ORIGINAL ARTICLE

Intraspecific and interspecific competition for mates: *Rana temporaria* males are effective satyrs of *Rana dalmatina* females

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Abstract

Reproductive interference can seriously affect the reproductive success of involved individuals and may lead to local exclusion of the competitively inferior species. The components of male competitiveness in direct bodily fights for females have been studied rarely in a heterospecific context. In explosively breeding anuran amphibians, males are often coercive and indiscriminate, which frequently leads to interactions among heterospecific males. We experimentally assessed the competitiveness of male *Rana dalmatina* (RD) and *R. temporaria* (RT), two species with overlapping breeding both in time and space. The mating speed of the RD males decreased over the course of the breeding season, whereas RT males retained their swiftness. In addition, the RD males were rarely able to replace the RT males from amplexus with RD females, while takeovers frequently occurred among the RD males. Further, larger RD males were more successful in maintaining amplexus and in achieving takeovers when facing smaller conspecifics. Our results suggest that male body size is important for intraspecific competition among the RD males, but the RT males outcompete the RD males of all sizes, perhaps due to their larger body size. Hence, RT males are likely to be effective satyrs of RD females, because they may lower the reproductive success of the latter. Such interspecific differences in the competitiveness of males may represent an important mechanism that contributes to the arousal of asymmetric reproductive interference between species.

Significance statement

Reproductive interference—interactions between species during mating with negative consequences on the fitness of involved individuals—is widespread in nature. Even though differences in the competitiveness of males of interfering species may have severe consequences, competitiveness of males has rarely been studied in an interspecific scenario in vertebrates. Males of anuran amphibians are often indiscriminate and coercive and engage in bodily fights for the possession of both conspecific and heterospecific females, which may often compromise the reproductive success of involved males and females. Here, we demonstrate that interspecific differences among ranid males can be large in the swiftness of pair formation, in the ability to defend the mating position and to perform takeovers. These differences are likely to lower the reproductive performance of the competitively inferior species, potentially leading to its local extinction.

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Introduction

Reproductive interference occurs when interspecific interactions during mating or mate acquisition negatively affect fitness (Gröning and Hochkirch 2008). The most common cause of reproductive interference is imperfect species recognition (Gröning and Hochkirch 2008), which is most likely to arise in mating systems ruled by male-male competition and sexual coercion where males are under strong selection not only for superior competitive abilities but also for indiscriminateness and a prompt reaction to mating opportunities (Andersson 1994; Clutton-Brock and Parker 1995; Lengagne et al. 2006). When two species with such a mating system co-occur, indiscriminate males may also harass heterospecific females and mate with them coercively (Kyogoku and Nishida 2012; Noriyuki et al. 2012) thus acting as "satyrs" (Ribeiro and Spielman 1986). Costs of reproductive interference paid by satyr males may involve time, energy, and sperm invested in non-rewarding fights and matings with heterospecifics (Gröning and Hochkirch 2008; Bath et al. 2012). At the same time, females coerced by satyr males may also pay substantial costs because they are deprived from choosing an optimal sire for their offspring (Qvarnström and Forsgren 1998) and may lose a considerable portion of their reproductive investment if hybrids are counterselected (Ribeiro and Spielman 1986; Hettyey et al. 2009a; Noriyuki et al. 2012). Ultimately, reproductive interference may influence population dynamics very much like resource competition (Kyogoku and Nishida 2012); it may limit the persistence of populations and affect species composition of animal communities (McLain and Shure 1987; Kuno 1992; Kishi et al. 2009).

Anuran amphibians are popular model organisms of studies on reproductive interactions. Water bodies used for reproduction are often visited by several species simultaneously, resulting in frequent encounters between breeding heterospecifics (e.g., Licht 1969; Engeler and Reyer 2001; Pfennig 2007; Lengagne et al. 2008; Hettyey et al. 2014). In species exhibiting explosive breeding (*sensu* Wells 1977), the reproductive season is short, males largely outnumber females over large parts of the breeding season, and intense male-male competition overrules direct female choice (Davies and Halliday 1979; Engeler and Reyer 2001; Hettyey et al. 2003, 2009a). Males are selected for large body size (Davies and Halliday 1979; Liao and Lu 2012; Rausch et al. 2014), swiftness in pairing (high mating speed; Lengagne et al. 2006), and indiscriminateness (Wells 1977; Engeler and Reyer 2001; Hettyey et al. 2005).

