Sexual networks: measuring sexual selection in structured, polyandrous populations

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Sexual selection is traditionally measured at the population level, assuming that populations lack structure. However, increasing evidence undermines this approach, indicating that intrasexual competition in natural populations often displays complex patterns of spatial and temporal structure. This complexity is due in part to the degree and mechanisms of polyandry within a population, which can influence the intensity and scale of both pre- and post-copulatory sexual competition. Attempts to measure selection at the local and global scale have been made through multi-level selection approaches. However, definitions of local scale are often based on physical proximity, providing a rather coarse measure of local competition, particularly in polyandrous populations where the local scale of pre- and post-copulatory competition may differ drastically from each other. These limitations can be solved by social network analysis, which allows us to define a unique sexual environment for each member of a population: ‘local scale’ competition, therefore, becomes an emergent property of a sexual network. Here, we first propose a novel quantitative approach to measure pre- and post-copulatory sexual selection, which integrates multi-level selection with information on local scale competition derived as an emergent property of networks of sexual interactions. We then use simple simulations to illustrate the ways in which polyandry can impact estimates of sexual selection. We show that for intermediate levels of polyandry, the proposed network-based approach provides substantially more accurate measures of sexual selection than the more traditional population-level approach. We argue that the increasing availability of fine-grained behavioural datasets provides exciting new opportunities to develop network approaches to study sexual selection in complex societies.

1. Introduction

Darwin [1] defined sexual selection as a selective process operating on individual variation in the number and reproductive quality of reproductive partners owing to intrasexual competition. Over the past 40 years, sexual selection has emerged as a potent agent of Darwinian evolution [2], and driver of fundamental evolutionary processes such as speciation [3–5], local extinction rates [6] as well as rates of mutation and the tempo of molecular evolution [7,8]. The way sexual selection affects these phenomena depends on the strength with which it acts on individuals within a population. Therefore, a main goal in evolutionary biology has been to both measure sexual selection and understand the forces that determine its strength [9].

A major catalyst in the study of sexual selection was the development of quantitative measures to determine the targets of selection, and the strength and direction of selection acting on these traits [10]. This approach is based on the decomposition of variance in individual male reproductive success into three multiplicative components as thus:

\[ T = (M \times N \times P) + e, \] (1.1)
where $T$ is the total variance in male reproductive success, $M$ is variation in male mating success (number of females mated by a male), $N$ is the average number of eggs produced by the females successfully mated by a male in a given time unit, $P$ represents variation in the average proportion of a clutch of eggs fertilized by a male and $e$ represents a source of error [11]. Together, $M$ and $N$ contribute to generate variation in male mating success, and thus opportunity for pre-copulatory sexual selection. Finally, $P$ arises from post-copulatory competition that occurs when individual females mate with, or obtain sperm from, multiple males, a mating system referred to as polyandry. This classical approach considers the relationship between individual variation in the expression of phenotypic traits and a given measure of reproductive success ($M$, $N$, $P$ or $T$) standardized within a population, to generate selection gradients [12]. Such standardized measure of selection enables critical comparisons of the operation of sexual selection across different populations, different traits and sexes. An important implicit assumption of this population-level approach to sexual selection is that mating interactions are not structured, i.e. a focal individual is just as likely to encounter the same frequency distribution of phenotypes of prospective partners and/or competitors in any section (e.g. social, spatial or temporal) of the population, so that intrasexual competition measured at the level of the population is representative of patterns of intrasexual competition at the local scale. However, a growing body of empirical work has recently challenged the assumption of population-level homogeneity in competitive structure on grounds of two inter-related factors: (i) population structure and (ii) polyandry.

