



## REPRODUCTIVE INTERFERENCE BETWEEN ANIMAL SPECIES

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## ABSTRACT

*Although sexual interactions between species (reproductive interference) have been reported from a wide range of animal taxa, their potential for determining species coexistence is often disregarded. Here, we review evidence from laboratory and field studies illustrating that heterospecific sexual interactions are frequently associated with fitness loss and can have severe ecological and evolutionary consequences. We define 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. We distinguish seven types of reproductive interference: signal jamming, heterospecific rivalry, misdirected courtship, heterospecific mating attempts, erroneous female choice, heterospecific mating, and hybridization. We then discuss the sex-specific costs of these types and highlight two typical features of reproductive interference: density-dependence and asymmetry. Similar to competition, reproductive interference can lead to displacement of one species (sexual exclusion), spatial, temporal, or habitat segregation, changes in life history parameters, and reproductive character displacement. In many cases, patterns of coexistence might be shaped by reproductive interference rather than by resource competition, as the presence of a few heterospecifics might substantially decrease reproductive success. Therefore, interspecific sexual interactions should receive more attention in ecological research. Reproductive interference has mainly been discussed in the context of invasive species or hybrid zones, whereas its influence on naturally-occurring sympatric species pairs has rarely been addressed. To improve our knowledge of the ecological significance of reproductive interference, findings from laboratory experiments should be validated in the field. Future studies should also focus on ecological mechanisms, such as temporal, spatial, or habitat partitioning, that might enable sexually interacting species to coexist. Reproductive interference also has implications for the management of endangered species, which can be threatened by sexual interactions with invasive or common species. Studies of reproductive interference might even provide new insights for biological pest control.*

## INTRODUCTION

**I**NTERACTIONS BETWEEN SPECIES are important determinants of community composition. While predation, mutualism, and competition have been frequently investigated (e.g., Gurevitch et al. 1992; Bronstein 1994; Chase et al. 2002; Elewa 2006; Kaplan and Denno 2007), sexual interactions between animal species (reproductive interference) (Walker 1974) are still regarded as unusual by many ecologists (Mallet 2005). Consequently, this topic is missing even in modern ecology textbooks (Begon et al. 2005). In contrast to the ecological effects, the evolutionary significance of sexual interactions between species has often been addressed in the speciation literature, in studies of reinforcement and reproductive character displacement (Dobzhansky 1937; Brown and Wilson 1956; Butlin 1989; Servodio and Noor 2003; Coyne and Orr 2004). Some evolutionary biologists have concluded from models of reinforcement that extinction of one species is a likely outcome when sexually interacting species occur sympatrically (e.g., Paterson 1978; Liou and Price 1994), but they have done so without addressing the significance of these findings for community ecology. Interspecific communicative interference was first observed by behavioral biologists (Faber 1929), and, since then, interspecific sexual interactions have been documented in a wide range of animal taxa (Table 1). There is accumulating evidence that, in many cases, reproductive interference is associated with decreased fitness for one or both species. These costs might have dramatic ecological consequences, such as displacement of species by related species that share similar signal channels (Kuno 1992). We propose the term “sexual exclusion” for such displacement processes (Hochkirch et al. 2007), in order to distinguish them from the principle of competitive exclusion (Gause 1934).

Another reason why reproductive interference may have received relatively little attention in the ecological literature might be due to nomenclatural inconsistency. Subtypes of reproductive interference have been termed

as follows: “signal interference” (Schwartz 1987; Singer 1990), “communication interference” (Groot et al. 2006), “mistaken identity” (Schultz and Switzer 2001), “acoustic interference” (Littlejohn and Martin 1969; Ficken et al. 1974), “competition for acoustic signal space” (de Kort and ten Cate 2001), “interspecific acoustic interactions” (Schwartz and Wells 1984), “masking interference” (Gerhardt 1994; Amézquita et al. 2006), “cross-attraction” (Linn et al. 1988), “interspecific sex attraction” (Tamhankar 1992), “interspecific competition for mating territories” (Maier and Waldbauer 1979), “inappropriate mate-selection” (Butler and Stein 1985), “interspecific mate choice” (Ptaček 1998), “breeding interference” (Pearl et al. 2005), “interspecific social interactions” (Ficetola and De Bernardi 2005), “heterospecific pairing” (Chow-Fraser and Maly 1988), “pseudocompetition” (McLain and Shure 1987), “heterospecific sexual harassment” (McLain and Pratt 1999), “mating interference” (Ribeiro 1988; Nascy et al. 1989), “satyr effect” (Ribeiro and Spielman 1986), “satyrism” (Ribeiro 1988), “reproductive interactions” (Bull and Burzacott 1994), and “sexual interference” (Dame and Petren 2006). Even this list might be incomplete. Here, we use the term “reproductive interference” as a generic term for all of these interactions. We use this term not because it is necessarily the most appropriate, but instead because it is the most widespread in the recent literature (e.g., Walker 1974; Andrews et al. 1982; Kuno 1992; Söderbäck 1994; Fujimoto et al. 1996; Takafuji et al. 1997; Jackson and Tinsley 1998; Westman et al. 2002; Hettyey and Pearman 2003).

We define 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. Although interference, in its original sense, is defined as a type of competition (Birch 1957), reproductive interference differs from competition by the absence of one of its fundamental features (Begon et al. 1996): a shared limited resource. In fact, mates represent the resource that individuals compete for, but they can

only be regarded as a limited resource in an intraspecific context (Jennions and Petrie 1997). Fitness loss caused by reproductive interference does not result from competition for mates, but instead from wasting time, energy, nutrients, or gametes in heterospecific sexual interactions. Hence, reproductive interference is a type of "mistake," rather than competition in its original sense. It is caused by incomplete species recognition systems and, thus, is in between negative heterosis (if hybrids are involved) (Spencer et al. 1986) and competition (de Kort and ten Cate 2001). As we will show in this review, reproductive interference has many features in common with competition, as both are usually associated with fitness loss and are density-dependent and, in most cases, asymmetric.

The significance of reproductive interference as a determinant of species coexistence in nature is still a matter of controversy (Kuno 1992; Wauters and Gurnell 1999; Hettyey and Pearman 2003; Ficetola and De Bernardi 2005; Friggens and Brown 2005), since laboratory experiments and field observations often yield different results (e.g., Andrews et al. 1982 versus Bull and Burzacott 1994; Hettyey and Pearman 2003 versus Ficetola and De Bernardi 2005; Gröning et al. 2007 versus Hochkirch et al. 2007). In most of these cases, reproductive interference was found under laboratory conditions rather than in the field, possibly due to higher encounter frequencies with heterospecifics (Coyne and Orr 1989; Gröning et al. 2007). This phenomenon is well-known from practical experience in zoological gardens, where closely related species readily hybridize in mixed populations (Benirschke and Kumamoto 1991). Similar to competition, the significance of reproductive interference for species coexistence is difficult to assess. Some authors argue that exclusion is even more probable as a result of reproductive interference than due to resource competition and might, thus, explain the stability of parapatric or allotopic distributions of several closely related species (Ribeiro and Spielman 1986; Bull 1991; Kuno 1992). The-

oretically, sexual exclusion is a likely result of reproductive interference, if the reproductive success of one species is more heavily reduced than that of the other or if one of the species involved is much more abundant (Ribeiro 1988; Kuno 1992; Reitz and Trumble 2002; Westman et al. 2002), but evidence for such processes is still sparse.

As the mechanisms of signal production are evolutionarily constrained by the anatomy of the organisms involved, overlap of signal channels is more likely in related taxa (de Kort and ten Cate 2001). In fact, reproductive interference has mainly been documented in congeneric species (e.g., Crankshaw and Matthews 1981; Singer 1990; Fujimoto et al. 1996; Deering and Scriber 2002; Hettyey and Pearman 2003; Dame and Petren 2006). Smith and Florentino (2004) compared the male response of *Arrenurus* mites (Acari: Arrenuridae) to heterospecific sex pheromones and showed that it is restricted to members of the same species group. Despite this phylogenetic trend, reproductive interference also occurs between distantly related taxa (Chow-Fraser and Maly 1988), particularly if acoustic or olfactory long-distance signals are involved (Mazor and Dunkelblum 1992), or if other taxa resemble conspecific rivals (Schultz and Switzer 2001). Some authors argue that signal overlap is more likely to be found between allopatric species, which have not been exposed to any long-term selective pressures resulting in signal divergence (Coyne and Orr 1989). Hence, reproductive interference has received much attention in secondary contact zones (e.g., Servedio and Noor 2003) and between invasive and native species (e.g., Rhymer and Simberloff 1996); however, it might also affect the coexistence of naturally sympatric species (Hochkirch et al. 2007).

