Sexual selection in complex communities: Integrating interspecific reproductive interference in structured populations

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The social structure of populations plays a key role in shaping variation in sexual selection. In nature, sexual selection occurs in communities of interacting species; however, heterospecifics are rarely included in characterizations of social structure. Heterospecifics can influence the reproductive outcomes of intrasexual competition by interfering with intraspecific sexual interactions (interspecific reproductive interference [IRI]). We outline the need for studies of sexual selection to incorporate heterospecifics as part of the social environment. We use simulations to show that classic predictions for the effect of social structure on sexual selection are altered by an interaction between social structure and IRI. This interaction has wide-ranging implications for patterns of sexual conflict and kin-selected reproductive strategies in socially structured populations. Our work bridges the gap between sexual selection research on social structure and IRI, and highlights future directions to study sexual selection in interacting communities.

KEY WORDS: Interspecific reproductive interference, parasitism, predation, sexual selection, social evolution, social structure.

Decades of evidence have underscored the importance of sexual selection in driving the evolution of traits that mediate the outcome of intrasexual competition over reproductive success, often at the expense of members of the opposite sex (Darwin 1871; Andersson 1994; Arnqvist and Rowe 2005). Research has shown that the social environment plays a key role in shaping variation in sexual selection between populations (Kasumovic et al. 2008; Eldakar et al. 2009; Oh and Badyaev 2010; Rankin 2011; Bailey and Moore 2012; McDonald et al. 2013; Buzatto et al. 2015; Pizzari et al. 2015; Fisher et al. 2016; Cardoso et al. 2017; McDonald and Pizzari 2018). Social structure describes the genetic and/or phenotypic composition of populations, and the pattern in which individuals interact (West-Eberhard 1979, 1983; Krause et al. 2014; Farine et al. 2015). Sexual selection research scrutinizing the complexity of social structure has typically focused on single-species systems (Gomez-Llano et al. 2018; terHorst et al. 2018). However, in nature, sexual selection occurs in communities and interactions between species can quali-

tatively and quantitatively change the evolutionary outcomes predicted in single species systems (Weber et al. 2017; terHorst et al. 2018).

A key process whereby heterospecifics can influence intrasexual competition within a species is by interfering with intraspecific sexual interactions. Interspecific reproductive interference (IRI) occurs when heterospecifics engage in sexual interactions that influence the reproductive success of the individuals involved (Gröning and Hochkirch 2008; Burdfield-Steel and Shuker 2011). For example, interspecies courtship, sexual harassment, and matings can all reduce female reproductive success (Gröning and Hochkirch 2008; Burdfield-Steel and Shuker 2011; Cothran 2015; Kyogoku 2015; Grether et al. 2017; Shuker and Burdfield-Steel 2017). IRI can have severe ecological and evolutionary outcomes. For example, matings between male *Callosobruchus chinensis* and *C. maculatus* females can drive the exclusion of *C. maculatus* through harm to *C. maculatus* females (Kishi et al. 2009; Kyogoku and Sota 2015). In mosquitoes,
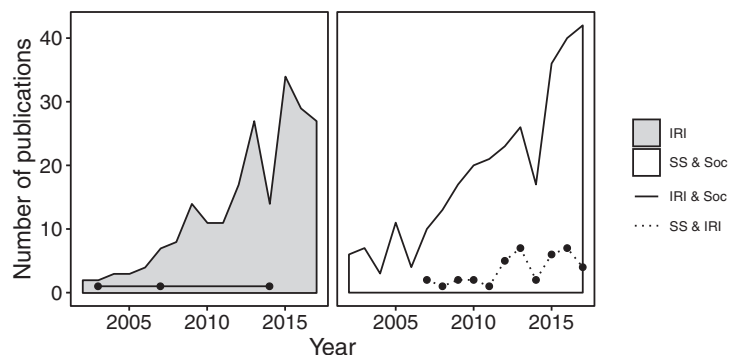
Figure 1. Reproductive interference research overlooks social structure and sexual selection research overlooks reproductive interference. Figure shows the number of publications from 2002 to 2017 with keywords relevant to reproductive interference (gray) or sexual selection and social structure (white). Lines show the number of publicaitons for the same period with keywords relevant to reproductive interference and social structure (solid) or sexual selection and reproductive interference (dotted). For full details of literature searches, see supplementary information.

Aedes albopictus ejaculates sterilize female *A. aegypti* causing population reductions and rapid evolutionary change in *A. aegypti* in nature (Bargielowski et al. 2013), whereas in plants, heterospecific pollen transfer limits coexistence of sexual and asexual lineages (Whitton et al. 2017). However, IRI research has typically focused on the role of differences in the size of interacting heterospecific populations with little consideration of population structure (Kishi et al. 2009; Kishi and Nakazawa 2013). Thus, although studies of sexual selection and social structure rarely incorporate heterospecifics, studies of heterospecific interactions rarely incorporate social structure (Fig. 1).