In anurans, the outcome of intraspecific competition for mates is often decided by differences in body size. Large males usually rely on their superiority in male-male fights for females, whereas smaller males often try to intercept females already on their way to the breeding grounds or use satellite or sneaker tactics (Davies and Halliday 1979; Loman and Madsen 1986; Höglund and Robertson 1988; Bourne 1993; Byrne and Roberts 2004; Lodé et al. 2004). Intense intrasexual competition can also endure after gamete release in the form of sperm competition (Jennions and Passmore 1993; D'Orgeix and Turner 1995; Roberts et al. 1999; Lodé et al. 2005; Sztatecsny et al. 2006; Rausch et al. 2014).

Despite their potential importance for breeding success of individuals and for the coexistence of species, behavioral mechanisms of male-male competition in anuran amphibians and their relationship with physical traits of males have been studied rarely in the heterospecific context. In hybridogenetic waterfrogs, where heterospecifics compete for females, *Pelophylax lessonae* males are faster in achieving amplexus with females than are *P. esculentus* males (Lengagne et al. 2006), whereas *P. esculentus* males are more aggressive, call more often, and orient more frequently toward females (Bergen et al. 1997). These differences in male behavior, presumably along with mating preferences of females (Abt and Reyer 1993; Engeler and Reyer 2001), result in higher mating success of males of the parental species, *P. lessonae*. However, even less is known about behavioral mechanisms in interfering species pairs that do not hybridize. For example, in European brown frogs, skewed species abundance ratios may lead to a drop in fertilization success in the less abundant species (Hettyey and Pearman 2003; Hettyey et al. 2014; but also see Ficetola and De Bernardi 2005), but the underlying behavioral mechanisms of competition have not been evaluated.

In our study, we aimed at quantifying competitive abilities of males of two European brown frogs, *Rana dalmatina* (RD) and of its close relative, *R. temporaria* (RT). Reproductive interference between these two species has an asymmetric outcome in natural populations; increasing abundance ratio of RT has a negative effect on the fertilization success of RD, but the opposite effect has not been detected (Hettyey et al. 2014). We hypothesized that in the competition for females, large males were superior compared to small males and the RT males were superior compared to the RD males. We tested these hypotheses by investigating how mating speed, the ability to remain in amplexus, and the ability to achieve takeovers were influenced by the size and type of males. We also tested for a role of female size that may indicate the presence of a male mating preference or difficulties in maintaining amplexus with too large or too small females. As we performed the experiment in two consecutive rounds covering a large part of the breeding season, we could also test for signs of reproductive exhaustion in males (e.g., Gibbons and McCarthy 1986; Hettyey et al. 2009b).

Materials and methods

The study species

We studied the interactions between RT and RD, which are two closely related ranid frogs of the Palearctic (Green and Borkin 1993; Vences et al. 2013). In Hungary, RD is widespread, while RT is restricted to cooler regions of the Northern and Transdanubian mountain ranges, where the two species are found in sympatry (Dely 1967; Puky et al. 2005). Members of both species are medium-sized frogs, but while sexes are of similar size in RT, males are smaller than females in RD, so the RT males usually are larger than the RD males (Nöllert and Nöllert 1992). In the study area, both species reproduce in early spring. The breeding season of RT is characteristically short and explosive (ca. 1 week of breeding activity), whereas RD is a more prolonged breeder (ca. 3–4 weeks long reproductive period; Hettyey et al. 2003). Both species frequently use small temporary ponds for reproduction (Vági et al. 2013; Hettyey et al. 2014), where the RD males call from territories (Lesbarrères and Lodé 2002; Lodé et al. 2005) and the RT males form dense choruses where wrestling for females dominates (Elmberg 1986; Ryser 1989). Males of both species readily grab heterospecific females and stay in amplexus with them for hours (Reading 1984; Hettyey and Pearman 2003; Hettyey et al. 2009a). Interspecific matings yield no viable offspring, nullifying reproductive success of involved individuals (Hettyey et al. 2009a, 2014).

