

# Reproductive interference between *Rana dalmatina* and *Rana temporaria* affects reproductive success in natural populations

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**Abstract** Experimental evidence suggests that reproductive interference between heterospecifics can seriously affect individual fitness; support from field studies for such an effect has, however, remained scarce. We studied reproductive interference in 25 natural breeding ponds in an area where two ranid frogs, *Rana dalmatina* and *Rana temporaria*, co-occur. The breeding seasons of the two species usually overlap and males of both species are often found in amplexus with heterospecific females, even though matings between heterospecifics produce no viable offspring. We estimated species abundance ratios based on the number of clutches laid and evaluated fertilization success. In ponds with low spatial complexity and a species abundance ratio biased towards *R. temporaria*, the average fertilization success of *R. dalmatina* eggs decreased, while this relationship was not detectable in spatially more complex ponds. Fertilization success of *R. temporaria* did not decrease with

increasing relative numbers of heterospecifics. This asymmetry in fitness effects of reproductive interference may be attributed to *R. temporaria* males being more competitive in scramble competition for females than *R. dalmatina* males. Our study is among the first to demonstrate that in natural breeding populations of vertebrates interference among heterospecifics has the potential to substantially lower reproductive success at the population level, which may in turn affect population dynamics.

**Keywords** Anura · Fertilization success · Scramble competition · Sexual coercion · Population dynamics

## Introduction

Reproductive interference, i.e. when interspecific interactions during mate acquisition adversely affect fitness, occurs in a wide variety of taxa in the animal kingdom

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(Gröning and Hochkirch 2008). The mechanisms involved in reproductive interference are similar to those of resource competition (McLain and Shure 1987; Hochkirch et al. 2007; Kishi et al. 2009) and can have varied consequences, including character displacement, niche segregation, lowered reproductive success, and costs associated with mortality, energy and time (for reviews see Servedio and Noor 2003; Gröning and Hochkirch 2008). Consequently, reproductive interference can impact community composition, contribute to speciation, and affect the persistence of populations and species (Kuno 1992; Liou and Price 1994; Rhymer and Simberloff 1996; Coyne and Orr 2004). Most studies of interspecific effects on mating and reproduction have been carried out in the laboratory, and the effects of reproductive interference under natural conditions have remained largely unaddressed (Gröning and Hochkirch 2008).

The cause of reproductive interference is often imperfect species recognition (Gröning and Hochkirch 2008), while effective mate choice reduces interference and contributes to stable species coexistence (Hellriegel and Reyer 2000; Som et al. 2000). In systems where sexual coercion by indiscriminate heterospecific males is pervasive and overruns female mating preferences, pre-mating reproductive isolation may break down and individuals may pay substantial costs (Trivers 1972; Arnqvist and Rowe 2005). Intense intrasexual competition and strongly male-biased operational sex ratios may nonetheless maintain coerciveness and indiscriminateness of males (Johnstone et al. 1996; Kvarnemo and Simmons 1998; Candolin and Salesto 2009). However, the circumstances under which coerciveness and indiscriminateness of males lower reproductive success have rarely been evaluated in natural populations (Gröning and Hochkirch 2008).

