



Male mate choice contributes to behavioural isolation in sexually dimorphic fish with traditional sex roles



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ARTICLE INFO

Article history:

Received 26 January 2017

Initial acceptance 3 March 2017

Final acceptance 3 May 2017

MS. number: A17-00091R

Keywords:

behavioural isolation

darter

Etheostoma

male mate choice

preference

sexually dimorphic

Behavioural isolation between closely related species with exaggerated male mating traits is traditionally thought to be mediated by female preference for conspecific male ornaments. The role of male mate choice in maintaining boundaries between highly sexually dimorphic species is therefore comparatively neglected. However, mounting theoretical and empirical evidence supports the existence of male mate choice both within, and increasingly, between species with exaggerated male ornaments. We therefore tested the role of male mate choice in the maintenance of species boundaries for two sexually dimorphic species of darters (Percidae: *Etheostoma*). Using dichotomous choice assays, we measured male preferences of sympatric species *Etheostoma barrenense* and *Etheostoma zonale* for size-matched conspecific and heterospecific females, thus reducing the possibility that males would select for general indicators of fecundity. Our results show that males of both species strongly prefer conspecific females. A comparison with published data showed that the strength of preference for conspecific mates is just as strong for males as it is for females in *E. barrenense*. We also estimated the relative contribution of male mate choice, female mate choice and male–male competition to behavioural isolation. We found that male mate choice contributes as much as female mate choice to total behavioural isolation and thus likely plays an important role in behavioural isolation in these sexually dimorphic species. Our results suggest that the contribution of male choice to behavioural isolation should be studied in a larger variety of animal species to appreciate the relative roles of the sexes in the maintenance of species boundaries.

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In many animals, males benefit more than females from increased mating success, leading to a greater intensity of sexual selection on male mating traits (Andersson, 1994; Bateman, 1948). These differences between the sexes are due in part to differences in gamete investment and in part to a lack of male parental care, which leads to higher potential reproductive rates in males and a skewed operational sex ratio, with an overabundance of available males relative to females (Emlen & Oring, 1977). These sex differences are often used to explain the sexual dimorphism common in many polygynous species, where males are indiscriminate and showy while females are choosy and drab. In contrast, mating traits in monomorphic species are hypothesized to have equal intensities of sexual selection (Trail, 1990), or alternatively to be driven by similar natural selective forces between the sexes, with sexual selection playing a weak role in trait evolution (Björklund, 1984).

While parental investment, potential reproductive rates and the operational sex ratio have typically been used to predict mate choice, Edward and Chapman (2011) suggested that mating effort is also an essential factor in the evolution of mate choice. Mating effort includes investments that increase the number of mates available to an individual at the cost of reducing the ability to invest in future matings (Edward & Chapman, 2011). For example, increased investment in mate guarding or courtship displays may increase individual fertilization success, but it also subsequently reduces the ability to invest in future matings (Møller & Birkhead, 1991; Pilastro & Bisazza, 1999). By increasing the cost of mating investment, mating effort therefore can tip the balance in favour of the benefits of exhibiting mate choice. Because mating effort is typically a male investment, male mate choice may evolve in species that do not fit the traditional predictions for male mate choice (e.g. polygynous species with traditional sex roles).

Female choice itself also may create an opportunity for male mate choice to arise. If female preferences for attractive males creates large variation in male mating success, with a majority of males obtaining few or no matings, then a minority of males have the potential to mate with multiple females. Thus, even if the

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operational sex ratio is male biased, female preferences may create a scarcity of favoured males. If a male's capacity to mate with all available females is limited, and the costs of choice do not outweigh its benefit, then mate choice by high-quality males could be favoured (Edward & Chapman, 2011). For example, in the two-spotted goby, *Gobiusculus flavescens*, high-condition males are more successful at attracting mates, more successful in male–male competition and more likely to express mate preferences than low-condition males (Amundsen & Forsgren, 2003).

Male mate choice has been observed in several species of insects (reviewed by Bonduriansky, 2001), fishes (Côte & Hunte, 1989; Rowland, 1982; Sargent, Gross, & Van Den Bergh, 1986) and mammals (Kuester & Paul, 1996; Schwagmeyer & Parker, 1990) among others. However, the traits most often reported to be preferred by males are indicators of fecundity (e.g. large body size), which can be uniform across females of many species (Bonduriansky, 2001). Thus, evidence for male mate preference does not necessarily imply that male mate choice contributes to behavioural isolation (Hochkirch, Gröning, & Bücke, 2007; Kozak, Reiland, & Boughmann, 2009). In other systems, however, male choice appears to be important in maintaining species boundaries, for example, in Lepidoptera (Roelofs & Comeau, 1969), *Drosophila* spp. (von Schilcher & Dow, 1977) and snails (Johannesson et al., 2008). Notably, however, these species do not have exaggerated sexually dimorphic sexual ornamentation. Male preference for conspecific females has been demonstrated in some species of sexually dimorphic fishes (Gregorio, Berdan, Kozak, & Fuller, 2012; Knight & Turner, 1999; West & Kodric-Brown, 2015), but male choice in species with exaggerated male ornaments is rarely implicated in behavioural isolation. Rather, behavioural isolation between such species is thought to be primarily driven by female preference for conspecific male ornaments (Fisher, 1930; Lande, 1981; West-Eberhard, 1983), leaving the role of male choice in the behavioural isolation of sexually dimorphic species a neglected question.

