



Social network position experiences more variable selection than weaponry in wild subpopulations of forked fungus beetles

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Funding information

Division of Environmental Biology, Grant/Award Number: DEB-1911485; Division of Integrative Organismal Systems, Grant/Award Number: IOS-1355003 and IOS-1355029; National Science Foundation

Handling Editor: Eric Vander Wal

Abstract

1. The phenotypic expression and fitness consequences of behaviours that are exhibited during social interactions are especially sensitive to their local social context. This context-dependence is expected to generate more variation in the sign and magnitude of selection on social behaviour than that experienced by static characters like morphology. Relatively few studies, however, have examined selection on behavioural traits in multiple populations.
2. We estimated sexual selection in the wild to determine if the strength and form of selection on social phenotypes is more variable than that on morphology.
3. We compared selection gradients on social network position, body size, and weaponry of male forked fungus beetles *Bolitotherus cornutus* as they influenced mating success across nine natural subpopulations.
4. Male horn length consistently experienced positive sexual selection. However, the sign and magnitude of selection on individual measures of network centrality (strength and betweenness) differed significantly among subpopulations. Moreover, selection on social behaviours occurred at a local scale ('soft selection'), whereas selection on horn length occurred at the metapopulation scale ('hard selection').
5. These results indicate that an individual with a given social phenotype could experience different fitness consequences depending on the network it occupies. While individuals seem to be unable to escape the fitness effects of their morphology, they may have the potential to mediate the pressures of selection on behavioural phenotypes by moving among subpopulations or altering social connections within a network.

KEYWORDS

Bolitotherus cornutus, hard selection, interacting phenotypes, male combat, mating success, permutation, soft selection, spatial variation

1 | INTRODUCTION

Social behaviours, by definition, are expressed during interactions among conspecifics. Phenotypic variation in such traits arises both from properties of the focal individuals that exhibit the behaviours, and from social partners in their immediate neighbourhood

(Dawkins, 1982; Krebs & Dawkins, 1984; McGlothlin, Moore, Wolf, & Brodie III, 2010; Moore, Brodie III, & Wolf, 1997). As a result, both the expression and the fitness consequences of social behaviours are expected to be especially sensitive to the details of the social context, ranging from group level properties such as density and sex ratio, to the distributions of specific traits in individual social partners

(Bailey, Marie-Orleach, & Moore, 2018; Eldakar, Wilson, Dlugos, & Pepper, 2010; Formica et al., 2011; Pruitt & Goodnight, 2014).

This extreme context dependency suggests that selection on individual social behaviours is likely to be local, rather than global (Bailey et al., 2018; McDonald, Farine, Foster, & Biernaskie, 2017). It is an individual's behaviour, relative to those with which it interacts, that is expected to mediate its fitness. In this way, selection on social traits is analogous to soft selection, wherein both traits and fitness are important on the relative scale within subpopulations (De Lisle & Svensson, 2017; Goodnight, Schwartz, & Stevens, 1992; Hunt, Breuker, Sadowski, & Moore, 2009; McDonald, James, Krause, & Pizzari, 2013). Conversely, non-social phenotypes like morphology may influence fitness through their absolute, rather than relative, values. For example, an individual may have to achieve a minimum size to successfully defend a territory, acquire a mate or survive winter. Selection in this case better fits a hard selection model, and it is an individual's value relative to the global or metapopulation mean phenotype that influences fitness (De Lisle & Svensson, 2017). There are, of course, situations in which morphological traits, especially those used in social interactions, might experience selection that is based on locally relative values (e.g. where the larger males of a group have an advantage, regardless of absolute size). In such cases we would expect selection on morphology to be more soft than hard.

Selection gradients on non-social traits commonly vary among populations, but most often in magnitude rather than sign (Siepielski et al., 2013). The critical components of the local social environments that influence social behaviours are often determined by a small number of conspecifics, so the potential exists for even finer scale variation in selection. However, differences in selection among local subpopulations or social neighbourhoods within subpopulations rarely have been explored for any trait, let alone for social behaviours. In a recent review of spatially variable selection (Siepielski et al., 2013), <1% of the traits considered involved behaviours of any kind. Furthermore, most studies of subdivided populations do not specify whether they assume local or global selection but rather default to a hard model (De Lisle & Svensson, 2017). We predict that local variation in social environments can generate qualitative differences in the strength and direction of selection on social behaviours that are greater than those experienced by non-social traits like morphology.

One of the most fundamental social behaviours is the pattern of interactions among conspecifics—which individuals interact, how often and in what contexts. These interactions influence the expression and consequences of all other social behaviours (McDonald, 2007; Oh & Badyaev, 2010; Ryder, McDonald, Blake, Parker, & Loiselle, 2008; Silk, Alberts, & Altmann, 2003; Silk et al., 2009; Wey, Burger, Ebensperger, & Hayes, 2013). Social network analysis quantifies these interactions at both the individual and group levels (Croft, James, & Krause, 2008; Krause, James, & Croft, 2010; Proulx, Promislow, & Phillips, 2005; Sih, Hanser, & McHugh, 2009; Snijders, Blumstein, Stanley, & Franks, 2017; Wey, Blumstein, Shen, & Jordan, 2008). Network-level variables describe differences among groups in the shapes of networks or the

overall patterns of interactions exhibited by groups or subpopulations, whereas individual network metrics quantify the position of each individual within its social network space. Individual network metrics describe behaviours that simultaneously incorporate both properties of an individual (e.g. aggression and activity) and the influences of the conspecifics around them (reviewed in Croft et al., 2008; Krause, Croft, & James, 2007; Wey et al., 2008; Whitehead, 1997). As such, they represent an ideal category of traits in which to evaluate whether traits with context-dependent expression and consequences experience more variable selection than more static phenotypes like morphology.

At least some aspects of social network position are repeatable phenotypes of individuals (Aplin et al., 2015; Formica, Wood, Cook, & Brodie III, 2017; Frumkin et al., 2016; Jacoby, Fear, Sims, & Croft, 2014) that likely have heritable genetic components (Brent et al., 2013; Fowler, Dawes, & Christakis, 2009; Lea, Blumstein, Wey, & Martin, 2010). In a number of taxa, the position that an individual occupies within a network correlates strongly with fitness (Brent et al., 2013; Formica et al., 2012; McDonald, 2007; Oh & Badyaev, 2010; Ryder et al., 2008; Silk et al., 2003, 2009; Wey & Blumstein, 2012). Network position can affect the exposure of an individual to disease, parasites, information, aggression, social mediation and other positive and negative fitness consequences (Bohm, Palphramand, Newton-Cross, Hutchings, & White, 2008; Dey, Reddon, O'Connor, & Balshine, 2013; Drewe, 2010; Flack, Girvan, De Waal, & Krakauer, 2006; Gordon, 1996; Nandi, Sumana, & Bhattacharya, 2014; Nunn, Jordan, McCabe, Verdolin, & Fewell, 2015; Pinter-Wollman et al., 2013; Royle, Pike, Heeb, Richner, & Kolliker, 2012; Snijders et al., 2017; VanderWaal, Atwill, Isbell, & McCowan, 2014). Despite the fact that network position itself and its ramifications are expected to vary depending on group membership, no studies have evaluated if selection on network position is consistent in space or time.