Here, we outline the need for studies of sexual selection to incorporate heterospecifics as part of the social environment and to account for the social complexity of these interacting populations. We use simulations to show that classic predictions for the effect of social structure on sexual selection are altered by IRI. We discuss the broader implications of IRI for patterns of sexual conflict and kin-selected reproductive strategies and highlight future research directions. Our work bridges the gap between sexual selection research and IRI, demonstrating that models of sexual selection in socially structured populations should incorporate the structure of the wider community.

Fitness Consequences of Interspecific Interference

IRI is widespread, occurring between both closely and distantly related species (for detailed discussions, see Gröning and Hochkirch 2008; Grether et al. 2017; Shuker and Burdfield-Steel 2017). The fitness effects of IRI can be incurred by one or both species, but research suggests the magnitude of costs is often asymmetric (Gröning and Hochkirch 2008; Kishi 2015). Fitness effects of IRI can arise as a result of direct interactions (Fig. 2).

For example, males may reduce the fitness of heterospecific females by harassing them, causing injury or through the production of inviable hybrids. Similarly, males of one species can reduce the fitness of heterospecific males by excluding them from mating territories or otherwise limiting their access to conspecific females (Gröning and Hochkirch 2008; Shuker and Burdfield-Steel 2017; Gomez-Llano et al. 2018). IRI can therefore lead to individuals of different species effectively competing for the same resource (i.e., gametes of the opposite sex; Gröning and Hochkirch 2008; Drury et al. 2015), which can affect the fitness of intrasexually competing individuals by eroding or otherwise limiting access to that resource. Fitness effects can also arise through less direct routes. For example, interference competition between heterospecific males may indirectly reduce the fitness of females by reducing their access to conspecific sperm, decreasing fertility. In some cases, IRI may increase the fitness of conspecifics. Recently, Gomez-Llano et al. (2018) showed that IRI arising from competition between *Calopteryx splendens* and *C. virgo* males increases female *C. splendens* fecundity by reducing conspecific harassment. By impacting the fitness of individuals engaged in intrasexual competition, IRI will likely shape mechanisms of intra- and intersexual selections on male reproductive strategies.

These effects may occur as part of short-term transient changes in sexual selection driven by recent colonization events, range shifts, and biological invasions (Sánchez-Guillén et al. 2013; Chunco 2014). For example, potential for IRI arises among related species of animals, with overlapping ranges and weak or no prezygotic isolation (Sasa et al. 1998; Presgraves 2002; Lijtmaer et al. 2003). Simultaneous spawning and cross-fertility is well documented among pairs of externally fertilizing sympatric species (Coyne and Orr 2004; Geyer and Palumbi 2005; Nosil 2012; Yeates et al. 2013), and heterospecific mating interactions
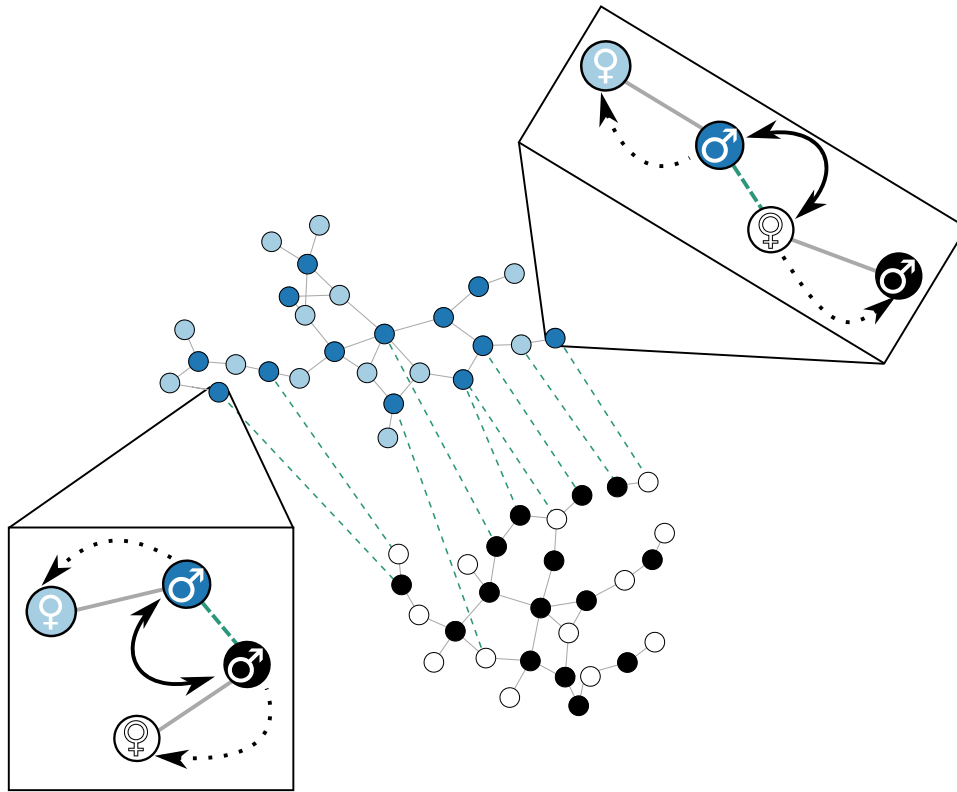
Figure 2. Heterospecifcs are a key component of the social environment. An example network of male–female sexual and male–male competitive interactions between individuals of a population of a focal species and a hetersospecific species. Dark blue nodes represent focal males and light blue nodes represent focal females. Black nodes represent hetersospecific males and white nodes represent heterospecific females. Gray edges between nodes indicate intraspecific interactions and green dotted edges indicate interspecific interactions. Subsets of the network are highlighted for two focal males. The fitness of individuals in interacting heterospecific pairs may be directly affected by their interaction (solid black arrows) and the fitness of their potential or actual sexual partners may subsequently be affected indirectly by the heterospecific interaction (dotted black arrows).

