

Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*)

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Abstract

Social networks describe the pattern of intraspecific interactions within a population. An individual's position in a social network often is expected to influence its fitness, but only a few studies have examined this relationship in natural populations. We investigated the fitness consequences of network position in a wild beetle population. Copulation success of male beetles positively covaried with strength (a measure of network centrality) and negatively covaried with clustering coefficient (CC) (a measure of cliquishness). Further analysis using mediation path models suggested that the activity level of individuals drove the relationships between strength and fitness almost entirely. In contrast, selection on CC was not explained by individual behaviours. Although our data suggest that social network position can experience strong sexual selection, it is also clear that the relationships between fitness and some network metrics merely reflect variation in individual-level behaviours.

Introduction

Interactions with social partners can have profound effects on the fitness of the participants (West-Eberhard, 1979; Frank, 1998, 2007). Quantifying the role interactions play in social evolution is difficult because interactions with conspecifics are often complex and their effects may be farther-reaching than the outcome of a single dyadic interaction. In the wild, social interactions are often fluid and dynamic with individuals moving in and out of social groups. In many systems, individuals do not interact with all social partners equally, and some social partners have a greater effect on the focal individual's behaviours and fitness than others. Phenomena such as interacting phenotypes (Moore *et al.*, 1997), reciprocity (Bleakley & Brodie, 2009; McGlothlin *et al.*, 2010), eavesdropping (McGregor, 1993; Mennill & Ratcliffe, 2004) policing (Flack *et al.*, 2006) and social learning (Kendal *et al.*, 2009) have all been hypothesized to

extend the effects of dyadic interactions to multiple individuals.

Network analyses have gained popularity as a means of describing the more complex aspects of social structure in a population of interacting individuals because they consider not only pairwise contacts, but also multi-level connections and patterns of structure that are impossible to characterize as occurring between two individuals. Social network analysis can be used to describe the components of the social structure of a population as a whole, including its centrality, cohesion (e.g. cliquishness) or flow (e.g. flow of information or disease) (Krause *et al.*, 2007; Croft *et al.*, 2008). Additionally, social network analyses can describe many of these attributes for individuals within a social network. An individual's position in a social network may be influenced by its own behaviours but is also inherently a function of the conspecifics with which it interacts (Wey *et al.*, 2008). Thus, social network position may be a context-dependent trait whose expression depends directly upon the other individuals in the network.

Several recent studies have demonstrated that individuals' network positions predict differences in fitness in animal systems. In baboons, a female's sociality (based on

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grooming and proximity) strongly influenced her offspring's survival (Silk *et al.* 2003; Silk *et al.* 2009). In wire-tailed manakins, a male's centrality in a coordinated display network on the lek covaried with the number of offspring he sired (Ryder *et al.* 2008; Ryder *et al.* 2009). Moving among social groups appears to be part of an alternative reproductive tactic in house finches (Oh & Badyaev, 2010). These results suggest that we might consider an individual's network position as an extended phenotype that can covary with individual fitness and thereby experience natural and sexual selection (Dawkins, 1982; Lande & Arnold, 1983; Turner, 2004).

As is true for any character, a covariance with fitness might not indicate that direct selection is operating through causal effects of network position. Such a statistical relationship may also be due to indirect selection that results from underlying behavioural and morphological traits that themselves directly influence fitness as well as network position. For example, in a system where more aggressive individuals have higher fitness and aggression also causes individuals to be more central to the network, a simple regression of fitness on social network metrics might incorrectly identify network position as a target of selection. This situation is analogous to the morphology-performance-fitness paradigm (Arnold, 1983), in which morphology has causal effects on performance and either or both might causally influence variance in fitness. Path analysis has been an effective tool for disentangling direct from indirect selection when there are hierarchical relationships between traits and may be useful for asking whether the relationship between social network position and fitness is causal, or simply an artefact of covariance with an underlying variable (Kingsolver & Schemske, 1991; Brodie & Ridenhour, 2003; Kingsolver & Huey, 2003).