Mating trials

At the onset of the breeding season in 2008, we collected 20 RT males, 140 RD males, and 40 RD females from two ponds (47° 42′ 27″ N, 19° 02′ 24 E, and 47° 44′ 20″ N, 19° 00′ 43″ E) in the Pilis-Visegrádi Mountains, Hungary. We searched ponds with headlights and captured animals by hand in the early evening hours. As the populations are close to each other (ca. 4-km distance) and are situated along the same stream with further breeding ponds interspersed, we regarded the sampled populations being parts of the same metapopulation and did not distinguish between frogs based on their origin. We transported the experimental animals to a nearby pond (which was also used for breeding by both species), where we accommodated them separated by sex and species in large plastic boxes (ca. 50 × 30 × 30 cm) half filled with pond water and placed in the shade. We measured body length (snout-urostyle length—SUL) with a plastic ruler (to the nearest 1 mm) and body mass with a portable scale (to the nearest 0.1 g). We marked the RD males individually with small, numbered labels of adhesive tape fixed to waistbands made of thread. We observed no signs of behavioral change due to the waistbands, which we removed at the end of the experiment.

We started trials after dusk by placing 20 RD females individually into plastic boxes (48 × 35 × 25 cm) filled with 10 cm (around 15 L) of pond water, half of them with a conspecific male, the other half with an RT male. We checked the boxes every 20 min until amplexus was formed. None of the females laid eggs in the boxes. As soon as a pair formed amplexus, we noted the time and transferred the pair into nearby plastic tubs (80 cm in diameter, 40 cm deep) filled with 15 cm (ca. 30 L) of pond water. Tubs contained a handful of sedge leaves as shelter and as substrate for egg laying and one small, one medium, and one large RD male as competitors. Sex and species ratios were similar to those in the original breeding aggregations (Hettyey et al. 2003, 2014). We checked the experimental tubs every 20 min in the first hour, later once per hour. At night, we used dim red headlights to minimize disturbance. We noted which males were in amplexus and if egg-clutches were laid. We estimated fertilization success by taking a few subsamples totalling about 100 eggs from each clutch, and rearing embryos under laboratory conditions until developing individuals could clearly be discerned from nondeveloping eggs (Gosner stage 19–20; Gosner 1960). We also recorded the horizontal and vertical positions of the pair and assessed the number of eggs laid to investigate cryptic female choice (for results, see Hettyey et al. 2009a). If no further amplexus was formed within 2 h after egg laying, we considered the trial finished, removed animals, and released them at their site of collection.

We ran two consecutive rounds of trials to increase sample size. We did not wait until all females deposited their eggs but terminated the first round of trials 115 h after start to 11 h after the last egg-deposition and 55 h after the last observed takeover. Thereafter, we removed experimental animals, emptied and refilled tubs with fresh pond water, added sedge leaves, and performed the second round of trials as described above with a new set of animals. The second round lasted for 69.5 h until 7 h after the last egg deposition and 8 h after the last observed takeover. We terminated the experiment because a sudden drop in temperature stopped the breeding activity in the experimental tubs and in the nearby natural populations.

During competition trials, it was not possible to record data blindly because difference between the two treatments (tubs with only the RD males or with an RT and three RD males) was obvious for the observer at first glance. Fertilization data were blindly evaluated to minimize observer bias.

Statistical methods

Males initially put together with a female did not enter amplexus in 3 out of 40 trials, so we excluded these from all analyses. We mistakenly did not measure the body size of four RT males, lowering the sample size by four in the analyses including RT male SUL. In two trials, apparent matings with conspecific males resulted in close to 0 % fertilization success and in one more trial by amplexus with a heterospecific

yielded 74 % fertilization. As we did not directly observe egg-laying events in these trials, we can only speculate on the cause and cannot be sure what caused the unexpected outcome, so we excluded these trials as well. Finally, a male escaped from two experimental trials, and in two more cases, the female was abandoned by the amplexing male, as if the female would not have carried eggs. Thus, we could use data from the 30 trials in our analyses on takeovers.