To determine whether the strength and direction of selection targeting social behaviours is more variable than that experienced by non-social traits, we compared patterns of phenotypic selection on social network position and morphological characters among nine subpopulations of the forked fungus beetle *Bolitotherus cornutus* over a breeding season. We estimated selection gradients on morphological traits (body size and horn length) known to be important in sexual selection in males in this species, and on individual social network position using three commonly utilized network metrics.

2 | MATERIALS AND METHODS

2.1 | Study species

Forked fungus beetles *B. cornutus* are tenebrionid beetles (Coleoptera) that live on fungi of the species *Ganoderma applanatum*, *Ganoderma tsugae* or *Fomes fomentarius* that grow on decaying logs or stumps (Liles, 1956). Adults consume the fungus brackets,

females oviposit on bracket surfaces and the larvae develop entirely inside the brackets (Pace, 1967) until they eclose as adults after 1–2 years (Wood et al., 2018). Most adults spend an entire breeding season on a single log, leading to repeated social interactions within a single subpopulation (Formica, Donald-Cannon, & Perkins-Taylor, 2016; Formica et al., 2011, 2012). Logs separated by as little as a few metres function as socially distinct units with limited movement of individuals among social neighbourhoods. While previous studies have estimated between 12.5% and 25% migration among subpopulations during the breeding season (Ludwig, 2008; Whitlock, 1992; Wood et al., 2018), we observed only three adult males moving among our subpopulations during this study and all three moved at the end of the observation period. Courtship, copulation, mate guarding and male–male combat occur mostly on the surface of the brackets. During courtship, males mount females head to abdomen, then during copulation the males reverse direction and remain facing head to head with females during the mate guarding stage (Brown & Bartalon, 1986; Brown, Macdonell, & Fitzgerald, 1985). Mate guarding typically lasts for several hours and has been demonstrated to be a reliable indicator of insemination success (Conner, 1988, 1989). Sufficient migration occurs to maintain genetic homogeneity among subpopulations (Wood, Donald, Formica, & Brodie III, 2013).

Bolitotherus cornutus are sexually dimorphic with respect to thoracic horns that males use in combat over access to females (Brown, 1980; Conner, 1988, 1989). Body size also predicts grip strength that prevents males from being dislodged by other males during courtship and mate guarding (Benowitz, Brodie III, & Formica, 2012). Horn and body size have been shown to be under strong sexual and social selection in males of this species, especially in lower density populations (Conner, 1988, 1989). Large males, and those who associate with smaller social partners, are more successful at inseminating females (Formica et al., 2011). The density-dependence of sexual and social selection for male horn and body size (Conner, 1989; Formica et al., 2011) in *B. cornutus* suggests that the strength of selection on morphology may in fact vary at the subpopulation level. Previous selection analyses of body size and horn length in this species have all assumed hard selection on globally relativized traits and fitness (De Lisle & Svensson, 2017).

Social connections among individual *B. cornutus* determine the opportunity for courtship and mating, access to egg laying sites and agonistic behavioural interactions that mediate space use and access to mates. Social interactions do not require direct contact in *B. cornutus*; individuals reorient themselves and wave their antennae towards each other when they are within a few body lengths, suggesting chemical, acoustic and/or visual communication are important in mediating social interactions. Many social behaviours are initiated at a short distance, with individuals reorienting before beginning a combat charge or courtship approach (Mitchem, Debray, Formica, & Brodie III, 2019). Females are able to distinguish losing from winning males based on substrate borne chemical cues (Mitchem et al., in prep), suggesting information about past behavioural outcomes may transmit through network connections.

Previous work indicates that network positions may be evolutionary important phenotypes in *B. cornutus* (Formica et al., 2012). In artificially assembled and manipulated laboratory populations, some network metrics (strength and betweenness) were repeatable across two time periods even in the face of a social disturbance (Formica et al., 2017), suggesting that those properties could experience consistent selection across a breeding season. However, a third metric (clustering coefficient) was not consistently expressed over time. In a single wild population of *B. cornutus*, male mating success was strongly predicted by both individual strength and clustering coefficient in male-only networks (Formica et al., 2012).

2.2 | Study populations

We followed nine subpopulations of *B. cornutus* (distinct logs or tree stumps supporting fungus populations) located within the Pond Drain metapopulation near the Mountain Lake Biological Station, Giles County, VA (37.3671°, –80.5360°) from June through August 2015. Subpopulations were selected based on feasibility of access and observation, proximity to other subpopulations and a minimum size of at least 25 individuals (to allow robust network estimation). The fallen logs hosting five of the subpopulations were infected with only *G. applanatum*, three with *G. applanatum* and *F. fomentarius* and one with only *G. tsugae*. Subpopulations had between eight and 148 fungus brackets of varying age and quality (Table 1).

During June 2015, all individuals were captured, imaged, labelled and returned to the population and bracket of their capture within 48 hr. Each individual was imaged on a flatbed scanner (Epson Perfection V600 Photo) at 2,100 dots per inch. Images were then imported into Image J (Abramoff, Magelhaes, & Ram, 2004) to measure the elytra length (mm) of all beetles and the thoracic horn length (mm) of males. Elytra length is an indicator of overall body size and is strongly correlated with thoracic horn length in males ($r \sim 0.90$; Conner, 1988; Formica et al., 2011). Thoracic horn length has been shown to influence mating success of males independent of body size (Conner, 1988). Each beetle was labelled with a unique three-letter code, printed at 4.5 point font on fluorescent paper and affixed with a light-cured clear acrylic (Tuffleye Wet-A-Hook Technologies). Throughout the study, any newly discovered, unlabelled beetles were captured, imaged, labelled and returned as above.

