



Counterstrategies by female frogs to sexual coercion by heterospecifics

Attila Hettyey^{a,b,*}, Sandra Baksay^{b,1}, Balázs Vági^{b,1}, Herbert Hoi^a

^a Konrad Lorenz Institute for Ethology, Austrian Academy of Sciences

^b Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University

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In mating systems with intense male–male competition for mates, males may coerce females into matings that impose fitness costs. Females able to alleviate negative fitness effects of sexual coercion by enforcing their mating preferences should have a selective advantage. What behaviours females of externally fertilizing species use to reduce costs of coercion, and how effective these behaviours are, is largely unknown. We experimentally evaluated mechanisms of mate choice in a system where indiscriminate and genetically nonmatching heterospecific males coerce females into matings and females are apparently passive participants of the mating game. We performed experiments using two frog species (*Rana dalmatina* and *R. temporaria*) which are sympatric and are often observed in heterospecific matings but do not produce viable offspring. We paired *R. dalmatina* females with a conspecific or a heterospecific male, placed pairs together with unmated *R. dalmatina* males and monitored female behaviour. Females paired with heterospecific males did not try to attract the attention of conspecific males, but they delayed egg laying. Females exerted cryptic female choice by laying fewer eggs when paired with heterospecific males. Finally, some females laid a small clutch of eggs, apparently to increase the likelihood of being released by their heterospecific mate and subsequently mate with a conspecific male. Female *R. dalmatina* thus have subtle but effective means to avoid the complete loss of a year's reproductive effort. In a broader context, females may be able to enforce their mating preferences even in externally fertilizing species where direct female choice is overrun by male–male competition.

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Sexual coercion by males is widespread in the animal kingdom (Clutton-Brock & Parker 1995), because in the majority of species males gain more by mating repeatedly (Bateman 1948), invest less in offspring (Trivers 1972), are more limited in the number of available mates (Emlen & Oring 1977) and have higher intrinsic maximum reproductive rates (Clutton-Brock & Parker 1992). Females often suffer high costs from sexual coercion in the form of increased energy expenditure and exposure to predation, injury or even death (Clutton-Brock & Parker 1995), but coercion may also reduce fitness of females by limiting their ability to choose between potential mates (Qvarnström & Forsgren 1998). Selection arising from this type of sexual conflict may favour females that can circumvent male control and are able to manipulate the outcome of a mating event to their own benefit.

Selection favouring females that succeed in enforcing their interests when facing sexual coercion may be especially strong

when coercion occurs between heterospecifics. In this case, coercing males are generally incompatible with females and this may result in low fertilization success, low offspring quality or offspring nonviability (e.g. Kruuk et al. 1999; Pfennig & Simovich 2002; Valero et al. 2008). We may thus expect to find counterstrategies to sexual coercion in species pairs or groups that interfere during reproduction (Gröning & Hochkirch 2008) and such systems should provide excellent opportunities for studying the behavioural responses to coercion. Also, theory predicts that reproductive interference can not only have severe consequences for individuals but also affect the persistence of whole populations or even species (Kuno 1992; Rhymer & Simberloff 1996; Hochkirch et al. 2007). Despite their potential significance for behavioural ecology, evolutionary biology and conservation, behavioural counterstrategies to coercive reproductive interactions between heterospecifics have remained largely unexplored (Gröning & Hochkirch 2008).

Studies on within-species sexual coercion have proposed a number of behavioural mechanisms that females may use to reduce its costs. To decrease levels of sexual harassment, females may avoid areas with high male abundance (Parker 1970), form shoals (Pilastro et al. 2003; Dadda et al. 2005), forge coalitions (Smuts & Smuts 1993), or associate with territorial (Clutton-Brock

* Correspondence: A. Hettyey, Konrad Lorenz Institute for Ethology, Austrian Academy of Sciences, Savoyenstrasse 1a, 1160 Vienna, Austria.

E-mail address: hettyeyattila@yahoo.de (A. Hettyey).

¹ S. Baksay and B. Vági are at the Behavioural Ecology Group of the Department of Systematic Zoology and Ecology, Eötvös Loránd University, Pázmány Péter sétány 1/C, 1117 Budapest, Hungary.

et al. 1992) or dominant males (Clutton-Brock et al. 1988). Once paired, females may delay egg deposition, sperm transfer or actual fertilization (Clutton-Brock & Parker 1995), incite male–male competition (Cox & Le Boeuf 1977; Wiley & Poston 1996; Hoi 1997; Hoi & Hoi-Leitner 1997) or induce sperm competition (Smith & Reichard 2005) if this enhances the chances of their ova being sired by a superior male. Females may exercise cryptic female choice by selecting sperm from specific males (Pizzari & Birkhead 2000), by adjusting their investment in the production of a clutch and in the amount of parental care they provide according to the quality of their mates (Eberhard 1996). Females may also deceive males to make them invest more in reproduction (sensu Smith et al. 2007) and parental care (sensu Valera et al. 1997) or to prevent infanticide (Zinner & Deschner 2000).