To explore the relationships between individual network position, underlying traits, and fitness, we examined the social structure and copulation success of males in a wild population of forked fungus beetles (*Bolitotherus cornutus*). Forked fungus beetles have relatively simple social structure and are known to experience strong sexual and social selection on male combat traits (Conner, 1988, 1989b; Formica *et al.*, 2011). Males interact with other males in mating arenas, with some males establishing relatively long-term tenures in one physical position, whereas other males move more frequently among possible mating sites. Previous fieldwork has demonstrated that the social context of the mating arena has direct effects on the mating success of individual males. Males whose social partners are smaller tend to gain more copulations, and males in lower density groups experience stronger selection on body size (Conner, 1989b; Formica *et al.*, 2011). The density of males further influences patterns of assortment such that males tend to associate with the opposite sized individuals in low, but not high, density populations. New interactions with novel males might further be expected to have different fitness consequences than repeated interactions

with the same males. These observations suggest that both the number and identity of social partners that a male interacts with might affect his mating success. Network metrics describe many of the patterns of interactions among males that are thought to be important in this system. The goal of this study was to determine whether an individual's position within a social network could explain variance in male copulation success beyond that of individual behaviours and physical traits. We first conducted simple univariate analyses to determine whether network position covaried with fitness. We then used a hierarchical path analysis to dissect direct and indirect selection to evaluate whether these relationships describe unique pathways to fitness beyond behavioural and morphological characteristics of individuals.

Methods

Forked fungus beetles (*B. cornutus*; Coleoptera: Tenebrionidae) live their entire lives on or near the fruiting bodies of wood-decaying shelf fungi (Liles, 1956; Pace, 1967). They are ideal for social network studies because they perform the majority of their social and mating behaviour on the surface of these fungi (Conner, 1988), remain in one population throughout a breeding season, can live for several years, and nearly all of the individuals in a population can be surveyed through scan sampling (Formica *et al.*, 2010, 2011). When beetles are not on the surface, they remain inside of the log or holes in the fungal brackets where there is limited space for social interactions and no space for mating to occur (Conner, 1988).

Bolitotherus cornutus have stereotyped mating behaviours that consist of males mounting females, facing head to abdomen and performing a twitching behaviour (Conner, 1989a). Females apparently have no control over which males court them, but have complete control over mating, as they must open their anal sternite to allow copulation. After a successful copulation, males mate guard by remaining on the dorsum of the female and facing head to head for several hours. This guarding posture typically lasts from 0.5 to 5 h and has been demonstrated to be a reliable indicator of copulation success (Conner, 1989a). We used the number of times a male was observed guarding a unique female each night as our estimate of male fitness (Formica *et al.*, 2011). Although this component of fitness does not include all aspects of reproductive success (e.g. cryptic female choice or sperm competition), it is an excellent measure of males' access to females and likely includes most components of noncryptic sexual selection. Copulation success ranged from 0 to 3 unique guarding events, with a mean of 0.43 ± 0.10 SE.

Study site and scan sampling protocol

Our study population was a deme within the larger Pond Drain metapopulation of *B. cornutus* near Mountain Lake Biological Station in the Appalachian Mountains of

southwest Virginia (37.376°N, 80.522°W). The Pond Drain metapopulation has been extensively studied for over 20 years. Previous work has demonstrated that beetles freely move among brackets within a deme, but infrequently among demes (Ludwig, 2008), resulting in local genetic differentiation at the deme level ($F_{ST} = 0.06$; Whitlock 1992). Young adults disperse to new demes shortly after emergence, suggesting that the social environment of each deme should be relatively stable for the most of the breeding season (Bondrup-Nielsen, 2005).