2.3 | Social networks

Trained observers searched every subpopulation during two scan periods (06:00–09:00 and 21:00–24:00) nearly every day from June 23 until August 23 ($n = 119$ scan periods). A scan consisted of searching for beetles on and around all fungus brackets and the surface of the log at each subpopulation. The location, behaviour and social partners of all individuals were recorded. Social interactions were defined as occurring when beetles were observed within 5 cm (~ 5 body lengths) of another individual and were scored as dyadic events

TABLE 1 Demographic and network characteristics of the nine subpopulations

Subpopulation ID	Demographic factors			Network factors					
	No. of females	No. of males	Total subpop. size	Sex ratio (males/total)	No. brackets used	Male density (ind./bracket)	Connectedness (edge density)	Average path length	Global clustering coefficient
PDR-609	14	13	27	0.48	20	0.65	0.313 (<0.001)	1.56 (0.097)	0.513 (0.012)
PDR-618	15	12	27	0.44	32	0.38	0.131 (<0.001)	3.40 (<0.001)	0.545 (<0.001)
PDR-614	12	17	29	0.59	31	0.55	0.063 (<0.001)	3.07 (<0.001)	0.315 (<0.001)
PDR-611	16	13	29	0.45	21	0.62	0.140 (<0.001)	2.80 (<0.001)	0.387 (<0.001)
PDR-613	17	15	32	0.47	8	1.88	0.143 (<0.001)	2.21 (0.562)	0.277 (0.049)
PDR-602	20	22	42	0.52	46	0.48	0.093 (<0.001)	2.52 (0.170)	0.234 (0.027)
PDR-619	42	28	70	0.40	107	0.26	0.047 (<0.001)	3.65 (<0.001)	0.379 (<0.001)
PDR-607	52	50	102	0.49	148	0.34	0.073 (<0.001)	2.90 (<0.001)	0.489 (<0.001)
PDR-331	117	81	198	0.41	97	0.84	0.060 (<0.001)	2.50 (<0.001)	0.317 (<0.001)



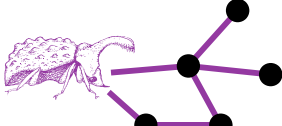

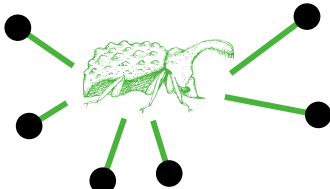
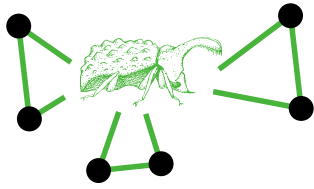
Note: Values in parentheses represent *p*-values from network-level permutations. Bold values indicate that the observed network structure of the subpopulation is significantly different from random networks. See section 'Network-level metrics' in text for details.

rather than via group membership (i.e. there was no 'gambit of the group'; Franks, Ruxton, & James, 2010). Previous work indicates that close physical proximity is an important determinant of individual interactions in *B. cornutus* (Formica et al., 2012, 2017; Mitchem et al., 2019). Spatial proximity is a common method for constructing social networks (e.g. Aplin et al., 2015; Leu, Farine, Wey, Sih, & Bull, 2016; Snijders et al., 2017; Wey et al., 2013). Both males and females were observed and included in the construction of the networks. Observations of sexual behaviour (courtship and guarding behaviours) were not included in the construction of the social networks to avoid non-independence between the reproductive behaviours used as fitness correlates and the network positions for which selection gradients were estimated (see below). Any individual that was not seen at least three times during the breeding season was removed from all analyses to avoid including mistaken identifications. Three males (out of 251) moved between two subpopulations during the breeding season; because these males were seen only 3–4 times on their new population, and were unlikely to influence the social networks, we removed these observations from network and selection analyses.

We constructed separate weighted, undirected social networks for each of the nine subpopulations from these proximity data using the simple ratio index (SRI). The SRI is an association index that weights the level of social interactions between individuals and corrects for biases introduced during observation periods where neither individual is observed but may be interacting unseen (Croft et al., 2008; Ginsberg & Young, 1992).

Three weighted network metrics, chosen because they are common metrics used in animal social network analysis and have been previously studied in this system (Formica et al., 2010, 2012, 2017), were calculated for every individual (Box 1) using the *TNET* package (Opsahl, 2009) in R. *Strength* is a measure of centrality to a network that scores the weighted number of interactions. We set the tuning factor (alpha) to 0.5, where each unique partner increases the focal individual's strength by one and each repeated interaction with that partner only increases the strength by 0.5 (Opsahl, 2009). *Betweenness* is a more emergent measure of an individual's centrality to a network that requires complete knowledge of the network. Betweenness is calculated by drawing the shortest path between all pairs of individuals in the network, then counting the number of those paths that pass through the focal individual (Opsahl, 2009; Wasserman & Faust, 1994). Individuals that lay between two distinct components of a network will have the largest betweenness values and those that are on the periphery of the network will have a betweenness of zero. *Clustering coefficient* is a measure of cliquishness that is calculated as the proportion of times that a focal individual's social partners interact with each other (Croft et al., 2008). Beetles that form equally weighted triangles in a network will have high clustering coefficient values and those that have many partners that do not interact with one another will have low to zero values of clustering coefficient. Individuals that have zero or one social partner have undefined clustering coefficients because they have zero possible

BOX 1 Measures of individual social network position

Metric	Definition	Low	High
Strength	<ul style="list-style-type: none">• A measure of centrality• Calculated as the weighted measure of the number of interactions		
Betweenness	<ul style="list-style-type: none">• An emergent measure of centrality that requires complete knowledge of the network• Calculated by counting the number of shortest paths between all pairs of individuals in the network that pass through the focal individual		
Clustering Coefficient	<ul style="list-style-type: none">• A measure of cliquishness• Calculated as the proportion of times that a focal individual's social partners interact with each other		

triangles in the network ($N = 41$ males). Therefore, these males were excluded from any further analysis involving clustering coefficient.

2.4 | Network-level metrics

To characterize the subpopulation in overall network structure, we calculated several network-level properties. We chose network-level metrics that described group contexts that seemed likely to influence the magnitude and direction of selection. *Connectedness* (edge density) is an unweighted measure of how linked the nodes of a network are to each other. It is a simple ratio of the number of actual edges divided by the number of all possible edges (Wasserman & Faust, 1994). We used igraph's `edge_density` function to calculate the connectedness of each population's social network. *Average shortest path length* is a measure of network-level connectivity, calculated as the average of the shortest paths between every pair of nodes in the network. We used the `distance_w` function in the `TNET` package for R to find the shortest path lengths for each population, incorporating weighted edges (Opsahl, 2009). The *global clustering coefficient* measures cliquishness in a population, or extent to which the interaction partners of any one individual are also partners with each other. We used the `tnet` function `clustering_w` (Opsahl, 2009), which divides the total number of closed triplets (sets of three nodes in which each node interacts with both of the other nodes in the set) by the total number of open and closed triplets (sets of three nodes in which some, but not all individuals interact with each other). In addition, the `clustering_w` function

assigns weight to each triplet based on the weights of the edges that connect its nodes.

2.5 | Selection analysis

We estimated sexual selection gradients on males ($n = 251$) using the number of successful spermatophore transfers (scored as observed mate guarding) as our fitness correlate. The appropriate scale of relativization (local or global) for fitness and phenotypes depends on how variation in traits mediates variation in fitness (De Lisle & Svensson, 2017). Based on previous work and the natural history of the system, we expected morphology to experience global (hard) selection, and social network traits to experience local (soft) selection. However, reasonable counterarguments about the mode of selection could be made so we analysed both hard (globally relative fitness and standardized phenotypes) and soft selection (local, within subpopulation relative fitness and locally standardized phenotypes) models for all traits.