As the RD males were smaller than the RT males (RD SUL 55.9 ± 0.91 mm; RT SUL 78.13 ± 1.88 mm; mean $\pm$ SE; Mann-Whitney U test; $U = 1.5$, $N = 35$, $P < 0.001$) and we were interested in the effects of both male type and male body size on male competitiveness, we calculated standardized scores relative to the mean from SUL values for males of the two species separately and used these values in the analyses as measures of relative male size. To analyze the variation in mating speed, we used generalized linear models (GZLMs) with Poisson error distribution and an identity link function. We entered rank-transformed values of time until amplexus as the dependent variable; round of trials and male type (RD or RT) as fixed factors; and relative male SUL and female SUL as covariates.

We investigated what influenced the ability of initially amplexed males to maintain their position on the female for a longer time period using linear mixed-effects models (LMMs). Because in trials where egg-deposition occurred males had to maintain amplexus for less time than in trials where females did not lay eggs before termination, we excluded these trials, resulting in 22 replicates. To enhance homogeneity of variances and normality of model residuals, we entered log-transformed values of amplexus duration as the dependent variable. We entered male type as a fixed factor and relative SUL of the male that was initially in amplexus and female SUL as covariates.

When evaluating what may contribute to the ability of males to achieve successful takeovers, we had to rely on 17 trials where takeovers had occurred. We only included the first takeovers to avoid pseudoreplication. We used generalized linear mixed-effects models (GZLMMs) with binomial error distribution and logit link function and compared models using likelihood-ratio tests. We entered successfulness of males as the dependent variable, male SUL and its interactions with round of trials and species of the male initially in amplexus as fixed factors, and tub as a random factor. The structure of the data did not allow investigating the effects of the relative SUL of the male initially in amplexus and of the female SUL on successfulness of individual males, because these variables assumed different values in each trial while being the same within each trial.

We entered two-way interactions into initial models and applied a backward stepwise removal procedure (Grafen and Hails 2002) to avoid overparameterization and problems that may arise from the inclusion of non-significant terms

(Engqvist 2005). We calculated statistics in the analysis on mating speed using IBM SPSS Statistics 20. We run LMM in R (version 3.1.1) using the "lme" function in the package "nlme" and GZLMM using the "glmer" function in the package "lme4."

Results

Mating speed

The time it took males to amplex the female differed between the two species (GZLM: LR $\chi^2 = 35.27$, $N = 37$, $P < 0.001$) and between the first and the second round of trials (LR $\chi^2 = 14.85$, $N = 37$, $P < 0.001$). However, the interaction between species and round of trials also was significant (LR $\chi^2 = 35.44$, $N = 37$, $P < 0.001$), indicating that in the first round of trials, there was no detectable difference between males of the two species, but the RD males became slower in the second round of trials, while the RT retained their swiftness (Fig. 1). The mating speed of males was unrelated to their relative body size (LR $\chi^2 = 1.54$, $N = 33$, $P = 0.22$) and to female size (LR $\chi^2 = 0.27$, $N = 37$, $P = 0.6$). The remaining two-way interactions were all nonsignificant (all $P > 0.13$).