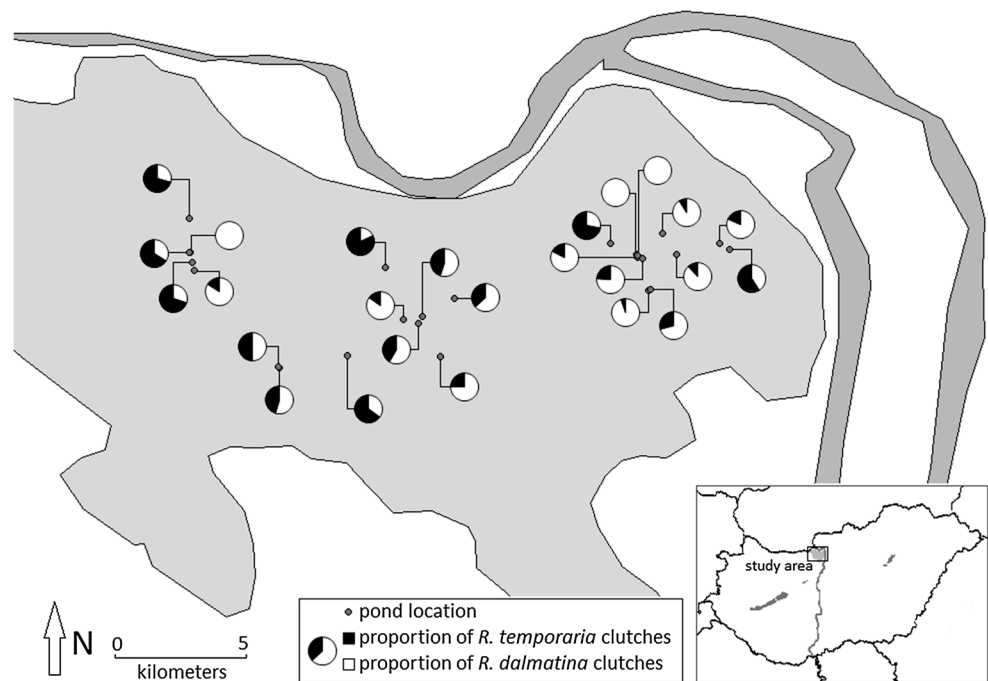
Anuran amphibians provide ideal model systems for studying the causes and consequences of reproductive interference. In many anurans, operational sex ratios are strongly male biased throughout the reproductive season and males use sexual coercion to obtain matings (Wells 1977). As the reproductive activity of different species often overlaps both temporally and spatially and males appear indiscriminate, matings between heterospecifics can readily be observed (Arak 1983; Reading 1984; Gergus et al. 1999; Engeler and Reyer 2001; Hettyey and Pearman 2003). Anuran males can pay costs of misdirected matings in terms of energy (McLister 2003; Lengagne et al. 2007), sperm (Gibbons and McCarthy 1986; Hettyey et al. 2009b, 2012) and lost mating opportunities (Höglund 1989; Hettyey et al. 2009a). When mating with heterospecific males, females may lose an entire year's reproductive investment (Abt and Reyer 1993; Hettyey et al. 2009a), which may lead to the evolution of female discrimination against heterospecific males (Lamb and Avise 1986; Engeler and

Reyer 2001) and, in cases where coercion overrules female choice, to the appearance of behaviours ameliorating costs of interspecific mating (D'Orgeix 1996; Reyer et al. 1999; Hettyey et al. 2009a).

In an experimental study on reproductive interference between *Rana dalmatina* and *Rana latastei*, Hettyey and Pearman (2003) report that when heterospecific males dominate numerically, pre-mating reproductive isolation breaks down; frequency of matings between heterospecifics drastically increases, and the number of viable embryos drops precipitously. They conclude that when species abundance ratios are strongly biased, reproductive interference has the potential to affect population dynamics of the less abundant species. In contrast, Ficetola and De Bernardi (2005) assessed reproductive success of *R. latastei* in natural populations, but did not report effects of reproductive interference on reproductive success. They suggest that under natural conditions, mate recognition may be more effective and niche segregation may be possible thanks to the larger area and greater spatial complexity in natural than in experimental settings, weakening reproductive interference and its effects (also see Verrel 1990; Michalak and Rafinski 1999). As Ficetola and De Bernardi (2005) also point out, experimental conditions may be overly stressful, simplistic or unrealistic and lead to spurious results (Verrel 1990; Skelly 2002; Bezemer and Mills 2003; Joron and Brakefield 2003), suggesting that predictions arising from experimental studies have to be tested under natural conditions in order to validate the relevance of their results. However, limited sample size and statistical power (Hettyey and Pearman 2006) suggest that a statistically adequate test of the predictions of Hettyey and Pearman (2003) under natural conditions remains to be done.

In the present study, we investigate whether reproductive interference between two ranids, *Rana dalmatina* and *Rana temporaria*, affects reproductive success in natural populations. As in the *R. dalmatina*–*R. latastei* system, males of *R. dalmatina* and *R. temporaria* readily amplex heterospecific females and remain in prolonged amplexus even though viable offspring are not produced (Hettyey et al. 2009a), consistent with previous reports of indiscriminate amplexus by ranid males (Reading 1984; Engeler and Reyer 2001; Hettyey and Pearman 2003; Hettyey et al. 2005). We examine whether fertilization success in egg clutches of *R. dalmatina* and *R. temporaria* is related to species abundance ratios in ponds where the two species co-occur. We predict that average fertilization success correlates positively with species relative abundance and is low in ponds where the species is substantially outnumbered by heterospecifics. We also predict that the effects of reproductive interference should be asymmetric, with *R. temporaria* suffering lower costs, because: (1) females of this species may be

