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Females trade off the uncertainty of breeding resource suitability with male quality during mate choice in an anuran

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In many species, females may be particularly selective about the expected direct benefits of choosing a potential mate or the male's genetic contribution to their offspring. Growing evidence suggests that female choosiness can also be influenced, for instance, by local abiotic factors, the social environment or the presence of heterospecifics. In amphibians that breed in highly temporary ponds with limited trophic resources (such as the yellow-bellied toad, *Bombina variegata*), competition during larval development may have a strong impact on the fitness of offspring. Accordingly, one might expect females to apply hierarchical decision making, balancing intraspecific competition risks during larval growth against the relative indirect benefits associated with the quality of the male. To investigate this issue, we conducted experiments in seminatural enclosures to test whether the preference of yellow-bellied toad females for good call attractiveness (determined by fundamental frequency) is affected by the risk of larval competition within the pond occupied by the callers. Overall, our results showed that females have a preference for low-frequency calls when prior information does not enable them to assess the relative quality of ponds. However, when prior information enables females to unambiguously determine relative pond quality, females appear to apply hierarchical decision making in which the quality of a pond prevails over call cues related to the quality of the male.

In many species, females may be particularly selective when they come to mate based on the expected benefits they might receive: either direct benefits resulting from male gifts or parental care, or indirect benefits related to a male's genetic contribution (Andersson, 1994). Males differ in heritable traits, and females would be expected to choose those bearing genes that will improve the offspring's genetic quality. This is affected by two main components: nonadditive genetic variance (the 'compatible genes' model) and additive genetic variance (the 'good genes' model) (Neff & Pitcher, 2005; Puurtinen, Ketola, & Kotiaho, 2009). In line with the latter, a clear female preference for costly male advertisements such as visual or acoustic signalling has frequently been documented (Iwasa & Pomiankowski, 1994). Yet evidence of enhanced offspring fitness resulting from female choosiness is more rare and, when reported, the benefit appears relatively weak (Head, Hunt, Jennions, & Brooks, 2005; Hine, Lachish, Higgie, & Blows, 2002; Neff & Pitcher, 2005; Petrie, 1994; Sheldon, Merilö, Qvarnström, Gustafsson, & Ellegren, 1997; Welch, Semlitsch, & Gerhardt, 1998). This low indirect benefit may result from environmental variance markedly blurring the effect of male sexual characteristics as well as offspring fitness (Kirkpatrick & Barton, 1997; Welch, 2003). There is now growing evidence suggesting that female choosiness is not trivial and can involve multimodal cues (Candolin, 2003; Gomez, Théry, Gauthier, & Lengagne, 2011) related to expectancy about different aspects of fitness (i.e. direct and indirect benefits) or unrelated (for instance, complementary or redundant information about male quality), and that these can be processed either as an amalgamated criterion or hierarchically (Candolin, 2003; Hebets et al., 2016). It is also now acknowledged that female choosiness is often context dependent (Bussiere, Hunt, Stölting, Jennions, & Brooks, 2008; Chaine & Lyon, 2008; Fricke, Perry, Chapman, & Rowe, 2009; Qvarnström, 2001). For example, it can vary greatly depending on the local environment (Edward & Gilburn, 2007; Grazer, Demont, Michalczyk, Gage, & Martin, 2014; Robinson, Sander van Doorn, Gustafsson, & Qvarnström, 2012), the social environment (Jann, Blanckenhorn, & Ward, 2000; Punzalan, Rodd, & Rowe, 2010; Richardson & Lengagne, 2010; Schwartz, Buchanan, & Gerhardt, 2001) and the presence of heterospecifics (Pfennig, 2000, 2007; Rundle, Chenoweth, & Blows, 2008;

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Svensson, Eroukhmanoff, Karlsson, Runemark, & Brodin, 2010). Such environmental constraints can increase the costs of searching for a mate, thus potentially leading to a reduction in the female's sampling and assessment accuracy, making them more permissive when it comes to less attractive males (Candolin, 2003). However, a clearer understanding of the outcome of a female's choices requires investigating the mechanisms underlying decision making, in particular how all this different information is processed and how uncertainty assessment is incorporated in the decision-making process (Castellano & Cermelli, 2011; Luttbeg, 1996, 2002).