can also occur between sympatric internally fertilizing species (Coyne and Orr 2004; Nosil 2012). IRI may be particularly relevant to recently diverged populations in secondary contact and hybrid zones (Nosil 2012; Matute 2015). In such cases, the reduction in ova available to focal males may be severe. A recent study has demonstrated that heterospecific inseminations in some nematode species (*Caenorhabditis*) have lethal consequences for the sperm recipient (Ting et al. 2014). Similarly, males of various *Callosobruchus* seed-beetle species possess elaborate genital spines that have recently been shown to reduce the fecundity of heterospecific females following mating (Kyogoku and Sota 2015), while in frogs (*Rana*), heterospecifics can reduce the frequency of conspecific amplexus and the percentage of viable embryos laid by females (Hettyey and Pearman 2003). When hybrids are inviable or infertile, heterospecific matings will remove ova available for conspecific fertilization and reduce the absolute reproductive success of individual females. Under these conditions, IRI may play a role in the evolution of reinforcement of female preference for conspecific males (Liou and Price 1994; Servedio and Noor 2003; Pfennig 2007).

Alternatively, IRI may be more persistent. For example, when the cost of IRI to interacting species is not enough to result in species exclusion or when the asymmetries in costs of IRI are balanced by reversed asymmetries in resource competition (Kishi and Nakazawa 2013; Drury et al. 2015; Ruokolainen and Hanski 2016), IRI may drive more stable changes in patterns of sexual selection and drive the long-term maintenance of reproductive strategies.

IRI Alters Conventional Expectations in Structured Populations

Social structure is driven by behavioral, environmental, and demographic processes (e.g., via limited dispersal; Hamilton 1964; Wolf et al. 1999; Croft et al. 2005; Krause et al. 2014; Farine et al. 2015). In socially structured populations, competitive interactions can be nonrandomly distributed. This can result in a covariance between trait values of interacting individuals, for example, when large competitive individuals tend to compete against other similarly large individuals ("positive assortment," e.g., due to limited

dispersal). This covariance can obscure or accentuate the relationship between traits and relative fitness at the population level (Wallace 1968, 1975; Goodnight et al. 1992; Benton and Evans 1998; Wolf et al. 1999; McDonald et al. 2013). In the case of positive assortment, the relative benefits of body size are reduced and population-level selection for body size will be weakened (Goodnight et al. 1992; McDonald et al. 2013). Negative assortment, when large individuals compete with individuals smaller than the population mean, will instead accentuate sexual selection on size (Wolf et al. 1999; McDonald et al. 2017). Negative assortment may emerge as the consequence of male strategies to occupy less competitive social groups, where individuals preferentially assort with less competitive rivals, potentially increasing their relative reproductive success (Oh and Badyaev 2010; Gasparini et al. 2013).

Social structure therefore modulates the relative influence of the phenotypes of local competitors on an individual's fitness, increasing the importance of the phenotypes of local competitors and reducing the importance of the mean phenotype of the population as a whole (Wallace 1975; Goodnight et al. 1992; Wolf et al. 1999; Whitlock 2002; Agrawal 2010; Laffafian et al. 2010). This property has been referred to as both the "softness" of selection or the "scale of competition" (Frank 1998; Whitlock 2002; Gardner and West 2004; Agrawal, 2010; McDonald et al. 2013; De Lisle and Svensson 2017). When populations are not structured (i.e., competition occurs at random), the local competitive environment is similar across all individuals and local patterns of selection are representative of sexual selection at the level of the population (global competition). When populations are structured, the local competitive environment is crucial in determining individual fitness, and population-level patterns of selection may not represent local patterns of selection (Goodnight et al. 1992; Benton and Evans 1998; McDonald et al. 2013).