The deme used for this study was located on a fallen oak (*Quercus* sp.) log containing a large patch of *Ganoderma applanatum* with many fungal brackets. The landscape of the log was gridded using numbered galvanized steel nails arranged in a Mercator-like coordinate system (Formica *et al.*, 2010). Previous work has demonstrated that > 80% of the beetles ever observed can be marked in 3 days (unpublished data). The log was surveyed several days prior to behavioural observation, and all individuals on the deme were captured and the dorsal side of each beetle was photographed with a Nikkor 105-mm micro lens and Nikon D200. The photographs contained a 2-mm stage micrometer in the same plane as the focal trait for scale. Elytra length was measured using the software IMAGEJ (Wet A Hook Technologies LP, San Antonio, TX, USA; Abramoff *et al.*, 2004). Each beetle was labelled with a unique identification tag printed on fluorescent paper and affixed with a light-cured acrylic (Tuffleye™ Wet-A-Hook Technologies). The tags fluoresced when exposed to ultraviolet light and were easily observed from a few metres away. Unlabelled individuals that appeared during the study period were collected and labelled at the end of each night. All beetles were returned within 24 h of initial capture.

Scan sampling was conducted 4–5 times a night for 19 nights, resulting in a total of 84 scans. A scan consisted of several researchers searching the entire surface of the log and fungal brackets for *B. cornutus* using dark red light (so as not to disturb mating behaviour). Every location on the log was searched by two researchers during each scan. At the end of the night, the log was scanned for a final time using white and UV light to ensure that no individuals were missed during the data collection scans, and unlabelled beetles were collected at this time. Although all individuals in the population were censused and observed, here we use only observations of males to construct the social networks and analyse selection because previous work suggests that the major cause of sexual selection are male–male social interactions including combat (Brown & Bartalon, 1986; Conner, 1988, 1989b; Formica *et al.*, 2010, 2011; K. M. Benowitz, D. Edmund, I. Brodie & V. A. Formica, unpublished).

Delineation of social partners

Little is known about how social information is gathered and transmitted in *B. cornutus*. Although social interac-

tions clearly include direct contacts, it is also likely that important communication occurs at some local distance in insect species that communicate with conspecifics via chemical cues (d’Ettorre & Moore, 2008). Therefore, in a method modelled after other shared space-use social networks (e.g. Vohnhof *et al.*, 2004; Wolf & Trillmich, 2008), we chose to define probable social partners as males that were located within 5 cm of each other. These observations were recorded as individual associations (by spatial proximity), and not as group membership; therefore, we do not need to employ the additional statistical steps needed to deal with the ‘gambit of the group’ (Whitehead & Dufault, 1999; James *et al.*, 2009).

Previous studies of social networks have also used spatial proximity and physical association as means to delineate social partners (e.g. Croft *et al.*, 2004). Association data, as compared to physical contact, may provide greater insight to overall social structure for two reasons: first, spatial proximity may be the result of unobserved social interactions that have occurred prior to the observation, and second, it is highly probable that socially pertinent information is often passed from individual to individual without physical contact (Whitehead, 2004). Potential information transmitted through spatial proximity could include the sex or size of the nearby individuals; in many systems, complex information such as relatedness and reproductive status can be gathered by social patterns without contact (e.g. Colwell *et al.*, 1978; Epple *et al.*, 1987; doNascimento & Morgan, 1996; Smith & Abbott, 1998; Washabaugh & Snowdon, 1998; White *et al.*, 2002; Fitzgerald *et al.*, 2004; Byrne & Keogh, 2007; Scordato & Drea, 2007; Morgan, 2009). The distance of spatial proximity was based on biology of the system – 5 cm corresponds to approximately four body lengths of *B. cornutus*. Beetles reorient themselves to engage other beetles during encounters on fungal brackets while still several centimeters apart, demonstrating that they are aware of each other’s presence before they come into physical contact. This distance includes some, but not all, individuals on the same fungal bracket, but no individuals located on other brackets.

We constructed a weighted and symmetrical social network for male beetles using socPROG (Whitehead, 2008; Fig. 1). Our association index matrix was calculated using the Simple Ratio Index (SRI). SRI measures the proportion of times two individuals were seen together out of the total number of times those individuals were observed (Croft *et al.*, 2008). This index controls for differences in the total number of times an individual was scored in the study, thereby reducing observation bias and adjusting for total activity level of different individuals in the network metrics.