We conducted four separate selection gradient analyses following the methods of Lande and Arnold (1983; Brodie III, Moore, & Janzen, 1995). As with all observational selection analyses, the directionality of causation (i.e. behavioural variation determines fitness variation or vice versa) is assumed and cannot be tested directly. We used the number of unique guards (i.e. insemination success) as the dependent variable and included number of observations, elytra size, thoracic horn size, the total number of observations, network strength, network betweenness and subpopulation as fixed effects. We also included subpopulation by strength, subpopulation by betweenness and subpopulation by thoracic horn as interactions in the

model to determine if selection gradients varied among subpopulations. We investigated two applications of this general linear model. In the hard selection model, fitness was relativized to the global average and all quantitative traits were standardized to metapopulation mean and variance. In the soft selection model, fitness was relativized to the mean of each subpopulation and all quantitative traits were standardized to the local subpopulation average. A second pair of selection models were analysed on the same dataset in which clustering coefficient and the clustering coefficient by population interaction were included and strength and betweenness and their interaction terms were dropped. It was necessary to analyse clustering coefficient separately from the other network traits because this variable was undefined for a large number of individuals (i.e. any male that did not interact in clique of shared nodes could not be assigned a clustering coefficient), reducing the overall sample of males to 210 and leaving some subpopulations with fewer than 10 males.

2.6 | Hypothesis testing and permutations

The fact that network position is the product of the behaviour of an individual and all of its social partners is what makes social network position such an interesting behavioural phenotype. However, this fundamental fact of network variables also creates non-independence that violates assumptions behind most hypothesis tests (Bejder, Fletcher, & Brager, 1998; Croft, Madden, Franks, & James, 2011; Farine, 2013, 2017; Lusseau, Whitehead, & Gero, 2008; Whitehead & Dufault, 1999). Randomization tests have been suggested as the most effective method for accounting for this non-independence. Permuting the raw data that are used to construct the network has been shown to be most robust and most likely to result in null distributions that account for aspects of network structure that are due to factors other than individual differences in behaviour and social associations (Farine, 2017).

We used a novel two-step permutation method to conduct significance testing for the selection models described above. The first permutation step randomized the field-collected raw observation data to generate 2,000 permuted datasets. Because our data are dyadic in nature (each social interaction between individuals was observed directly) we could not use existing methods that generally expect scoring via group composition (such as the R package *ASNIPE* (Farine, 2013)). Instead, we developed our own permutation protocol informed by previously suggested methods for dyadic interactions (Whitehead & Dufault, 1999) and largely modelled after Farine's 'pre-network' permutation method (2017). For each subpopulation, we generated a pool of all individual beetles that were seen on the subpopulation more than two times throughout the season. For a given scan period, every observed individual was replaced with another individual's ID that was drawn randomly (without replacement) from the population pool. All other data connected to that observation were retained, including the number of partners, the behaviour, the location of the observation and the time of day. This process was repeated for

each subpopulation and each scan period across the entire breeding season to generate a single permuted dataset. Each permuted dataset was then used to build a social network and estimate individual metrics for each subpopulation.

This permutation method retains the core structure of the social environment for a given population during a given period, and generates a null distribution of social networks and individual network metrics. Structural aspects of a network that are influenced by overall activity levels of a population, spatial dispersion of resources and abiotic factors that might affect patterns of social interactions should not differ between the observed networks and the permuted networks. Instead, differences between the observed and permuted networks should be due primarily to social behaviours of individual beetles that chose to be active and interact with specific social partners (Bejder et al., 1998; Farine, 2017).

After the first permutation step, the resulting network metrics (strength, betweenness and clustering coefficient) were then merged with the other individual phenotypic attributes for each beetle to create 2,000 complete permuted datasets. Each of these datasets now had some traits that had been permuted (e.g. strength and betweenness) and others that had been directly measured (e.g. thoracic horn and elytra). We therefore performed a second permutation step in which we shuffled all variables (without replacement) within each permuted dataset while retaining the link between individual beetle and fitness.

For each fully permuted dataset, we then ran the linear selection models as described above for the observed (unpermuted) dataset. The same linear model was then run for each of the 2,000 doubly permuted datasets to generate null distributions of F -values for all effects in all four selection analyses (Tables 2 and 3) and p -values were calculated as the percentage of permuted values that were greater than the observed F -value of each factor tested. One was added to the numerator and denominator of the final calculation to prevent p -values of zero (Davison & Hinkley, 1997; North, Curtis, & Sham, 2003). We evaluated permuted F -value distributions rather than permuted regression coefficients (β) because we were specifically interested in testing hypotheses about interactions between fixed effects (e.g. thoracic horn) and subpopulations; interaction terms from linear models have no single regression coefficient. Regression coefficients (β) reported herein were extracted from the observed linear model using the *EMMEANS* package in R (Lenth et al., 2018). Gradient estimates are reported without 95% CI because the permutations generate null distributions of statistics rather than estimates of error around a slope. We used the linear models to calculate effect sizes (η^2) of each variable in the model. Exact values of η^2 should be interpreted with caution, as the residuals from these models did deviate, somewhat, from normality.

To test whether subpopulation network structure deviated from a null structure, we calculated the values of connectedness, average shortest path length, and global clustering coefficient for each of our observed networks as described above. We then compared these observed values to the distributions of network values calculated from our 2,000 permuted datasets. p -values were calculated as the proportion of permuted values that were more extreme

TABLE 2 Double permutation results for hard (left) and soft (right) selection models that include the network metrics strength and betweenness ($N = 251$ males)

Hard selection				Soft selection			
	Standardized selection gradients (β) from observed data	p -value	Effect size ^a (η^2)		Standardized selection gradients (β) from observed data	p -value	Effect size ^a (η^2)
Number of observations	1.04	<0.001	0.250	Number of observations	0.895	<0.001	0.199
Elytra size (mm)	-0.26	0.140	0.001	Elytra size (mm)	-0.050	0.248	0.002
Thoracic horn (mm)	0.39	0.003	0.103	Thoracic horn (mm)	0.248	0.220	0.109
Strength	0.14	0.330	0.086	Strength	0.309	0.109	0.146
Betweenness	1.56	0.398	0.040	Betweenness	-0.191	0.246	0.046
Subpopulation ID	—	<0.001	0.119	Subpopulation ID	—	—	—
Subpopulation \times Horn interaction	—	0.081	0.038	Subpopulation \times Horn interaction	—	0.435	0.045
Subpopulation \times Strength interaction	—	0.460	0.023	Subpopulation \times Strength interaction	—	0.027	0.082
Subpopulation \times Betweenness interaction	—	0.110	0.046	Subpopulation \times Betweenness interaction	—	0.032	0.074

Note: p -values were calculated using a two-step permutation method and are the proportion of tests more extreme than the observed values (see Section 2.6 for complete details). Significant values are highlighted in blue.