Social structure will thus have ramifications for variation in population-level patterns of selection (Wallace 1975; Goodnight et al. 1992; Benton and Evans 1998; Wolf et al. 1999; McDonald et al. 2017) and consequently for the maintenance of variation in quantitative traits (Dempster 1955; Wallace 1975; Goodnight et al. 1992). Moreover, social structure can influence population mutation load (Whitlock 2002; Agrawal 2010), by sheltering deleterious mutations from selection (positive assortment) or exposing them to selection (negative assortment) with potentially strong ramifications for population viability (Gabriel et al. 1991; Higgins and Lynch 2001; Whitlock 2002; Agrawal and Whitlock 2012). However, in nonsexual contexts, both theory and experiment suggest that, when heterospecific competitors are included in models of social structure, expectations can be radically altered (Agrawal 2010; Ho and Agrawal 2012).

Consider a population of a focal species, A, where males are under sexual selection and where limited male dispersal results

in positive assortment by promoting the genetic (and hence phenotypic) similarity of local rivals. Positive assortment weakens sexual selection at the population level, even though males compete intensely locally. Next, consider the addition of a randomly distributed interfering species B such that B-males interfere with the reproduction of species A (i.e., IRI) and reduce the number of A-females and/or ova locally available to A-males. The addition of B-males therefore means that resources (ova) not acquired by an A-individual may be surrendered not only to other A-males but also to B-competitors. Importantly, A-males of low competitive ability will compete against other weak A-males and with B-males of average competitive ability. On the other hand, A-males of high competitive ability will compete with other competitive A-males and with B-males of average competitive ability. The relative intensity of interspecific competition will be greater than that of intraspecific competition for A-males of low competitive ability, whereas for A-males of high competitive ability, the relative intensity of interspecific competition will be lower than that of intraspecific competition. In other words, when competitively inferior A-males lose out, resources are more likely to go to heterospecific B-males because their local conspecific A-rivals are also poor competitors, whereas when the competitively superior A-males lose out, their resources will have a higher likelihood of going to other conspecific A-males because their average quality is higher. Thus, the fitness of A-individuals of lower competitive ability will be compromised to a greater extent when compared to high-quality conspecific rivals. This will have the crucial result of strengthening the correlation between competitive ability and fitness for the focal A-population.

Instead, if focal A-males were negatively assorted by competitive ability, the addition of a randomly assorted interfering heterospecific competitor would reduce the effect of assortment on selection. This occurs because now low-quality individuals compete not only with high-quality conspecifics but also with average-quality heterospecifics. Similarly, high-quality individuals no longer reap the rewards of low-quality conspecific competitors and suffer increased competition due to heterospecifics of average quality. Thus, although the negative assortment of population A acts to strengthen sexual selection on the competitive ability of A-males, IRI by B-males diminishes this effect, by reducing the variation in fitness outcomes across focal individuals of differing trait values, weakening population-level sexual selection.

To demonstrate how social structure and IRI interact to modulate sexual selection, we set up simple simulations (Fig. 3; for details, see supplementary material). We constructed populations containing an equal number of focal males with or without a competitive phenotype under positive directional sexual selection. Populations were positively, randomly, or negatively assorted by male trait and focal males competed either only with conspecifics
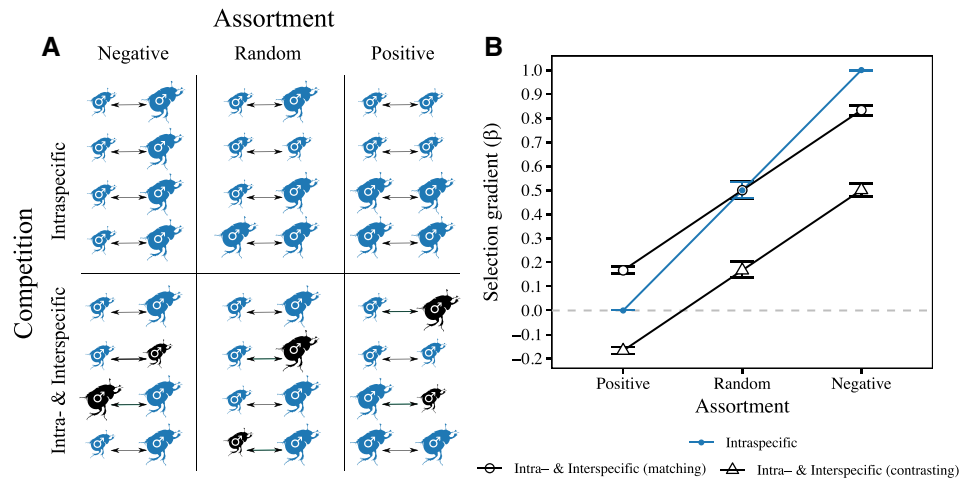
Figure 3. Interspecific reproductive interference (IRI) alters the effect of social structure on sexual selection. (A) Example populations of males with competition between conspecific (blue) and heterospecific males (black). Arrows link individuals in direct competition. The top three panels give three example groups with different patterns of assortment by a competitive trait (indicated by male size, small or large): negative assortment, random assortment, and positive assortment. The bottom three panels show the same populations but with 25% of conspecific competitors swapped for a randomly distributed heterospecific competitor. For simplicity, we assume that the two species have similar means and distributions in male competitive ability. (B) Selection gradients calculated from simulations with different levels of assortment with no heterospecifc competitors (intraspecifc; blue points), or with heterospecific competitors where the most competitive trait in intraspecific competition is the most (matching; black circles) or least (contrasting; black triangles) competitive trait when competing with heterospecifics. Error bars provide the 95% range of simulated values. Gray dashed line indicates no selection.