(a) Population structure

There is increasing evidence that most populations are not randomly assorted, but display complex social and phenotypic structure. Sexual selection is driven by social competition and, therefore, is likely to be profoundly affected by local structure in the social environment [13]. Benton & Evans [14] used a simulation approach to show that in species where females use a ‘best of $n$’ strategy when choosing mates, local spatial clumping of males by quality may obscure the covariance between trait and fitness at the population level. This happens when females are limited in the number of males they can sample. Local spatial clumping increases the chance that females will sample a non-random collection of males, i.e. choosing between only low-quality and only high-quality males. The effect of local variation in social environment on the strength and direction of sexual selection was demonstrated empirically in natural populations of the golden orb-web spider (Nephila plumipes), in which local differences in density and the operational sex ratio (ratio of reproductive males to females, OSR) result in fine-scale differences in the strength and direction of sexual selection on male morphology [15]. By correlating male quality at the population level, classical selection analysis implicitly assumes that any female could potentially select any male and, therefore, ignores the importance of local competitive structure resulting in biased estimates of sexual selection.

(b) Polyandry

Polyandry has substantial repercussions for the operation of sexual selection. First, by forcing the ejaculates of different males to compete for the fertilization of a set of ova, polyandry introduces a post-copulatory source of variance in male reproductive success that gives rise to post-copulatory episodes of sexual selection: sperm competition [16] and cryptic female choice [17]. Second, the fact that males must defend paternity can weaken sexual selection gradients on male re-mating rates (i.e. the Bateman gradient) [11]. Finally, the introduction of an additional (i.e. post-copulatory) round of intrasexual competition adds complexity to the structure of mating interactions. For example, females may mate with a male at a local patch and then move to a new patch to mate with another male. In this scenario, each male competes with his local neighbours to mate with a female, but his sperm will compete with the ejaculates of males from other parts of the population. Similarly, when females vary in number of mating partners, the intensity of sperm competition will also vary across females. If males who mate with many females also mate with the least promiscuous females (have higher exclusivity of mating), they may face lower sperm competition, and this may increase variation in reproductive success within males [18]. Such a pattern may steepen the relationship between number of mates and number of offspring produced. This would, therefore, be expected to increase the strength of pre-copulatory sexual selection on male competition for access to mates. Therefore, the structure of polyandrous mating patterns may have strong implications for the strength and direction of sexual selection. However, such patterns have rarely been quantified and this may be partially due to a lack of quantitative tools to characterize these patterns.

(c) Social network analysis

Network analysis is an approach to characterize how local interactions between individuals create population-level patterns and provide a quantitative tool to capture sexual patterns and dynamics. Social network analysis has become a widespread approach in behavioural biology to shed light on the complex dynamics of social systems [19,20]. Originally developed by sociologists to deal with the complexities of human behaviour [21], the social network approach has increasingly been used to address evolutionary questions, especially when it was realized that the success of behavioural strategies of individuals can be dependent on the structure of the social network of which they are part [22,23]. Models that take social heterogeneity explicitly into account in game theoretic analyses have made a number of interesting predictions (for example, regarding the evolution and maintenance of cooperation) that have yet to be tested [22–24]. The fact that network structure arises from individual interactions (bottom-up), but also selects for individual behavioural strategies (top-down) and, therefore, has important fitness consequences for individuals [25], is of particular relevance in the context of sexual interactions. We, therefore, focus here on ‘sexual networks’, networks composed of nodes representing individuals (males and/or females), and the connections between these individuals (edges) may represent any sexual interaction of interest, here defined to include copulations themselves.

(d) Aims

The aims of this study are twofold. First, we develop a novel quantitative framework to measure sexual selection based on
multi-level selection analysis in which local competition is defined by the sexual network. Second, we consider the impact that polyandry has on the operation of sexual selection in a structured population, and compare the sensitivity of our multi-level selection approach with that of the traditional population-level approach to the influence of polyandry on estimates of sexual selection. We show that multi-level selection approaches informed by network analysis can provide substantially more sensitive, unbiased estimates of sexual selection whenever populations display some degree of viscosity (i.e. limited dispersal) and polyandry. Finally, we discuss how the quantitative characterization of the structure of the mating network itself, the mating topology, can shed light on the operation of sexual selection in polyandrous populations.