In this review, we synthesize case studies from a wide range of animal taxa that demonstrate that reproductive interference may have substantial fitness consequences, and we analyze empirical studies on the topic published between 1929 and 2007. In order to find relevant studies, we searched two

TABLE 1  
*Analyzed cases of various types of reproductive interference across different taxa*

Study	Taxon	AI	CI	HR	MC	HA	EF	HM	Total
Laboratory experiments	Nematoda							3	3
	Arthropoda								
	Crustacea		6			6		7	8
	Arachnida		1		7	2	1	2	11
	Insecta								
	Orthoptera	27		1	4	3	3	3	32
	Heteroptera				1	1			1
	Homoptera				1			1	1
	Lepidoptera		4		4	4		5	9
	Coleoptera		5				5	3	8
	Diptera				4	1	2	4	10
	Hymenoptera		1			5			5
	Vertebrata								
	Teleostei		1		3	1	1	2	5
	Amphibia	2	1		1	1		1	5
	Reptilia				1			1	1
	Aves	1			1		4		4
Subtotal		30	19	1	27	24	16	32	103
Field experiments	Arthropoda								
	Crustacea						2	1	3
	Arachnida							1	1
	Insecta								
	Orthoptera				1	1		1	1
	Odonata			2		2		2	2
	Lepidoptera		1		1	1		2	3
	Diptera							1	1
	Vertebrata								
	Teleostei				1				1
	Amphibia	3						1	4
	Reptilia				1				1
	Aves	3		1	4	3		3	8
Subtotal		6	1	3	8	7	2	12	25
Field observations	Plathelminthes							1	1
	Arthropoda								
	Crustacea							1	1
	Arachnida							1	1
	Insecta								
	Orthoptera	9		1	2	1		1	10
	Odonata			2		1			2
	Heteroptera				2	2			2
	Lepidoptera			9	1				9
	Diptera			3		2			5
	Hymenoptera			2		3		3	5

*continued*

TABLE 1  
*Continued*

Study	Taxon	AI	CI	HR	MC	HA	EF	HM	Total
	Vertebrata								
	Teleostei				2			1	3
	Amphibia	3				7			10
	Reptilia				1				1
	Aves	2							2
	Mammalia				1				1
Subtotal		14	0	17	9	16	0	8	53
Total		45	19	20	38	44	18	46	167

The table comprises species pairs that occur in sympatry in parts of their ranges (including suture zones and invasive species). A total of 108 publications have been considered, reporting on 167 bi-species systems of reproductive interference (AI = Acoustic interference; CI = Chemical interference; HR = Heterospecific rivalry; MC = Misdirected courtship; HA = Heterospecific mating attempt; EF = Erroneous female choice; HM = Heterospecific mating). Systems that have been published more than once have been counted only once. Note that subtotals and totals can be smaller than 100%, as in many systems different kinds of reproductive interference co-occur, and some cases have been studied in the field as well as in the laboratory. All observed types of reproductive interference have been included, regardless of frequency, strength, or direction (asymmetry).

References: Faber (1929); Fulton (1934); Tinbergen et al. (1942); Weih (1951); Storm (1952); Lin (1961); Broughton (1965); Brodie (1968); Cody and Brown (1969); Licht (1969); Littlejohn and Martin (1969); Hill et al. (1972); McHugh (1972); Vick (1973); Ficken et al. (1974); Grant et al. (1975); Kaneshiro (1976); Brower (1977); Brown (1977); Samways (1977); Spickett and Malan (1978); Bitzer and Shaw (1979); Mac Nally (1979); Maier and Waldbauer (1979); Crankshaw and Matthews (1981); Severinghaus et al. (1981); Andrews et al. (1982); Brenowitz (1982); Fuyama (1983); Ratcliffe and Grant (1983); Schwartz and Wells (1983); Stadelbacher et al. (1983); Tierney and Dunham (1983); Schwartz and Wells (1984); Butler and Stein (1985); Bailey and Morris (1986); Landolt and Heath (1987); McLain and Shure (1987); Chow-Fraser and Maly (1988); Rutowski and Gilchrist (1988); Searcy and Brenowitz (1988); Takafuji (1988); Nasci et al. (1989); Scott and Jackson (1989); Brown and Alcock (1990); Phelan and Baker (1990); Singer (1990); Verrell (1990); Collins and Margolies (1991); Dame and Petren (1991); Koprowski (1991); Lewis and Cane (1992); Mazor and Dunkelblum (1992); Tamhankar (1992); Perring et al. (1993); Kronstedt (1994); Ravenscroft (1994); Ross et al. (1994); Söderbäck (1994); Verrell (1994); Dreisig (1995); Tomaru et al. (1995); Wiernasz (1995); Doherty and Howard (1996); Fujimoto et al. (1996); McClintock and Uetz (1996); Silva and Stouthamer (1997); Gregory et al. (1998); Jackson and Tinsley (1998); Jones and Hunter (1998); Jones et al. (1998); Ptacek (1998); McLain and Pratt (1999); Gray and Cade (2000); Tomaru et al. (2000); de Kort and ten Cate (2001); Hill and Hernault (2001); Price et al. (2001); Schultz and Switzer (2001); Collins and Luddem (2002); Deering and Scriber (2002); Westman et al. (2002); Yamada et al. (2002); Christy et al. (2003); Hettley and Pearman (2003); Lind et al. (2003); Scott et al. (2003); Ardeh et al. (2004); Dukas (2004); Fricke and Arnqvist (2004); Luddem et al. (2004); Magurran and Ramnarine (2004); McLennan (2004); Shine et al. (2004); Smith and Florentino (2004); Gray (2005); Gumm and Gabor (2005); Pearl et al. (2005); Scott et al. (2005); Wong et al. (2005); Amézquita et al. (2006); Fricke et al. (2006); Kandul et al. (2006); Marshall et al. (2006); Russel et al. (2006); Gröning et al. (2007); Hochkirch et al. (2007, forthcoming).

databases (Web of Science, Biological Abstracts) using the key phrase “reproductive interference” and the related aforementioned terms. We also screened ecological, evolutionary, and behavioral textbooks and reviews and searched the reference lists of papers to locate additional studies. However, we excluded studies of hybridization, since these have been subject to several reviews over the past few decades (e.g., Barton and Hewitt 1985; Rhymer and Simberloff 1996; Dowling and Secor 1997; Wirtz 1999; Burke and Arnold 2001; Bell and Travis 2005; Seehausen 2004; Mallet 2005). We analyzed 167 bi-species systems of reproductive interference (Table 1), including examples of

species that are either naturally (141 cases) or artificially (26 cases) sympatric in parts of their geographic ranges. A major goal of our review is to show that the ecological consequences of reproductive interference can be dramatic, even in the absence of hybridization. The effect that reproductive interference has on species coexistence might be similar to—if not even more important than—that of resource competition, and, therefore, it should be addressed in ecological research. Furthermore, we propose important topics for future research on reproductive interference and discuss the practical implications of this process for conservation biology and pest control.

#### TYPES OF REPRODUCTIVE INTERFERENCE

Within the course of mate acquisition, species utilize signals for mate attraction, courtship, or male combat (Bradbury and Vehrenkamp 1998). Often, these signals are believed to be sufficiently specific to avoid heterospecific sexual interactions (Paterson 1985). If the signals of two or more species are too similar, the chance of heterospecific interactions increases (McHugh 1972). In principle, such interactions are possible at any stage of mate acquisition, from signaling to copulation to fertilization.