or with both conspecifics and a heterospecific competitor (i.e., including IRI, Fig. 3A).

When competition is only intraspecific, our results confirm classic predictions (Goodnight et al. 1992; Wolf et al. 1999), showing that when competitors are maximally positively assorted by phenotype, the correlation between the competitive trait and reproductive success is completely obscured (Fig. 3B). Positive assortment reduces selection gradients on male traits relative to if males competed at random, because competing with more competitive males counteracts the benefits of being highly competitive. Instead, when populations are negatively assorted with respect to competitive ability, selection is accentuated as the males with the highest competitive ability consistently compete with the males with the lowest competitive ability (Fig. 3B).

However, for those simulations including heterospecific competitors and where the male trait that is most effective when competing with conspecifics is also the most effective when competing with heterospecifics ("matching" selection pressures), our results show that IRI can alter basic quantitative predictions of the effect of social structure on sexual selection. Although IRI does not affect the strength of selection when focal populations are randomly assorted (i.e., no structure), the addition of heterospecific competitors influences the strength of sexual selection at the population level when populations are socially structured. When focal competitors are positively assorted, the addition of randomly distributed heterospecific competitors increases the strength of

sexual selection (Fig. 3B). When focal competitors are negatively assorted on the other hand, the addition of heterospecific competitors weakens sexual selection by diminishing the competitive advantage of the most competitive focal males (Fig. 3B).

We also considered the case where the male trait that is most effective when competing with conspecifics is the least effective when competing with heterospecifics ("contrasting" selection pressures). This could arise if, for example, males with a particular size or color pattern are the best competitors in intrasexual interactions, but attract the most intense competition from heterospecifics (Gomez-Llano et al. 2018). When the focal population is randomly assorted (i.e., no structure) and selection on focal male phenotype is contrasting, IRI weakens selection on the focal male trait because heterospecifics reduce the fitness of males with the trait, even though these males are the best competitors intraspecifically (Fig. 3B). When assortment is positive, IRI results in a similar reduction in selection such that overall the focal male trait is selected against at the population level. When assortment is negative, IRI reduces selection on focal male trait but selection remains relatively strong because males with the trait have a strong competitive advantage over their weaker conspecific competitors (Fig. 3B). However, the magnitude of the difference between selection with and without IRI is even larger for negative assortment, and thus deviations from classic predictions are accentuated (Fig. 3). These results demonstrate that IRI modifies standard expectations for the effect of social structure

on sexual selection and these modifications are highly dependent on the way in which animal societies are structured.

So far, we have considered cases where the population of heterospecific competitors is randomly assorted. However, additional complexity can be added when we consider that heterospecific competitors may also be socially structured. When the heterospecific population is also structured, the outcomes for selection will depend on the assortment within each population (intraspecific assortment) and the assortment between both populations (interspecific assortment). For example, the dispersal barriers that generate positive assortment among individuals of the focal species may have a similar outcome for assortment within the heterospecific population. This could generate positive assortment in competitive ability within each population and also across both populations (i.e., the most [least] competitive focal individuals also compete with the most [least] competitive heterospecific individuals). This would mean the focal competitors with the most competitive traits would not only face the most intense intraspecific competition but also the most intense interspecific competition. Alternatively, resources favorable to the focal species may be unfavorable to the heterospecific competitor, resulting in the poorest quality focal competitors facing only the highest quality heterospecific competitors, and vice versa (i.e., positive intraspecific assortment but negative heterospecific assortment). By further varying the intensity of intra- versus interspecific competition across focal phenotypes, social structure within heterospecifics may therefore modify expected changes in sexual selection beyond those predicted if heterospecifics were randomly distributed. Future research must assess how heterospecific assortment and the covariance between the competitive ability of focal and heterospecific competitors (interspecific assortment) may alter the predicted effects of IRI on patterns of sexual selection.