2. Measuring sexual selection in structured populations

Several quantitative methods have been developed to estimate the fitness effects of an individual’s local competitive environment, including the ‘contextual approach’ [26–28] and the ‘neighbour analysis’ approach (analogous to social selection) [26,32–33]. These methods represent hierarchical expansions of Lande & Arnold’s [12] classic selection analyses, where selection is measured at more than one level of hierarchy (i.e. individual phenotype and the phenotype of the group), and have, therefore, been termed ‘multi-level selection analyses’. The goal of contextual analysis and neighbour analysis is to estimate both the effects of individual phenotype on fitness and the effects of an individual’s socio-competitive environment (local group) on individual fitness. To achieve this, each method partitions the effects both of individual phenotype (e.g. individual ornament size) and group phenotype (e.g. mean ornament size of group members) on individual fitness [26,32]. Specifically, the contextual analysis uses a multiple regression model of individual phenotype and group phenotype on individual fitness,

\[ \omega_i = \beta_1 z_{ij} + \beta_2 Z_j + e, \]  

(2.1)

where \( \omega_i \) and \( z_{ij} \) are the fitness and trait values for the \( i \)th individual in the \( j \)th group, respectively, \( Z_j \) is the trait value for the \( j \)th group and \( e \) is the residual variance. The regression coefficient \( \beta_1 \) is, therefore, the partial regression of individual fitness on individual character, controlling for group character, and \( \beta_2 \) is the partial regression individual fitness on group character, controlling for individual character. The fitness effects of an individual’s local social group on individual fitness are, therefore, described by \( \beta_2 \). The neighbour analysis is mathematically identical to the contextual analysis except for the calculation of what constitutes group phenotype (\( Z_j \)). In the contextual approach group phenotype for a focal individual is calculated as the mean trait value for all \( n \) individuals, \( \text{including the focal individual, of the } j \text{th group, i.e.} \)

\[ Z_j = \frac{1}{n_j} \sum_{i=1}^{n} z_{ij}. \]  

(2.2)

The neighbour analysis instead calculates group phenotype of all individuals in the group \( \text{omitting the focal individual. This approach has been extensively used in} \)

social selection studies [30,31], where an additional term named the ‘interactant covariance’ (\( C_{ij} \)) is also included, e.g.

\[ \omega_i = \beta_1 z_{ij} + C_{ij} \beta_2 Z_j + e, \]  

(2.3)

where \( C_{ij} \) is calculated as the covariance between individual phenotype and the group phenotype. The interactant covariance, therefore, describes the relationship between focal and group phenotypes, and translates the fitness effects of group phenotype (\( \beta_2 \)) into phenotypic selection at the population level. In practice, analyses using contextual or neighbour approaches to calculate group phenotype are likely to produce similar results [26]. However, there are a few key differences between the two approaches. For instance, if the researcher is also interested in selection on emergent group properties, such as the density of the focal individual’s group, then the contextual approach may be more appropriate [26]. This is because the neighbour approach calculates group phenotype explicitly as the mean trait value of the focal individual’s neighbours. Contextual and neighbour analyses represent valuable tools to measure selection in structured populations. Crucially however, the utility of either analysis depends on the identification of functionally relevant groups, which often represents a non-trivial challenge.

(a) The challenge of defining ‘local’

Few populations have easy-to-define, spatially structured groups with little between-group migration, such that individuals can be attributed to their respective groups with ease [33]; in the majority of cases, groups are likely to be difficult to define \( a \text{ priori} \), and competition may be likely to lie somewhere between completely local and completely global [34]. How then should the researcher investigating the effects of competitive context (group character) on individual fitness decide which individuals constitute a particular group? Despite the importance of this question, little work has been done to provide quantitative methods for competitive group identification. Methods to identify functional groups often require assumptions regarding space use and home range limits to infer social interactions. For instance, probabilistic home range models have recently been used to estimate local social environments [30]. However, these methods may not be appropriate to accurately identify functional groups of sexual interactions in species with complex within-range space use [35]. In fact, even within groups with home range overlap there can considerable variation in interaction patterns between individuals both within- and between-groups [36]. Some experimental studies of multi-level selection have adopted designs that allow for a more objective definition of groups (e.g. based on individual position on an experimental grid [37] or the sharing of the same experimental pools [38]). However, these definitions can be somewhat contrived, being dictated by the experimental layout rather than by the behaviour and ecology of the study organisms. Crucially, these approaches fail to consider that in polyandrous populations, the scale of mate competition may differ drastically from that of sperm competition. For example, in vector-pollinated species, the movement of pollinators will determine the local competition for fertilization [39]. Another important aspect is that some individuals share the same group phenotype, but may compete with vastly different numbers of individuals. This variation can be minimized in experimental studies of sessile organisms [37], but represents
a significant challenge for studies of more labile social systems. It is clear, therefore, that for multi-level selection approaches to provide unbiased estimates of sexual selection in natural populations, a method for determining groups is required that is explicitly based on patterns of individual behaviour, and that provides the flexibility needed to capture such variation across multiple episodes of selection operating on vastly different scales.