Based on the temporal course of mating behavior, we distinguish seven types of reproductive interference:

1. *Signal jamming* during mate attraction is the most indirect type of reproductive interference. During signal jamming, conspecific signals are degraded by the presence of heterospecific signals, thereby resulting in decreased conspecific mating success. Signal jamming complicates mate recognition by confusing individuals in their search for mates. Heterospecific signal jamming should be distinguished from other types of "environmental noise" (Linn and Roelofs 1995), such as abiotic (Endler 1992; Rosenthal and Ryan 2000), anthropogenic (Brumm and Slabbekoorn 2005), or conspecific noise (Gerhardt 1994).

2. *Heterospecific rivalry* is a type of reproductive interference in which heterospecifics are mistaken for conspecific individuals of the same sex (usually males) rather than mates. It is found mainly in territorial species, which are known to chase heterospecifics out of their mating territory (Schultz and Switzer 2001). However, heterospecific rivalry might often be associated with resource competition or predator-prey relationships (Severinghaus et al. 1981; Bolger and Case 1992), and, in these cases, it is difficult to distinguish reproductive interference from other types of interspecific interactions.

3. *Misdirected courtship* can occur if heterospecifics possess traits or produce signals that elicit courtship behavior. Courtship displays are usually performed or

initiated by males, which are often indiscriminate in mate choice, as they invest less energy in reproduction (Arnqvist and Rowe 2005). Hence, the costs associated with misdirected courtship mainly affect the male sex.

4. *Heterospecific mating attempts* may occur independently of courtship or female choice. Even if one mate (usually the female) does not tolerate a copulation (Andersson 1994), such attempts may still involve fitness costs for both sexes, particularly if sexual harassment is involved.

5. In most animal species, females are the choosy sex (Andersson 1994). *Erroneous female choice* is, therefore, another important type of reproductive interference, although it is believed to be relatively rare due to the high reproductive investment of females and the associated high costs of choosing heterospecific males (Wirtz 1999).

6. *Heterospecific matings* may happen if a lack or insufficiency of premating barriers exists in both sexes, or if one sex (usually the female) is not able to reject forced copulations of heterospecific mates ("satyr effect") (Ribeiro and Spielman 1986). The costs of heterospecific matings are particularly high if postmating barriers are complete (Liou and Price 1994). Therefore, we distinguish heterospecific matings from hybridization.

7. *Hybridization* is a rather special type (albeit the most well-known) of reproductive interference that occurs between taxa that are not yet fully reproductively isolated. The costs associated with hybridization can sometimes be lower than those of other types of reproductive interference, depending on the fitness of the hybrids (Fitzpatrick and Shaffer 2007; Pfennig 2007).

The boundaries between these types of reproductive interference are gradual, and, in many species pairs, more than one type has been documented (47 of the 167 cases summarized in Table 1). Nonetheless, we follow the classification system outlined above for reasons of consistency.



## SIGNAL JAMMING

In animal communication, the quality, transmission, or detection of signals might be disturbed by other signal sources. This phenomenon is known as signal jamming (Heiligenberg 1986). Species-specific signals, such as male calling songs, visual displays, or female sex pheromones, play a crucial role as premating barriers between closely related taxa (Bradbury and Vehrencamp 1998; Ptacek 2000). The efficient transmission or perception of conspecific mating signals can be reduced or inhibited by the signaling environment, including abiotic noise (Endler 1992), anthropogenic noise (Popper 2003; Slabbekoorn and Peet 2003; Fisher et al. 2006), conspecific signals (Gerhardt 1994), and signals produced by heterospecifics (Andrews et al. 1982). Only the latter mechanism can be assigned to reproductive interference. Signal jamming, or "signal interference" (Verrell 1994), is the most indirect type of reproductive interference, as it does not necessarily involve close contact between individuals. Nevertheless, it might decrease the probability of conspecific encounters (Gerhardt and Klump 1988) and may lead to reduced conspecific mating frequencies.

Acoustically communicating species are the best studied organisms with respect to signal jamming (45 cases) (Table 1). It has frequently been shown that noise produced by heterospecifics can represent a serious problem for intraspecific communication (Cody and Brown 1969; Wollerman 1999; Amézquita et al. 2006; Marshall et al. 2006). In noisy environments, the detection, identification, and localization of conspecific signals may be difficult, and animals can be forced to change the signal or switch communication channels (Lindquist and Hetherington 1996; Amézquita and Hödl 2004). Calls of species may be so similar that they either blanket the perception of conspecific songs ("auditory masking") (Marshall et al. 2006) or cause individuals to mistake heterospecifics for mates. In addition, a complex acoustic environment may also complicate the identification of high-quality mates

(Gerhardt and Klump 1988; Wollerman 1999; Wollerman and Wiley 2002). While the most obvious problem for acoustically interfering species is a reduced ability to recognize or locate mates (Bailey and Morris 1986; Schwartz and Gerhardt 1989; Wollerman 1999; Wollerman and Wiley 2002; Amézquita et al. 2006; Marshall et al. 2006), it might also influence male singing behavior (Weih 1951; Broughton 1965; Cody and Brown 1969; McHugh 1972; Ficken et al. 1974; Schwartz and Wells 1984). In some cases, male song production is even inhibited (Fulton 1934; Broughton 1965; Littlejohn and Martin 1969; McHugh 1972; Schwartz and Wells 1983).

Among taxa utilizing chemical signals, signal jamming has been reported particularly often among Lepidoptera, which may overlap in female sex pheromone components (Landolt and Heath 1987). Although pheromones usually consist of specific multicomponent blends that contain elements that are attractive to conspecifics and antagonistic to heterospecifics (Landolt and Heath 1987), males of some species also react to heterospecific females (Stadelbacher et al. 1983; Mazor and Dunkelblum 1992; Linn and Roelofs 1995). The stability of a parapatric suture zone of the Australian reptile ticks *Aponomma hydrosauri* and *Amblyomma albolimbatum* (Acari: Ixodidae) is thought to be mainly caused by such chemical signal jamming (Andrews et al. 1982). In addition to airborne pheromones, chemical communication plays an important role in aquatic environments. In many piscine species, males are attracted to chemical cues from ovulated females, and the temporal effort in conspecific courtship could decrease in the presence of heterospecifics (McLennan 2004).

Although visual communication systems are common in many animal taxa (Ptacek 2000; Rosenthal and Ryan 2000), there seem to be no documented cases in which the perception of visual signals is jammed by heterospecific signals. Nevertheless, visual signals can be modified or degraded by environmental factors due to refraction or reflection of light (Bradbury and Ve-

hrencamp 1998), as has been shown in cichlid fishes of Lake Victoria (Seehausen et al. 1997). Female sticklebacks (*Gasterosteus aculeatus*) are known to be attracted by red colored objects (ter Pelkwijk and Tinbergen 1937), and male *Anolis* lizards speed up their visual displays in response to movements of windblown vegetation (Ord et al. 2007). These studies suggest that visual signal jamming by heterospecifics is possible in principle. Similar mechanisms might be found in organisms using bioluminescence (Lloyd 1983).

#### HETEROSPECIFIC RIVALRY

Heterospecific rivalry is a special case of reproductive interference, as it involves male-male interactions and not male-female mating behavior. Moreover, it is often difficult to distinguish from other interspecific interactions. For example, many authors interpret male pursuit of heterospecifics as behavior reflecting interspecific resource competition (e.g., Maier and Waldbauer 1979; Severinghaus et al. 1981; Bolger and Case 1992; Jones et al. 1998) or predator defense (e.g., Leiser 2001). However, it has been argued that if the pursued heterospecifics resemble conspecifics (Dreisig 1995; Jones et al. 1998; Schultz and Switzer 2001), males are more likely to mistake these as conspecific rivals for mates than to compete with them for the same resource (Schultz and Switzer 2001). In a strict sense, interspecific rivalry can only be assigned to reproductive interference if heterospecifics are mistaken as conspecific competitors for mates. Yet, in many cases, even signals involved in rivalry between conspecifics might serve both functions: territoriality and mate attraction (Bradbury and Vehrencamp 1998). As many species use their territories for both mating and foraging, reproductive interference and resource competition may often be difficult to disentangle (Severinghaus et al. 1981).