Sexual Conflict

Sexual selection can contribute to the divergence between the fitness interests of males and females over reproductive outcomes (sexual conflict), by promoting male strategies that harm or otherwise reduce the reproductive success of females (Arnqvist and Rowe 2005; Parker 2006; Kokko and Jennions 2014). For example, sclerotized spines on the aedeagus of male seed beetles (*C. maculatus*) physically damage females during copulations reducing female life expectancy but increase male fertilization success in sperm competition (Hotzy and Arnqvist 2009). In the fruit fly (*Drosophila melanogaster*), male accessory gland products such as the Sex Peptide convey a reproductive advantage to the male while resulting in fitness costs for the inseminated female (Wigby and Chapman 2005; Wigby et al. 2009). Similarly, brightly colored male bluehead wrasse (*Thalassoma bifasciatum*)

attract more spawning females but are unable to fertilize all their eggs, imposing a fertility cost on individual partners (Warner et al. 1995). In some cases, female harm arises as the consequence of intense intrasexual competition among males. For example, male sexual harassment of females to attain matings can reduce feeding rates in female guppies (*Poecilia reticulata*; Magurran and Seghers 1994) and lead to female death in waterfowl (McKinney and Evarts 1998). This may result in a "tragedy of the commons" (Hardin 1968; Frank 1998; Rankin et al. 2007), by reducing the overall fitness of the mating group or population, with potentially strong implications for population viability (Le Galliard et al. 2005; Rankin et al. 2007).

When competition is positively assorted so that more competitive (and more harmful) males compete with each other, groups of males that are more competitive overall may have lower absolute reproductive success than those groups of less competitive (less harmful) males because of their negative effect on female fecundity and/or survival (Rankin et al. 2007, 2011). Sexual conflict therefore interacts with the social structure of populations to generate variation in group-level productivity. This has the counterintuitive effect of increasing the relative productivity of groups of males with lower mean competitive ability compared with groups with a higher mean competitive ability. At the population level, positive assortment can generate selection against those harmful male traits that are most successful at the local level (Eldakar et al. 2009, 2010; Eldakar and Gallup 2011; Pizzari et al. 2015).

IRI can influence sexual conflict by modulating sexual selection for male harm of females. Consider a situation in which A-males harm their conspecific females as they vie to mate, and suffer IRI from B-males. The standard expectation is that when the A-population is positively assorted by male competitiveness and female harm, groups with less competitive, and thus less harmful, A-males are more productive. IRI from B-males is likely to buffer this effect, because groups of less harmful and less competitive A-males will lose out to B-males more than groups of more competitive/harmful A-males (see above). Therefore, IRI may effectively weaken population-level selection against male harm in the A population (below we show how this prediction may be qualitatively changed when we consider the genetical structure of the focal population). Moreover, when B-males harm A-females, high-quality A-males may be better able to shelter A-females from heterospecific harm than poor A-male competitors, as they more effectively compete with and/or exclude B-males in a positively assorted population, increasing the productivity of high-quality male groups (akin to selection for the evolution of male protection against B-males). This result is equivalent to the prediction of increased population-level selection on male competitive traits in positively assorted populations with IRI (see "matching" selection Fig. 3B). Conversely, negative conspecific assortment will

promote sexual selection for conspecific male harm, and in this case, IRI is expected to act to weaken this process.

Kin-Selected Strategies

Indirect fitness effects can play a role in sexually selected traits in viscous populations and have been implicated in selecting for the evolution of cooperation among males to secure mating opportunities (Pizzari and Gardner 2012; Faria et al. 2015, 2017; Pizzari et al. 2015). For example, male wild turkeys (*Meleagris gallopavo*) form cooperative courtship coalitions, where helper males do not reproduce but gain inclusive fitness through increasing the reproductive success of their male relatives (Krakauer 2005). Similar strategies have been reported in nonlekking species suggesting that such indirect effects may be a general property of sexual selection in structured populations (Pizzari et al. 2015; Łukasiewicz et al. 2017; Lymbery and Simmons 2017; Rosher et al. 2017; Tan et al. 2017; Torices et al. 2018).

Social structure is a key modulator of social evolution because it shapes the relatedness of interacting individuals (Hamilton 1964). Positive assortment via limited dispersal is expected to influence the potential for kin-selected reproductive strategies by increasing the relatedness of interacting neighbors (i.e., genetic relatedness rather than phenotypic assortment alone; Hamilton 1963, 1964, 1971). However, assortment of similar genotypes can simultaneously also increase the intensity of competition between kin, which is expected to undermine the evolution of cooperation by cancelling out the indirect benefits of helping (Hamilton 1971; Taylor 1992a; Kelly 1994b; Queller 1994; Frank 1998; West et al. 2002; Gardner and West 2006; Rankin 2011; Faria et al. 2015). The evolution of altruistic reproductive strategies in socially structured populations therefore depends on the extent to which the reproductive success of individuals is influenced by their local competitors versus the population as a whole (i.e., whether competition is local or global).

