# Reproductive interference in insects

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## Abstract

1. Reproductive interference occurs when members of different species engage in reproductive interactions, leading to a fitness cost to one or both actors.

2. These interactions can arise through signal interference (“signal-jamming”), disrupted mate searching, heterospecific rivalry, mate choice errors, or misplaced courtship, mating attempts or copulation.

3. We present a definition of reproductive interference (RI) and discuss the extent to which a failure of species discrimination is central to a definition of RI.

4. We review the possible mechanisms of RI, using a range of insect examples.

5. We discuss some of the causes and consequences of RI, focusing in particular on mating systems and mating system evolution.

6. We conclude by considering future ways forward, highlighting the opportunities for new theory and for tests of old theory presented by reproductive interference.

## Introduction

Mating systems are sexual networks of individuals, describing how, where, when and how often animals come together to mate and raise offspring (Emlen & Oring 1977; Thornhill & Alcock 1983; Davies 1991). Alongside recent reappraisals of how best to quantify and model key mating system parameters (Kokko et al. 2014), there has been growing interest in recent years in – to borrow a popular expression – “when good mating systems go bad”, i.e. when unexpected and seemingly non-adaptive behavioural phenotypes arise during reproductive encounters. For instance, there is an increasing realisation that same-sex sexual behaviour is more widespread than previously thought, challenging our understanding of mate recognition and sexual function (including in insects: Bailey & Zuk 2009). Similarly, it is now clear that mating failure – the failure of individuals, particularly females, to produce offspring – is a more common phenomenon than predicted by our assumptions of strong natural and sexual selection on primary sexual function (Rhainds 2010). Mating failure can arise in a number of ways (Greenway et al. 2015), ~~but~~ with failure to achieve successful insemination despite successful intromission ~~is~~ perhaps being one of the more perplexing examples, but this too can be surprisingly common (e.g. 40-60% in *Lygaeus* seed bugs; Tadler et al. 1999; Dougherty & Shuker 2014; Greenway & Shuker 2015). Here we will consider another unexpected aspect of mating systems, again apparent in insects, reproductive interference.

Reproductive interference (RI) arises when individuals of different species sexually interact during reproduction, with one or both actors suffering a fitness cost. A ground-breaking review by Gröning and Hochkirch in 2008 revealed that costly heterospecific interactions were widespread in nature (167 bi-species systems, excluding the very many studies on hybridisation). However, the study of RI was perhaps hampered by the various synonyms used (at least 22 different names for the same phenomenon: Gröning & Hochkirch 2008). Their review also showed that heterospecific interactions were often studied by different groups of biologists, asking different kinds of questions. On the one hand, evolutionary biologists interested in speciation have very often studied heterospecific mating interactions and outcomes, given their obvious interest in reproductive isolation and population divergence (Coyne & Orr 2004). On the other, ecologists have been interested in RI in the context of its role in ecological character displacement (Dayan & Simberloff 2005). What perhaps was missing was the middle ground, between ecology and evolution. Here we hope to begin to fill that gap, considering the causes and consequences of reproductive interference in terms of mating system evolution in insects. We will begin by defining RI more completely, outline possible mechanisms by which RI can occur, and then provide empirical examples from insects. We will then consider the causes and consequences of RI, before concluding by outlining a few outstanding questions.

## Defining reproductive interference

Reproductive interference occurs when individuals of one species engage in reproductive behaviours with individuals of a different species that result in a loss of fitness for one or both species (Gröning and Hochkirch, 2008; Burdfield-Steel and Shuker, 2011). To this definition, Gröning and Hochkirch (2008) add that this behaviour towards a heterospecific arises due to a failure in species discrimination, which we will consider in further detail below. These authors also clarify the link between RI and ecological competition. As they note, “interference” interactions between individuals have been defined as a form of competition (e.g. Begon et al 2005), but there is an important difference, in that there is no shared resource over which competition can arise when we consider RI. Thus, whilst Gröning and Hochkirch (2008) confirm that RI will often share many of the features of ecological competition, such as density-dependence, it stands apart from competition as a separate ecological process, with its own set of evolutionary consequences. A similar point was made by Ribiero and Spielman (1986), in terms of “reproductive niches” and “trophic niches”. The extent to which the reproductive niches of different species overlapped would give a measure of reproductive interference, whilst overlap of trophic niches would give a measure of traditional resource competition, therefore separating reproductive interference from competition.

The reproductive behaviours that underlie RI can take many forms (see below; Figure 1). In cases where mating and successful sperm transfer occurs, RI can also lead to hybridisation (although cases of adaptive hybridisation may not constitute RI, see Pfennig and Simovich, 2002). Non-adaptive hybridisation comes with its own fitness consequences (Rhymer and Simberloff, 1996) and has been thoroughly studied in the context of reproduction isolation and speciation. In contrast, there is a greater need for studies focused on interactions where hybridisation does not occur (Gröning and Hochkirch, 2008, Kyogoku, 2015).

These interactions are expected to lead automatically to wasted reproductive effort, although the fitness costs of RI are likely to vary across the type of RI occurring, and the life history and mating system of the species involved. For example, heterospecific mating attempts are likely to carry the highest costs due to gamete wastage, energetic expenditure, and physical damage or death.

Gröning and Hochkirch (2008) identified a number of key patterns in their review, including the importance of RI for the ecological and evolutionary impacts of invasive species, and that the asymmetry of costs of RI to the two actors appears to be common. This asymmetry is important, as many of the ecological and thus evolutionary consequences of reproductive interference flow from this asymmetry, such as in terms of which species is more likely to be displaced, or be under stronger selection for reproductive character displacement. However, as will we confirm below, RI encompasses a diverse range of phenomena, and generalisations beyond these are so far limited.

## Mechanisms of reproductive interference in insects

A famous example of a misplaced mating attempt comes from the beetle *Julodimorpha bakewelli*, with males observed attempting to copulate with a beer bottle (Figure 2; Gwynne & Rentz 1983). This behaviour may arise from the fact that brown, stippled beer bottles provide enough attractive (or even "super-normal") stimuli to generate sexual behaviour (Gwynne & Rentz 1983) but it provides a clear example that mating attempts do not always run smoothly.

Insects provide numerous examples of RI, which we will review in terms of the different mechanisms of RI, starting with at-a-distance interactions. Our review is far from comprehensive, but hopefully illustrative in terms of the forms of reproductive interference.

First, RI may arise due to "signal jamming" or signal interference, whereby the signals produced by one species in some way disrupt the sending or receiving of those necessary for successful reproduction in another species. (This is distinct from conspecific "signal-jamming": Tobias and Seddon, 2009). Signal jamming has been widely studied in the Orthoptera, indeed making up a major component of the studies reviewed by Gröning and Hochkirch (2008). Patterns of con- and heterospecific signal discrimination observed in the field may therefore reflect current or indeed previous patterns of interactions or sympatry (Morris and Fullard 1983; Gwynne and Morris 1986), particularly in northern temperate habitats where glaciation cycles have repeatedly constructed and deconstructed communities with the coming and going of the ice sheets. Importantly, signal jamming may arise not just from females being unable to discriminate between different species-specific songs, it may also arise thanks to male responses to heterospecifics. For instance, male *Metrioptera brachyptera* bush crickets appear to be prevented from calling by the presence of the songs of *Metrioptera roeselii* (McHugh 1972).

Signal jamming can also occur in other communication systems and modalities. Insects offer very many examples of chemical communication, and many chemical communication systems are known to be susceptible to environmental disturbance (Fisher et al., 2006), and the presence of heterospecific signals could lower signal efficiency or block them entirely. Pheromonal signal jamming is well-known from Lepidoptera (e.g. Landolt & Heath 1987), but the phenomenon is more widespread. For instance, *Ips* bark beetles females can be attracted to heterospecific pheromones (Lewis and Cane 1992), whilst males of the mirid bug *Phytocoris difficilis* are attracted by the aggregation pheromone of the lygaeid *Oncopeltus fasciatus* (Zhang & Aldrich 2003).