**Fig. 1** Location of the breeding ponds studied. *Circles* indicate pond locations, *pie charts* depict species abundance ratios, *light grey area* shows the Pilis-Visegrádi Mountains, *darker grey ribbon* represents the River Danube. *Inset* Location of the study area within Hungary



more successful in resisting mating attempts by heterospecific males than the smaller *R. dalmatina* females, and (2) because *R. temporaria* males are larger and more able to displace amplexing heterospecific males than *R. dalmatina* males (B. Vági et al., unpublished data). We also investigate whether lower spatial complexity of ponds or higher population density lead to more pronounced effects of reproductive interference (Ficetola and De Bernardi 2005; Gröning et al. 2007).

## Materials and methods

### Study species

*Rana dalmatina* (Rd) and *R. temporaria* (Rt) are two closely related species with a largely overlapping European distribution. Both are explosive breeders (sensu Wells 1977), exhibiting short and intensive breeding periods. The reproductive periods of these species largely overlap in our study area (Hettzey et al. 2003). Female Rd normally lay about 800 eggs attached to branches, stones or aquatic vegetation, whereas Rt females deposit ca. 2,000 eggs on the bottom of ponds and lakes. At low densities, Rd males call from territories while Rt males form dense choruses, while at high densities scramble competition dominates in both species (Elmberg 1986; Ryser 1989; Lesbarrères and Lodé 2002; Lodé et al. 2005). Multiple male matings, sperm competition and multiple paternity have been documented for both species (Laurila and Seppä 1998; Lodé and Lesbarrères 2004; Vieites et al. 2004).

### Data collection

Our study area was located in the Pilis-Visegrádi Mountains (Hungary), a hilly woodland about 30 km to the north of Budapest (47°43'N, 19°00'E). Based on a previous study, we selected 25 breeding ponds where Rt and Rd are present (Vági et al. 2013) and where species abundance ratios were known to vary widely (B. Vági and T. Kovács, unpublished data) (Fig. 1). To be able to evaluate whether biotic and abiotic factors may affect interspecific interactions, we measured the size and spatial complexity of each pond at the onset of the breeding season. We selected these measures because we could propose clear predictions regarding their effect on the strength of reproductive interference. We calculated approximate pond size from length and width measurements (to the nearest 1 m) taken by a laser range finder (Precaster Enterprises, Taichung, Taiwan) and assuming an elliptic shape. We scored spatial complexity of ponds by eye as the percent of pond surface (metre squared) containing vegetation, rocks or branches (to the nearest 10 %).

We visited each pond every 2 days and counted and individually marked all egg clutches laid since our last visit with numbered flags made of wooden sticks and adhesive tape. We marked the position of each clutch on hand-drawn maps of ponds and identified the species of the female that had laid the clutch based on clutch size, shape, position and opacity of the egg jelly (Rd clutches are smaller, have a regular round shape, are attached to branches or aquatic vegetation separated from other clutches and exhibit a clear egg jelly; Rt clutches are larger, have an irregular

shape, are laid on the bottom in shallow parts of the pond in aggregations and exhibit a milky egg jelly). We took four samples of five eggs from each clutch to estimate fertilization success. We put these egg samples into plastic dishpans ( $15 \times 10 \times 7.5$  cm) covered with lids and containing 0.5 L of pond water, placed into shade on land, and raised embryos until developing eggs could be clearly discerned from dead eggs (ca. 3–10 days, depending on temperature). We counted developing embryos and used their ratios averaged over the four samples as an estimate for fertilization success in the clutch of origin. We used this method of estimating fertilization success because eggs ‘fertilized’ by heterospecific sperm also rotate, but then do not show any further signs of development (A. Hettyey, personal observation). Based on a subsample, fertilization success estimated from samples in dishpans represented that in original clutches very well. As in previous experiments we had never encountered infertile males of these two species in the study area (Hettyey et al. 2005, 2009a, 2010, 2011), we assume that one or more heterospecific males were involved in matings that yielded clutches with low fertilization success. After estimating fertilization success, eggs and embryos were poured back into their native pond. We used the total number of clutches laid by both species to obtain abundance estimates of reproducing individuals. This is a rough estimate of actual species abundances, because males usually outnumber females, and sex ratio (and, thus, the number of males relative to the number of clutches laid) may vary from population to population. However, measuring abundance in this way represented a trade off between the collection of exact data on sex-specific abundances of each species (which could only be gathered by enclosing breeding ponds with fencing) and sampling a sufficiently large number of populations.

