

# 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. The possible mechanisms of RI are reviewed, using a range of insect examples.

5. Some of the causes and consequences of RI are discussed, 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 tests of the old theory presented by reproductive interference.

**Key words.** Behaviour, competition, harassment, inter-specific interactions, satyr effect, sexual conflict.

## 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 (Rhains, 2010). Mating failure can arise in a number of ways (Greenway *et al.*, 2015), with failure to achieve successful insemination despite successful intromission 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 groundbreaking 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

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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 & Hochkirch, 2008; Burdfield-Steel & Shuker, 2011). To this definition, Gröning and Hochkirch (2008) add that this behaviour towards a heterospecific arises as a result of 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, while 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 Ribeiro 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, while 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; Fig. 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 & Simovich, 2002). Non-adaptive hybridisation comes with its own fitness consequences (Rhymer & 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 & 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 are 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* White (Buprestidae), with males observed attempting to copulate with a beer bottle (Fig. 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 & 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 & Fullard, 1983; Gwynne & 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* Linnaeus (Tettigoniidae) bush crickets appear to be prevented from calling by the presence of the songs of *Metrioptera roeselii* Hagenbach (Tettigoniidae) (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 & Cane, 1992), whereas males of the mirid bug *Phytocoris difficilis* Knight (Miridae) are attracted by the aggregation pheromone of the lygaeid *Oncopeltus fasciatus* Dallas (Lygaeoidea) (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 (2016) 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 to use males as pollinators (e.g. Gaskett, 2011, 2012), being a potential example of reproductive interference across kingdoms, and indeed other plants beyond



**Fig. 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): Daisuke Aochi, David Shuker, Piero Fariselli.



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

orchids employ similar sexual deception (e.g. the South African daisy *Gorteria diffusa* Thunberg (Asteraceae): Ellis & Johnson, 2010). Perhaps the classic case though is the sexual deception practised by *Photuris* fireflies (Fig. 1a; Lloyd, 1997; Lewis,

2016). Female *Photuris* mimic the signals of the females of *Photinus* and *Pyrractomena* 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 conspecifics of the opposite sex. The next form of RI also occurs prior to close-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 & Stamps, 2009). Schultz and Switzer (2001) studied the amberwing dragonfly *Perithemis tenera* Say (Libellulidae) (Fig. 1b) and showed that territorial males chased away butterflies and horse-flies that resembled conspecifics, but 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* Harris (Calopterygidae) (Tynkynen *et al.*, 2004; Fig. 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 (Peiman & Robinson, 2010; Ord *et al.*, 2011). 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.

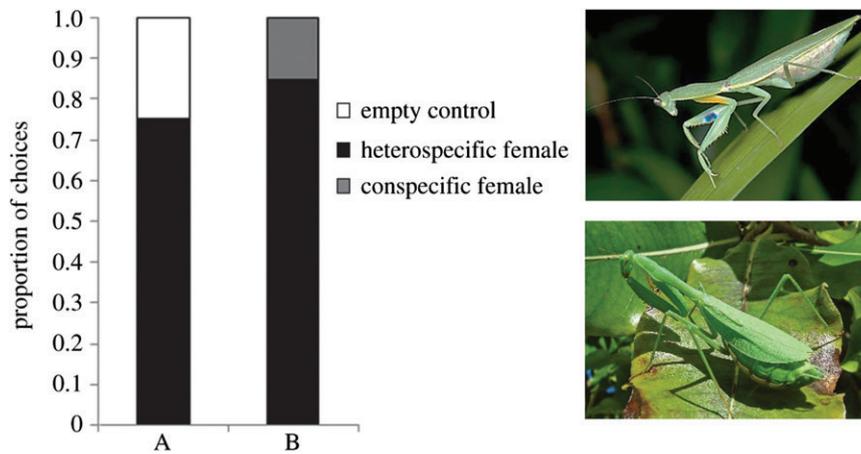
Once mate searching is completed, RI can then arise from errors in mate choice. We might expect mate choice errors to be rare, given the costs involved. A molecular analysis of hybridisation events looking at inheritance patterns of mitochondrial DNA suggested that unidirectional hybridisation was common however (Wirtz, 1999; see also Coyne & 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 & Rodríguez, 2012 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 (Ribeiro & 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* Linnaeus (Lygaeoidea) (Burdfield-Steel *et al.*, 2015; Evans *et al.*, 2015; Shuker *et al.*, 2015). Interestingly, there are a number of cases of males preferring heterospecifics over conspecifics, for example in male *Anasa andresii* Guérin-Méneville (Coreidae) squash bugs which prefer larger *Anasa tristis* DeGeer (Coreidae) females rather than conspecific females (Hamel *et al.*, 2015). A similar pattern is seen in the ground-hopper *Tetrix ceperoi* Bolívar (Tetrigidae), where males prefer the