^a η^2 were calculated from a linear model with only the observed data. Exact values of η^2 should be interpreted with caution, as the residuals from these models were not always normally distributed.

TABLE 3 Double permutation results for hard (left) and soft (right) selection models that include the network metric clustering coefficient ($N = 210$)

Hard selection				Soft selection			
	Standardized selection gradients (β) from observed data	p -value	Effect size ^a (η^2)		Standardized selection gradients (β) from observed data	p -value	Effect size ^a (η^2)
Number of observations	0.762	<0.001	0.250	Number of observations	0.763	<0.001	0.289
Elytra size (mm)	-0.191	0.710	0.001	Elytra size (mm)	0.030	0.114	0.003
Thoracic horn (mm)	0.297	0.141	0.103	Thoracic horn (mm)	0.155	0.485	0.119
Clustering coefficient	0.122	0.286	0.086	Clustering coefficient	0.158	0.242	0.004
Subpopulation ID	—	0.332	0.119	Subpopulation ID	—	—	—
Subpopulation \times Horn interaction	—	0.059	0.038	Subpopulation \times Horn Interaction	—	0.456	0.025
Subpopulation \times Clustering coefficient interaction	—	0.293	0.046	Subpopulation \times Clustering coefficient interaction	—	0.170	0.069

Note: p -values were calculated using a two-step permutation method and are the proportion of tests more extreme than the observed values (see Section 2.6 for complete details). Significant values are highlighted in blue.

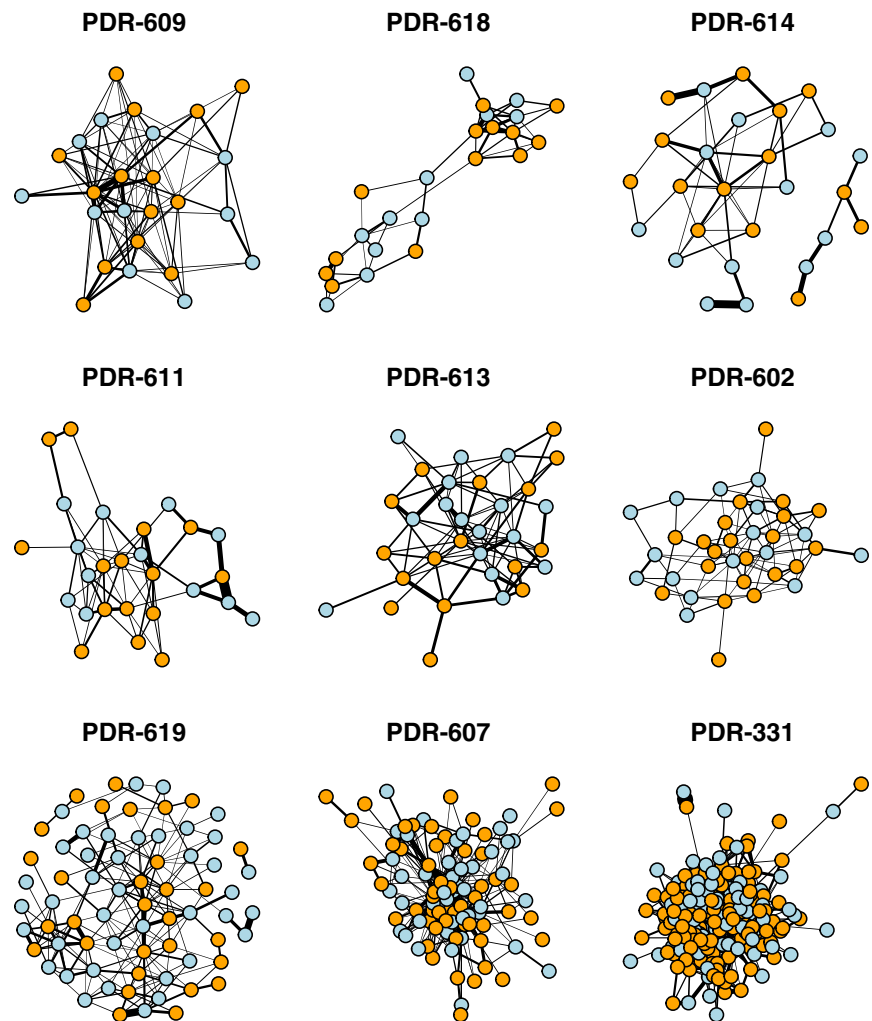
^a η^2 were calculated from a linear model with only the observed data. Exact values of η^2 should be interpreted with caution, as the residuals from these models were not always normally distributed.

than the observed values. These methods allowed us to determine whether subpopulation level features of the *B. cornutus* social networks deviate from the null expectation generated by local abiotic or demographic factors. All statistical analyses were done with program R version 3.5.2 (R Development Core Team, 2011).

3 | RESULTS

In total we observed 556 resident *B. cornutus* (251 males and 305 females) involved in 4,105 social interactions that did not include courtship or copulation behaviour. Each individual beetle

FIGURE 1 Visualizations of social networks in each of the nine subpopulations. Circles (nodes) represent individuals and lines connecting the circles (edges) represent observed social interactions. Thickness of edges indicates relative number of interactions between each pair of social partners. Blue nodes represent males and orange nodes females. The visualizations were constructed using the Fruchterman–Reingold method in iGraph for R (Csardi & Nepusz, 2006; Fruchterman & Reingold, 1991), which pulls nodes that are highly connected closer together. Subpopulations are arranged in order of subpopulation size from smallest in the upper left (PDR-609) to largest in the lower right (PDR-331). This order is maintained through subsequent figures. Unconnected individuals (those seen three or more times but never observed interacting with other individuals) are excluded from this visualization. See Figure S1 for alternative visualizations of the two largest subpopulations (PDR-607, PDR-331)