We only know of one study explicitly testing for behavioural counterstrategies to sexual coercion by heterospecifics in externally fertilizing species, where several mechanisms (e.g. postcopulatory mate choice) are not feasible and, consequently, different behaviours from those in internal fertilizers may be important (Clutton-Brock & Parker 1995; Eberhard 1996; Birkhead 1998; Gil et al. 1999). Reyer et al. (1999) found that female waterfrogs (*Rana lessonae* and *Rana erculenta*) laid a smaller clutch when amplexed by undesired, sexually parasitic males, while the reduction in the number of spawned eggs increased the female's residual reproductive value. Further studies on anuran amphibians have proposed that females may defer pair formation with coercive, nonmatching and generally indiscriminate males (Emlen 1976; Robertson 1986; Bourne 1992). Females may approach conspecific males or, when a heterospecific male comes close to them, they may flee (Abt & Reyer 1993) or assume a vertical body position in an attempt to hinder amplexus formation (Emlen 1976). Once amplexed, females may delay egg deposition to increase the likelihood of the amplexed male losing interest in them or another male attempting to displace the already amplexed one (Hettyey & Pearman 2003) or assisting in the displacement of undesired males. This can be achieved by producing release calls or behaving conspicuously in front of other, more suitable males to incite male–male competition (Emlen 1976; Davies & Halliday 1977; Abt & Reyer 1993). However, there is little information on what behaviours females indeed use and whether these behaviours raise the chances of mating with preferred mates.

Using externally fertilizing anurans, we aimed to determine whether females are able to discriminate between coercive conspecific and heterospecific males, look for behavioural mechanisms that females already in amplexus may use to lessen negative fitness effects of sexual coercion and investigate the effectiveness of these counterstrategies to coercion. We used the *Rana dalmatina* – *R. temporaria* species pair because heterospecific matings occur among members of these species (personal observation) as a result of overlapping breeding seasons and the indiscriminate coercive mating behaviour of males (Reading 1984; Hettyey & Pearman 2003; Hettyey et al. 2005). Eggs laid in heterospecific matings do not enter embryonic development (personal observation); this allowed us to quantify costs of coercion and any fitness benefits arising from behavioural responses of females to coercion attempts.

METHODS

The Study Species

Rana dalmatina (RD) and *R. temporaria* (RT) are closely related European brown frogs (Green & Borkin 1993). They have a largely overlapping European distribution with RD having a more southern distribution ranging from northern France to the southern Balkans and RT also being present in northern Fennoscandia (Nöllert & Nöllert 1992). Both frogs are medium sized with RD being

somewhat smaller than RT (Nöllert & Nöllert 1992). They are explosive breeders (Wells 1977) and their reproductive periods often coincide both spatially and temporally. The operational sex ratio is, in both species, strongly male biased throughout the breeding season. At low densities, males are stationary and call from territories (RD) or a chorus (RT), whereas at high densities intense scramble competition for mating opportunities arises in the form of prolonged wrestling and displacement attempts (Elmberg 1986; Ryser 1989; Lesbarrères & Lodé 2002; Lodé et al. 2005). As reported for other anuran species, intensive intrasexual competition may negatively affect fertilization success (Byrne & Roberts 1999) and lead to severe injuries or to the drowning of the female (Davies & Halliday 1979; Howard 1980; Hedengren 1987). Females are unable to repel mating attempts or terminate amplexus themselves. Males mate indiscriminately, which often leads to heterospecific matings in both directions (RD male with RT female and RT male with RD female, personal observation).

Experimental Procedures

We collected animals from two populations in the Pilis Mountains, Hungary (47°42'N, 19°02'E and 47°44'N, 19°01'E) at the beginning of the breeding season in March 2008. We captured males and females by hand while randomly searching the breeding ponds after dawn. We transported frogs to the site of the experiments located next to a third pond (47°43'N, 19°02'E), frequented by small populations of RD and RT. We kept individuals separated by sex in 35-litre plastic boxes filled with fresh pond water until the start of the experiment. We captured a total of 40 RD females, 140 RD males and 20 RT males. For each individual, we measured snout to vent length with a plastic ruler (± 1 mm) and body mass with a digital scale (± 0.1 g) and marked males for individual recognition with numbered waistbands. These consisted of a thick yarn bound around the waist of males and a 1 × 1 cm piece of self-adhesive tape stuck onto it. Waistbands did not seem to affect the behaviour of males. We removed waistbands before releasing males at the end of experiments.

We ran experimental trials in 20 plastic wading pools (80 cm diameter, 40 cm deep) containing ca. 15 cm of pond water, and a handful of sedge leaves providing cover and substrate for egg deposition. We assigned three RD males, one RD female and either a fourth RD male or an RT male to each container. The size of anuran breeding populations is highly variable over time, resulting in varying ratios of RT and RD at breeding sites. In the breeding ponds from which we collected animals, we have observed species ratios fluctuating between 1:2 and 1:20 (RT:RD) over the last decade (personal observation). Consequently, the ratio of male types in our experiment simulated conditions at the breeding site, where RD males usually largely outnumber RT males (Hettyey et al. 2003; personal observation). Density was also within the range that can be found in nature. We ran two consecutive rounds of trials, both started a few hours after dusk by placing three RD males into each wading pool and putting one RD female together with either a fourth RD male or an RT male into a covered plastic box (48 × 35 cm and 25 cm high, containing ca. 15 litres of pond water) placed next to each wading pool. Once amplexus had occurred, we moved the pair from the box to the wading pool containing three RD males. This allowed us to control species composition in initial pairs. Egg deposition never occurred in the plastic boxes or sooner than 8 h after we moved the pairs to the wading pools. We monitored each experimental unit every 20 min during the first hour and then every hour for the rest of the experiment. To collect information on whether a female was inactively hiding on the bottom or actively swimming around on the water surface, we noted vertical and horizontal positions of the female. We also

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