IRI may promote the evolution of kin-selected reproductive strategies in populations with positive genetic assortment (i.e., genetic structure) by relaxing reproductive competition among focal related males. This occurs because while retaining assortative social structure within conspecifics, the addition of an interspecific competitor decreases the reliance of individual fitness on the phenotypes of local conspecific competitors (i.e., retaining local kin interactions but reducing competition between kin). Few empirical studies have investigated the potential role of interspecific competition as a modulator of kin selection. However, in a nonsexual context, Kelly (1994a) showed theoretically that, in the presence of heterospecific competitors, the negative effects of competition are reduced among kin and instead increasingly felt by heterospecific competitors. This reduces the intensity of competition between local competi-

tors (i.e., kin), facilitating the evolution of kin-selected foraging strategies.

This effect can also be described in terms of the elasticity of the environment (Taylor 1992b; Gardner and West 2006). Taylor (1992a) showed that in inelastic populations (where local groups cannot accommodate increases in density), local competition between kin (i.e., positive assortment) limits the potential for altruistic behaviors because helping kin comes at a direct cost to the actor's personal reproductive success. However, in more elastic populations (local groups can accommodate increases in density), helping kin may pay because groups with more altruists can produce more offspring (Taylor 1992b). IRI creates elasticity, because the number of ova that are effectively taken away by heterospecifics represents the room for elastic expansion. Those groups composed of more altruists have the potential to fertilize more ova than groups of more selfish individuals, if they are better able to compete with heterospecifics and access this room for expansion. Thus, the direct costs of intrasexual cooperation to altruists may be outweighed by an increase in indirect benefits of helping local relatives. IRI can therefore reduce local competition between kin by shifting the competitive burden onto heterospecifics while maintaining intraspecific kin structure. This result is functionally equivalent to cases of sexual conflict (see above) where selection for male selfish restraint results in a reduction in harm to females and creates the elastic expansion (higher productivity) of groups with related and less competitive, and thus less harmful males (Rankin 2011; Faria et al. 2015; Pizzari et al. 2015)

If, however, cooperative strategies are less effective at competing with heterospecifics, IRI may hinder the evolution of kin-selected sexual cooperation. For example, if selfish male restraint causes an increase in female fecundity but this benefit cannot be directed toward kin or is otherwise not large enough to compensate for the ova removed by heterospecifics, selection for reduced male harm in positively assorted populations is counteracted by the effective "exploitation" of this trait by heterospecific competitors.

In principle, population structure may also create opportunities for the evolution of spite (Hamilton 1964, 1970; Gardner and West 2004; Pizzari and Foster 2008; Pizzari and Gardner 2012). Spite should be favored when relatedness is negative, that is, when population social structure results in individuals interacting with other individuals that are more genetically dissimilar to them than the average of the population (i.e., negative assortment, Grafen 1985). In the case of negatively assorted populations, IRI is likely to limit the potential for the evolution spiteful behaviors. This results from the same process that promotes the evolution of altruistic behaviors, by reducing the sensitivity of the fitness of focal individuals on their local, nonrandom subset of conspecific competitors and increasing its reliance on the mean phenotype of the population of conspecifics as a whole (i.e., globalizing

selection). That is, the inclusion of heterospecific competitors weakens the intensity of local competition among conspecifics while increasing the intensity of competition with heterospecifics. This effectively reduces the relative intensity of local competition between conspecifics. Thus, in positively assorted populations, IRI can promote kin-selected benefits of cooperation among related males. In negatively assorted populations, IRI can reduce the intensity of local competition amongst unrelated (i.e., "negatively" related) conspecific males, limiting the scope for the evolution of spiteful behaviors.

Looking Beyond IRI

IRI is only one of many potential interspecific interactions in natural communities. Other interactions such as predation and parasitism can also have strong effects on intrasexual competition. Many sexually selected traits involve visual and auditory displays that increase mating success but also the risk of predation or parasitism (Magnhagen 1991). A striking example of parasitoids inducing radical change in sexual traits is in field crickets (*Teleogryllus oceanicus*). Male song in crickets is used in courtship and agonistic male–male interactions. The parasitoid fly (*Ormia ochrace*) locates male *T. oceanicus* via their songs and lays larvae on these males, which subsequently kill those males (Zuk et al. 2006). Research has associated *O. ochrace* with the spread of the wingless allele in *T. oceanicus* that causes males to lack the structures used to sing, resulting 95% of males in some populations lacking song (Zuk et al. 2006; Pascoal et al. 2014).