Hard selection on morphology

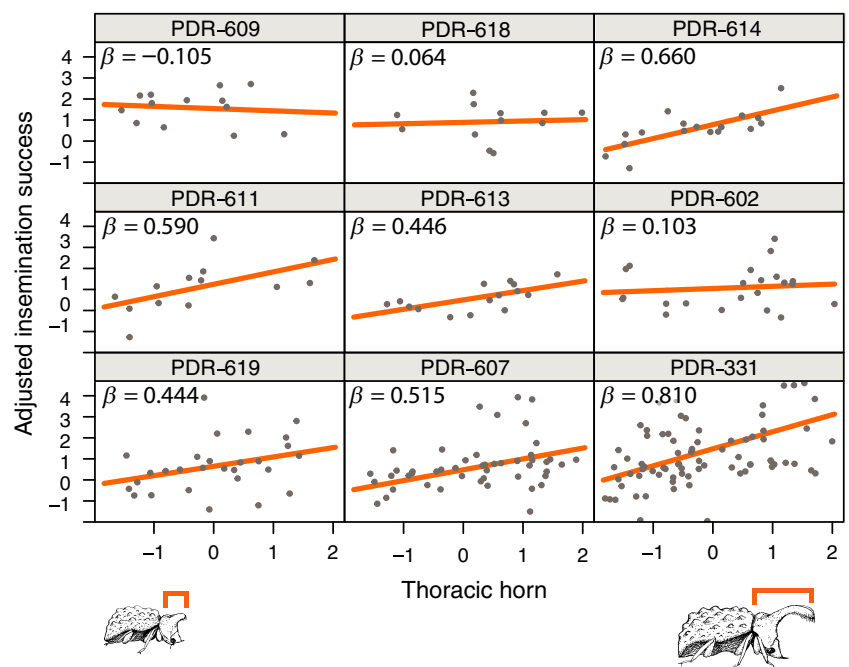


FIGURE 2 Subpopulation selection gradients (β) extracted from a linear model that assumes hard selection. Gradients are estimated from observed data with both phenotypes and fitness (insemination success) standardized to metapopulation means. Permutation tests indicate significance of overall effect of thoracic horn and no significant interactions among subpopulations. Confidence intervals for subpopulation gradients are not generated by the permutation test

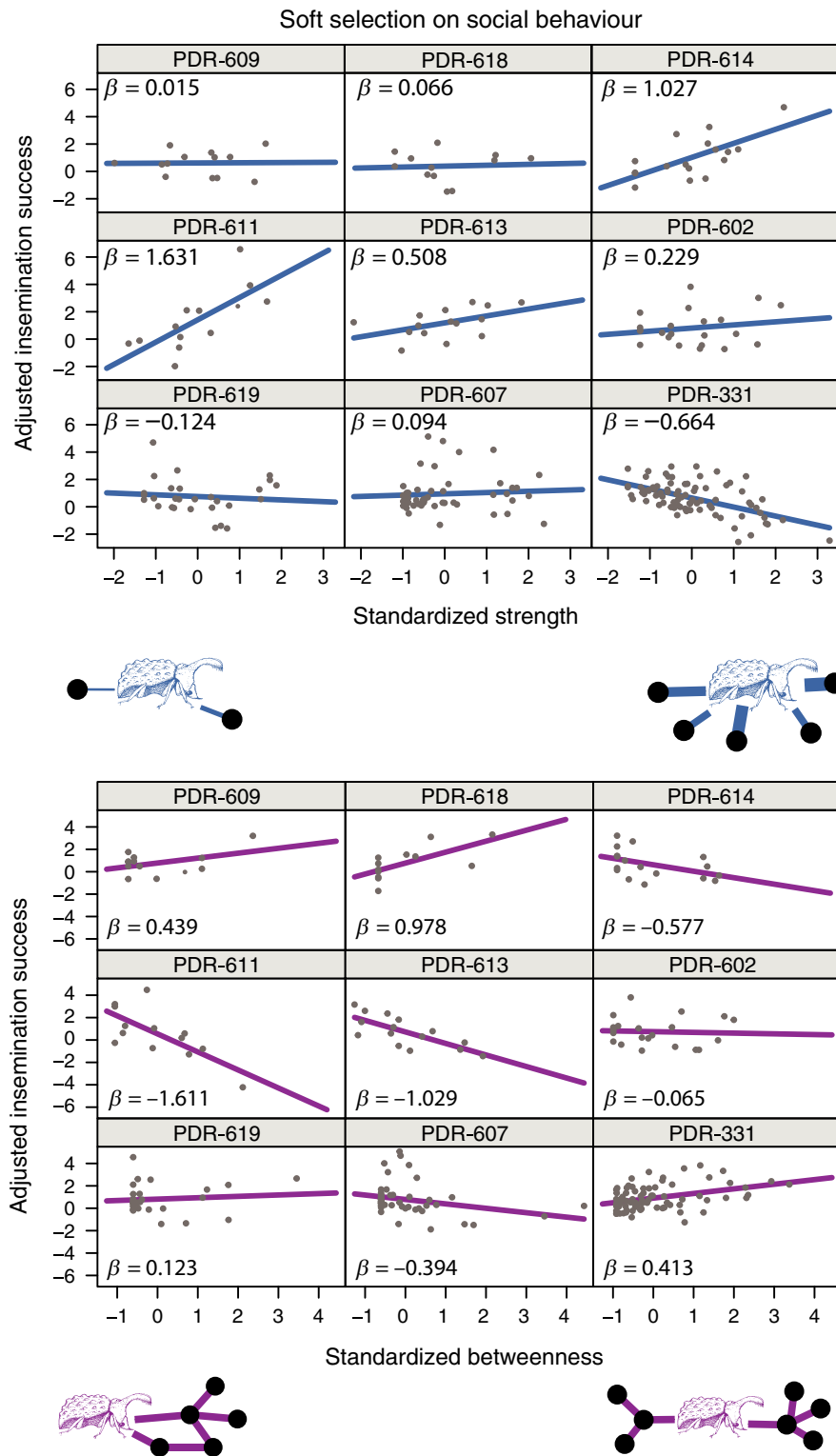


FIGURE 3 Subpopulation selection gradients (β) extracted from a linear model that assumes soft selection. Gradients for strength (top) and betweenness (bottom) are estimated from observed data with both phenotypes and fitness (insemination success) standardized to local subpopulation means. Permutation tests indicate no significant main effect of either behaviour, but significant interactions among subpopulations for each behaviour. Confidence intervals for subpopulation gradients are not generated by the permutation test

was observed between 3 and 81 times over 119 scan periods (mean = 23.8 ± 16.7 SD observations). Beetles also varied in the number of observed social interactions used to construct the social networks (range = 0–121, mean = 13.6 ± 18.45 SD, median = 7 interactions).

The nine subpopulations we observed varied in size, demographics and network structure (Table 1; Figure 1; Figure S1). Most of the subpopulations, especially the three largest, formed highly

connected networks, whereas others formed more sparsely connected structures. One subpopulation (PDR-614) exhibited two distinct modules, while another (PDR-618) had two nearly unconnected modules that were joined by two social interactions between two pairs of individuals. The social networks we observed were largely nonrandom in structure (Table 1). Connectedness and global clustering coefficient were different from randomly permuted networks for all subpopulations. Average path length

was similarly different from null expectations in six of the nine subpopulations.