Darters (Percidae: *Etheostoma*) are a diverse group of North American freshwater fish (Page & Burr, 1991), consisting of over 200 species, many of which are characterized by species-specific nuptial coloration (Kuehne & Barbour, 1983; Page, 1983). Coloration is largely limited to males and is expressed primarily during the breeding season (Page, 1983), suggesting that sexual selection has played a role in speciation. As such, much work has been done on the role of female mate choice and male–male competition in reproductive isolation in darters (Fuller, 2003; Martin & Mendelson, 2013; Mendelson, 2003; Mendelson, Imhoff, & Venditti, 2007; Williams & Mendelson, 2010, 2011, 2013). However, some evidence has begun to suggest a potential role for male mating preferences in behavioural isolation for some darter species as well. For example, in a comparative study across several pairs of darter species, Martin and Mendelson (2016) found that male courting preferences better predicted the strength of behavioural isolation than female spawning preferences, and Ciccotto, Gumm, and Mendelson (2013) showed that males of the darter species *Etheostoma luteovinctum* have strong association preferences for conspecific over heterospecific (*Etheostoma hopkinsi*) females.

Sympatric darter species *Etheostoma barrenense* and *Etheostoma zonale* are members of closely related subgenera (Porter, Fiumera, & Avise, 2002) that represent some of the most closely related darter species to co-occur without hybridizing in nature (Hubbs, 1955, 1967; Keck & Near, 2009). Males of the two species exhibit elaborate and divergent nuptial coloration, with male *E. barrenense* displaying primarily red-orange coloration with black blotches fused along the lateral line, while male *E. zonale* have alternating green and yellow bars along the body. Females of both species are drab in comparison to males, although they have some muted coloration and display the patterning of the conspecific males (Fig. 1). The two

species are largely syntopic where they co-occur (Williams & Mendelson, 2014) and display similar courtship and egg-laying behaviours, with neither sex in either species providing parental care (Page, Smith, Burr, & Mayden, 1985). Previous work with these species using dichotomous choice trials demonstrated strong association preferences in females for live conspecific males (Williams & Mendelson, 2010) and for conspecific male colour patterns on painted models (Williams & Mendelson, 2011), suggesting that female preferences contribute to behavioural isolation. In addition, however, in free-spawning assays, males of these two species exclusively courted conspecific females (Williams & Mendelson, 2010), suggesting that male choice also plays a role in behavioural isolation. However, males were not subject to the same dichotomous choice trials as females in this study, so whether assortative male courtship in free-spawning assays was a consequence of male preferences for female phenotypes is not clear.

Male *E. barrenense* and *E. zonale* also have been shown to exhibit increased aggression towards models painted to resemble conspecifics (Williams & Mendelson, 2013) and were more likely to chase away live conspecific males in seminaturalistic artificial stream environments (Williams & Mendelson, 2010), which suggests that male–male interactions also may contribute to behavioural isolation between these species. Therefore, we also considered the potential role of male–male competition in behavioural isolation. Male–male competition may influence speciation by facilitating divergence in male agonistic signals and aggressive responses through negative frequency-dependent selection or by promoting divergence in male traits, behaviours and/or resource use (Qvarnström, Vallin, & Rudh, 2012). For example, selective male exclusion of heterospecific individuals from preferred breeding sites has been shown to contribute to behavioural isolation between two species of *Ficedula* flycatchers (Vallin & Qvarnström, 2011).

In the present study, we sought to determine whether male preference for conspecific female visual signals contributes to behavioural isolation for sympatric darters *E. barrenense* and *E. zonale*, by measuring male association preference for physically and chemically isolated conspecific and heterospecific females. Additionally, we estimated the relative importance of male mate choice, female mate choice and male–male competition to behavioural isolation for this species pair using previously published data on female mate choice and male aggression bias (Williams & Mendelson, 2010) and our own measure of male mate preferences. Our results show strong association preference for conspecific females in males of both species and suggest that male choice can play a central role in the maintenance of species boundaries in this species pair.

METHODS

Fish Collection and Maintenance

We collected *E. barrenense* and *E. zonale* from the East Fork of the Barren River in Monroe Co., Kentucky, U.S.A. (36°44'51"N,

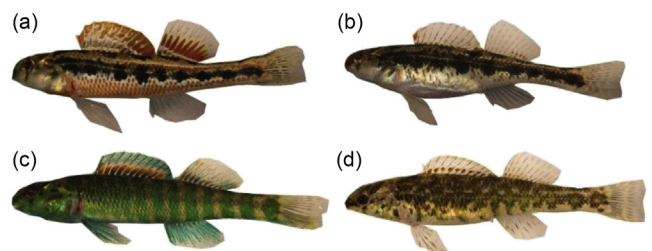


Figure 1. Focal species in breeding colours: (a) male and (b) female *Etheostoma barrenense*; (c) male and (d) female *Etheostoma zonale*.

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