Heterospecific rivalry due to mistaken identity has been reported from many territorial insect taxa, such as dragonflies (Singer 1990; Schultz and Switzer 2001), butterflies (Tinbergen et al. 1942; Bitzer

and Shaw 1979; Ravenscroft 1994; Dreisig 1995; Jones et al. 1998), and bees (Severinghaus et al. 1981), but it also occurs among nonterritorial grasshoppers (Hochkirch et al. forthcoming). Heterospecific rivalry can involve substantial costs, given that time, energy, and nutrients are wasted (Singer 1990). Males of many territorial insect species use a "perch-and-pursue" mating strategy (Dreisig 1995). They occupy and defend specific mating sites and will chase conspecific males, heterospecific insects, noninsect taxa, or even inanimate objects out of their mating territories (Fitzpatrick and Wellington 1983; Jones et al. 1998). A particularly good example of heterospecific rivalry is found in males of the amberwing *Perithemis tenera* (Odonata: Libellulidae), which ignore intruding heterospecific dragonflies but chase horse flies (*Tabanus* spp., Diptera: Tabanidae) and butterflies (*Ancyloxypha numitor*, Lepidoptera: Hesperidae), which are most similar to conspecifics in appearance (Schultz and Switzer 2001). In this case, alternatives to mistaken identity can be rejected, since horseflies and butterflies are neither prey nor predators of amberwings, do not compete for resources, and never disturb matings (Schultz and Switzer 2001).

#### MISDIRECTED COURTSHIP

Males of many species engage in indiscriminate courtship that is occasionally directed towards heterospecifics (Arnqvist and Rowe 2005). In species pairs with a high overlap in mate recognition traits, males may fail to recognize conspecific females and may prefer heterospecific females or even males. Misdirected courtship has been documented in many taxa (e.g., Mazor and Dunkelblum 1992; Verrell 1994; Ptacek 1998; Reitz and Trumble 2002; Scott et al. 2005, Hochkirch et al. 2006). Heterospecifics that resemble high-quality conspecifics may be perceived as especially attractive mates (Pfennig 1998). This might be particularly true if heterospecific females are larger than conspecific females, as a large female body size often indicates high fecundity (Luddem et al. 2004). Males of the invasive gecko *Hemidactylus frenatus* (Squamata:



Gekkonidae) were observed to preferably court the larger females of *Hemidactylus garnotii*, which is native to the Pacific Islands (Dame and Petren 2006). A preference for heterospecific females due to their larger body size has also been suggested to cause heterospecific courtship in groundhoppers (Hochkirch et al. 2006). In mate-choice experiments, *Tetrix ceperoi* males preferably courted the larger heterospecific *Tetrix subulata* females (Orthoptera: Tetrigidae) but were rejected (Hochkirch et al. 2007).

#### HETEROSPECIFIC MATING ATTEMPTS

In many animal species, males will attempt to copulate even if females do not display any signals that might solicit matings (Arnqvist and Rowe 2005). Interspecific mating attempts can follow interspecific courtship or can occur without any preceding courtship (Belovsky et al. 1996). Numerous examples of heterospecific mating attempts without sperm transfer exist, some of which overlap with cases of heterospecific courtship. In contrast to misdirected courtship, however, heterospecific mating attempts involve costs for both sexes, as females expend energy repelling males. Males of the groundhopper species *Tetrix ceperoi* and *Tetrix subulata* both frequently mount heterospecific females, males, and even flies, but, in most cases, they are repelled by the larger females. Nevertheless, as demonstrated in a field experiment, the reproductive success of *Tetrix ceperoi* decreased substantially in mixed enclosures (Hochkirch et al. 2007). The costs associated with mating attempts might be particularly high if harassment (aggressive mating behavior) is involved. This phenomenon has been termed "pseudocompetition" by McLain and Shure (1987), thus indicating the similar consequences of reproductive interference and competition. The seed bug *Neacoryphus bicrucis* (Heteroptera: Lygaeidae) limits the access to and colonization of *Senecio smallii* by five polyphagous insect species. These smaller species abandon their host plant as a result of the aggressive mating attempts of *Neacoryphus bicrucis*. It should be noted that, in this case, displacement does not result from resource com-

petition or defense (McLain and Shure 1987). On the other hand, female *Neacoryphus bicrucis* can also be harmed by heterospecific sexual harassment of another bug, *Margus obscurator* (Heteroptera: Coreidae). Both species co-occur on *Senecio tomentosum*, and males occasionally misdirect their aggressive mating behavior, inducing retreat of heterospecific females (McLain and Pratt 1999). A particularly well-known example of interspecific sexual harassment involves anuran amplexus behavior (Brodie 1968; Licht 1969; Brown 1977; Ross et al. 1994). In "explosive-breeding" anuran species with short breeding seasons and intense competition for mates, selection for female guarding may lead males to vigorously clasp any object, including heterospecifics, dead females, salamanders, floating debris, or the hands of observers (Pearl et al. 2005). It has been suggested that the endangered frog *Rana latastei* is threatened by the heterospecific amplexus behavior of the more widespread *Rana dalmatina* (Hettiey and Pearman 2003).

#### ERRONEOUS FEMALE CHOICE

In many species, female choice is known to be a more important determinant of pair formation than male discrimination (Andersson 1994). If males are indiscriminate, the extent and consequences of reproductive interference depend on the female's ability to recognize and reject inappropriate males. Depending on the temporal course of the female's influence, male courtship may be terminated prematurely, or copulation attempts may be inhibited or end without success (Wong and Candolin 2005). Despite their higher reproductive investment, females can also fail to correctly recognize conspecific males. Some female crickets seem to be insensitive to interspecific song differences (Doherty and Howard 1996; Gregory et al. 1998; Gray 2005). Attraction to heterospecific pheromones and misdirected courtship has also been documented in females in species with female courtship, such as *Ips* bark beetles (Coleoptera: Scolytidae) (Lewis and Cane 1992). Similar to male mate preferences,

erroneous female choice might be influenced by an ancestral sensory bias, as we will discuss in the following sections (Ryan 1998). In general, females become less choosy with decreasing availability of conspecific males and with increasing need for fertilization (Wirtz 1999).

#### HETEROSPECIFIC MATING

Reproductive interactions between species may culminate in interspecific matings with or without hybrid formation. If postmating barriers are complete, heterospecific matings may involve substantial costs, as time, energy, and nutrients are wasted (Servedio and Noor 2003). It should be noted that postmating isolation is a gradual process that can act at any time after sperm transfer and that may include sperm competition, lack of fertilization, aborted development, and reduced viability of hybrids (Howard 1999; Hill and L'Hernault 2001; Price et al. 2001). Conspecific sperm precedence is the most widely examined type of cryptic isolation and has been documented in several taxa (Howard 1999; Dixon et al. 2003). However, in many cases of heterospecific matings, information on hybrid offspring is simply missing. It remains unknown at which stage barriers act and whether a small proportion of hybrids are viable but have not yet been discovered. Compared to hybridization, heterospecific matings without hybrid formation have received relatively little attention. A well-studied example, however, of the ecological consequences of heterospecific matings without hybrid formation is that of the spider mites *Panonychus mori* and *Panonychus citri* (Acari: Tetranychidae). Interspecific matings of these species were observed in the laboratory as well as under field conditions (Takafuji 1988; Fujimoto et al. 1996; Takafuji et al. 1997). Males of *Panonychus citri* copulate with heterospecific females almost equally as often as with conspecifics, but, in cross-matings with *Panonychus mori* females, only a small proportion of eggs are fertilized and all die during embryonic development (Takafuji et al. 1997). Heterospecific matings in these species also severely affect subsequent conspecific mating success of fe-

males, as they produce no female offspring afterward (Fujimoto et al. 1996; Takafuji et al. 1997). Although reproductive interference implies the presence of sexual reproduction, interspecific matings may also affect species with asexual reproduction. Interspecific matings between sexual *Hemidactylus frenatus* and parthenogenetic *Hemidactylus garnotii* seem to disrupt parthenogenetic reproduction, although no hybrids are produced (Dame and Petren 2006).