#### Statistical analyses

We obtained Rt/Rd and Rd/Rt abundance ratios for each pond by dividing the number of Rt clutches by the number of Rd clutches and vice versa. We log transformed species abundance ratio to linearize its relationship with fertilization success and avoid potential problems due to heteroscedasticity. We calculated population densities for the two species by dividing clutch numbers by pond surface area. We averaged fertilization success over clutches for each population of Rt and Rd separately and entered these means as dependent variables into the analyses. We did not only analyse the number of clutches with zero fertilization success, because multiple males participating in a mating, pirate males and stray sperm present at the location of egg deposition may lead to some fertilizations even if the primary mate is a heterospecific male (Laurila and Seppä 1998; Lodé and Lesbarrères 2004; Vieites et al.

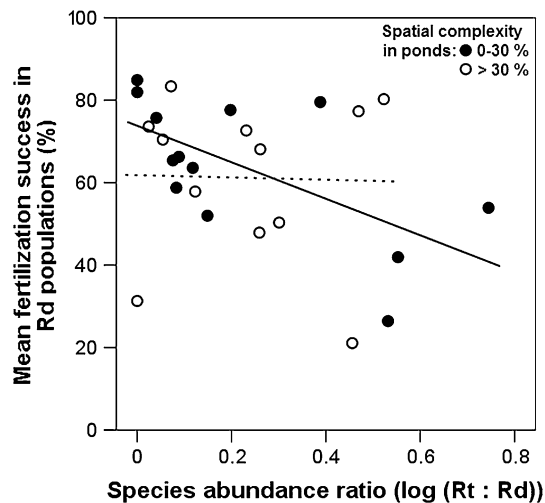
2004). Clutches showing low but some level of fertilization were indeed abundant. To analyse what influenced fertilization success in breeding ponds we used generalized linear models (GLM), entering pond size, spatial complexity of ponds, species abundance ratio and population density of the species analysed as covariates. We entered all two-way interactions into initial models and applied a backward stepwise removal procedure (terms were removed when  $P > 0.05$ ) to avoid problems potentially arising from the inclusion of non-significant terms. We obtained statistics for removed variables by re-entering them one by one into the final model. Model residuals were normally distributed in all tests. Statistical tests were two-tailed and were calculated using IBM SPSS Statistics 20.

#### Results

Rd was present in all ponds, whereas Rt was absent from three locations. The Rt:Rd ratio ranged between 0 (no Rt) and 4.56. The abundances of Rd and Rt were not related to each other (Pearson correlation,  $R = 0.03$ ;  $P = 0.89$ ).

Fertilization success in Rd was related to spatial complexity of ponds and species abundance ratio (GLM; spatial complexity of ponds,  $B = -0.408$ ,  $SE = 0.184$ ,  $F_{1,20} = 4.91$ ,  $P = 0.039$ ; Rt:Rd ratio,  $B = -81.98$ ,  $SE = 21.69$ ,  $F_{1,20} = 14.28$ ,  $P = 0.001$ ), but the interaction between spatial complexity and abundance ratio was also significant ( $F_{1,20} = 11.7$ ,  $P = 0.003$ ; Fig. 2). Fertilization success was positively correlated with pond size ( $B = 0.022$ ,  $SE = 0.009$ ,  $F_{1,20} = 6.53$ ,  $P = 0.019$ ) and unrelated to Rd density ( $F_{1,19} = 0.029$ ,  $P = 0.87$ ). Further two-way interactions remained non-significant (all  $P > 0.26$ ). To investigate the significant interaction between spatial complexity of ponds and species abundance ratio, we created two groups by assigning half of the ponds to the high spatial complexity category ( $n = 12$ ; spatial complexity index  $\geq 30$  %) and the other half to the low spatial complexity category ( $n = 13$ ; spatial complexity index  $< 30$  %). We performed separate analyses on these groups of ponds. These analyses revealed that average fertilization success of Rd clutches decreased with increasing Rt ratio in ponds exhibiting low spatial complexity ( $B = -44.28$ ,  $SE = 16.39$ ,  $F_{1,11} = 7.3$ ,  $P = 0.021$ ), while this relationship was absent in spatially more complex ponds ( $F_{1,10} = 0.006$ ,  $P = 0.94$ ; removing one data point representing low fertilization success in a pond lacking Rt did not qualitatively change the results).