Network metrics

Much of the previous animal social network literature has focused on unweighted, binary networks, which

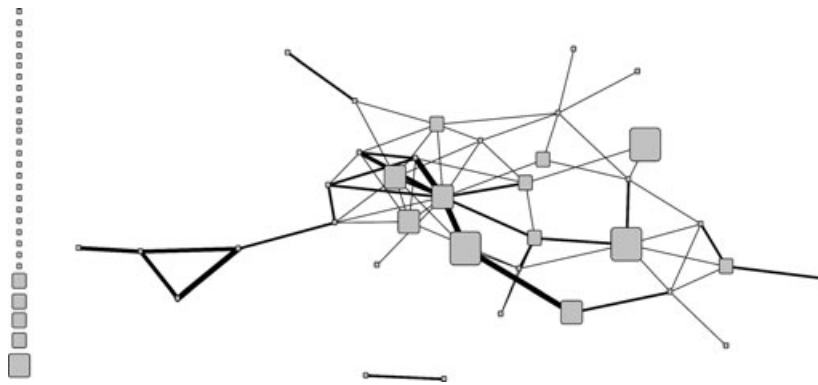


Fig. 1 Diagram of male *Bolitotherus cornutus* social network. Nodes (squares) represent individual male beetles, and edges (lines) connect beetles that were social partners during the sampling period. Size of nodes denotes copulation success (0, 1, 2 or 3 unique guarding events), and the thickness of the edges is scaled to denote weight of interaction (number of times observed in association; 1, 2, 3 or 4 association events). Unconnected nodes to the left represent males that were observed during the sampling period, but did not interact with other males.

ignore the influence of repeated interactions between individuals. Due to the stability of social groups in many systems, the frequency of interactions is likely to be important. We therefore used weighted network analyses, which scale the resultant metrics by the number of times two individuals interact or are observed in association with each other. *Strength* is the sum of social interactions of the focal individual; strength increases if an individual interacts with more social partners, or if it interacts more often with its partners. Like strength, *betweenness* is a measure of centrality in the network, but it scores how many of the shortest paths (taking into account the magnitude of the connections, i.e. frequency of interactions) between any two individuals in the network pass through the focal individual (Opsahl, 2009). Betweenness often captures information about the role individuals play in connecting subgroups within a population (Wasserman & Faust, 1994; Oh & Badyaev, 2010). *Affinity* is the weighted mean strength of a focal individual's social partners. It is a metric that is one step removed from the focal individual and can be thought of as how frequently a focal individual's social partners interact with other individuals in the network, or how central one's social partners are, within the network (Whitehead, 1997). *Clustering coefficient* (CC) is a measure of the proportion of a focal individual's social partners that are themselves partners and quantifies the cliquishness of its social environment (Whitehead, 2008). Strength, affinity and CC were calculated using *socprog* (Whitehead, 2009), and their formulations can be found in Whitehead (2008); weighted betweenness was calculated using the T-net package for R (Opsahl, 2009).

Statistical analysis

In our dataset, the sample size used to calculate each network metric differs. CC can only be calculated for individuals that have at least two social partners

($N = 27$), betweenness can only be calculated for those connected to the core network ($N = 34$), and affinity can only be calculated for individuals that have at least one social partner ($N = 36$), but strength can be calculated for all males in the population ($N = 65$) even if they have no social partners (i.e. if strength = 0). The different sample sizes for each metric make an analysis simultaneously containing all three metrics impossible without excluding individuals that were not well connected to the network (i.e. individuals with fewer than two social partners). The statistical independence of these metrics is unclear, as are the effects of including them in one multivariate model. Therefore, we conducted separate path analyses for each network metric.