#### HYBRIDIZATION

Hybridization between taxa with incomplete reproductive isolation is the most obvious and most frequently studied type of reproductive interference. As this phenomenon has often been discussed in the context of breeding programs (outbreeding), biological invasions, and evolution of premating barriers (e.g., Rhymer and Simberloff 1996; Dowling and Secor 1997; Noor 1999; Wirtz 1999; Servedio and Noor 2003; Bell and Travis 2005; Mallet 2005), this review focuses mainly on heterospecific matings without production of viable hybrids. The transition from partial to complete isolation is a gradual process (Coyne and Orr 2004). In many hybridizing species pairs, it has been shown that one cross is inviable (Wirtz 1999) or that the sexes differ in fertility or viability ("Haldane's rule") (Orr 1997). Although there are some examples in which the hybrids are fitter than their parents (e.g., Arnold and Hodges 1995; Fitzpatrick and Shaffer 2007; Pfennig 2007), it is generally assumed that hybridization represents a fitness loss compared to conspecific matings (Coyne and Orr 2004). However, the costs of heterospecific matings without hybrid formation should be even higher, since, in hybridization, at least genes are transferred to the next generation. The costs of hybridization do not only depend on hybrid fitness but also on the reproductive system. Species with a high parental investment, such as many mammal species, might suffer high costs for hybridization (Pierotti and Annett 1993).

## COSTS OF REPRODUCTIVE INTERFERENCE

Reproductive interference may affect all aspects of breeding performance (e.g., mate finding, territoriality, frequency of conspecific courtship and mating, fecundity of females, fertility of eggs) and should, thus, influence the fitness of the individuals involved (Ficetola and De Bernardi 2005). However, the significance of fitness loss due to reproductive interference has been disputed (e.g., Ravenscroft 1994), since the costs may be extremely variable. The fitness loss may depend on the type of reproductive interference, on the frequency of interactions, and, particularly, on the life history parameters of the species involved. Moreover, the costs of reproductive interference are usually not only species-specific, but also sex-specific (Watson et al. 1998). At least superficially, direct types of reproductive interference, such as heterospecific matings and hybridization, may seem to be associated with the highest costs, given that they involve gamete wastage (Bull and Burzacott 1994; Liou and Price 1994; Rhymer and Simberloff 1996). Nevertheless, fitness loss is not necessarily strongly related to the type of interaction, and it has been shown that costs can also be high for sexually incompatible species (Verrell 1990; Hochkirch et al. 2007). Unfortunately, only few studies (37 species pairs) quantify fitness loss in terms of reduced mating frequencies or reproductive success. More studies are needed that measure the effects of reproductive interference on lifetime reproductive success, which is suggested to be the best fitness estimate available (Newton 1989).

## TYPE-SPECIFIC COSTS

Even the most indirect type of reproductive interference—signal jamming—can involve high fitness costs (McHugh 1972). Theoretically, it can be even more costly than hybridization, if the heterospecific signal completely swamps the signals of conspecifics and, thus, inhibits conspecific matings. Signal jamming can hamper mate acquisition and reduce conspecific mating frequencies (Ardeh et al. 2004). Laboratory experiments with salamanders (Cau-

data: Plethodontidae) have shown that the conspecific mating frequency of *Desmognathus ochrophaeus* is depressed in the presence of *Desmognathus fuscus* due to interference of olfactory signals (Verrell 1994). Heterospecific rivalry, on the other hand, is usually believed to cause only low fitness costs (Ravenscroft 1994; Schultz and Switzer 2001), although some authors argue that heterospecific pursuits are indeed quite costly, as they require energy and may increase the risk of injury and predation (e.g., Singer 1990). In addition, loss of territory and mating opportunities may occur (Bitzer and Shaw 1979; Singer 1990). However, the costs for both the pursuer and the chased individual have rarely been measured in terms of lifetime reproductive success.

Fitness loss is more obvious in species that misdirect their courtship or mating attempts, particularly if heterospecifics are more attractive than conspecifics. These errors are costly in terms of wasted time and energy at the expense of conspecific breeding performance (Wells and Taigen 1989; Collins and Margolies 1991; Ardeh et al. 2004). Andrews et al. (1982) showed that heterospecific courtship between two tick species resulted in reduced conspecific courtship activity in both species. Males of *Amblyomma albolimbatus* performed the typical guarding behavior, including physically blocking the genitalia of female *Aponomma hydrosauri*. This behavior impeded the access for conspecific males for at least twenty days. Mating attempts that involve interspecific sexual harassment are particularly detrimental. Struggling of females to escape courting males may heavily increase energy expenditure (Watson et al. 1998), reduce foraging opportunities (Rowe et al. 1996), limit access to preferred microhabitats (such as oviposition sites) (McLain and Pratt 1999), or enhance the risk of predation (Arnqvist and Rowe 2005). Moreover, sexual harassment may substantially reduce the fecundity of females (McLain and Pratt 1999).

Heterospecific matings and hybridization are often considered to be the types of

reproductive interference with the highest fitness losses (Verrell 1994), as they involve gamete wastage and can lead to sterile offspring or inviable eggs (Barton and Hewitt 1985; Bull and Burzacott 1994). In extreme cases, females are damaged or even killed by heterospecific matings due to morphological incompatibilities (Ribeiro and Spielman 1986; Sota and Kubota 1998). However, this phenomenon has only been reported in allopatric species, such as the avian parasite bugs of the genus *Hesperocimex* (Heteroptera: Cimicidae), when females of *Hesperocimex sonorensis* and *Hesperocimex coloradensis* are killed during copulation with males of *Hesperocimex cochimiensis* (Ryckman and Ueshima 1964).

#### SEX-SPECIFIC COSTS

Fitness costs of reproductive interference are likely to vary between the sexes (Pfennig 1998). Females often pay higher costs for heterospecific matings because of their higher reproductive investment (sometimes they mate only once), whereas frequent indiscriminate matings may actually maximize male fitness (Arnqvist and Rowe 2005). Mating with heterospecific males may increase sperm competition, hamper fertilization, or disrupt the development of zygotes, thus reducing female reproductive success ("satyr effect") (Ribeiro and Spielman 1986). *Trogoderma glabrum* beetles are effectively sterilized by heterospecific matings, since they never remate (Vick 1973). This is also assumed for *Aedes aegypti* (Diptera: Colicidae) females, which are seemingly rendered sterile by mating with males of the invasive *Aedes albopictus* (Nasci et al. 1989). However, in rare cases, females may benefit from heterospecific matings, if mating with a heterospecific male is a prerequisite for embryogenesis (Gumm and Gabor 2005) or if they receive a nuptial gift (Vahed 1998).

Males can also suffer reproductive costs, especially due to investment of time and energy into heterospecific courtship or into mating attempts that do not result in successful reproduction (Kandul et al. 2006). In species using volatile pheromones for male attraction, male fitness loss could be high as

a result of the high energetic costs of misdirected long-distance flights. In some insect species, males produce costly nutritive spermatophores ("nuptial gifts") (Vahed 1998), which are wasted in heterospecific matings. In extreme cases, interspecific matings can even be lethal for males, as has been shown in *Heliothis* moths (Lepidoptera: Noctuidae) (Stadelbacher et al. 1983). However, in some taxa (e.g., *Drosophila*, *Poecilia*), males are able to learn to avoid costly heterospecific interactions and refine their courtship behavior with experience (Dukas 2004; Magurran and Ramnarine 2004). Males of *Poecilia latipinna* even benefit from heterospecific matings, as they become more attractive to their conspecific females by mating with gynogenetic *Poecilia formosa* ("mate copying") (Schlupp et al. 1994; Schlupp and Ryan 1996).