For such interspecific interactions to have the similar consequences for sexual selection as IRI (i.e., interact with the social structure of the focal species), their fitness effects must mediate access to mates or their gametes in a way that is dependent on the expression of male traits. For example, predation could reduce the availability of females or their ova, but do so more severely for more or less competitive males. In the cricket *Gryllodes supplicans*, males call from burrows and are protected from predators, whereas females attracted to male calls are subsequently predated by geckos (Sakaluk and Belwood 1984; Magnhagen 1991). Thus, high-quality males that, for example, sing for longer or louder may attract more predation of their females than poor-quality males. This could in principle similarly interact with social structure to determine sexual selection on males. Future research should examine the potential for interspecific trophic interactions to interact with social structure to intensify or relax sexual selection within a species.

Future Directions

Addressing the role of IRI requires methodologies to characterize the social structure of interacting populations. This can be achieved empirically through the use of social network analy-

sis (Croft et al. 2008; Sih et al. 2009; Krause et al. 2014). Social network analysis provides a framework to characterize the social structure of populations using detailed spatial and behavioral datasets (Farine and Whitehead 2015), and has previously been used to quantify social structure in mixed-species groups (Farine et al. 2012; Kiffner et al. 2014). The use of multilayer networks that simultaeneosly charaterize structure of multiple networks (e.g., within and across species) may provde a key tool to understand the feedback between social and competitive processes in one species, on the social strcture and reproductive outcomes in another (Pilosof et al. 2017; Silk et al. 2018).

Importantly, social network datasets can be combined with multilevel selection approaches to estimate the fitness effects of an individual's social environment (McDonald et al. 2013, 2017; Cramer et al. 2017). Multilevel selection analyses are a multiple regression approach to estimate the relative contributions of fitness effects of the trait value of a focal individual, and the trait values of its social partners (Heisler and Damuth 1987; Wolf et al. 1999; Okasha 2004; Bijma and Wade 2008; Gardner 2015; Goodnight 2015). This approach is beginning to be used to study interspecific interactions. For example, Campobello et al. (2015) showed that the reproductive success of individual Jackdaws (*Corvus monedula*) was affected not only by their own nest attendance and that of their conspecific neighbors but also by the nest attendance of neighboring Lesser kestrels (*Falco naumanni*). Using social networks that include both focal species and heterospecifics, in combination with multilevel selection analyses, could allow estimates of how sexual selection is shaped by the traits of conspecific competitors, the traits of their heterospecific competitors, and how patterns of assortment in both popualtions translate those fitness effects into population-level patterns of sexual selection in the focal species.

Finally, while we have focused on competitive structure in the competing sex, social structure in both sexes is likely crucial in determining reproductive outcomes. For example, population-level covariances between competing male phenotypes and female fecundity may mediate these population-level patterns of selection (e.g., while large males compete with large males, they may also compete over a larger local resource pool). Selection outcomes will therefore depend on the relative magnitude of the covariance between the traits of competing males and the covariance between the size of resource pool (i.e., female fecundity) and male traits. Moreover, female evolutionary responses will likely mediate the expected change in intensity of sexual selection on males, and female behavior itself may be a key driver of social structure (e.g., via differential patterns of polyandry; McDonald et al. 2013). Future research should address this complexity. Laboratory experiments where heterospecific presence and social structure can be both manipulated and

Table 1. Example of the effects of interspecific reproductive interference (IRI) on sexual selection, driven by the change in the scale at which selection operates in socially structured focal populations. The potential outcomes outlined below are expressed relative to random assortment in focal populations and for cases where the heterospecific interfering species is randomly assorted and the most competitive trait in intraspecific competition is also the most competitive trait in interspecific competition (outcomes will change under different sets of assumptions).

Focal species assortment	Potential effects on sexual selection	Potential effects on kin-selected strategies	Potential effects on male harm of females
Positive	Intensify sexual selection	May promote altruistic strategies	Increase or decrease selection for male harm
Negative	Weaken sexual selection	May impede spiteful strategies	Increase or decrease selection for male harm

characterized may be a key first step to test the predictions presented here.

Conclusions

The social structure of populations is often complex, with important repercussions for the operation of sexual selection. IRI adds a further layer of complexity in ecological communities. IRI can interact with population structure to shape population-level correlations between the traits and fitness of a focal species, with far-reaching, and often overlooked, implications for the maintenance of variation in sexual traits, mutational load, sexual conflict, and the evolution of kin-selected reproductive strategies. In Table 1, we summarize some of the effects of IRI. The role of IRI may become increasingly prominent as climate change and anthropogenic globalization catalyze the introduction of nonnative species, range shifts, and expansions, placing together species with little or no shared recent coevolutionary history (Kearns et al. 1998; Biesmeijer et al. 2006; Traveset and Richardson 2006; Sánchez-Guillén et al. 2013; Chunco 2014). Future research should investigate the way in which rapid changes in ecological assemblages driven by these global processes can impact populations through IRI-mediated effects on sexual selection and social behavior.

AUTHOR CONTRIBUTIONS
G.C.M. and T.P. conceived the article. G.C.M. conducted the analysis. G.C.M., T.P., and A.G. wrote the article.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.