(b) A network-based approach

Network data explicitly build up population structure using interactions between individuals. Networks capturing intra- and intersexual interactions can be used to describe which individuals are in local competition. Such local competitive environments are emergent properties of the network and, therefore, there is no requirement to define a priori an arbitrary local group. Below, we describe a simple approach to estimate the effects of social structure and local competitive environment on fitness, based on the application of information on local competition derived from networks to multi-level selection analyses. The use of network information to study sexual selection is not in itself new. For example, Oh & Badyaev [40] used a network approach to determine local competitive environments in a wild population of house finches (Carpodacus mexicanus). The study used network techniques to delineate ‘communities’ in the social networks of the finch population, and investigated the role of population social structure as a modulator of an individual’s attractiveness to partners relative to competitors in its local competitive environment. Communities were defined as collections of individuals that interact more often with each other than the rest of the population, and were identified using network modularity, which measures the level of compartmentalization of interactions/associations within a network [41]. To quantify selection on the individual taking into account the local competitive context, Oh & Badyaev [40] standardized individual trait value at the level of the local group (community) rather than the population. The study found that individuals are capable of influencing the selection regime that they experience by modifying their own social context. In particular, males with low secondary sexual ornament elaboration, and hence lower attractiveness, were able to increase their relative attractiveness by modifying their local competitive context via increased social lability. This is a promising approach, which demonstrates how consideration of network structure can help reveal subtle reproductive strategies, and add substantial resolution to our understanding of sexual selection in a population. However, this approach too suffers from some rigidity. First, community detection techniques fail to capture variation in interactions within individual communities (figure 1), which can be considerable [36,42], and which may have a large impact on the variation in competitive environments experienced between individuals. Second, this approach does not explicitly account for weak ties between communities (figure 1). The importance of such weak ties has long been recognized in sociological research [43,44]. Consider a hypothetical population with community structure similar to that in figure 1. Females inspect the attractiveness of a subset of the male population, and select the most attractive male(s) encountered. Community composition with respect to male attractiveness is non-random such that all communities have similar levels of variation in male attractiveness, but each community differs in its mean attractiveness. Females tend to interact and inspect only males within their community and so mate with the most attractive male from that community. Global selection measures would, therefore, underestimate sexual selection for male attractiveness. However, local selection measures purely based on community membership ignore inter-community ‘bridges’. These bridges lie somewhere between local, i.e. within the community, and global, and may be important determinants of reproductive success. For instance, if inter-community bridges are formed by choosy females, then competition over such ‘bridge’ females will comprise males from different communities, whereas competition over less choosy females will be restricted within a community. The distribution of such bridges in the network could lead to biased estimates of selection, which may be particularly important in species where females use adjustable thresholds when making mate choice decisions, but also suffer high search costs [45]. To achieve unbiased estimates of selection, group membership must, therefore, take into account individual variation in socio-competitive group.

To resolve these shortcomings and provide a framework for group identification of broad generality, we propose that the competitive environment of a focal individual is described by the pattern of the ‘connectedness’ the focal individual shares with other individuals in a competitive network. An individual’s competitive group can then be defined as the individuals with which it shares fitness-affecting interactions [33]. Using such an approach, an individual’s local social environment is defined based on social/competitive interactions, which may or may not correlate with the spatial assortment of individuals, potentially capturing ‘cryptic’ social structure overlooked by spatial methods. Consider a hypothetical network capturing the pattern of ejaculate transfer from males to females (figure 2a). Such a network enables one to explain $P$ (variation in paternity share) by capturing patterns of post-copulatory competition. Edges are drawn between males and females for each independent set of ova for which the males compete for fertilization (e.g. batches of ova across different females or separate batches of ova produced successively by the same female). Two males are in sperm competition if they both transfer sperm to the same female within a certain time window such that their ejaculates co-occur at the time the same batch of ova is fertilized.