Sexual selection on morphological traits was detected in the hard selection model that evaluated globally relativized traits and fitness, but not in the soft selection model (Table 2; Figure 2). However, in both the hard and soft selection models thoracic horn explained ~10% of the variation in fitness (see η^2). Thoracic horn length of males was under strong positive selection across the metapopulation, and there was no significant interaction between thoracic horn length and subpopulation in either model. No selection on elytra size of males was detected. In the models with reduced sample size that included clustering coefficient, no selection on thoracic horn or elytra size was detectable. Number of observations, a covariate included to control for individual differences in overall activity, positively predicted mating success in all models and consistently explained between 20% and 29% of variation in fitness across all of the selection models.

Selection for network position varied considerably among the nine subpopulations for both strength and betweenness, with significant interaction terms for both behaviours in the soft selection model (Table 3; Figure 3). Each these interactions explained 7.4% and 8.2% of the variation in fitness. Point estimates of betas should be viewed with caution because of the absence of confidence intervals, but ranged from strongly positive to strongly negative for both traits (Figure 3). The hard selection model showed no significant effects of behaviour or population interactions on relative mating success and no interaction terms explained more than 5% of the variance in fitness. No selection was detected on clustering coefficient in either the hard or soft selection models.

4 | DISCUSSION

Our observations of free-ranging beetles reveal that social behaviours experienced sexual selection that operated locally and varied substantially across nine subpopulations. In contrast, male weaponry consistently experienced positive directional selection in those same subpopulations. Selection on morphology was only evident when evaluated as hard selection at the metapopulation level, indicating that a male's absolute horn size was the important predictor of mating success, rather than his horn size compared to local competitors. This pattern of variable soft selection on social behaviour and consistent hard selection on morphology supports the hypothesis that local differences in social context could lead to substantial variance in the form of selection on social traits even within a single metapopulation. The reasons for these differences in the direction and magnitude of selection are not discernable from the current data, but could relate to population size, density, network structure or other demographic factors (Figures S2 and S3). As with all correlational studies of selection in the wild, it is impossible to determine for certain the causal links behind covariance between a trait and fitness. In the case of social behaviour, it is even possible that fitness differences lead to changes in assortment and thereby social network position.

4.1 | Subpopulations differ in social context

Our focal subpopulations varied markedly in overall social network structure and demographic properties that might be expected to influence fitness relationships. Most aspects of social network structure were demonstrably nonrandom in every one of the subpopulations. Nonrandom metrics associated with edge density, path length and clustering suggest that *B. cornutus* networks tend to be densely connected, with few degrees of separation between the majority of beetles in a subpopulation. Although we were not able to test whether network structure differed statistically among subpopulations, visual inspection of network plots (Figure 1) and the range of values of key metrics (Table 1) reveals substantial qualitative differences. It is important to note that all network metrics reported here were calculated based on social proximity of individuals of both sexes (not including courtship and reproductive behaviours). This network reflects the pattern of interactions that mediates other important behaviours including fighting, courting and access to food and reproductive resources. Network structure of single sex (e.g. male only) interactions, or of different kinds of interactions (e.g. reproductive behaviour or physical 'touches') would undoubtedly differ (Croft et al., 2008; Farine & Whitehead, 2015).

Demographic properties also varied among subpopulations, though most spanned only a narrow range of values. Density has been implicated as a factor influencing sexual selection in a variety of species including *B. cornutus* (Conner, 1989; Formica et al., 2011). Although our observations of total individuals per fungus bracket ranged six-fold, only one of the subpopulations exceeded the thresholds of one or two males per bracket that were considered high density in previous studies (Conner, 1989; Formica et al., 2011). Sex ratio was consistently even or only slightly male biased. Only overall population size varied dramatically, with some populations including an order of magnitude more individuals than others.

The observed differences in social context existed despite the subpopulations occupying a limited geographic area. Pairs of subpopulations were separated by 18–500 m, and all of the logs occurred in a total area of forest <1 km². Factors, whether social or environmental, that structured the observed variation in social and demographic parameters occurred at the level of individual logs within the forest.

4.2 | Selection on morphology

Selection gradients on horn length of males were generally positive, with some of the smaller subpopulations appearing to experience little or no detectable directional selection. We found no evidence of directional selection on elytra size in our study. These results echo previous studies that found strong selection favouring longer horns (relative to elytra size), but undetectable or weak selection against large body size (Conner, 1988). In analyses that treated male morphology on a multivariate rotation, sexual selection strongly favoured a principal component representing overall

size (that included both elytra and horn size; (Formica et al., 2011). It was somewhat surprising that male weaponry did not experience more variable selection, given the behavioural scenario in which thoracic horns are used by *B. cornutus*. Males use their horns in physical battles with one another that influence access to courtship opportunities with females (Brown, 1980; Conner, 1988; Mitchem et al., 2019). Previous studies indicate that horn length does not influence mating success in high density subpopulations (Conner, 1989) and that the multivariate body size of social partners further favoured large body size of males through social selection (Formica et al., 2011). These lines of evidence suggest that an individual's horn size relative to that of other males in its social group might be the most important influence on mating success, but our soft selection model did not support this view. Instead, absolute horn size (standardized relative to the metapopulation mean) was the only predictor of relative fitness, suggesting that simply having larger horns than one's neighbours is not enough to skew mating success. Despite differences in significance of its effect, thoracic horn size did explain approximately 10% of the variation in fitness in both hard and soft selection models. This result is not surprising since the difference between hard and soft selection should be limited whenever phenotypic distributions are fairly similar across subpopulations as they were for morphology in our study. The comparison of hard and soft selection models generally supports the interpretation that selection on morphology (in this case weaponry) does not operate in a locally context-dependent fashion with subpopulations.

4.3 | Selection on network traits

An individual male's centrality (strength and betweenness) in its social network strongly influenced mating success, but the strength and sign of the relationships varied among subpopulations. On the other hand, cliquishness (clustering coefficient) had no detectable consequence for mating success (but see Section 2 regarding reduced sample size for this test). These results partially contradict an earlier study of a single subpopulation of *B. cornutus* in which centrality was positively, and cliquishness negatively, correlated with individual mating success in males (Formica et al., 2011). Repeatability studies in *B. cornutus* indicate that individual strength and betweenness measures are more consistently expressed than clustering coefficient (Formica et al., 2017). Changing expression of some social network traits could lead to differences in how they relate to fitness variation across studies.

Among subpopulations, centrality measures experienced selection that apparently ranged from strongly negative to strongly positive. Our soft selection analysis suggests that an individual's strength and betweenness are important relative to the other individuals within its own network. Individuals with locally high strength or betweenness could experience either increased or decreased mating success, depending on the network they found themselves in. Point estimates of the selection gradients suggest that selection does not necessarily operate in the same direction on the two

centrality measures, underscoring the different aspects of centrality that each metric captures.