Pond-breeding amphibians are a useful biological model for investigating context dependence in sexual selection. In these species, males usually produce advertisement calls, and females display choosiness in regard to particular call features, especially call frequency (dominant or fundamental; Bosch & Márquez, 2005; Burke & Murphy, 2007; Richardson, Joly, Léna, Plénet, & Lengagne, 2010), which is related to the caller's size (Wells, 2010). Female mate choice has also been linked to other call features, including pulse rate (Castellano & Rosso, 2006; Wagner & Sullivan, 1995), call rate (Smith & Roberts, 2003; Taylor, Buchanan, & Doherty, 2007) and call duration (Castellano, Rosso, Laoretti, Doglio, & Giacoma, 2000; Tarano & Herrera, 2003). While many studies have highlighted the fact that calling performance and male attractiveness are reliable predictors of offspring fitness components such as larval growth (Forsman & Hagman, 2006; Gerhardt & Huber, 2002; Jaquiéry, Broquet, Aguilar, Evanno, & Perrin, 2010; Reinhold, 2011; Welch et al., 1998), others have also suggested that such indirect benefits depend on the environmental context (Doty & Welch, 2001; Welch, 2003). The aquatic habitat required for larval development is the primary breeding resource in pond-breeding amphibians; this habitat varies across species from very small ephemeral water bodies to large permanent ponds (Cayuela, Besnard, Bechet, Devictor, & Olivier, 2012; Van Buskirk, 2005; Werner, Skelly, Relyea, & Yurewicz, 2007). For amphibians that breed in ephemeral water bodies, offspring fitness is strongly affected by competition between conspecifics for limited trophic resources (Morey & Reznick, 2004; Newman, 1998; Wells, 2010). Competition experienced during larval development can severely reduce offspring fitness as it can result in decreased body size at metamorphosis, a life-history trait that affects overwinter survival (Cabrera-Guzmán, Crossland, Brown, & Shine, 2013; Morey & Reznick, 2001; Schmidt, Hödl, & Schaub, 2012), dispersal ability (Chelgren, Pearl, Adams, & Bowerman, 2008; Chelgren, Rosenberg, Heppell, & Gitelman, 2006), juvenile growth (Altwegg, 2003) and size at sexual maturity (Altwegg & Reyer, 2003). In addition, high tadpole density decreases growth rate at the larval stage and consequently prolongs the exposure of tadpoles to predation (for a review, see Relyea, 2007), epidemic diseases (Touchon, Gomez-Mestre, & Warkentin, 2006) and desiccation (Denver, Mirhadi, & Phillips, 1998; Enriquez-Urzelai, San Sebastián, Garriga, & Llorente, 2013). Since the degree of larval competition may affect spawning decisions (Dillon & Fiaño, 2000; Halloy & Fiaño, 2000; Matsushima & Kawata, 2005; Resetarits & Wilbur, 1989, 1991), one might expect females to apply hierarchical decision making regarding both the environmental conditions prevailing in potential breeding ponds and the relative indirect benefits associated with male quality.

We investigated this issue in the yellow-bellied toad, *Bombina variegata*, an anuran that breeds in relatively small and highly temporary water bodies (Barandun & Reyer, 1998; Cayuela, Besnard, & Joly, 2013; Cayuela, Cheylan, & Joly, 2011). This species displays the four criteria distinguishing resource-based lek species: (1) the breeding resources (in this case, small temporary ponds) are occupied by males and act as an arena (or lek) to which females come to mate and in which most of the mating occurs (Schneider & Eichelberg, 1974; Schneider, Hussein, & Akef, 1986); (2) males do not provide direct benefits such as parental care or resources (except perhaps external fertilization) (Buschmann, 2002; Schneider & Eichelberg, 1974); (3) as in other anurans, males likely do provide indirect benefits through the effects of genetic contribution (Forsman & Hagman, 2006; Jaquiéry et al., 2010; Welch et al., 1998); (4) males actively defend call sites, but not spawning sites (Wells, 2010), and produce advertisement calls to attract females and/or deter competitors (Sanderson, Szymura, & Barton, 1992; Schneider et al., 1986; present study). In this species, the metamorphosis success and the local recruitment strongly depend on low desiccation risk and low competition experienced during larval development (Barandun & Reyer, 1997; Barandun, Reyer, & Anholt, 1997; Cayuela, Arsovski et al., 2016), so one would expect breeders to be particularly sensitive to these environmental factors when making mating decisions. Indeed, in a recent study we demonstrated that breeders strongly prefer occupying, mating and spawning in larvae-free ponds (Cayuela, Lengagne, Kaufmann, Joly, & Léna, 2016). This recent study also showed that females preferred the heavier male in a pair when each solely occupied a larvae-free pond, but this mating preference vanished when both males shared the same larvae-free pond. In all contexts, females usually mated successively with the same male and bred in ponds only when they did not contain larvae.

Following these results, one could hypothesize that pond quality overrides male quality in a female's decision-making process (Cayuela, Lengagne et al., 2016). The main objective of the present study was to investigate in detail the rules that govern female decision making in order to test this hypothesis. To do this, we envisioned two possibilities. First, females are unable to resolve uncertainty associated with the relative quality of a pond before a visit. This could occur if females do not use direct cues (notably waterborne odours) to determine pond quality, or if the available information does not allow an accurate assessment of the relative pond quality. In such cases, females might bet on the most attractive males if the preferred trait indicates either the intrinsic quality of the bearer or his ability to locate the most suitable ponds. However, if females were allowed to breed a second time, one would expect their subsequent decision to no longer depend on the male occupying each pond, but rather on the information gathered about the pond itself during the first visit. In the second, alternative, situation, direct cues would enable females to unambiguously determine the relative quality of a pond without visiting it. In this case, females would be able to select the most suitable pond whatever the relative quality of the male occupying it.

To investigate these two possible scenarios, we conducted pond choice experiments in seminatural enclosures that mimicked the situations described above. Pond quality was manipulated using larval competition as done in Cayuela, Lengagne et al. (2016) to be either of good quality (i.e. larvae-free) or of poor quality (i.e. presence of larvae). To manipulate the attractiveness of the male associated with each pond, we created soundtracks with contrasting call frequency as this call feature is usually related to female preference in anurans (females have been shown to prefer low-frequency calls; Bosch & Márquez, 2005; Burke & Murphy, 2007; Wells, 2010). Call frequency has also been found to be related to the size of the male in our model species, with larger males making lower-frequency calls (present study, see below). Three experiments were performed in which females had to choose between a pond associated with a low-frequency call and another associated with a high-frequency call. In the first two experiments, the ponds had an identical quality level, either at the upper quality limit (both ponds larvae-free, experiment A), or at the lower quality level (both ponds containing larvae, experiment B). In experiment C, pond quality was inversely contrasted with call attractiveness for