Initially, univariate analyses were conducted to determine whether each network metric covaried with fitness (Fig. 2a, c, e, g; Table S1). Values for an individual's position in a social network are not independent from the values of the other members of the population and network, so randomization techniques are often employed for significance testing (Croft *et al.*, 2008; James *et al.*, 2009). We conducted bootstrap procedures with 10 000 permutations and report *P*-values and parameter estimates calculated using the 95% CI bias-corrected percentile method. Although simpler methods could be employed to conduct these univariate analyses, we used the bootstrapping procedures in AMOS for direct comparison with the multivariate tests below; we have included results from the permutation tests in UCINET (Borgatti *et al.*, 1999) in the Table S2 for comparison with other work.

To evaluate individual characters and behaviours that could influence network metrics as well as fitness, we conducted path analyses including each network metric (Fig. 2b, d, f, h; Tables S3–S6). The bias-corrected bootstrap method allows for non-normality in input variables for path models and should approximate permutation tests typically used in univariate network analyses. These path models included elytra length (a reliable measure of

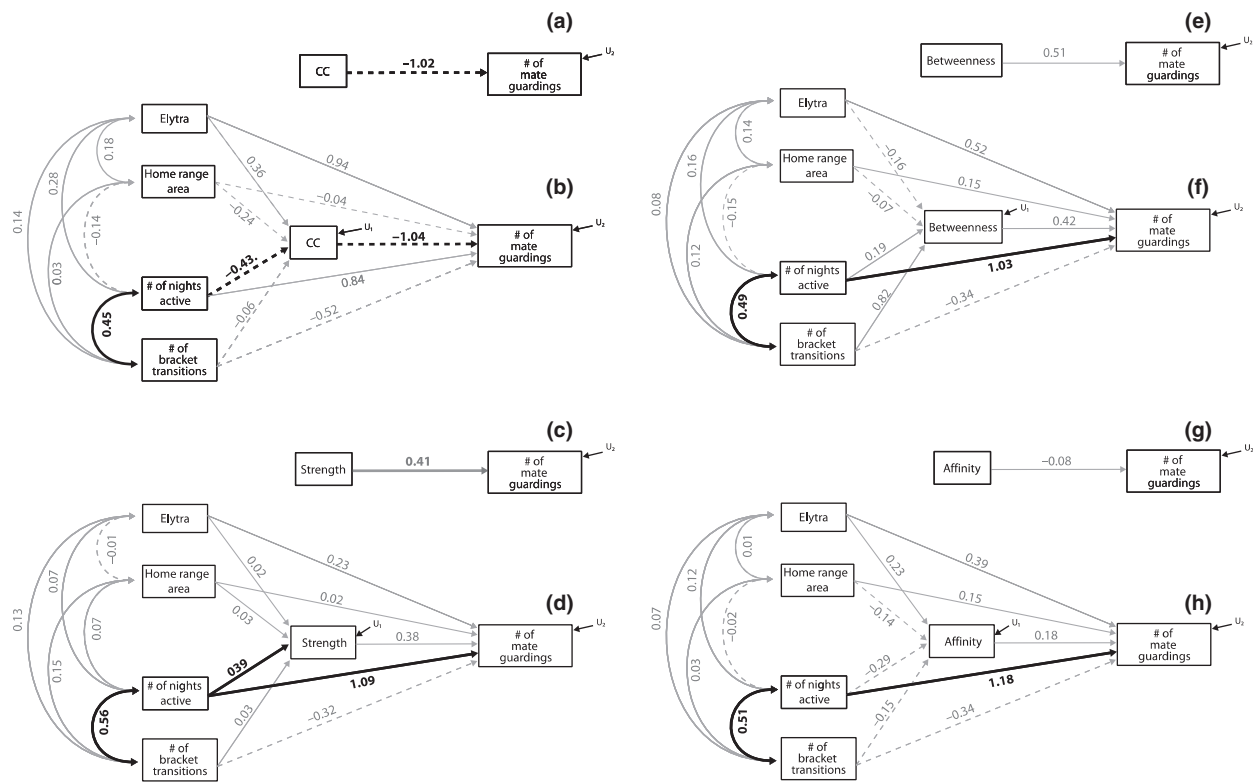


Fig. 2 Path diagrams illustrating the analyses and results for the four network metrics we considered: clustering coefficient (a, b), strength (c, d), betweenness (e, f), and affinity (g, h). Black values and paths are significant ($P < 0.05$); dashed lines denote negative coefficients. a, c, e and g are univariate analyses that were conducted with the same methods (95% CI bias-corrected bootstrapping) as the multivariate analyses. Both the univariate and multivariate models were run separately for each of the three network metrics. Statistical details of the univariate tests can be found in Table S1. Path coefficients for error terms (U_1 and U_2) and further statistical details for each model can be found in Tables S3–S6. We used the number of mate guarding events (copulation success) as our fitness component in all analyses.

body size, which covaries strongly with horn length) (Formica *et al.*, 2011), activity (the number of nights an individual male was observed on the surface of the log or fungus brackets during at least one scan), the home range area of each male and the number of transitions between brackets. The home range area was determined using a 65% kernel density estimation method (as in Formica *et al.*, 2010, 2011); this method uses the spatial location of observations of one individual to estimate a probabilistic core area utilized by that individual over the course of our observation period. Individuals with larger home ranges may have the opportunity to interact with more potential mates and other males (social partners in the network). The number of bracket transitions measures the number of times beetles were observed to move between mating arenas (different fungus brackets).

Results

The overall social network of male forked fungus beetles was weakly connected. Approximately one-third of the males were observed on more than one occasion, some of which interacted with females, and yet never associated