While the variability of selection on social network traits is clear, no contextual properties of subpopulations obviously align with the observed differences. Several variables, including population size, male density per bracket, number of brackets and network-level characteristics including connectedness and shortest path length all varied substantially among the subpopulations. Unfortunately, the error associated with estimates of subpopulation gradients and the small number of replicate subpopulations preclude rigorous statistical analysis. We plotted bivariate relationships and estimated Spearman's rho (Figures S3 and S4) as an exploratory exercise and found no significant trends. Male density per fungus bracket has been shown to influence the strength of selection on weaponry in other studies (Conner, 1989; Formica et al., 2011), but did not appear to align with differences in selection on either morphology or behaviour in our study. Selection on strength trended more positively in populations with male biased sex ratios and more connected network structure, and more negatively in larger populations. Selection on betweenness trended more positively in networks with higher global clustering. These relationships are suggestive at best, and require further data to substantiate.

The underlying reasons for selection on network characters are unclear, but we suspect that they relate to mating interference among males and harassment of females that increases with the frequency and pattern of interactions. The networks we analysed included both sexes, so strength and betweenness reflect connections among males and females. For example, high strength values could reflect a large number of social interactions among males or between males and females. Relatively high strength or betweenness may represent different underlying social dynamics in small and large populations. For males, high strength in large populations may lead to more aggressive or competitive interactions with other males that become distractions from mate acquisition, whereas in smaller populations the higher centrality reflects access to mates. Similar behavioural explanations are thought to underlie differences in selection on morphology that correlated with male density in this system in previous studies (Conner, 1989; Formica et al., 2011).

An alternative, and fairly speculative, explanation for the varying fitness effects of betweenness involves the flow of information through social networks. Connections among individuals provide information about resources, location of mates and properties of same-sex competitors (Darden, James, Ramnarine, & Croft, 2009; Darden, Steffensen, & Dabelsteen, 2008). Beetles likely transmit information about past experiences through chemical signals, some of which are known to change to reflect outcomes after behavioural interactions (Mitchem et al., in prep). If information about the past successes or actions of social partners biases the outcome of current events, (such as with winner-loser effect dynamics or mate copying, Dugatkin & Drueen, 2004; Oliveira, McGregor, & Latruffe, 1998) then variation in mating success might be correlated to access to this kind of information, as captured in network position. Contest outcomes

even have the potential to cascade through multiple interactions to influence the behaviour of individuals not directly involved (e.g. a past winner is more likely to play a loser in the next round, who would then be more likely to play a winner and so on, so that the original winner's effect might reach multiple connections through the network).

This kind of information cascade may have different consequences in subpopulations of different overall sizes or with different network structure. Small dense networks may have more positive feedback because they contain fewer pathways connecting relatively fewer individuals. Larger networks, by virtue of size alone, may experience more negative interactions such as male–male competition and aggression/dominance interactions that are subsequently transmitted across networks, so that a single interaction indirectly impacts a larger number of individuals.

5 | CONCLUSIONS

Our results suggest that the scale on which we evaluate adaptive evolution of social behaviours like network position will be critical. In metapopulations that are spatially or socially subdivided, selection may be detectable only when social traits and fitness are evaluated relative to the social group in which they operate. Moreover, this subdivision creates opportunities for the form of selection to vary dramatically in a context-dependent fashion that is similar to frequency-dependent, or soft, selection (De Lisle & Svensson, 2017; Goodnight et al., 1992). These soft selection dynamics allow for a multilevel process in which group effects on individual fitness contribute to adaptive evolution (Goodnight et al., 1992).

Variation in the direction of selection is likely to have more significant consequences for the downstream patterns of evolution than differences in magnitude alone (Siepielski et al., 2013). Our study suggests that social network position may be more likely than other characters to experience differences in the sign of selection among subpopulations. This pattern in turn would lead to more rugged fitness landscapes across the span of a metapopulation. The ramifications of complex fitness landscapes will depend on a number of other factors including availability of genetic variation, genetic architecture underlying phenotypes and genetic structure of the metapopulation. At one extreme, diversifying local adaptation could result if traits of interest have the potential to respond locally to variable selection, and sufficient subdivision among subpopulations to allow independent evolutionary trajectories. Conversely, limited genetic differentiation among subpopulations, such as has been observed in forked fungus beetles (Wood et al., 2013), may lead the same sort of rugged fitness surface to promote genetic and phenotypic variation that is more homogeneously distributed across the entire metapopulation.

The consequences of variable selection may be especially important when the targets are social behaviours. As interacting phenotypes, social behaviours function as both targets and agents of selection, creating feedback loops that can generate rapid evolutionary change

and widespread correlated responses to selection (McGlothlin et al., 2010; Moore et al., 1997; Wolf, Brodie III, Cheverud, Moore, & Wade, 1998). Social behaviours mediate selection on other characters, such as weaponry used in social interactions, and even have been argued to lead the evolution of other phenotypes (Fisher, 1915; Mayr, 1960; Moore et al., 1997; West-Eberhard, 1979, 1984). Because behaviours are inherently more labile than morphological traits, it is also possible that individuals can adjust either behaviour or the social context in which they find themselves, further impacting their experience of the adaptive landscape (Flack et al., 2006; Formica & Tuttle, 2009; Saltz, Geiger, Anderson, Johnson, & Marren, 2016). In these ways, the effects of varying selection on social behaviour are expected to cascade throughout the multivariate phenotype.

ACKNOWLEDGEMENTS

This work was made possible by the continuing field efforts of Beetle Crew and student collaborators, Desta Pulley, Adam Kapilow, Shelby Daniel-Wayman and Hazel Galloway who helped collect field data. We thank the Mountain Lake Biological Station, including J. Jones and T. McNamara, who provided facilities and logistical support. We are very grateful to Andrew Reuther of Swarthmore's ITS department for help getting the R Studio Server and parallel processing working. Ariel Kahrl drew the original sketches of forked fungus beetles used in the figures. White Pine Lodge and The Mountain Lake Lodge provided access to field sites, without which this work would have been impossible. Financial support for this work was provided by the National Science Foundation (awards IOS-1355029 to V.F. and IOS-1355003 and DEB-1911485 to E.B.III), the Robert Enders Field Research Award and Norman A. Meinkoth Field Biology Award from Swarthmore College, the Swarthmore Biology Department and a Howard Hughes Medical Institute grant to Swarthmore College.

AUTHORS' CONTRIBUTIONS

V.F. and E.B.III conceived the ideas and designed methodology; V.F., E.B.III and H.D. collected the data; All authors contributed to data analysis; V.F. and E.B.III led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.0k6dj9xm> (Formica, Donald, Marti, Irgebay, & Brodie III, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Formica V, Donald H, Marti H, Irgebay Z, Brodie III E. Social network position experiences more variable selection than weaponry in wild subpopulations of forked fungus beetles. *J Anim Ecol*. 2021;90:168–182. <https://doi.org/10.1111/1365-2656.13322>