At-a-distance signalling also presents the opportunity for inter-specific sexual deception, where predators use deceptive sexual signals to lure prey. Mokkonen and Lindstedt (2015) listed several examples of sexual deception, including that of bolas spiders that attract male moths to their lures with pheromones that resemble those of female moths (Stowe et al., 1987, Haynes et al., 2002). A number of orchid species mimic female insects to attract males in order to use males as pollinators (e.g. Gaskett 2011, 2012), being a potential example of reproductive interference across kingdoms, and indeed other plants beyond orchids employ similar sexual deception (e.g. the South African daisy *Gorteria diffusa*: Ellis and Johnson 2010). Perhaps the classic case though is the sexual deception practised by *Photuris* fireflies (Figure 1a; Lloyd 1997; Lewis 2016). Female *Photuris* mimic the signals of the females of *Photinus* and *Pyractomena* fireflies. By doing so, they attract males from those species and predate upon them. However, the complexity does not stop there, as male *Photuris* also mimic the females of other species, this time presumably to try to attract their own females (Lloyd 1997).

These cases fall at the blurry edge of RI though. While they do fit the definition of RI from the perspective of the prey species, they are the result of “intentional” deception on the part of the predatory species. As with the “sexual parasitism” described below, the evolutionary dynamics that result from these interactions should differ from more “classic” examples of RI since, although the prey species will undergo selection to avoid these interactions, there will be opposing selection in the predator to enhance them. This differs from most cases of RI where we would expect interspecific interactions to be either costly or selectively neutral for the two actors, not advantageous.

As well as long-distance attraction, males and females may actively search for mates. During mate searching, individuals may be attracted by the presence of heterospecifics to areas that reduce success, either by an increase in misdirected courtship or mating (see below), or by visiting an area with low numbers of con-specifics of the opposite sex. The next form of RI also occurs prior to close-range range interactions, namely heterospecific rivalry for mates. In this case, individuals, often males, mistakenly perceive members of another species as potential rivals for mates and behave aggressively towards them. This is most commonly seen in territorial species, including bees (Severinghaus et al. 1981), butterflies (Ravenscroft 1994; Dreisig 1995; Jones et al. 1998), and dragonflies (Singer 1990; Schultz & Switzer 2001; see also Ord and Stamps, 2009). Schultz and Switzer (2001) studied the amberwing dragonfly *Perithemis tenera* (Figure 1b) and showed that territorial males chased away butterflies and horse-flies that resembled conspecifics, but actually tended to ignore individuals of five other dragonfly species that look less like conspecifics. Heterospecific rivalry has also been found to drive character displacement in wing spots, a sexually selected trait, in the damselfly *Calopteryx splendens* (Tynkkynen et al., 2004; Figure 1c). Heterospecific rivalry can also occur in non-territorial species though, as in *Tetrix* groundhoppers (Hochkirch et al 2008).

Heterospecific rivalry might be considered non-adaptive when territories are held solely for reproduction, rather than for resources (Ord et al., 2011, Peiman and Robinson, 2010). However, aggression to all-comers, conspecific or not, might be favoured if successful defence against rival males leads to the side effect of occasional attacks on heterospecifics (see below for an analogous argument for mating attempts). As Gröning and Hochkirch (2008) point out though, when males are defending resource-based territories, and when heterospecifics also use those resources, it will often be hard to disentangle inter-specific competition from reproductive interference.

Once mate searching is completed, RI can then arise from errors in mate choice. We might expect mate choice errors to be rare, given the costs involved. A molecular analysis of hybridisation events looking at inheritance patterns of mitochondrial DNA suggested that unidirectional hybridisation was common (Wirtz 1999; see also Coyne and Orr 2004). Wirtz (1999) suggested that this arose because females are the only sex likely to change mating preferences enough when conspecific mate partners are rare, as males are always likely to be more permissive in their mate choices than females (see also Fowler-Finn & Rodriguez 2011 for an example of plasticity in mate preference as a result of experience in a treehopper).

Misdirected courtship occurs when an organism directs courtship behaviour towards an individual of a different species and this may then lead to hetero-specific mating attempts (Ribiero & Spielman 1986; Cothran et al., 2013), hetero-specific mating, and even hybridisation. Our work on lygaeid seed bugs illustrates all these outcomes for *Lygaeus equestris* (Shuker et al. 2015; Burdfield-Steel et al 2015; Evans et al 2015). Interestingly, there are a number of cases of males preferring heterospecifics over conspecifics, for example in male *Anasa andresii* squash bugs which prefer larger *Anasa tristis* females rather than conspecific females (Hamel et al., 2015). A similar pattern is seen in the ground-hopper *Tetrix ceperoi*, where males prefer the larger *T. subulata* females, even though those females reject them (Hochkirch et al 2007).

In the absence of hybridisation, heterospecific matings are predicted to carry the greatest fitness costs. In addition to the usual costs of mating (e.g. Shuker et al., 2006), heterospecific matings also carry the risk of physical damage from incompatible morphologies (Rönn et al., 2007, Kyogoku and Nishida, 2013, Kyogoku and Sota, 2015). This is the case in *Hesperocimex* bed bugs, which are haematophagous bird parasites and which copulate via traumatic insemination. Females of both H. *sonorensis* and *H. coloradensis* die after copulating with males of a third species, *H. cochimiensis*, in the former case following what appears to be a strong melanisation response (i.e. an immune system response to wounding) leaving blackened abdomens (Ryckman & Ueshima 1964). Similar inter-specific effects of traumatic insemination have been recorded for male *Cimex hemipterus* bedbugs mating with female *Cimex lectularius* (Walpole 1988, Newberry 1989). In addition to morphological damage, there is also the threat of attack from the perceived "mate". Males of the mantid *Orthodera novaezealandiae* are attracted to the pheromone of females of the invasive species *Miomantis caffra*, and attempt to copulate with them. As *M. caffra* females show high levels of sexual cannibalism, such attempts frequently end in the male's death (Figure 3; Fea et al., 2013). Extreme costs need not only arise from damage or predation though. Heterospecific matings can render females sterile, as in female *Aedes aegypti* mosquitos when they mate with male *Aedes albopictus* (Nasci et al 1989; see also Carrasquilla & Lounibos 2015). Similarly, females of the dermestid beetle *Trogoderma glabrum* often failed to mate with a conspecific after mating with the heterospecific *Trogoderma inclusum*, effectively sterilising them (Vick 1973). However, sometimes the costs are grave for males as well, for instance if the heterospecific mating involves the transfer of a costly nuptial gift, or indeed if heterospecific matings are similarly fatal for the male (e.g. *Heliothis* moths: Stadelbacher et al 1983). That said, the swapping of nuptial gifts between heterospecific partners may benefit the recipient (typically the female) provided that conspecific matings are also obtained, as suggested by Shapiro (1999) in the context of interactions between two *Orchelimum* katydid species, but such benefits are perhaps unlikely to be common.

Despite these costs, misdirected mating attempts are well known in the insect literature, and we provide just two brief examples. Our own work has shown that five species of lygaeid seed bugs, including three genera and species that either do or do not naturally co-occur, will all attempt mating and achieve successful intromission with each other, in something like 10% of mating trials (Shuker et al 2015). Moreover, *Lygaeus equestris* females suffer similar costs of inter-specific harassment when kept with male *Spilostethus pandurus* as they do when kept with conspecific males (Figure 4; Shuker et al 2015; Burdfield-Steel et al 2015). Related Heteroptera also provide some of the neatest examples of the ecological consequences of RI by mating attempts. Mating harassment by male *Neacoryphus bicrucis* displace five other species (beetles, bugs and a bushcricket) from their *Senecio smallii* food-plants (McLain & Shure 1987), whilst female *N. bicrucis* are in turn harrassed by a different bug (a coreid), *Margus obscurator*, and themselves are displaced from food-plants (McLain & Pratt 1999).