**Figure 1.** A network demonstrating heterogeneous interaction patterns. Colours represent community membership and red dotted lines represent the absence of interactions between community members.
A similar approach can be used to build networks describing the focal male’s competitive context will then work where edges between males represent events of sperm competition. The focal male’s competitive context will then work where edges between males represent events of sperm competition.

pre-copulatory inter- and intrasexual competitive interactions to explain $M$ and/or $N$. Here, each edge may represent whether two males displayed to the same female (intersexual), e.g. within a lekking system, or direct male–male competition (e.g. fighting contests in horned beetles [46]). In the case of direct male–male competition, the local competitive environment would be described directly by the focal individual’s one-step ego network without the need for projection. When males mate only once at most, such as in species with male terminal investment [47], it will be possible to represent the sperm competitive network using binary network data alone (i.e. presence or absence of an edge). When edges are binary, the contextual analysis using individual local group phenotype as determined by the focal’s ego network would take the following form:

$$\omega_i = \beta_2 z_i + \beta_4 z_{i(local)} + \epsilon,$$

(2.4)

where $\omega_i$ and $z_i$ are the fitness and trait value for the $i$th individual, respectively, $\epsilon$ is the residual variance and $z_{i(local)}$ is the group phenotype for $i$th individual’s local competitive group, calculated as

$$Z_{i(local)} = \frac{\sum_{j=1}^{n_i} z_j + z_i}{n_i + 1}.$$

(2.5)

Equation (2.5) is the mean of all individuals with which the focal individual competes, including the focal individual; where $z_i$ is the focal male’s trait value and $z_j$ is the trait value for the $j$th individual with which the focal competes. In network nomenclature, $z_i$ is the focal node’s attribute and $z_j$ is the attribute for the $j$th node with which the focal node is connected. However, in many cases males mate multiply and may compete over several batches of ova. Therefore, edges between males must be ‘weighted’. These weights give value to the edges between males (figure 2b,d), and represent the number of independent competitive events between males. For instance, when two males both transfer sperm to the same two females (or the same female but across two unique sets of ova), the edge between these males will have a weight of two. Within the period of study (e.g. across a reproductive season), the edges between males can then be weighted to represent the number of independent competitive events. In the example in figure 2, weights indicate that although several males compete with each other, some do so to at greater or lesser extent than others. To include this information when estimating selection gradients, the weight between two males ($p_{ij}$) can formally be calculated as,

$$p_{ij} = \sum_{q=1}^{n_j} \frac{\theta_{ij}^{pq}}{\sum_{q=1}^{n_j} \theta_{ij}^{pq}},$$

(2.6)

where $\theta_{ij}^{pq}$ represents whether the $i$th and $j$th males both competed for the $q$th batch of eggs of the $p$th female (zero when they did not compete, unity if they did). These weights can then be used when calculating the mean trait value for a male’s competitive group, by weighting male traits by the number of separate occasions in which the males competed. In this case, local mean trait value using contextual analysis would be calculated as follows:

$$Z_{i(local-weighted)} = \frac{\sum_{j=1}^{n_i} (p_{ij} z_j)}{\sum_{j=1}^{n_i} p_{ij} + \sum_{j=1}^{n_i} p_{ij}}.$$

(2.7)