Ability to remain in amplexus

In trials where egg-deposition did not occur, relative male body size in itself did not significantly influence the ability of males to remain in amplexus for longer (LMM, $F_{1,17} = 1.01$, $P = 0.33$). However, the RT males could defend their positions longer than the RD males can ($F_{1,17} = 23.74$, $P < 0.001$), and the interaction between male type and relative male size was
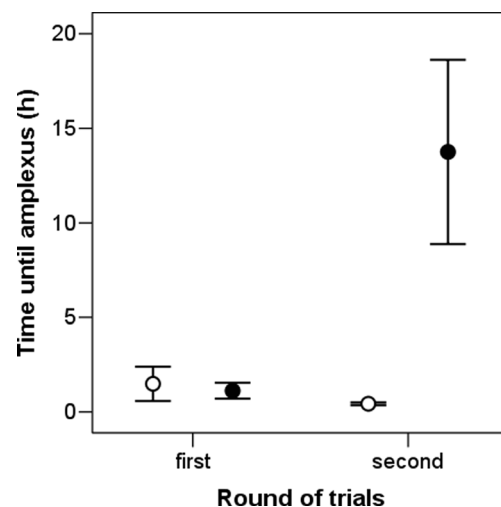

Fig. 1 Time until males of the two species amplexed the RD female at the beginning of the two rounds of trials. *Empty circles* represent the RT males and *full circles* represent the RD males. The means $\pm$ SE of untransformed data are shown

also significant ($F_{1,17} = 8.2$, $P = 0.011$); larger RD males remained in amplexus for longer than did their smaller conspecifics (LMM only including RD males: $F_{1,10} = 11.81$, $P = 0.006$), whereas no such relationship was observable in RT males (LMM only including RT males: $F_{1,6} = 1.39$, $P = 0.28$; Fig. 2). The effects of female size ($F_{1,16} = 1.45$, $P = 0.25$) and of the other two-way interactions were nonsignificant (all $P > 0.7$).

Ability to achieve takeovers

Larger RD males were more able to achieve successful takeovers than were their smaller conspecifics (GZLMM, LR $\chi^2 = 12.82$, $N = 17$, $P < 0.001$; Fig. 3), but only when the male initially in amplexus was a conspecific. When an RT male was in amplexus, the body size of the competing RD males did not play a role in determining which one could replace the amplexing males (LR $\chi^2 = 14.04$, $N = 17$, $P < 0.001$). The effect of the round of trials was nonsignificant (LR $\chi^2 = 0.19$, $N = 17$, $P = 0.91$).

Fertilization success

When only conspecific males were present, females laid eggs in 13 trials and fertilization success was 95.6 ± 3.15 % (mean $\pm$ SD). When an RT male was also present, females laid eggs in only six trials and the fertilization success was 0 % in three cases and 57.9, 20.4, and 93.9 % in the other three trials. In the latter three cases, females laid a second clutch with a conspecific male after laying some of their eggs with the RT male (also see Hettyey et al. 2009a); hence, the nonzero fertilization success.
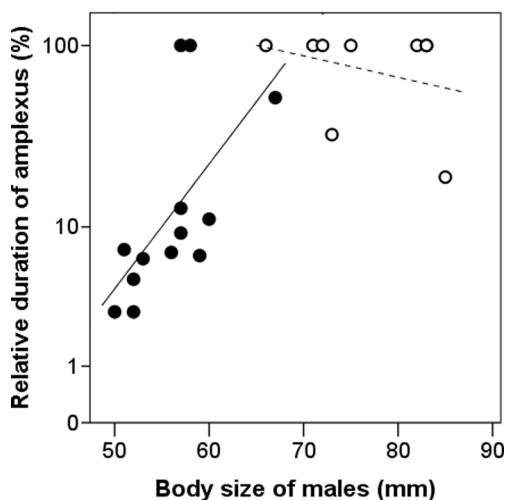

Fig. 2 The relationship between snout-urostyle length of males initially in amplexus with an RD female, male species, and the time they could stay in amplexus relative to the length of the round of trials. *Empty circles* represent the RT males and *full circles* represent the RD males. Please note that the y-axis (duration of amplexus) is on a logarithmic scale
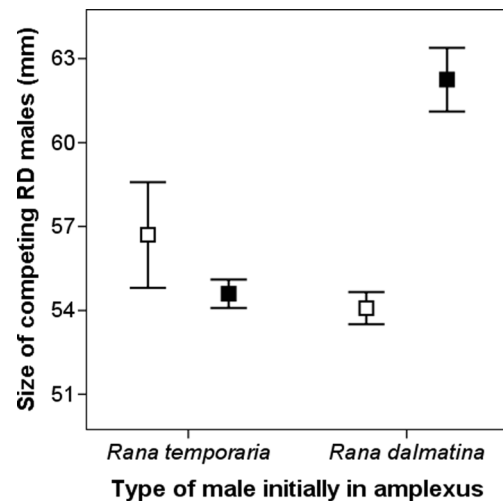