A rather particular form of RI occurs in gynogenetic species. Gynogenesis (or “pseudogamy”) is a form of parthenogenesis that requires sperm to trigger embryonic development. Despite this dependence on sperm, embryos produced in this manner contain only maternal chromosomes. Thus, gynogenetic species are almost exclusively female and require matings with males of closely-related species in order to reproduce. There are a few known examples in insects (in Coleoptera, Lepidoptera, Hemiptera and Collembola: Normark 2014), but it is easily missed without careful study. As the males that mate with these females pass no genes to the offspring produced, gynogenetic species can be thought of as “sexual parasites”. A similar form of sexual parasitism is hybridogenesis, as found in the *Bacillus rossius* stick insects (Mantovani & Scali 1992). In hybridogenesis, sperm from a closely-related sexual species is used to fertilise eggs, but all the offspring develop as females, and when they produce their own haploid gametes, they only use their mother’s chromosomes, so that the males never produce grand-offspring (reviewed by Lehtonen et al. 2013; Normark 2014). Gynogenetic and hybridogenetic species are perhaps a special case however as, typically, there are no mating interactions between truly parthenogenetic species and so no reproductive interference (as defined above). With the exception of gynogenetic species, parthenogenetic species will only influence RI when they become a target for misdirected mating interactions (for instance, if there are closely related sexual and asexual species, which is of course the case in a variety of insects: Normark 2014).

Post-mating, pre-zygotic reproductive interference can also occur via inter-specific sperm competition. Data from a range of insects suggest that con-specific sperm are favoured over heterospecific sperm (e.g. Howard et al 1998; Howard 1999; Simmons 2001), a phenomenon known as homogamy. For instance, Price (1997) showed that three sibling species of *Drosophila* exhibited conspecific sperm precedence, a phenomenon seemingly associated with seminal fluid products. Nonetheless, heterospecific sperm can disrupt sperm uptake, storage and usage.

In conclusion, reproductive interference takes a very wide range of forms in insects. Moreover, multiple forms of RI can often occur simultaneously, for instance, when both signal jamming and erroneous mate preferences result in heterospecific mating attempts (Andrews et al., 1982). In the next section, we will consider some of the causes and consequences of reproductive interference.

## Causes and consequences of reproductive interference

What causes reproductive interference? The ecological factors influencing RI have already been thoroughly reviewed, as have some of the ecological consequences of RI, such as species coexistence, sexual exclusion, and ecological character displacement (Kuno 1992; Gröning & Hochkirch 2008; recent examples include Kyogoku, 2015; Noriyuki & Osawa 2016; Ruokolainen & Hanski 2016). Given space constraints though, we will focus on the evolution of mating systems, including the evolutionary causes and consequences of polyandry, sexual selection, and sexual conflict on RI. However, ecological and evolutionary processes will be intimately linked, and we do not wish to stress the importance of one over the other.

In terms of causation, it is important to separate proximate and ultimate causes. For instance, a failure to discriminate stimuli at the proximate level begs the question as to why better discrimination has not evolved, or why a permissive discrimination system, that allows failure under some circumstances, has evolved. It is also worth considering what we mean by “errors” or “mistakes” in reproductive behaviour (for a discussion of how we use words in studies of sexual behaviour, see for instance Dougherty et al. 2013). If we assume that natural selection, first and foremost, favours con-specific reproductive interactions (apart from sexual deception say), then perhaps we can tentatively identify true “errors”. Here RI has no ultimate cause, and is involved either with an underlying pathology of one or both of the actors (damaged sensory structures for instance), or is truly a stochastic misplaced behaviour. On the other hand, there may be “adaptive errors”, whereby some plasticity in behaviour or permissiveness in response to signals is adaptive, even though RI may sometimes ~~result~~ occur as a side effect.

Proximate causes of RI can be broken down into those that are based on a failure of species recognition and those that occur independently of species recognition. Gröning and Hochkirch (2008) defined reproductive interference as “any kind of interspecific interaction during the process of mate acquisition that adversely affects the fitness of at least one of the species involved and that is caused by incomplete species recognition”. Presumably, many of the examples given in the previous section do involve a failure of species recognition. However, this is not always explicitly tested. Moreover, whilst a failure of species discrimination may often be the observed *outcome* of RI, it need not necessarily be its *cause*. A clear example of this comes from signal jamming. “Contaminating” signals from hetero-specifics may mask variation among conspecific signals, making mate choice difficult or effectively random (Pfennig, 2000). This may be costly, and it is certainly reproductive interference, but there need not be an actual species discrimination decision here, as there may only be conspecific mating options, or a garbled set of signals that are indecipherable. More generally, signal jamming may reduce choosiness *within* a species, compromising mate choice in a way that is costly to the chooser, without leading to a failure of species discrimination (we extend this point in Figure 5). As such, while we can generally assume that failures in species discrimination play some role in RI – and we certainly do not wish to underplay its role – they may not be the driving force shaping the behavioural outcomes, and we recommend a definition of RI that is not predicated on a failure of species discrimination.

In terms of ultimate causes of RI, when might RI be a side effect of an adaptive strategy? In a species that mates only once, such a mistake would be disastrous and reduce the fitness of the affected individual to zero. Under such conditions, we would expect very strong selection for species discrimination or reproductive character displacement that reduced the likelihood of hetero-specific encounters. The parasitoid wasps *Nasonia vitripennis* and *N. giraulti* overlap in Eastern North America, and have been found parasitising blow-fly pupae hosts in the same bird nests (Grillenberger et al. 2009). As with many parasitoids, the two species are mostly monandrous, with females typically mating once before dispersing to find new hosts (Boulton et al 2015). The two species are reproductively isolated by endosymbiont-based incompatibilities, with the two species hosting different and bi-directionally incompatible strains of the bacteria *Wolbachia* (Breeuwer & Werren 1990; Bordenstein & Werren 1998). Whilst there are also mate preferences for con-specifics, heterospecific matings can occur in the laboratory.

Crucially though, the two species have very different patterns of mating, with *N. vitripennis* typically mating outside of the host puparium after adult eclosion, whilst *N. giraulti* mates within the puparium; this difference in mating behaviour is suggested to have evolved to limit inter-specific~~s~~ mating (Drapeau & Werren 1999). More generally, we should expect species with a limited degree of multiple mating to exhibit extremely low reproductive interference. In contrast, in species that mate multiply, interspecific matings, while they may waste both time and mating effort, are expected to extract a lesser cost in terms of lifetime fitness, and these species may therefore be more tolerant to RI. We know of no formal test of that prediction yet.

Turning to mating systems theory more explicitly, some of the classic ways to view mating systems is through measures such as the operational sex ratio (OSR; Emlen & Oring 1977; Thornhill & Alcock 1983) and the Bateman gradient (Bateman, 1948; Kokko et al. 2014). Indeed, the operational sex ratio should influence the extent of RI in multiple ways. For instance, high skew in OSR (with one sex being rare for whatever reason) may make heterospecific interactions, and hence RI, more likely, as the common sex searches for possible mates. If mates are rare, then overly restrictive mate searching or mate choice thresholds maybe costly due to the possibility of missing out on mating entirely. Thus mate encounter rate should shape how permissive individuals are in terms of their species discrimination, and to what extent the need to mate leaves reproductive interference as a possible side-effect (for classic mate-searching and mate choice theory see Parker 1979 and Parker and Partridge 1998; a similar rationale has been used to suggest that polyandry should be considered the null situation for females, given the risks to females of going unmated: Kokko and Mappes 2013). We suspect that many occurrences of RI will be explained this way. The OSR may also influence the severity of the fitness costs, as it will influence an individual's chances of re-mating or not, or increase the intensity of courtship, or other forms of RI.