**Figure 2.** (a) An intersexual network showing the pattern of ejaculate transfer between males (blue) and females (pink). Red nodes highlight the two-step ego network for focal node male $\mathcal{O}3^a$. (b) Male–male sperm competition network projection of (a) in which female nodes have been removed. Red nodes highlight the one-step ego network for $\mathcal{O}3^a$. Numbers over edges represent the number of independent competitive events between male nodes. The method of projection adopted here is the simple summation of shared ties between males. (c) An intersexual network showing the pattern of ejaculate transfer between males (blue) and females (grey) and their batches of ova (pink) for which the males competed. Red nodes highlight the two-step ego network for focal node male $\mathcal{O}3^a$. Numbers over edges represent the number of independent batches of ova for which the male competed for fertilization. (d) Male–male sperm competition network projection of (c) in which female and ova nodes have been removed. Red nodes highlight the one-step ego network for $\mathcal{O}3^a$. Numbers over edges represent the number of independent competitive events between male nodes. The method of projection adopted here is the simple summation of shared ties between males.
Equation (2.7) is the weighted mean of trait value of the focal \( i \)th male’s competitive group, where \( \rho_i \) is the number of competitive ties between the \( i \)th and \( j \)th male in the male–male competitive network (as in equation (2.6)) and \( \sum_{j=1}^{\rho_i} w_{ij} \) is the total strength of male node \( i \) in the male–
female sexual network (i.e. the sum of the edge weights between the \( i \)th male node and all \( j \)th female nodes). Note that the above calculations are equally applicable to neighbour analysis by omitting the focal individual’s trait and node strength from group phenotype calculations.

(c) Weighting edges

So far we have described weighting edges by the number of independent competitive events. However, edges could also be weighted by other factors with potentially strong impact on reproductive success, and which might confound our estimates of sexual selection on male trait \( z \). These factors may reflect the phenotype/genotype of the male (independent of \( z \)) or of the female, e.g. fecundity; the interaction between partners’ phenotype/genotype, e.g. relatedness; social interactions among partners, e.g. the re-mating rates of an individual male with an individual female or the social environment, e.g. such as local variation in population density or OSR. Information on the number of individuals with which a focal individual competes can be derived from sufficiently detailed sexual networks. As networks are built based on interactions between individuals, emergent properties such as density or individual OSR can be calculated without the pseudoreplication of individuals and included in a contextual analysis model [38].

3. The impact of polyandry on sexual networks and sexual selection: a simulated example

(a) Contextual analysis

In §2, we proposed a new quantitative framework which integrates multi-level selection with network analysis. In this section, we demonstrate the use of this approach in measuring changes in sexual selection under different regimes of polyandry. Specifically, we adopt simple simulations to change the degree of polyandry (i.e. the number of males mated by each female in a population), and measure the sexual selection gradient on a male trait \( z \) using both standard population-level (global) selection analysis and the novel network-based multi-level selection approach proposed in §2 to illustrate how these estimates are differentially sensitive to changes in polyandry.

We generated replicate sets of 1000 populations of 100 individuals (50 females and 50 males). Males and females were placed randomly within a two-dimensional environment of fixed dimensions (1 \( \times \) 1). In all populations, males were provided with one phenotypic trait (\( z \)). To do so, we used male position along one axis of the two-dimensional space, resulting in a continuous uniform distribution of male trait \( z \) values from left to right. This creates an environmental gradient in \( z \) such that males to the left of the environment possess a lower phenotypic trait value compared with males on the right. For simplicity, we assumed that in all populations each female produced only one set of ova. In all cases, we imposed post-copulatory sexual selection on \( z \) such that males mated to females fertilize a proportion of a female’s ova proportional to their trait value (i.e. males with a larger trait value fertilize a larger proportion of a set of ova). More explicitly, the proportion of the \( j \)th female’s ova fertilized by the \( i \)th male (\( W_{ij} \)) that mated with her was calculated as

\[
W_{ij} = \frac{z_i}{\sum_{j=1}^{\rho_i} w_{ij} + z_j},
\]

where \( z_i \) is the trait value for the \( i \)th male and \( z_j \) is the trait value for the \( i \)th male’s \( j \)th sperm competitor within female \( j \). We then calculated post-copulatory reproductive success for each male (\( W_i \)) as the mean proportion of eggs fertilized across all \( j \)th females with whom he mated [11]. Clearly, a similar approach can be used to focus on different episodes of sexual selection.