with other males (unconnected nodes on the left of Fig. 1). Additionally, a number of males were ‘pendants’ in the network, having only interacted with one other male throughout the observed breeding season.

Of the four network metrics, only CC explained a significant amount of variance in fitness (Table S3; Fig. 2a) in univariate analyses; however, strength showed a positive relationship that was marginally significant (at $P = 0.06$; Table S4; Fig. 2c). Affinity and betweenness had no significant relationship with fitness (Tables S5 and S6; Fig. 2e, g).

Of the individual-level characters, only activity significantly predicted fitness or network position (Fig. 2b, d, f, h). Activity directly predicted CC and strength, but not betweenness or affinity. For the models that contained strength, betweenness or affinity, activity also directly predicted fitness. In the mediation models, the path from CC to fitness was the only relationship between network metrics and fitness that was significant when individual characters were included in the model. Elytra length, home range area and the number of bracket transitions did not significantly predict the network position or fitness in any of the path models (Tables S3–S6).

Discussion

We found that position in a social network covaries with copulation success in a wild population of beetles. Strength, a measure of network centrality, was positively related to copulation success, whereas cliquishness, as measured by CC, was negatively related. At least some of these pathways to fitness appear to be driven by variation in a simple individual-level behaviour, activity. Males that were active on more nights had higher measures of centrality in the network, and this mediation path effectively accounted for the relationships between fitness and strength. However, CC remained a significant predictor of male copulation success, even after considering the potential mediation effects of activity. Thus, some measures of network position appear to influence individual differences in fitness above and beyond the effects of individual behaviours.

One current challenge to the application of network analyses in behavioural and evolutionary studies is whether these measures of social context provide additional information that is not captured by considering individuals as independent agents. Our data indicate that the answer to this challenge is complex, at least in terms of explaining variation in copulation success. Male beetles that are present on the surface of the log or brackets for more nights (i.e. are more active) tend to gain more copulations and also tend to be more central in the network. We were unable to detect any additional power of centrality to explain fitness differences beyond this indirect relationship. Although we might consider centrality to be experiencing indirect selection, many will find it unsurprising that more active individuals attain more copulations, and so this result indicates that, at least in this system, we gain little knowledge of the fitness consequences of social behaviour by including considering strength, affinity or betweenness (but see Oh & Badyaev, 2010).