In the case of Rt, fertilization success was not related to any of the covariates (pond size:  $F_{1,20} = 2.32$ ,  $P = 0.14$ ; spatial complexity of ponds:  $F_{1,20} = 0.54$ ,  $P = 0.47$ ; species abundance ratio:  $F_{1,20} = 0.51$ ,  $P = 0.48$ ; Rt density:  $F_{1,20} = 1.23$ ,  $P = 0.28$ ). All two-way interactions were non-significant as well (all  $P > 0.14$ ).



**Fig. 2** Relationship between *Rana temporaria*:*Rana dalmatina* (*Rt*:*Rd*) species abundance ratio and mean fertilization success in *Rd* egg clutches in 25 natural populations. For illustrative purposes only, we created two categories of ponds based on spatial complexity to depict the significant interaction between spatial complexity in ponds and species abundance ratio. We determined the cut-off value to be 30 % to obtain two categories with similar numbers of ponds. *Full circles, solid line* represent ponds with low spatial complexity; *empty circles, dotted line* represent ponds with high spatial complexity. Removing the data point representing low fertilization success in a pond lacking *Rt* and with high spatial complexity did not change results qualitatively

## Discussion

The relative abundance of *Rt* and *Rd* has a pronounced effect on fertilization success in natural populations of *Rd*. With increasing numerical dominance of *Rt*, the population-wide mean fertilization success decreases from around 80 % to ca. 40 % in *Rd* clutches. However, the strength and consequences of reproductive interference seem to be affected by the spatial complexity present in ponds. In locations where structure is more or less absent from the water surface, interference affects *Rd* fertilization success, whereas in ponds with the surface area broken up by vegetation, rocks and trunks, this effect is not detectable. Finally, fertilization success in *Rt* clutches appears unaffected by interference, so that interference and resulting costs are asymmetric.

The occurrence of detectable consequences of reproductive interference under natural conditions confirms previous experimental results (Hettley and Pearman 2003), while the observation that effects may be modulated by environmental factors supports previous cautionary notes on the applicability of experimental results to natural conditions (Verrel 1990; Skelly 2002; Bezemer and Mills 2003; Joron and Brakefield 2003; Ficetola and De Bernardi 2005). Among other factors, higher spatial complexity and more

available space may enhance reproductive segregation. Indeed, our results seem to support this hypothesis in that we did not detect a decrease in *Rd* fertilization success with an increasing ratio of *Rt* in ponds exhibiting higher levels of spatial complexity. The mechanism leading to the observed pattern may be that in ponds with simple structure, females are more likely to be noticed and approached by many males, including heterospecifics, whereas in ponds with vegetation and other types of spatial structure hiding may effectively lower the frequency of interspecific matings. Nonetheless, we note that among ponds exhibiting high spatial complexity, our sample contains few locations with strongly *Rt*-biased abundance ratios (see Fig. 2), while Hettley and Pearman (2003) predicted pre-mating reproductive isolation to break down only at relatively high ratios. The sample size of the present study does not allow firm conclusions to be drawn about the shape of the curve representing the relationship between the species abundance ratio and mean fertilization success under natural conditions, and the possibility that reproductive interference also has an effect on mean fertilization success in ponds with dense vegetation cannot be ruled out. The positive effect of pond size on fertilization success in *Rd* clutches may also be seen as support for the importance of the possibility for spatial segregation between the two species. However, this line of evidence is weakened by the result that the effect of pond size prevails independently of species abundance ratio.