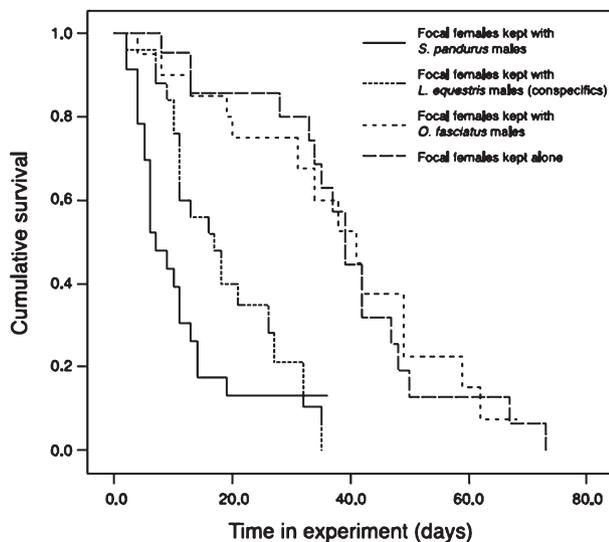
larger *T. subulata* Linnaeus (Tetrigidae) females, even though those females reject them (Hochkirch *et al.*, 2007).

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 & Nishida, 2013; Kyogoku & 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* Ryckman (Cimicidae) and *H. coloradensis* List (Cimicidae) die after copulating with males of a third species, *H. cochimiensis* Ryckman & Ueshima (Cimicidae), in the former case after 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* Fabricius (Cimicidae) bedbugs mating with female *Cimex lectularius* Linnaeus (Cimicidae) (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* Colenso (Mantidae) are attracted to the pheromone of females of the invasive species *Miomantis caffra* Saussure (Mantidae), 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 (Fig. 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* Linnaeus (Culicidae) mosquitoes when they mate with male *Aedes albopictus* Skuse (Culicidae) (Nasci *et al.*, 1989; see also Carrasquilla & Lounibos, 2015). Similarly, females of the dermestid beetle *Trogoderma glabrum* Herbst (Dermestidae) often failed to mate with a conspecific after mating with the heterospecific *Trogoderma inclusum* LeConte (Dermestidae), 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* Scopoli (Lygaeoidea) as they do when kept with conspecific males (Fig. 4; Burdfield-Steel *et al.*, 2015; Shuker *et al.*, 2015). Related Heteroptera also provide some of the neatest examples of the ecological consequences of RI by mating



**Fig. 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).



**Fig. 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 (conspicifics); 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).

attempts. Mating harassment by male *Neacoryphus bicrucis* Say (Lygaeoidea) displace five other species (beetles, bugs, and a bushcricket) from their *Senecio smallii* Britton (Asteraceae) food-plants (McLain & Shure, 1987), while female *N. bicrucis* are in turn harassed by a different bug (a coreid), *Margus obscurator* Fabricius (Coreidae), 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 to reproduce. There are a few known examples of 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* Rossi (Bacillidae) 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). Except 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

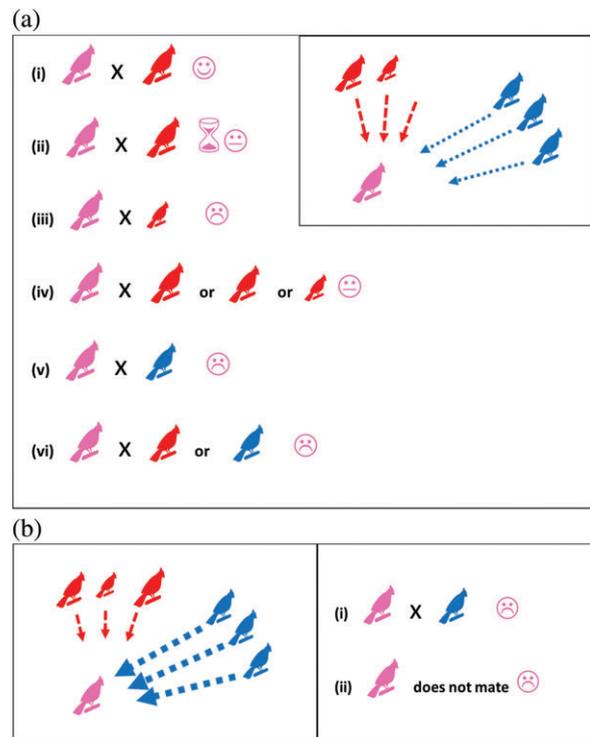
jamming and erroneous mate preferences result in heterospecific mating attempts (Andrews *et al.*, 1982). In the next section, we will consider some of the causes and consequences of reproductive interference.

### 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. In contrast, there may be 'adaptive errors', whereby some plasticity in behaviour or permissiveness in response to signals is adaptive, even although RI may sometimes 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, while 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



**Fig. 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 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 (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.

choice in a way that is costly to the chooser, without leading to a failure of species discrimination (we extend this point in Fig. 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* Walker (Pteromalidae) and *N. giraulti* Darling (Pteromalidae) 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). While there are also mate preferences for conspecifics, 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, while *N. giraulti* mates within the puparium; this difference in mating behaviour is suggested to have evolved to limit inter-specific 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 may be 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 & 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 & 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 & Partridge, 1998; Gavrillets, 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 & Day, 2001, 2002; seed bugs: Shuker *et al.*, 2006). Conflict over mating can take many forms and may even continue after fertilisation (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 & 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. McPeck and Gavrillets (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. While 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 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 *et al.* (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 & David, 2016). The ecological consequences of RI 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 Fig. 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 can 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.

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