The Bateman gradient may also shape the nature and extent of RI. If Bateman gradients are steep (i.e. fitness increases sharply with increased numbers of matings, being typically steeper for males than females: Janicke et al 2016), then selection for less selective mating behaviour may lead to higher RI. However, increased RI may then feed back into the system, as high RI may eventually reduce the slope of the Bateman gradient (as selection favours individuals that mate less, but more selectively). Therefore, reproductive interference may be both a consequence of the mating system and also a cause of mating system structure. As yet, a formal theoretical consideration of OSR and Bateman gradients in the context of the ecological and evolutionary consequences of reproductive interference is lacking, and experimental tests of these ideas would be very welcome.

Turning to what other factors may influence RI we will first consider courtship. Courtship plays a number of roles (Alexander et al. 1997). Not the least of which will be mate choice, and we might assume that courtship also plays a major role in species discrimination (Ritchie et al., 1999). At first glance then, it seems likely that courtship will reduce the chances of an individual mating with other species, even if it may make them vulnerable to other forms of RI, such as misplaced courtship or signal jamming. However, evidence that species with pre-copulatory courtship are less susceptible to RI is not as abundant as might be expected (Gray, 2005). Moreover, it remains an open question for those interested in the interaction between sexual selection and speciation whether inter-specific mate choice maps to intra-specific mate choice in terms of preferred signals and the underlying genetics.

One factor identified as having close ties to both courtship and RI is sexual conflict. Sexual conflict occurs when the evolutionary interests of the sexes differ (Parker 1979; Lessells, 1999; Chapman et al., 2003; Arnqvist & Rowe 2005). Despite much of the discussion about within- and among-population sexual conflict taking place in the context of reproductive isolation and speciation (e.g. Parker and Partridge, 1998, Gavrilets, 2000), much of the theory developed can also be applied to RI. Here we will focus on conflict over mating frequency (Parker, 1979).

Sexual conflict over mating usually involves males coercing females to mate at a rate above (or in some cases below) the female optima (e.g. seaweed flies: Shuker and Day, 2001, 2002; seedbugs: Shuker et al., 2006). Conflict over mating can take many forms and may even continue after fertilization (e.g. in flies:

Chapman et al., 1995, Wigby et al., 2009, Perry et al., 2013). The co-evolution of male coercion and female resistance can result in males having greater mating success with females from different populations, as these will lack the co-evolved resistance present in females of their own population. Furthermore, if, as has been suggested (Parker, 1979, Parker and Partridge, 1998), females are likely to show robust species discrimination, processes that manipulate or circumvent female choice may increase the likelihood of RI. It should be noted, however, that these models assume that hybridisation is possible between the populations, and so only include true reproductive interference at the limits of their parameter space. McPeek and Gavrilets (2006), on the other hand, explored the role of encounters with heterospecific males on female mate preferences when they are post-reproductively isolated and not able to form hybrids. Whilst focusing on speciation, they showed that the presence of heterospecifics increased selection for mate preferences, which meant that in a population divergence context, heterospecifics would increase the likelihood of speciation (and of course reduce the extent of RI).

A rather different aspect of behaviour may influence the outcome of RI, namely learning. Learning has the potential to reduce or increase the incidence of RI depending on the circumstances in which it occurs. Learned mate preferences have now been displayed in multiple species (e.g. in *Drosophila*: Dukas 2004, Dukas et al 2006; in damselflies: Svensson et al., 2010, Verzijden & Svensson 2016; in psyllids: Stockton et al. 2017). While acquiring a mate preference based on experience may allow for greater species discrimination, there are situations where individuals may actually acquire preferences for the “wrong” mate, for instance if the focal species is locally rare, or simply outnumbered by the “interfering” species. However, an example from the butterfly *Bicyclus anynana* provides a potential solution to this problem. In this species, males have varying numbers of eye-spots on their wings, which are thought to play a role in mate-choice. A recent study found that naïve females have an innate preference for males with two eyespots (the most common phenotype found in nature). When exposed to males with increased ornamentation (i.e. four eyespots) shortly after emergence, the females developed a preference for this phenotype, however they did not show any change in preference if exposed to males with no eyespots. This suggests that mate-preference learning is biased in this species. While the exact cause of this bias is still under investigation, the presence of closely related species in sympatry with *B. anynana* that possess fewer eyespots does raise the possibility that this bias has arisen in order to prevent females from acquiring preferences for hetero-specific males (Westerman et al., 2012).

To finish this section, given the range of possible factors influencing RI, it is clear that predicting when RI will occur will not be a straightforward task. RI can happen in many different ways, and indeed we can find examples of it from almost every kind mating system and ecology (Gröning & Hochkirch 2008). The species-specific nature of RI may also explain why the fitness costs it inflicts often appear to be asymmetric (i.e. one species suffers more than another; Gröning et al., 2007). There has been an attempt to generate and test predictions about inter-specific mating interactions though, albeit in the context of hybridisation rather than RI *per se* (Ord et al 2011). The authors constructed predictions associated with social context (including the cost of mate searching), sex differences in discrimination, familiarity (e.g. sympatric versus para- or allopatric species; again mate-search costs are important here), and the reliability of species-specific cues. Testing these predictions in the context of hybridisation using meta-analysis, Ord and colleagues (2011) failed to find consistent effects of any of these factors on the response of individuals to heterospecifics. Instead, they concluded that the benefits of species discrimination appear to be highly species specific. Aspects of species biology that were implicated included the spacing patterns of conspecifics, the intensity of sexual selection, and predation pressure (Ord et al., 2011). Thus, if we extend this finding from hybridisation to reproductive interference, current evidence suggests that multiple aspects of species biology and ecology will influence not just the likelihood of RI occurring, but also its consequences. Given then that RI is often the outcome of several different factors working together, its causes may be difficult to generalise.

## Concluding remarks

There has been a renewed interest in reproductive interference in recent years (e.g. Burdfield-Steel & Shuker 2011; Kyogoku 2015 and associated papers; Otte et al. 2016; Yassin and David 2016). The ecological consequences of RI still remain to the forefront – if we exclude work in relation to speciation – but broader questions are being addressed too, and here we have focused on mating systems in particular. To conclude, we would like to make three points.

First, as argued above, since RI can arise without a failure of species discrimination as a proximate cause, we suggest a more inclusive definition of RI that does not require this failure (see Figure 5). Second, there have been calls for more studies of RI in the field (Gröning & Hochkirch 2008; Kyogoku 2015), not least as field and laboratory studies may yield different results (Gröning et al 2007). Whilst we agree that field conditions may vary considerably from the laboratory, in terms of population density, encounter rate, habitat complexity and so forth, the laboratory still has much to offer in terms of facilitating experimental studies of the causes and consequences of RI. These include both manipulating ecological factors and allowing long-term experimental evolution studies. We therefore suggest that both field and lab studies be combined, with the aim not just to ascertain the occurrence of RI under field-realistic conditions, but also to experimentally test hypotheses about why RI happens and how it influences ecological and evolutionary dynamics. Moreover, given the lack of generalities about reproductive interference at present, laboratory studies will continue to provide important data for synthetic and hypothesis-testing meta-analyses, as we are unlikely to be able to collect field-data as quickly as we can lab-data.

Our final point is that RI provides us with opportunities to generate new theory and also to test existing theory. Here we consider mating systems and sexual selection theory, but the same will no doubt be true in other sub-disciplines. Explicit models of reproductive interference in terms of mating system parameters remain to be formulated, even though existing models (such as those of Parker & Partridge 1998) speak to some of the questions we might wish to ask. Ideally, we would like to map out the landscape of RI in terms of aspects of the mating system, such as operational sex ratio, encounter rate, mate searching, costs and benefits of mating (including Bateman gradients), levels of polyandry, and pre- and post-copulatory sexual selection. As some of the discussion above has suggested, we are able to generate plausible verbal hypotheses that could link Bateman gradients with both higher and lower RI. A more systematic body of theory might help us unpick this tangled bank of effects, but more importantly perhaps, it will also throw new light on our existing body of theory and stimulate tests of that theory using heterospecifics, either as "controls" or to provide a greater range of possibilities (e.g. extreme outbreeding: Burdfield-Steel et al 2015). This will put our theory really through its paces. Finally, mating systems biology is only beginning to appreciate the value of network-based analyses (e.g. Muniz et al 2015; Fisher et al 2016), but in the light of this symposium, modelling and interpreting reproductive interference in terms of the socio-sexual network of con- and heterospecifics may provide a useful tool to draw out and test predictions about this puzzling yet beguiling behaviour [NOTE TO EDITORS: we are happy to include references to other symposium papers if appropriate].