#### ASYMMETRIES IN COSTS BETWEEN SPECIES

If the species in a given pair differ in their life history parameters, then the costs associated with reproductive interference are likely to be asymmetric, with one species suffering higher costs than the other (Fujimoto et al. 1996; Takafuji et al. 1997; Wirtz 1999; Deering and Scriber 2002; Marshall et al. 2006; Hochkirch et al. 2007). This effect is further complicated by a possible asymmetry in the response of both sexes (Figure 1). Although fitness costs of heterospecific interactions could be symmetric in theory, our analysis suggests that this is rare in nature because it is extremely unlikely that both sexes of both species are indiscriminate to exactly the same degree (Wirtz 1999). Furthermore, each species in a given pair is likely to differ in several reproductive and ecological traits, such as reproductive periods and capacities, abundance and dispersion, ecological specialization, and response to environmental fluctuations. However, the literature we surveyed also revealed that cases of extreme asymmetry (unidirectional reproductive interference), in which the fitness of only one species is affected, are rare (13 cases). Most heterospecific interactions involve costs for both participants in terms of wasted time and energy (119 cases). Moreover, male investment in heterospecific



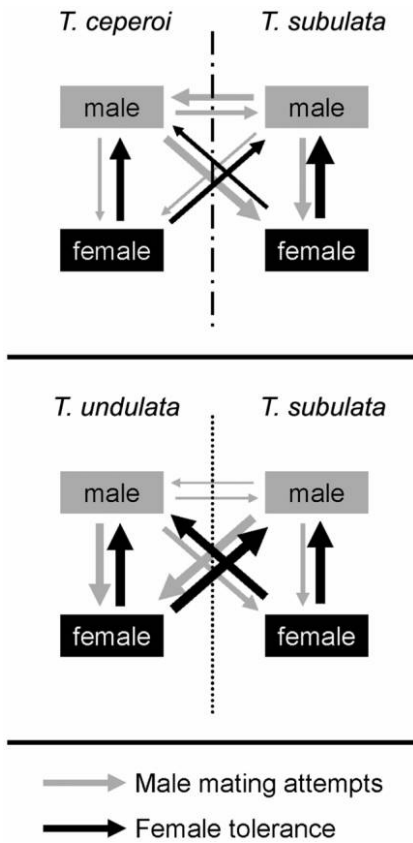


FIGURE 1. TWO TYPES OF ASYMMETRIC REPRODUCTIVE INTERFERENCE

Asymmetric mate preferences in groundhoppers of the genus *Tetrix* in laboratory experiments. Arrow depths are proportional to the percentage of mating attempts and female tolerance. In the first example, both males of *T. ceperoi* and *T. subulata* prefer to court females of *T. subulata*, whereas the females clearly prefer conspecifics. The mating success of *T. ceperoi* is substantially reduced due to its strong investment in heterospecific mating attempts, resulting in reduced reproduction (Hochkirch et al. 2007). In the case of *T. subulata* and *T. undulata*, females do not discriminate between con- and heterospecific males, possibly because both species use a similar courtship display (Hochkirch et al. 2006). Since *T. subulata* males prefer to court *T. undulata* females, interspecific matings occur (Hochkirch et al. forthcoming).

matings might decrease the fitness of that male, the fitness of heterospecific females, and the fitness of conspecific females (Ryckmann and Ueshima 1964; Hochkirch et al. 2007). Unidirectional reproductive

interference seems to occur mainly in signal jamming (11 cases), which lacks any direct interaction. Indeed, song production in the bush cricket *Metrioptera brachyptera* is inhibited by stridulating *Metrioptera roeselii*, whereas the latter species seems not to be adversely affected by the songs of *Metrioptera brachyptera* (McHugh 1972). Unidirectional effects have also been reported from hermaphrodite nematodes, where heterospecific matings may be reproductively neutral for the females (Hill and Hernault 2001), and from sexual parasitic fishes, in which females of a hybrid species even require heterospecific matings for successful reproduction (Gumm et al. 2006). We hypothesize, however, that, in most cases, the "superior" species is likely to have fitness costs as well, although these costs might only be detected sometimes at high heterospecific densities (Hochkirch et al. 2007). Asymmetries in the costs of reproductive interference are often caused by differences in the species recognition abilities of the species involved (Wirtz 1999). There is accumulating evidence that sensory biases may influence the directionality of reproductive interference (Ryan 1998). As stated earlier, a preference for heterospecific females due to their larger body size has been observed in birds (Ludde et al. 2004), frogs (Schmeller et al. 2005), and many insects (Bonduriansky 2001; Thornhill and Alcock 2001; Suzuki et al. 2005).

#### DENSITY DEPENDENCE

Similar to competition, the costs of reproductive interference can be strongly influenced by the relative abundance of each species (Ribeiro and Spielman 1986; Kuno 1992; Wirtz 1999; Hettyey and Pearman 2003). Even if two species would be similarly affected by reproductive interference, the species with a lower initial abundance will suffer the stronger fitness loss, comparable to negative heterosis (Foster et al. 1972). If the sexual relationship between two species is initially asymmetric, density is likely to modify the degree of asymmetry. This has been shown in the groundhoppers *Tetrix ceperoi* and *Tetrix subulata*. While *Tetrix subulata* is generally less affected in this sys-



tem, its reproductive success is also reduced at high densities (Hochkirch et al. 2007).

Density dependence in reproductive interference has been documented in a large number of studies (e.g., Hubbs 1955; McHugh 1972; Collins and Margolies 1991; Söderbäck 1994; Fujimoto et al. 1996; Takafuji et al. 1997; McLain and Pratt 1999; Westman et al. 2002; Hettyey and Pearman 2003; Pearl et al. 2005; Hochkirch et al. 2007). The relative abundance and sex ratio of each species, as well as their spatial and temporal activity, influence the frequency of heterospecific encounters and interactions (Verrell 1994; Gröning et al. 2007). Reproductive interference may become increasingly important with growing difference in the relative abundance of each species, as the rarer species will have difficulty finding conspecific mates and females may become less choosy (Hubbs 1955; Söderbäck 1994; Takafuji et al. 1997; Wirtz 1999; Gröning et al. 2007). This has been shown in the displacement process of the noble crayfish *Astacus astacus* by the invasive signal crayfish *Pacifastacus leniusculus* (Decapoda: Astacidae) in Fennoscandia (Söderbäck 1994). After the decline of the *Astacus astacus* populations in Fennoscandia, practically all individuals mated with the invasive *Pacifastacus leniusculus*, leading to an almost complete cessation of successful reproduction of the former species (Westman et al. 2002). Acoustic interference has also been shown to be density-dependent, since signal identification becomes more difficult with the increasing call overlap that results from a growing number of singing individuals (Marshall et al. 2006). In some cases, reproductive interference may only have significant effects at high population densities and/or when species cannot segregate spatially (e.g., song inhibition between *Metrioptera roeselii* and *Metrioptera bicolor*) (McHugh 1972).

#### ECOLOGICAL CONSEQUENCES OF REPRODUCTIVE INTERFERENCE

Evidence that reproductive interference affects species coexistence is still sparse. Some authors suggest that small-scale dispersion patterns are affected by reproductive interference (McLain and Shure 1987;

McLain and Pratt 1999). This might subsequently lead to geographical segregation, which has been proposed by Takafuji et al. (1997) for the spider mites *Panonychus mori* and *Panonychus citri*. Generally, gamete wastage in suture zones is believed to prevent dispersal and to lead to the maintenance of narrow parapatric boundaries (Barton and Hewitt 1985; Bull 1991). Furthermore, sexual exclusion has mainly been discussed in the context of invasive species. Inappropriate mate selection is thought to be the main determinant of displacement of native crayfish *Orconectes sanborni* (Decapoda: Astacidae) by invasive *Orconectes rusticus* in Ohio (Butler and Stein 1985) and of native *Aedes aegypti* by introduced *Aedes albopictus* (Nasci et al. 1989). In many cases, reproductive interference may act in combination with other factors, such as competition, predation, exploitation, or habitat loss (Söderbäck 1994; Westman et al. 2002; Pearl et al. 2005).

#### MECHANISMS OF COEXISTENCE

Even if reproductive interference adversely affects species coexistence, some diluting or segregating mechanisms can still allow species to coexist in sympatry (Figure 2). Habitat partitioning in time or space is a widespread mechanism of coexistence (Cody and Brown 1969; Singer 1990; Kuno 1992; Konuma and Chiba 2007) and has also been reported from sexually interacting species (Jackson and Tinsley 1998). Habitat segregation is often difficult to link to reproductive interference, since it might be caused by different fundamental niches and may be influenced by the evolutionary history of the species involved—a problem which has been referred to as the “ghost of competition past” (Connell 1980). Thus, niche partitioning could become genetically fixed in response to the selective pressure of reproductive interference (Singer 1990), but, in these cases, it may be difficult to determine whether reproductive interference was the ultimate reason for such niche partitioning.