For each replicate set of populations, we allowed females to mate with a set number (\( p \)) of their nearest males in the two-dimensional environment. We generated replicate sets for a distribution of levels of polyandry (\( p \)) ranging from \( p = 2 \) (where females always mate with only their two nearest males, e.g. female degree = 2) to \( p = 50 \), where each female mates with all males in the population. This results in 1000 replicate populations for each level of polyandry. For all populations at each level of polyandry, we extracted both the male–female sexual network and male–male sperm competitive network, with edges between males weighted by the number of independent competitive events (e.g. in this case a weight of 2 represents that both males mated the same two females as calculated in equation (2.6)). For each male we then calculated the mean phenotype of his competitive group (\( Z_{loc\text{-weighted}} \)) as in equation (2.7) and obtained male reproductive success (\( W \)). We standardized all selection gradients by dividing male fitness by the population mean fitness and standardizing both male trait and male group trait to have a mean of zero and a standard deviation of unity.

Figure 3 illustrates the way polyandry affects the sexual selection gradient (\( \beta \)) on \( z \) measured using both population-level selection analysis and contextual multi-level selection analysis based on network information. As expected, \( \beta \) measured using population-level (global) selection analysis increases with the level of polyandry in the population, because polyandry increases the level of sperm competition and the covariance between the male trait \( z \) and male reproductive success at the population level. Estimates of sexual selection on \( z \) using network-based contextual analysis, however, reveal a more nuanced pattern. This approach demonstrates that local selection on \( z \) is consistently higher than estimates of \( \beta \) based on traditional population-level selection analysis. Such discrepancy is due to the fact that population-level selection analysis fails to account for local variation in the sperm competitive environment experienced by the ejaculates of individual males owing to the environmental gradient in male \( z \). The contextual approach instead explicitly estimates selection on a male’s competitive group trait, which at all levels of polyandry shows negative selection (figure 3). This means that male reproductive success is affected not only by the absolute trait value (\( z \)), but also by the composition of the social group within which a particular male (or his ejaculate) competes. In this case, there is negative individual selection on competing in highly competitive groups; in other words, males are selected against sharing females with other males with large \( z \). It is this effect of male competitive
group that, although often implicitly assumed using traditional population-level techniques, is not quantified, resulting in biased estimates of sexual selection in structured populations [30]. The greatest discrepancy between post-copulatory sexual selection gradients (β) on male trait z estimated by traditional population-level selection analysis and by network-based contextual analysis is observed at low-to-intermediate levels of polyandry (i.e. where the positive correlation between male’s trait value (z) and the trait value of his competitors (Z_{local-weighted})) is expected to be strongest). Only when polyandry is complete (i.e. each female mates with every male in the population \( p = 50 \)) do we find complete agreement between both selection approaches as expected [48]. These results illustrate how population structure can obscure the effect of polyandry and bias estimates of sexual selection when this is measured purely at the global (population) scale.

(b) Neighbour analysis

We can use the same simulation to measure changes in sexual selection using the neighbour approach based on equation...
(2.3). This approach also includes the interactant covariance term \( C_{ij} \) that was calculated as the Pearson product–moment correlation between male \( z \) and \( Z_{(local-weighted)} \). This analysis generates a pattern of local and global sexual selection gradients that are virtually identical to those generated by the contextual analysis for most of the parameter range of polyandry with the exception of very low polyandry, where contextual estimates of \( |\beta| \) on male \( z \) exceed those of neighbour \( |\beta| \) (figure 3). This discrepancy is due to the fact that because the contextual analysis measures \( Z_{(local-weighted)} \) including the focal individual the difference between male \( z \) and \( Z_{(local-weighted)} \) is lower than in the neighbour analysis. This means that in the contextual analysis, a more limited amount of phenotypic variation (compared with the neighbour analysis) will result in the same change in standardized fitness, and thus in steeper selection gradients. As the level of polyandry increases, however, the contribution of the focal individual to \( Z_{(local-weighted)} \) becomes more negligible because group size increases, leading to a rapid alignment of contextual and neighbour estimates.