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## Author contributions

DMS and ERB-S conceived of and wrote the manuscript.

## Conflict of interest

DMS and ERB-S declare no conflicts of interest

## References

Alexander, R.D., Marshall, D.C. and Cooley, J.R. (1997) Evolutionary perspectives on insect mating. In Choe, J.C. and Crespi, B.J. (eds). *The evolution of mating systems in insects and arachnids*, pp.4-31. Cambridge University Press, Cambridge.

Andrews, R.H., Petney, T.N. and Bull, C.M. (1982) Reproductive Interference between 3 parapatric species of Reptile Tick. *Oecologia*, 52: 281-286.

Arnqvist, G. and Rowe, L. (2005) Sexual conflict. Princeton University Press, Princeton.

Bailey, N.W. and Zuk, M. (2009) Same-sex sexual behavior and evolution. *Trends in Ecology & Evolution*, 24: 439-446.

Bateman, A. (1948) Intra-sexual selection in *Drosophila*. *Heredity*, 2: 349–368.

Bath, E., Tatarnic, N. and Bonduriansky, R. (2012) Asymmetric reproductive isolation and interference in neriid flies: the roles of genital morphology and behaviour. *Animal Behaviour*, 84: 1331-1339.

Begon, M., Townsend, C.R. and Harper, J.L. (2005) *Ecology: From individuals to ecosystems.* Blackwell, Oxford.

Bonduriansky, R. (2001) The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biological Reviews*, 76: 305-339.

Bordenstein, S.R. and Werren, J.H. (1998) Effects of A and B *Wolbachia* and host genotype on interspecies cytoplasmic incompatibility in *Nasonia*. *Genetics*, 148: 1833-1844.

Boulton, R.A., Collins, L.A. and Shuker, D.M. (2015) Beyond sex allocation: the role of mating systems in sexual selection in parasitoid wasps. *Biological Reviews*, 90: 599-627.

Breeuwer, J.A. and Werren, J.H. (1990) Microorganisms associated with chromosome destruction and reproductive isolation between two insect species. *Nature*, 346: 558.

Burdfield-Steel, E. R., Auty, S. and Shuker, D. M. (2015) Do the benefits of polyandry scale with outbreeding? *Behavioral Ecology*, 26: 1423-1431.

Burdfield-Steel, E. R. and Shuker, D. M. (2011) Reproductive interference. *Current Biology*, 21: R450-R451.

Chapman, T., Arnqvist, G., Bangham, J. and Rowe, L. (2003) Sexual conflict. *Trends in Ecology & Evolution*, 18: 41-47.

Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F. and Partridge, L. (1995) Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature*, 373: 241-244.

Cothran, R. D., Stiff, A. R., Chapman, K., Wellborn, G. A. and Relyea, R. A. (2013) Reproductive interference via interspecific pairing in an amphipod species complex. *Behavioral Ecology and Sociobiology*, 67: 1357-1367.

Coyne, J. A. and Orr, H. A. (2004) *Speciation*. Sinauer Associates Sunderland, MA.

Davies, N.B. (1991) Mating systems. In Krebs, J.R. and Davies, N.B. (eds) *Behavioural ecology: an evolutionary approach*, 3rd edition, pp.263-94. Blackwell, Oxford.

Dayan, T. and Simberloff, D. (2005) Ecological and community-wide character displacement: the next generation. *Ecology Letters*, 8: 875-894.

den Hollander, M. and Gwynne, D. T. (2009) Female fitness consequences of male harassment and copulation in seed beetles, *Callosobruchus maculatus*. *Animal Behaviour*, 78: 1061-1070.

Doherty, J. A. and Howard, D. J. (1996) Lack of preference for conspecific calling songs in female crickets. *Animal Behaviour*, 51: 981-989.

Dougherty, L.R., Burdfield-Steel, E.R. & Shuker, D.M. (2013) Sexual stereotypes: the case of sexual cannibalism. *Animal Behaviour*, 85: 313-322.

Dougherty, L.R. & Shuker, D.M. (2014) Pre-copulatory sexual selection in the seed bug *Lygaeus equestris*: a comparison of choice and no-choice paradigms. *Animal Behaviour*, 89: 207-214.

Dreisig, H. (1995) Thermoregulation and flight activity in territorial male graylings, *Hipparchia semele* (Satyridae), and large skippers, *Ochlodes venata* (Hesperiidae). *Oecologia*, 101: 169-176.

Dukas, R. (2004) Male fruit flies learn to avoid interspecific courtship. *Behavioral Ecology*, 15: 695-698.

Dukas, R., Clark, C.W. and Abbott, K. (2006) Courtship strategies of male insects: when is learning advantageous? *Animal Behaviour*, 72: 1395-1404.

Edward, D. A. and Chapman, T. (2011) The evolution and significance of male mate choice. *Trends in Ecology & Evolution*, 26: 647-654.

Ellis, A.G. and S.D. Johnson (2010) Floral mimicry enhances pollen export: the evolution of pollination by sexual deceit outside of the Orchidaceae. *American Naturalist*, 176: E143-E151.

Emlen, S.T. and Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science*, 197: 215-223.

Evans, G.M.V., Nowlan, T. & Shuker, D.M. (2015) Patterns of reproductive isolation within- and between- species characterised by a sexual conflict over mating. *Biological Journal of the Linnaean Society*, 116: 890–901.

Fea, M. P., Stanley, M. C. and Holwell, G. I. (2013) Fatal attraction: sexually cannibalistic invaders attract naive native mantids. *Biology Letters*, 9(6).

Fisher, D.N., Rodríguez-Muñoz, R. and Tregenza, T. (2016) Comparing pre-and post-copulatory mate competition using social network analysis in wild crickets. *Behavioral Ecology*, 27: 912-919.

Fisher, H. S., Wong, B. B. M. and Rosenthal, G. G. (2006) Alteration of the chemical environment disrupts communication in a freshwater fish. *Proceedings of the Royal Society B-Biological Sciences,* 273: 1187-1193.

Fowler-Finn, K.D. and Rodríguez, R.L. (2012) Experience-mediated plasticity in mate preferences: mating assurance in a variable environment. *Evolution*, 66: 459-468.

Gaskett, A.C. (2011) Orchid pollination by sexual deception: pollinator perspectives. *Biological Reviews*, 86: 33-75.

Gaskett, A.C. (2012) Floral shape mimicry and variation in sexually deceptive orchids with a shared pollinator. *Biological Journal of the Linnaean Society*, 106: 469-481.

Gavrilets, S. (2000) Rapid evolution of reproductive barriers driven by sexual conflict. *Nature*, 403: 886-889.

Gray, D. A. (2005) Does courtship behavior contribute to species-level reproductive isolation in field crickets? *Behavioral Ecology*, 16: 201-206.

Greenway, E.V., Dougherty, L.R. & Shuker, D.M. (2015) Mating failure. *Current Biology*, 25: R534-R536.

Greenway, E.V. & Shuker, D.M. (2015) The repeatability of mating failure in a polyandrous insect. *Journal of Evolutionary Biology*, 28: 1578-1582.

Grillenberger, B.K., Van De Zande, L., Bijlsma, R., Gadau, J. and Beukeboom, L.W. (2009) Reproductive strategies under multiparasitism in natural populations of the parasitoid wasp *Nasonia* (Hymenoptera). *Journal of Evolutionary Biology*, 22: 60-470.

Gröning, J. and Hochkirch, A. (2008) Reproductive interference between animal species. *Quarterly Review of Biology*, 83: 257-282.