Fig. 3 Effects of type of male initially in amplexus and of snout-urostyle length of the competing RD males on their ability to achieve successful takeovers (*empty squares*: unsuccessful RD males; *full squares*: successful RD males). The means $\pm$ SE of untransformed data are presented

Discussion

Our results suggest that even though the larger RD males performed better in intraspecific competition for mates than did their smaller conspecifics, all of the RD males were outcompeted by the RT males, which consequently are effective satyrs of RD females (*sensu* Ribeiro and Spielman 1986).

In the first round of trials, males of both species amplexed females more or less immediately, whereas in the second round, RT males maintained their swiftness in amplexing the female, but the RD males became substantially slower. In a mating system ruled by male-male competition and sexual coercion, the first male reacting to the appearance of a female may secure a large benefit; the pair may remain unnoticed until egg-deposition, and even if other males discover them, a male already in amplexus has a high chance of being able to defend its position on the female (Loman and Madsen 1986) and to secure high fertilization success, even if the mating involves multiple males (Roberts et al. 1999; Lodé and Lesbarrères 2004; Sztatecsny et al. 2006). One reason for the observed pattern in mating speed may be interspecific differences in the mating system. Bodily fights for females determine the outcomes of contest competition in dense breeding aggregations of RT (Elmberg 1986; Ryser 1989). In contrast, while direct fights for females also occur in RD, advertisement calling is an important component of male-male competition and males defend territories, providing opportunities for female choice (Lesbarrères and Lodé 2002; Lodé et al. 2004). Consequently, mating speed may be more important for the reproductive success of the RT than for the RD males. In addition, under natural conditions, males of the more prolonged breeder RD may have more time between matings to mobilize their sperm or energetic reserves, whereas RT

males cannot afford to lose their vigilance during the short and intensive "explosive" reproductive period (Wells 1977; Elmberg 1990; Hettyey et al. 2003, 2005), hence, their observed high mating speed also in the second round of trials.

Mating speed was not correlated with the relative size of males. It thus appears that small males do not compensate for their inferiority in direct male-male fights for females by the means of higher mating speed. In anuran species where alternative mating tactics exist, satellite or sneaker males are often smaller than their competitively superior territorial rivals (Davies and Halliday 1979; Byrne and Roberts 2004). In addition, the only chance of the small RD males, which are outcompeted by larger males in direct bodily fights for females, may be to intercept females as soon as possible and thereafter try to remain undetected by other, larger males. Indeed, "caller" and "searcher" alternative mating tactics have been proposed to be present in RD (Lodé et al. 2004, 2005). Consequently, it was surprising to observe that size-dependent variation in mating speed was lacking. It is possible that the larger bodily strength and experience of larger, older males offset the otherwise quicker response of smaller males. Also, because females are a scarce resource even for larger males, selection may maximize responsiveness also in the case of the latter. The result that mating speed was not affected by female size confirmed previous results on the indiscriminateness of the RD males (Hettyey et al. 2005) and suggests that mate choice is lacking also in the RT males.

Once amplexus had been formed, the RT males were more successful than were the RD males in defending their position on the female against attacks of the competing RD males. Among the RD males, larger ones could stay in amplexus for longer, while among RT males, size did not affect amplexus duration. Thus, body size predicts the RD males' ability to defend the female against conspecifics (see also Davies and Halliday 1978, 1979; Howard and Kluge 1985; Byrne and Roberts 2004; Rausch et al. 2014), but male body size has no bearing for interspecific competition for females in our study system; the physical dominance of the RT males over the RD males usually prevails, most likely due to the larger size of the former. Some studies found that large male advantage is not due to SVL but forelimb or nuptial pad characteristics (Lee 1986; Höglund and Säterberg 1989), and RT males also seem superior in these terms with their thick forelimbs and heavily keratinized nuptial pads. Our observation that female size did not affect the length of amplexi further confirms male indiscriminateness and indicates that males may be equally efficient in clasping and defending mates of different sizes (for similar results, see Elmberg 1991; Bourne 1993; but see Höglund 1989).