On the other hand, some metrics (i.e. CC) do seem to capture additional information beyond properties of the individual that explain differences in fitness. Males that occupy more cliquish positions in the network have relatively low copulation success, even considering morphology, activity and space use. High CC is associated with relatively closed social groups, whereas beetles with lower CC interact more broadly with conspecifics. The direct relationship between CC and copulation success suggests that males that move among groups have more opportunities for matings. This effect must depend on the actions of other beetles, however, because the individual's number of bracket transitions did not affect CC or fitness. Another possibility is that more aggressive individuals gain more copulations because they drive away subordinate social partners. Subordinate males that leave because of directed aggression (i.e. move to another section of log) would be less likely to encounter each other and would not form

localized cliques and thereby lower the CC of the original, aggressive male.

Just as with any regression study of selection, it is possible that important, unmeasured individual variables explain some of the causal relationship between CC and copulation success. Although our path modelling approach can suggest causal relationships among variables, to truly determine whether the cliquishness of individuals contributes to variation in fitness among individuals, experimental manipulations of network structure and position would be necessary. Our conclusions are further limited because we were able to estimate selection in only a single population of beetles for one breeding season. Replicated samples in additional demes across space and time are needed to establish the generality of these results.

The observed selection on cliquishness in *B. cornutus* suggests that multi-individual interactions as captured in network analyses have fitness consequences. Yet, it is still difficult to characterize the level of organization that is ultimately responsible for variation in the metrics. An individual's position in a social network is inherently a context-dependent trait that could be influenced by phenomena occurring (nonexclusively) on at least three levels: (1) the focal individual, (2) the immediate social partners (neighbourhood) and (3) the population, where phenomena such as density and sex ratio could have important top-down effects on the entire social network and thereby affect individual metrics. For example, in populations with high densities, the social network might become swamped by the number of conspecific interactions and variance in cliquishness and centrality might be limited, thus preventing the detection of covariance with fitness. Consistent with this scenario, previous work on *B. cornutus* indicates the intensity of sexual selection is weaker at high densities (Conner, 1989b). The population in this study was relatively high density compared with those used in previous studies of sexual and social selection (1.6 males per utilized bracket; Formica *et al.*, 2011), leaving open the possibility that selection on network metrics may be different in populations with lower densities. Replicated studies in additional demes are needed to determine the generality of our results.

If aspects of network position are truly emergent (i.e. are not predictable from the individual behaviours of the interactants) and covary with fitness, then social networks may be a method for detecting context-dependent extended phenotypes that have been previously unexplored. Nonetheless, it is difficult to predict how, or even if, these traits can evolve across generations. For social network position to evolve, network metrics would need to be consistent within an individual (across variable social contexts) and must be in some sense heritable. Although these criteria may be met for some social networks (e.g. Fowler *et al.*, 2009; Frere *et al.*, 2010), our understanding of the basis of network position is still in its infancy. Certain types of individual-level

behaviour that govern social network structure (such as activity level or aggression) might evolve and in turn cause network position to change indirectly across generations. Our results suggest that measures of centrality (e.g. strength) could evolve through a correlated response to selection on activity. Even though CC appears to be under direct selection, it is clearly a complex trait involving the behaviours of social partners as well as those of the focal individual and would need nontypical modes of inheritance to evolve.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Results from univariate path analysis (number of mate guarding events (copulation success) regressed on each network metric) using the 95% CI bias corrected bootstrap method.

Table S2 Results from univariate permutation tests with the number of unique mate guarding events (copulation success) regressed on each network metric.

Table S3 Results of mediation path model analysis that includes the weighted network metric clustering coefficient (CC) (Fig. 2b).

Table S4 Results of mediation path model analysis that includes the weighted network metric strength (Fig. 2d).

Table S5 Results of mediation path model analysis that includes the weighted network metric betweenness (Fig. 2f).

Table S6 Results of mediation path model analysis that includes the weighted network metric affinity (Fig. 2h).

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