The effect of reproductive interference is asymmetric in the species pair studied. While in *Rt* the mean fertilization success seems unaffected by the relative number of heterospecifics, *Rd* exhibits lowered reproductive success when outnumbered by *Rt* in ponds with little opportunity for spatial segregation. Examples of asymmetric reproductive interference are abundant in the literature (e.g. Fujimoto et al. 1996; Marshall et al. 2006; Hochkirch et al. 2007) and may be caused by differences in reproductive and ecological traits, such as in the degree of indiscriminate-ness (Wirtz 1999) or differential body size (Ludde et al. 2004; Schmeller et al. 2005; Suzuki et al. 2005). In the *Rd*-*Rt* system, the asymmetry may be due to differences in male competitiveness: *Rd* males cannot displace the larger *Rt* males from the back of females, whereas *Rt* males are able to take over the position of *Rd* males (Hettley et al. 2009a; B. Vági et al., unpublished data). Also, the larger *Rt* females may be more able to resist mating attempts from heterospecifics than the smaller *Rd* females (Bruning et al. 2010). Another explanation for the asymmetric property of the costs of interference in the studied species pair may be deduced from aggregation models of coexistence (Ives 1988; Kuno 1988). Aggregation may enhance fitness of a species in the presence of reproductive interference because it lowers the probability of encounters with heterospecifics



(Westman et al. 2002; Hettyey and Pearman 2003; Ficetola and De Bernardi 2005; Gröning et al. 2007). Indeed, in our study system, Rt, the species which forms aggregated choruses in breeding ponds, appears to be unaffected by reproductive interference, whereas Rd, the species that is territorial and is dispersed evenly, suffers from interference. This phenomenon may also contribute to the observed asymmetry in fertility costs.

Reproductive interference may also entail more subtle costs than lowered population-level reproductive success. While interference does not seem to affect fertilization success in Rt, individual Rt males are likely affected. As Rt males are indiscriminate, like males of many other anuran amphibians (Reading 1984; Engeler and Reyer 2001; Marco and Lizana 2002; Hettyey et al. 2005), they maintain prolonged amplexus with heterospecific females (Hettyey et al. 2009a), and, thus, may lose mating opportunities with conspecific females and lose energy and sperm while investing into matings with no returns. On the one hand, this may lower re-mating and fertilization ability of males when subsequently encountering conspecific females (Gibbons and McCarthy 1986; Lengagne et al. 2007; Hettyey et al. 2009b, 2012). On the other hand, the effective population size of reproductively active males may be lowered, potentially leading to lowered population-wide genetic variability in the next generation and genetic bottlenecks (Conner and Hartl 2004). Further, the temporal disappearance of males from the pool of potential sires (i.e. while in amplexus with a heterospecific female) may push the mating system towards random mating with respect to the genetic quality of successful males, further slowing the spread of evolutionary adaptations and leading to genetic drift. Consequently, even if a population is not affected by reproductive interference immediately (i.e. in terms of recruitment rate), it may experience a lowered ability to evolve.

We had expected population density to affect fertilization success in both species, because the availability of potential mates and the strength of intraspecific mate competition may depend on population densities (Gröning et al. 2007; Hochkirch et al. 2007). However, we did not detect a relationship between population density and fertilization success in either species. In the case of Rt, the lack of such a correlation may partly be explained by the breeding phenology of this species; males call in dense, lek-like choruses and almost all egg clutches are laid within the chorus. Consequently, even though Rt males also actively search for females outside of choruses and several choruses may be formed within a single pond, density calculated as a mean value for the whole surface area of the pond may not represent actual densities in all areas very well, especially in larger ponds. In Rd, where males call from territories and are scattered out evenly over most of the entire

breeding pond, density should reflect mate availability and the strength of intraspecific mate competition rather well. Nonetheless, further studies will be necessary to affirm our observation and to assess under what circumstances density may become unimportant for the determination of the effects of reproductive interference.

In conclusion, we find evidence that reproductive interference between species can negatively influence population-wide reproductive success under natural conditions (for similar results see Kruuk et al. 1999; Pfennig and Simovich 2002). Such interference may compromise the persistence of populations of subordinate species and hinder the colonization of new habitats, where colonizers are generally at low density (Kuno 1992; Rhymer and Simberloff 1996; Hochkirch et al. 2007). The frequency and severity of similar interspecific reproductive interactions are likely to increase because climate change is predicted to lead to shifts in species distributions (Parmesan and Yohe 2003). Also, many formerly introduced species have become invasive and are spreading in distribution (for reviews see Grosholz 1996; Rahel and Olden 2008), anthropogenic alterations of the environment may thwart segregation among species (e.g. Fisher et al. 2006), and species that come newly into contact are likely not adapted to the presence of each other (Coyne and Orr 1989). Consequently, further research on interspecific interactions during reproduction is needed and detailed insights into the effects and mechanisms of reproductive interference will be of fundamental importance for the conservation of biological diversity.

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