Our results on the ability of males to achieve successful takeovers mirror those obtained on their ability to maintain amplexus. In intraspecific competition, the larger RD males were more able to take over the position of conspecifics than

were the smaller RD males (for similar results, see e.g., Howard and Kluge 1985; Bourne 1993; Byrne and Roberts 2004), but if an RT male was in amplexus with the female, the size of the RD males appeared to be unimportant. This result again emphasizes the competitive superiority or RT males. In the few cases where an RD male succeeded in replacing a heterospecific rival, the RT male may have lost its motivation, but this explanation remains speculative, and its evaluation would require continuous observation of the animals.

The question of to what extent our experimental results suggesting that RT males are effective satyrs of RD females can be generalized to natural populations arises (Michalak and Rafinski 1999; Skelly and Kiesecker 2001; Ficetola and De Bernardi 2005). In natural habitats, the frequency of interbreeding between interfering species may be lowered by more possibilities for spatial separation (Ficetola and De Bernardi 2005; Gröning et al. 2007; Hettyey et al. 2014). Also, visual, acoustic, or chemical communication, which potentially play a role in reproductive isolation (Belanger and Corkum 2009; Sztatecsny et al. 2012; Preininger et al. 2013; Starnberger et al. 2014), may be more effective under natural conditions. Finally, the simultaneous presence of RT and RD females may also lower the frequency of heterospecific matings (Ficetola and De Bernardi 2005). Consequently, the severity of reproductive interference may be mitigated by several mechanisms under natural conditions. However, heterospecific amplexi between RD and RT can readily be observed in natural breeding populations. In addition, we showed in a previous study that the costs of interference between RD and RT are asymmetric in natural populations with RD suffering more from interspecific interactions during reproduction (Hettyey et al. 2014). Consequently, our experimental results on the competitive superiority of the RT males over the RD males appear to be relevant for reproductive interference in natural breeding populations.

Another important question is why species discrimination did not evolve in males of the studied species. Apart from the aforementioned mechanisms lowering the frequency of interference between spatially and temporally co-occurring species, selection for species discrimination may also be weakened by female behaviors that decrease costs of misdirected mating effort paid by males (Reyer et al. 1999; Hettyey et al. 2009a). In addition, peak reproductive activity may overlap in some years but not in others due to interannual variation in weather conditions (Reading 1984, 1998). Further, interfering species may largely use different breeding habitats as a result of variation in habitat preferences and in environment-dependent larval competitiveness and survival (Hödl 1977; Gottsberger and Gruber 2004; Escoriza and Boix 2014). Finally, the evolution of male mating preferences may not get past the initial mistake-laden steps in mating systems that are dominated by intense male-male fights and are characterized by strongly male-biased sex ratios (Hettyey et al. 2009a).

Indiscriminateness and high mating speed may be beneficial for individual males in intrasexual competition among conspecifics, but these characteristics may turn detrimental in the presence of heterospecifics (Kandul et al. 2006; Lengagne et al. 2006); competitively superior RT males may forfeit mating opportunities while amplexing heterospecific females and spend costly sperm in nonrewarding matings (Gröning and Hochkirch 2008; Bath et al. 2012). Interspecific differences in competitiveness and coerciveness of males, which have evolved under different selection regimes in the respective mating systems (for similar results, see e.g., Lengagne et al. 2008), may fundamentally determine the population-level outcome of reproductive interference and lead to asymmetry therein (Wirtz 1999; Hochkirch et al. 2007; Hettyey et al. 2014), leading to the local or even regional disappearance of the competitively inferior species (Kuno 1992; Rhymer and Simberloff 1996).

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