Gröning, J., Lucke, N., Finger, A. and Hochkirch, A. (2007) Reproductive interference in two ground-hopper species: testing hypotheses of coexistence in the field. *Oikos*, 116: 1449-1460.

Gwynne, D.T., and Morris, G.K. (1986). Heterospecific recognition and behavioral isolation in acoustic Orthoptera (Insecta). *Evolutionary Theory*, 8: 33-38.

Gwynne, D.T. and Rentz, D.C.F. (1983) Beetles on the bottle: male buprestids mistake stubbies for females (Coleoptera). *Austral Entomology*, 22: 79-80.

Hamel, J. A., Nease, S. A. and Miller, C. W. (2015) Male mate choice and female receptivity lead to reproductive interference. *Behavioral Ecology and Sociobiology*, 69: 951-956.

Haynes, K. F., Gemeno, C., Yeargan, K. V., Millar, J. G. and Johnson, K. M. (2002) Aggressive chemical mimicry of moth pheromones by a bolas spider: how does this specialist predator attract more than one species of prey? *Chemoecology*, 12: 99-105.

Herberstein, M., Schneider, J. and Elgar, M. (2002) Costs of courtship and mating in a sexually cannibalistic orb-web spider: female mating strategies and their consequences for males. *Behavioral Ecology and Sociobiology*, 51: 440-446.

Hochkirch, A., Gröning, J. and Bucker, A. (2007) Sympatry with the devil: reproductive interference could hamper species coexistence. *Journal of Animal Ecology*, 76: 633-42.

Hochkirch, A., Bücker, A. and Gröning, J. (2008) Reproductive interference between the common ground-hopper *Tetrix undulata* and the slender ground-hopper *Tetrix subulata* (Orthoptera, Tetrigidae). *Bulletin of Entomological Research*, 98: 605-612.

Howard, D.J., Gregory, P.G., Chu, J. and Cain, M.L. (1998) Conspecific sperm precedence is an effective barrier to hybridization between closely related species. *Evolution*, 52: 511-516.

Howard, D.J. (1999) Conspecific sperm and pollen precedence and speciation. *Annual Review of Ecology and Systematics*, 30: 109-132.

Janicke, T., Häderer, I.K., Lajeunesse, M.J. and Anthes, N. (2016) Darwinian sex roles confirmed across the animal kingdom. *Science advances*, 2: 1500983.

Jones, M.J., Lace, L.A., Harrison, E.C. and Stevens-Wood, B. (1998) Territorial behavior in the speckled wood butterflies *Pararge xiphia* and *P. aegeria* of Madeira: a mechanism for interspecific competition. *Ecography*, 21: 297-305.

Kokko, H., Klug, H. and Jennions, M.D (2014) Mating systems. In Shuker, D.M. and Simmons, L.W. (eds) *The evolution of insect mating systems*, pp. 42-58. Oxford University Press, Oxford.

Kokko, H. and Mappes, J. (2013) Multiple mating by females is a natural outcome of a null model of mate encounters. *Entomologia Experimentalis Et Applicata*, 146: 26-37.

Kuno, E. (1992) Competitive exclusion through reproductive interference. *Researches on Population Ecology*, 34: 275-284.

Kyogoku, D. (2015) Reproductive interference: ecological and evolutionary consequences of interspecific promiscuity. *Population Ecology*, 57: 253-260.

Kyogoku, D. and Nishida, T. (2013) The mechanism of the fecundity reduction in *Callosobruchus maculatus* caused by *Callosobruchus chinensis* males. Population *Ecology*, 55: 87-93.

Kyogoku, D. and Sota, T. (2015) Exaggerated male genitalia intensify interspecific reproductive interference by damaging heterospecific female genitalia. *Journal of Evolutionary Biology*, 28: 1283-1289.

Landolt, P.J. and Heath, R.R. (1987) Role of female-produced sex pheromone in behavioral reproductive isolation between *Trichoplusia ni* (Hübner) and *Pseudoplusia includens* (Walker)(Lepidoptera: Noctuidae, Plusiinae). *Journal of Chemical Ecology*, 13: 1005-1018.

Lehtonen, J., Schmidt, D.J., Heubel, K. and Kokko, H. (2013) Evolutionary and ecological implications of sexual parasitism. *Trends in Ecology & Evolution*, 28: 297-306.

Lewis, S. (2016) *Silent Sparks: The Wondrous World of Fireflies*. Princeton University Press, Princeton.

Lewis, E.E. and Cane, J.H., (1992) Inefficacy of courtship stridulation as a premating ethological barrier for *Ips* bark beetles (Coleoptera: Scolytidae). *Annals of the Entomological Society of America*, 85: 517-524.

Lloyd, J.E. (1997) Firefly mating ecology, selection and evolution. In Choe, J.C. and Crespi, B.J. (eds) *The evolution of mating systems in insects and arachnids*, pp.184-192. Cambridge University Press, Cambridge.

Lessells, C.M. (1999) Sexual conflict in animals. In Keller, L. (ed) *Levels of Selection in Evolution*, pp.73-99. Princeton University Press, Princeton.

Mantovani, B. and Scali, V. (1992) Hybridogenesis and androgenesis in the stick-insect *Bacillus rossius-grandii benazzii* (Insecta, Phasmatodea). *Evolution*, 46: 783-796.

McHugh R. (1972) Aspects of acoustic interaction in the bushcricket genus *Metrioptera* (Orth., Tettigoniidae). Unpublished Ph.D., University of London.

McLain D. K., Pratt A. E. (1999) The cost of sexual coercion and heterospecific sexual harassment on the fecundity of a host-specific, seed-eating insect (*Neacoryphus bicrucis*). *Behavioral Ecology and Sociobiology*, 46: 164 –170.

McLain D. K., Shure D. J. (1987) Pseudocompetition: interspecific displacement of insect species through misdirected courtship. *Oikos* 49:291–296.

McPeek, M.A. and Gavrilets, S. (2006) The evolution of female mating preferences: differentiation from species with promiscuous males can promote speciation. *Evolution*, 60: 1967-1980.

Mokkonen, M. and Lindstedt, C. (2016) The evolutionary ecology of deception. *Biological Reviews*, 4: 1020-1035.

Morris, G.K., and Fullard, J.H. (1983).Random noise and congeneric discrimination in *Conocephalus* (Orthoptera: Tettigoniidae). In D.T. Gwynne and G.K. Morris (eds) *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*, pp. 73-96. Westview Press, Boulder, Colorado.

Muniz, D.G., Guimarães, P.R., Buzatto, B.A. and Machado, G. (2015) A sexual network approach to sperm competition in a species with alternative mating tactics. *Behavioral Ecology*, 26: 121-129.

Nasci R. S., Hare S. G., Willis F. S. (1989) Interspecific mating between Louisiana strains of *Aedes albopictus* and *Aedes aegypti* in the field and laboratory. *Journal of the American Mosquito Control Association*, 5(3):416–421.

Normark, B.B., 2014. Modes of reproduction. In Shuker, D.M. and Simmons, L.W. (eds) *The evolution of insect mating systems*, pp. 1-19. Oxford University Press, Oxford.

Noriyuki, S. and Osawa, N. (2016) Reproductive Interference and Niche Partitioning in Aphidophagous Insects. *Psyche: A Journal of Entomology*, 2016: 4751280.

Ord, T. J., King, L. and Young, A. R. (2011) Contrasting theory with the empirical data of species recognition. *Evolution*, 65: 2572-91.

Ord, T. J. and Stamps, J. A. (2009) Species identity cues in animal communication. *American Naturalist*, 174: 585-93.

Otte, T., Hilker, M. and Geiselhardt, S. (2016) Phenotypic plasticity of mate recognition systems prevents sexual interference between two sympatric leaf beetle species. *Evolution*, 70: 1819–1828.

Parker, G. A. (1979) Sexual selection and sexual conflict. In Blum, M.S. & Blum, B.N. (eds.) *Sexual selection and reproductive competition in insects*, pp. 123-166. Academic Press, New York.