Negative effects of reproductive interference can also be reduced by dilution ef-

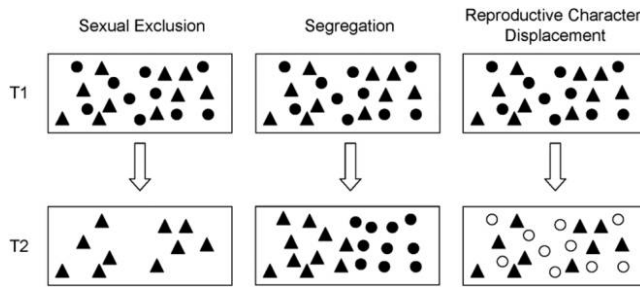


FIGURE 2. CONSEQUENCES OF REPRODUCTIVE INTERFERENCE

Three possible consequences of reproductive interference. Two species with overlapping signal channels (black circles and triangles) come in contact at three sites at time 1 (T1). Originally, reproductive interference is asymmetric with one species (the “inferior” species, represented by black circles) suffering higher costs than the other (the “superior” species, represented by black triangles). On the first site, sexual exclusion leads to extinction of the “inferior” species. On the second site, niche segregation (e.g., spatial, temporal, or habitat segregation) enables the species to coexist. On the third site, reproductive character displacement leads to a divergence of the species recognition systems. Consequently, the circle populations of sites two and three will be reproductively isolated at time 2 (T2).

fects from intraspecific aggregations (Ficetola and De Bernardi 2005) or local abundance (Westman et al. 2002; Hettyey and Pearman 2003). If the number of heterospecific encounters in the “inferior” species is low, either due to dominance or clumped occurrence, reproductive interference is less likely to play an important role in population dynamics (Verrell 1994). This has been shown in the groundhoppers *Tetrix ceperoi* and *Tetrix subulata*, which have a considerable niche overlap but differ in niche breadths. *Tetrix ceperoi* has a stronger preference for bare ground, leading to a clumped dispersion, whereas *Tetrix subulata* has a broader niche and is more evenly dispersed. Thus, *Tetrix ceperoi* dominates on small patches of bare ground and faces lower costs within these aggregations, while *Tetrix subulata* may escape from interference at places that are not suitable for *Tetrix ceperoi* (Gröning et al. 2007). Different life history strategies may be another means by which species can avoid the negative effects of reproductive interference. High reproductive capacities may compensate for costs of occasional heterospecific interactions. Moreover, high dispersal abilities might allow species to escape to unoccupied sites before sexual exclusion can occur. Hence, coexistence could be possible in a metapopulation context (Levins 1969). There is a strong need

for more studies on these potential mechanisms, which may enable sexually interacting species to coexist.

#### EVOLUTIONARY CONSEQUENCES OF REPRODUCTIVE INTERFERENCE

In some ways, the widespread occurrence of reproductive interference is surprising, as species are expected to evolve mechanisms to avoid such costly interactions (Paterson 1978). Hence, reproductive interference is believed to occur mainly between allopatric or invasive species, which lack long-term selective pressures leading to divergence of their species recognition systems (Coyne and Orr 1989). However, the literature that we surveyed revealed that reproductive interference also occurs in many species pairs that are sympatric in large parts of their geographic ranges (133 cases).

There are various reasons why pre-mating barriers between sympatric species may be incomplete. First, mate recognition systems may be subject to stabilizing selection, as their evolution requires changes in the signal quality as well as in the preference for this signal (Coyne and Orr 2004). Second, sympatric species might occur in different habitats—a pattern that has been termed “allotopy” (Rivas 1964). Metapopu-

lations of such species might co-occur in a mosaic pattern on a large spatial scale, although the coexistence of single populations could be hampered. Third, the aforementioned ecological mechanisms (such as density effects and segregation) might mitigate the costs of reproductive interference within single populations. These mechanisms could also have evolved to decrease the costs of reproductive interference.

Another consequence of reproductive interference might be the evolution of premating barriers (Figure 2). According to the reinforcement hypothesis (Dobzhansky 1937), selection against hybridization should favor the evolution of premating isolating mechanisms. Reinforcement is defined as the divergence of premating barriers "resulting from selection against hybrids" (Butlin 1989:159). It has been shown that this process becomes more likely with increasing postmating isolation (Spencer et al. 1986; Butlin 1989; Liou and Price 1994; Servedio and Noor 2003). In nonhybridizing species, the divergence of mate recognition systems is usually referred to as "reproductive character displacement" (Brown and Wilson 1956; Butlin 1989; Andersson 1994; Mullen and Andrés 2007). The role of reinforcement in speciation is still disputed (e.g., Spencer et al. 1986; Butlin 1989; Servedio and Noor 2003; Higgie and Blows 2007), given that extinction (sexual exclusion) seems to be a more likely outcome of reinforcement models (Paterson 1978; Liou and Price 1994; Turelli et al. 2001). Some authors argue that reinforcement is not suited to drive speciation because it requires the evolution of some degree of postmating isolation in allopatry before it can operate (Coyne and Orr 1989; Gray and Cade 2000). However, reinforcement and reproductive character displacement should not be regarded as sympatric speciation processes. Although reinforcement requires sympatry with another species, the speciation process mainly affects allopatric populations of the same species (Noor 1995). If allopatric populations of one species occur in different species assemblages throughout the geographic range, they might be exposed to dif-

ferent signaling environments, thus leading to reproductive character displacement.

Reproductive interference not only affects speciation but might also intensify the female's conflict between species and mate-quality recognition. This may be most likely when heterospecifics resemble high-quality mates or use similar signals (Pfennig 1998; Pfennig 2000). For example, female spadefoot toads (*Spea multiplicata*) are known to compromise on mate quality in areas of sympatry with *Spea bombifrons* in order to ensure conspecific matings. In allopatry, where heterospecific matings are unlikely, females of *S. multiplicata* increase reproductive success by mating with high-quality males. This trade-off between species and mate-quality recognition is most likely to occur in species whose ranges have overlapped recently and who have not yet evolved reliable species recognition systems (Pfennig 2000). Given that the benefits of mate-quality recognition can be substantial, selection may favor females that are able to assess both mate quality and species identity simultaneously or males that produce distinct species-specific signals (Pfennig 1998).

Learning behavior is another evolutionary response by which organisms may decrease the costs from reproductive interference (Dukas 2004; Magurran and Ramnarine 2004). However, Dukas et al. (2006) have recently shown that male insects only benefit from learning to discriminate heterospecific females if the encounter rate with receptive females is high, the courtship displays are of long duration, and the subsequent mating success is high. Under most circumstances, evolutionary fixed discrimination abilities seem to be as beneficial as learning.

#### THE IMPORTANCE OF COMBINED LABORATORY AND FIELD STUDIES

Our analysis (Table 1) shows that there is a strong bias towards laboratory experiments (103 cases), compared to field experiments (25 cases) and field observations (53 cases). There are only a few systems in which reproductive interference has been studied in the laboratory as well as in the field (13 cases). This might be influenced

by a publication bias towards experimental studies. Moreover, extensive observations are required to detect reproductive interference in nature and quantify its costs. The significance of reproductive interference might often be underestimated, since in many cases interspecific interactions are rare events but can have dramatic effects when they do occur (Goldberg and Lande 2006). There are only a few cases in which results from laboratory experiments on reproductive interference were confirmed in the field. Males of the guppy species *Poecilia reticulata* and *Poecilia picta* (Cyprinodontiformes: Poeciliidae) are known to mate with heterospecific females under both laboratory and field conditions (Russel et al. 2006), and Takafuji et al. (1997) were able to confirm asymmetric reproductive interference of the spider mites *Panonychus mori* and *Panonychus citri* in the field and in the laboratory. In addition, song inhibition between bush cricket species has been observed in song experiments as well as under natural conditions (McHugh 1972).

