. (2015), and Philson et al. (2022)). In one of the few investigations of selection on group social network traits, Royle et al. (2012) found that nestling great tits in families with higher mean strength better resolved conflicts over parental investment and were more likely to survive. Instead of considering networks within family groups, we used contextual analyses to quantify how selection simultaneously operates on individual-level and group-level social network traits of unrelated groups. Our results show that a full understanding of the social and ecological variables that shape the evolution of social networks requires a multilevel selection framework applied across sexes and environments.

Predicting how social networks evolve in response to multilevel selection is an ongoing challenge (Fisher & McAdam, 2017). First, for social networks to respond to multilevel selection, there must be some transmissible component of network structure across generations. Although additive genetic variance has been found for some aspects of individual social network position (Brent et al., 2013; Fowler et al., 2009; Lea et al., 2010), the potential for heritability of emergent social network traits is currently unknown. Furthermore, we know little about the relationship between individual-level and group-level social network traits (Cantor et al., 2020). Due to the complexity of emergent group traits, we do not expect

emergent group-level and their analogous individual-level network traits to share common loci. However, a separate study in experimental populations of forked fungus beetles found that emergent social network structure depended on the personalities of individual group members, suggesting that individual and group network traits may be more correlated than anticipated (Cook et al., 2022). If correlated across levels, selection at one level may either accelerate or constrain evolution at another level (Bijma & Wade, 2008). The evolutionary response to multilevel selection may be further complicated by sex-specific patterns of multilevel selection. In this study, males with higher individual connectedness (strength) and individual centrality (betweenness) secured more mates, but females produced more eggs when in less connected (dense) networks. Depending on the genetic relationship between individual and group connectedness, evolutionary increases in connectedness of males may be constrained by reduced reproductive output of females in more connected networks. More work exploring the genetic underpinnings and coupling of individual and emergent group traits is required for understanding the evolutionary implications of sex- and context-dependent multilevel selection on social networks.

## Conclusion

Social network analyses provide a unique opportunity to quantify social behaviors at both the individual and group levels. By applying a multilevel selection framework, we demonstrated that selection can operate on emergent properties of social networks without acting on analogous individual-level social network traits. We further demonstrated that selection on group network traits in one sex can oppose selection on analogous individual behaviors in the other sex. These conflicting patterns of selection across levels and between sexes may constitute a form of multilevel sexual conflict that shapes the evolution of sex-specific social behavior, both at the individual and network levels. The fitness consequences of emergent group phenotypes are difficult to parse, but may turn out to be important forces driving the evolution of social behavior.

## Supplementary material

Supplementary material is available online at *Evolution* (<https://academic.oup.com/evolut/qpac012>)

## Data availability

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.qjq2bvqkc> (Costello et al., 2022).

## Author contributions

R.A.C. designed the study with input from E.D.B. III and V.A.F., R.A.C. and P.A.C. collected the data, R.A.C. analyzed the data with assistance from P.A.C. and V.A.F., R.A.C. led the writing of the manuscript, all authors contributed to the development of the ideas and drafting of the manuscript.

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*Conflict of interest:* The authors declare no conflict of interest.

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