Parker, G. A. and Partridge, L. (1998) Sexual conflict and speciation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353: 261-274.

Peiman, K. S. and Robinson, B. W. (2010) Ecology and evolution of resource-related heterospecific aggression. *Quarterly Review of Biology*, 85: 133-58.

Perry, J. C., Sirot, L. and Wigby, S. (2013) The seminal symphony: how to compose an ejaculate. *Trends in Ecology & Evolution*, 28: 414-422.

Pfennig, K. S. (2000) Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behavioral Ecology*, 11: 220-227.

Pfennig, K. S. and Simovich, M. A. (2002) Differential selection to avoid hybridization in two toad species. *Evolution*, 56: 1840-8.

Price, C.S. (1997) Conspecific sperm precedence in *Drosophila*. *Nature*, 388: 663-666.

Rantala, M. J. and Kortet, R. (2003) Courtship song and immune function in the field cricket *Gryllus bimaculatus*. *Biological Journal of the Linnean Society*, 79: 503-510.

Ravenscroft, N. O. M. (1994) Environmental influences on mate location in male chequered skipper butterflies, *Carterocephalus palaemon* (Lepidoptera: Hesperiidae). *Animal Behaviour* 47:1179 –1187.

Rhainds, M. (2010) Female mating failures in insects. *Entomologia Experimentalis et Applicata*, 136: 211–226.

Rhymer, J. M. and Simberloff, D. (1996) Extinction by Hybridization and Introgression. *Annual Review of Ecology and Systematics*, 27: 83-109.

Ribeiro, J. M. C. and Spielman, A. (1986) The satyr effect: a model predicting parapatry and species extinction. *American Naturalist* 128:513–528.

Ritchie, M. G., Halsey, E. J. and Gleason, J. M. (1999) *Drosophila* song as a species-specific mating signal and the behavioural importance of Kyriacou & Hall cycles in *D. melanogaster* song. *Animal Behaviour*, 58: 649-657.

Rogers, D. W. and Greig, D. (2009) Experimental evolution of a sexually selected display in yeast. *Proceedings of the Royal Society B: Biological Sciences*, 276: 543-549.

Rosenthal, G. G. (2013) Individual mating decisions and hybridization. *Journal of Evolutionary Biology*, 26: 252-255.

Rönn, J., Katvala, M. and Arnqvist, G. (2007) Coevolution between harmful male genitalia and female resistance in seed beetles. *Proceedings of the National Academy of Sciences*, 104: 10921-10925.

Ruokolainen, L. and Hanski, I. (2016) Stable coexistence of ecologically identical species: conspecific aggregation via reproductive interference. *Journal of Animal Ecology* 85: 638-47.

Ryckman, R. E. and Ueshima, N. (1964) Biosystematics of the *Hesperocimex* complex (Hemiptera: Cimicidae) and avian hosts (Piciformes: Picidae; Passeriformes: Hirundinidae). *Annals of the Entomological Society of America* 57: 624–638.

Schultz, J. K. and Switzer P. V. (2001) Pursuit of heterospecific targets by territorial amberwing dragonflies (*Perithemis tenera* Say): a case of mistaken identity. *Journal of Insect Behavior* 14:607– 620.

Severinghaus, L. L., Kurtak, B.H. and Eickwort G. C. (1981) The reproductive behavior of *Anthidium manicatum* (Hymenoptera: Megachilidae) and the significance of size for territorial males. *Behavioral Ecology and Sociobiology,* 9: 51–58.

Shapiro, L.H. (1999). Reproductive costs to heterospecific mating between two hybridizing katydids (Orthoptera: Tettigoniidae). *Annals of the Entomological Society of America*, 93: 440-446.

Shuker, D. M., Ballantyne, G. A. and Wedell, N. (2006) Variation in the cost to females of the sexual conflict over mating in the seed bug, *Lygaeus equestris*. *Animal Behaviour*, 72: 313-321.

Shuker, D. M., Currie, N., Hoole, T. and Burdfield-Steel, E. R. (2015) The extent and costs of reproductive interference among four species of true bug. *Population Ecology*, 57: 321-331.

Shuker, D. M. and Day, T. H. (2001) The repeatability of a sexual conflict over mating. *Animal Behaviour*, 61:755-762.

Shuker, D. M. and Day, T. H. (2002) Mate sampling and the sexual conflict over mating in seaweed flies. *Behavioral Ecology*, 13: 83-86.

Sillen-Tullberg, B., Gamberale-Stille, G. and Solbreck, C. (2000) Effects of food plant and group size on predator defence: differences between two co-occurring aposematic Lygaeinae bugs. *Ecological Entomology*, 25: 220-225.

Simmons, L. W. (2001) *Sperm competition and its evolutionary consequences in the insects*. Princeton University Press, Princeton.

Singer, F. (1990). Reproductive costs arising from incomplete habitat segregation among three species of *Leucorrhinia* dragonflies. Behaviour 115: 188 –201.

Stadelbacher, E. A., Barry, M. W., Raina, A. K. and Plimmer, J. R. (1983) Fatal interspecific mating of two *Heliothis* species induced by synthetic sex pheromone. *Cellular and Molecular Life Sciences* 39(10): 1174–1176.

Stockton, D.G., Martini, X. and Stelinski, L.L. (2017) Male Psyllids Differentially Learn in the Context of Copulation. Insects, 8: 16.

Stowe, M. K., Tumlinson, J. H. and Heath, R. R. (1987) Chemical Mimicry - Bolas spiders emit components of moth prey species sex-pheromones. *Science*, 236: 964-967.

Svensson, E. I., Eroukhmanoff, F., Karlsson, K., Runemark, A. and Brodin, A. (2010) A role for learning in population divergence of mate preferences. *Evolution*, 64: 3101-3113.

Tadler, A., Nemeschkal, H.L. and Pass, G. (1999) Selection of male traits during and after copulation in the seedbug *Lygaeus simulans* (Heteroptera, Lygaeidae). *Biological journal of the Linnean Society*, 68: 471-483.

Thornhill, R. and Alcock, J. (1983) *The evolution of insect mating systems*. Harvard University Press, Cambridge.

Tobias, J. A. and Seddon, N. (2009) Signal Jamming Mediates Sexual Conflict in a Duetting Bird. *Current Biology*, 19: 577-582.

Tregenza, T. and Wedell, N. (1998) Benefits of multiple mates in the cricket *Gryllus bimaculatus*. *Evolution*, 52: 1726-1730.

Tregenza, T. and Wedell, N. (2002) Polyandrous females avoid costs of inbreeding. *Nature*, 415: 71-3.

Tynkkynen, K., Rantala, M. J. and Suhonen, J. (2004) Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. *Journal of Evolutionary Biology*, 17: 759-767.

Verzijden, M.N. and Svensson, E.I. (2016) Interspecific interactions and learning variability jointly drive geographic differences in mate preferences. *Evolution*, 70: 1896-1903.

Vick, K.W. (1973) Effects of interspecific matings on *Trogoderma glabrum* and *T. inclusum* on oviposition and remating. *Annals of the Entomological Society of America*, 66: 237–239.

Walpole, D.E. (1988) Cross-mating studies between two species of bedbugs (Hemiptera: Cimicidae) with a description of a marker on inter-specific mating. *South African Journal of Science*, 84: 215-216.

Westerman, E. L., Hodgins-Davis, A., Dinwiddie, A. and Monteiro, A. (2012) Biased learning affects mate choice in a butterfly. *Proceedings of the National Academy of Sciences*, 109: 10948-10953.

Wigby, S., Sirot, L. K., Linklater, J. R., Buehner, N., Calboli, F. C. F., Bretman, A., Wolfner, M. F. and Chapman, T. (2009) Seminal Fluid Protein Allocation and Male Reproductive Success. *Current Biology*, 19: 751-757.

Wirtz, P. (1999) Mother species–father species: unidirectional hybridization in animals with female choice. *Animal Behaviour*, 58: 1-12.