4. The ‘mating topology’ and ‘sex webs’

In addition to providing information to determine the local structure of phenotypic competition, it has more recently become clear that network structure itself may modify the strength and direction of selection. By forcing the ejaculates of males to compete, polyandry may reduce the relationship between mating success and paternity, and increase the importance of sperm competition intensity. A large body of work has focused on how males act to reduce the risk of sperm competition through mate guarding [49,50] or by preferentially mating with females that pose low risk or intensity of sperm competition [51]. These behaviours can have a profound impact on the spatio-temporal distribution of mating within a population, the mating topology. Yet we know very little about the way the mating topology generates local variation in the level of sperm competition (the sperm competitive environment) experienced by individual males. For instance, if males who mate with many females also mate with the least polyandrous females (i.e. have higher exclusivity of mating), they may face lower sperm competition and this may increase variation in reproductive success within males [18]. In networks, this would be described as negative degree assortment between male and female nodes (males with many mating partners, high mating degree, tend to be connected to females with low mating degree and vice versa). In ecological networks such as that of plant–pollinator or plant–herbivore systems, where edges are drawn across different trophic levels or plants and their pollen vectors, negative degree assortment generates a nested pattern of interactions where ‘specialists’ (those with few connections) from both sets of nodes tend to be connected to ‘generalist’ nodes of the other set (figure 4) [52,53]. In a nested sexual network, the ‘specialist’ male nodes with few mating partners may suffer relatively high sperm competition, whereas those males who mate with many females will have high exclusivity of mating across a subset of those females (figure 4). Such a pattern may steepen the relationship between number of mates and number of offspring produced, thus increasing the strength of pre-copulatory sexual selection (i.e. selection on competition for access to mates). An alternative way to characterize such patterns of mating specialization is through network tools commonly used to study ecological specialization in food webs across trophic levels [54]. Here, similar approaches can be used to characterize ‘sex webs’ and measure the degree of male and female specialization, and their relationship. However, the mating topology has rarely been quantified and this may be partially due to a lack of adequate quantitative tools available. Characterization of the mating topology will allow for a more comprehensive understanding of how polyandry and population structure interact to determine both the strength and direction of pre- and post-copulatory sexual selection.

5. Conclusions

The realization that natural populations typically display degrees of both polyandry and viscosity means that the operation of sexual selection can differ markedly across the mating topology within the population. Standard quantitative tools to measure sexual selection at population level are often inadequate to capture such complexity. Here, we propose that a way to resolve this issue is to use a multi-level selection approach in which local and global scales are defined based on information independently derived as emergent property of sexual networks. The study of sexual networks can elucidate the fine-grained structure of intersexual interactions within populations and its implications for variation in reproductive success and the operation of sexual selection.

The heuristic potential of this approach is vast and largely untapped. For example, how variation in female polyandry and complex behavioural processes such as assortative mating govern the pre- and post-copulatory competitive landscape, and its resulting effect on the operation of sexual selection, represent exciting avenues of research that are yet to be fully explored. A particularly relevant future step emerging from the present work will be to investigate the effect of the ‘scale’ of polyandry; in other words how far females and/or males move before females mate with a new male. It is
plausible that even under relatively low levels of polyandry, patterns of local sexual selection will converge towards global sexual selection if substantial mixing (e.g. dispersal) occurs between mating events. Conversely, reduced dispersal might exacerbate the difference between local and global selection even under relatively high levels of polyandry.

Characterizing the sexual network of a population is a non-trivial challenge. The novel approach proposed here requires high-resolution behavioural data, comprehensive information of the mating and fertilization events representative of the whole population. However, studies of natural or semi-natural populations have become sufficiently sophisticated to generate this type of data. The application of recent technological advancements, such as complex visual recording systems [55,56], as well as proximity loggers that allow the recording of interactions between individuals remotely [57–59] and, importantly, also allow the inference of specific behavioural interactions [60], may facilitate obtaining such detailed interaction patterns in species where such observations may have before been unfeasible in experimental and natural populations. Furthermore, experimental studies using semi-natural populations combined with network data will provide an opportunity to measure with exceptional accuracy the pattern of interactions, and help develop an understanding of how fine-scale assortment patterns may affect our measurement of selection using standard techniques.

We are grateful to Andy Gardner for helpful discussions. We thank two anonymous reviewers for constructive comments. G.C.M. was supported by a PhD scholarship from the Biotechnology & Biological Sciences Research Council and Aviagen. T.P. was supported by a research grant from the Natural Environment Research Council and the Philip Leverhulme Prize.

References