#### CONFLICTING RESULTS OF FIELD AND LABORATORY DATA

Studies that involve complex ecological, social, or behavioral interactions between individuals or species often reveal poor concordance between laboratory and field experiments (Bezemer and Mills 2003). Such conflicting results have also been reported in studies on reproductive interference. In an outdoor experiment, Bull and Burzacott (1994) were not able to confirm the hypothesis that reproductive interference prevents the coexistence of two Australian reptile tick species (Andrews et al. 1982). Fice-tola and De Bernardi (2005) argue that it is unlikely that interference with *Rana dalmatina* affects the reproductive success of *Rana latastei* under natural conditions, although this has been shown in experimental cages (Hettzey and Pearman 2003). Also, males of some noctuid moth species respond to heterospecific pheromone components in a flight tunnel, but do not exhibit any interspecific

cross-attraction in the field (Mazor and Dunkelblum 1992). Conflicting results from laboratory and field experiments do not necessarily imply that reproductive interference has no significance in the field. Under natural conditions, several ecological mechanisms (as discussed earlier) might influence interactions between species and produce different results (Marshall and Jain 1969; Verrell 1994; Dame and Petren 2006).

#### LIMITATIONS OF LABORATORY EXPERIMENTS

There is little doubt that laboratory experiments offer an opportunity to study mechanisms under controlled conditions without confounding environmental variables (Magellan and Magurran 2006). Nevertheless, they also have some limitations compared to more complex situations in the field (Zhang et al. 2004). Interspecific mating frequencies may depend on whether potential mating partners are presented simultaneously (choice tests) or sequentially (single stimulus tests). Male *Desmognathus fuscus* salamanders are attracted to heterospecific females in nonchoice tests, whereas they prefer conspecific females when they can compare them simultaneously (Verrell 1990). Moreover, limited space in experimental arenas may increase the rate of interactions between species (Gröning et al. 2007). In large enclosures, individuals may have the opportunity to avoid heterospecific encounters, but, in small arenas, they may be forced to come in close contact (Verrell 1990). Therefore, a higher frequency of interspecific matings may be an experimental artifact due to artificially high densities (Söderbäck 1994, Wirtz 1999). Such density effects of mate choice should be addressed in future experimental studies. Another problem is that habitat-specific factors cannot easily be duplicated in a laboratory setting or even in field enclosures, although they may be of crucial importance for mate finding (e.g., Feder et al. 1994). Hence, results and predictions from experiments are sometimes difficult to transfer to field situations. This illus-



trates that, in addition to experiments, observations in free-ranging populations are essential to understanding the real significance of reproductive interference in nature (Verrell 1994; Deering and Scriber 2002; Scott et al. 2005).

#### PRACTICAL APPLICATIONS

Sexual exclusion is an important issue for the management of endangered species (Hettyey and Pearman 2003; Ficetola and De Bernardi 2005), especially with respect to invasive species. Reproductive interference with the exotic bullfrog *Rana catesbeiana* may play a role in the decline of many native frog species (Storm 1952; Lind et al. 2003; Pearl et al. 2005). Similarly, reproductive interference may also be involved in the displacement of native crayfish *Orconectes sanborni* by invasive *Orconectes rusticus* in Ohio (Butler and Stein 1985). The replacement of *Astacus astacus* in Swedish and Finnish lakes by *Pacifastacus leniusculus* has been attributed to the combined effects of harvest, competition, predation, and reproductive interference (Söderbäck 1994; Westman et al. 2002). The potential effects of reproductive interference also need to be considered in reintroduction programs. In a Lake Ontario tributary, the establishment of reintroduced Atlantic salmon seems to be hampered by courtship of exotic salmonids that may lead to reduced reproductive success of *Salmo salar* (Scott et al. 2005). On the other hand, we assume that reproductive interference might also impede the colonization of invasive species if a region is already occupied by closely related species. Indeed, it has been shown that invaders who are distantly related to the occupants phylogenetically are more successful colonizers than closely related species ("naturalization hypothesis") (Darwin 1859; Strauss et al. 2006).

In addition to the introduction of foreign species, anthropogenic alterations of the environment might increase the frequency of interspecific reproductive encounters and interactions. Samways (1977) reports that acoustic signal jamming between the bush crickets *Platycleis intermedia* and *Platycleis affinis* in southern France is

naturally prevented by their different habitat requirements. Due to anthropogenic habitat modification, interspecific acoustic interactions are more likely to occur. Similarly, Fisher et al. (2006) demonstrate that anthropogenic alteration of the chemical environment disrupts species recognition in swordtail fish (*Xiphophorus*). Many conservation projects focus on improving habitat connectivity, although such activities might also bring sexually interacting species into contact. Furthermore, recent climate change has caused range extensions of many species (Parmesan and Yohe 2003), raising the possibility of sexual interactions between species that are not presently sympatric.

Although the hypothesis of sexual exclusion still needs to be tested experimentally, it has been suggested that reproductive interference might also offer opportunities for pest control (Ribeiro 1988; Ardeh et al. 2004). Some authors have proposed that local extinction of a species is even more likely to result from reproductive interference than from competition (e.g., Kuno 1992), and competitive exclusion has been successfully applied in biological control of exotic Homoptera (Reitz and Trumble 2002). Brower (1977) argues that, in some moths of the family Pyralidae, attempts to use reproductive interference for pest control will fail, since these species do not produce any hybrid offspring. However, as outlined earlier, sexual exclusion seems even more likely in the absence of hybridization (Liou and Price 1994). On the other hand, reproductive interference can also impose problems for pest control. For example, *Eretmoceris mundus* (Hymenoptera: Aphelinidae) is an important biological control agent for *Bemisia tabaci* (Homoptera: Aleyrodidae). Ardeh et al. (2004) argue that reproductive interference with *Eretmoceris eremicus* might reduce the ability of *Eretmoceris mundus* to control the pest.

#### CONCLUSIONS AND FUTURE DIRECTIONS

There is accumulating evidence that reproductive interference occurs in a wide range of animal taxa and may act at any stage in the course of mate acquisi-



tion. Although it is often associated with fitness loss, future studies should measure these costs in terms of lifetime reproductive success in order to accurately evaluate their evolutionary significance. Sexual interactions might hamper the coexistence of species utilizing similar signal channels, but, despite this, studies on the ecological consequences of reproductive interference are still sparse. In many cases, displacement, spatial segregation, or niche partitioning might be caused by reproductive interference rather than by resource competition. This issue becomes particularly relevant in light of biological invasions or range expansions driven by climate change, which will probably increase the contact of formerly separated taxa (Olden 2006). Reproductive interference may not only be important in the context of invasive species, but also for species that are currently shifting their ranges because of climate change.

Sexual interactions between species have so far mainly been studied in laboratory experiments. In order to assess the ecological significance of reproductive interference, future studies should focus on the validation of laboratory results under natural conditions. Furthermore, there is a strong need for investigations into mechanisms that reduce costly interspecific sexual interactions in the field. Ecological mechanisms of coexistence might include temporal, spatial, or habitat segregation, dilution effects from intraspecific aggregations or local abundance, and different colonization abilities or population growth rates. As is the case for competition, it will be difficult to distinguish currently acting mechanisms from evolutionary responses

to former selective pressures associated with reproductive interference.

In some taxa (e.g., mammals, reptiles, bugs, cicadas, and many noninsect invertebrate taxa), information on reproductive interference is sparse or completely missing. Since virtually all animal taxa utilize signals for locating mates, reproductive interference may be more widespread than is presently recorded. It may also be found in other types of communication, such as vibrational, visual, and electrical signals. Until now, the majority of studies (72% of those examined) considered congeneric species, although all types of reproductive interference have also been documented between species in different genera. Most of these cases involve acoustic signal jamming (33%) and heterospecific rivalry (20%). More information on the ecological significance of reproductive interference between distantly related taxa is needed (e.g., noisy frog species affecting acoustically communicating insects). Moreover, most studies on its evolutionary and ecological consequences focus on species pairs with narrow zones of sympatry. The ecological and evolutionary potential of reproductive interference in species with broadly overlapping geographic ranges is little studied and should receive more attention.

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