Zhang, QH. & Aldrich, J.R. (2003) Pheromones of milkweed bugs (Heteroptera: Lygaeidae) attract wayward plant bugs: *Phytocoris* Mirid sex pheromone. *Journal of Chemical Ecology*, 29: 1835-1851.

## Figure legends

Figure 1. Reproductive interference in insects takes many forms. (A) Fireflies (Coleoptera: Lampyridae) exhibit both signal-jamming and sexual deception; (B) Males of the amberwing dragonfly *Perithemis tenera* perform heterospecific rivalry, chasing heterospecifics away from their territories; (C) Wing-spot evolution is driven by heterospecific rivalry in *Calopteryx* damselflies, and these species can also alter mate preferences after exposure to heterospecifics; (D) Insects can also mediate reproductive interference between other organisms, for instance when pollinating bees move pollen between different plant species, inhibiting conspecific pollen tube growth. Photo credits (clockwise from top left): TBC, TBC, TBC, David Shuker

Figure 2. A male *Julodimorpha bakewelli* beetle attempting to mate with a beer bottle. Photo credit: Darryl Gwynne.

Figure 3. Male *Orthodera novaezealandiae* select chambers in a Y-choice maze containing females of *Miomantis caffra*, versus an empty control chamber (Treatment A) or a chamber with females of their own species (Treatment B), with *M. caffra* females preferred in both treatments. From Fea et al. (2013). Inset top: a female *Orthodera novaezealandiae*; inset bottom: a female *Miomantis caffra*. Photo credits: Bryce McQuillan (under CC-2.0) and Phil Bendle (under CC-3.0)

Figure 4. Reproductive interference from male *Spilostethus pandurus* reduces longevity in female *Lygaeus equestris*, in a similar way to exposure to conspecific males. Solid line: focal *L. equestris* females kept with *S. pandurus* males; dotted line: focal females kept with *L. equestris* males (conspecifics); dashed line: focal females kept with *O. fasciatus* males; extended dashed line: focal females kept alone. Log-rank tests: *P*<0.001. From Shuker et al. (2015).

Figure 5. Species discrimination failure is not necessary for reproductive interference to occur. Species discrimination (SD) is defined as any behaviour that leads to non-random reproductive interactions with respect to species identity (con- versus heterospecifics). (A). Inset: Females (pink) receive courtship signals from conspecific males (red) and heterospecific males (blue). There are six possible reproductive interference (RI) outcomes if heterospecific signals disrupt conspecific signals: (i) Female mates with preferred male following usual mate assessment (no RI; successful SD); (ii) Female mates with preferred male following more costly (e.g. prolonged) mate assessment (RI; successful SD); (iii) Female mates with less preferred male (RI; successful SD); (iv) Female mates with randomly chosen conspecific male (RI; successful SD); (v) Female mates with heterospecific male (RI; failure in SD); (vi) Females mate randomly with con- or heterospecifics (RI; failure in SD). In the first four cases (i-iv), there is successful ~~signal~~ species discrimination, but in (ii-iv) mate choice is either prolonged or disrupted, leading to costs to the female, and so reproductive interference. (B) Left panel: Females (pink) again receive courtship signals from

conspecific males (red) and heterospecific males (blue), but in this case heterospecific signals swamp conspecific signals. Right panel: Two possible outcomes are shown: (i) Female mates with hetero-specific (no RI; failure in SD); (ii) Female does not mate (RI; successful SD). In terms of (i), even though females in this case have no “choice” (in the sense that they only have access to heterospecific signals), we still consider this a failure of species discrimination.

Figures

Figure 1.

**Figure 2**

**Figure 3**

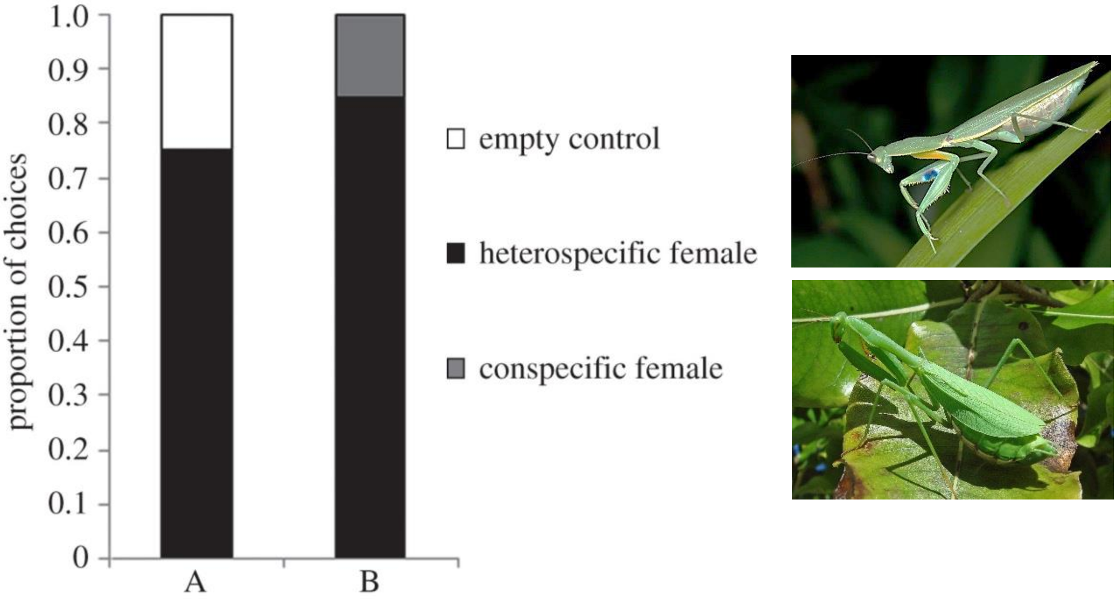
proportion of choices
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
A
B
☐ empty control
■ heterospecific female
▨ conspecific female

**Figure 4**

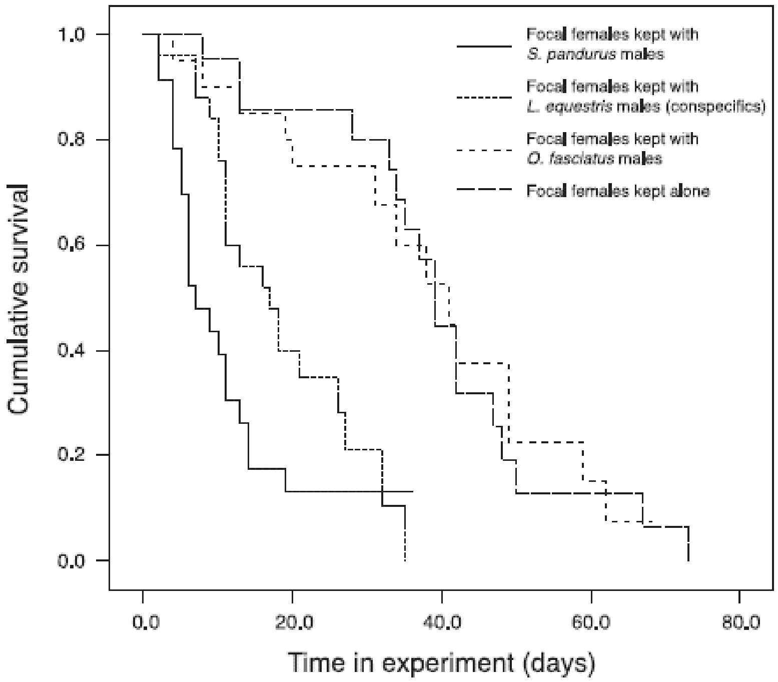
Focal females kept with
S. pandurus males
Focal females kept with
L. equestris males (conspecifics)
Focal females kept with
O. fasciatus males
Focal females kept alone
Cumulative survival
0.0
0.2
0.4
0.6
0.8
1.0
0.0
20.0
40.0
60.0
80.0
Time in experiment (days)

Figure 5