



## Sexually asymmetric colour-based species discrimination in orangethroat darters



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Female mate preferences, male mate preferences and male–male competition can all potentially play roles in promoting speciation by sexual selection. The orangethroat darter, *Etheostoma spectabile*, is a sexually dichromatic fish in which males compete for access to females. We quantified male and female responses to conspecific versus heterospecific fish under normal light, dim light and blue light, the last of which impaired colour perception. We found that behavioural isolation was likely mediated primarily by male behavioural discrimination against heterospecific fish, with females showing no evident mate preferences. Furthermore, male aggression towards conspecific rivals was reduced in blue light, suggesting that the evolution of male coloration may contribute to speciation through male–male interactions.

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Sexual selection has long been hypothesized to drive speciation through coevolution of male ornaments and female preference, which results in behavioural isolation when two populations diverge in both traits to such a degree that females of one population no longer recognize males of the other population as potential mates (Fisher, 1930; Lande, 1981). Under traditional sexual selection theory, females are expected to show conspecific mate recognition for the same reason that they are expected to be choosy in selecting mates: female gametes are more costly to produce than male gametes, hence the cost of making a 'mistake' with a mate of inferior quality or incorrect species should be correspondingly higher for females than for males (Bateman, 1948; Wirtz, 1999).

However, male preferences for females have also been reported from multiple taxa, and may be selectively advantageous if males invest heavily in reproductive behaviours (e.g. parental care; Bonduriansky, 2001). Just as choosy females should be reticent to mate with heterospecific males due to negative fitness consequences, choosy males may similarly be predicted to discriminate

against heterospecific females; as a result, the evolution of behavioural isolation may rely on both sexes (Kozak, Reisland, & Boughmann, 2009; O'Rourke & Mendelson, 2010; Svensson, Karlsson, Friberg, & Eroukhmanoff, 2007). Further complicating the picture is male–male competition, which is increasingly recognized as a selective force underlying male ornament diversification (West-Eberhard, 1983). By promoting male trait divergence and/or modulating the effect of female preferences, male–male competition may directly contribute to speciation (Dijkstra & Groothuis, 2011; Hunt, Breuker, Sadowski, & Moore, 2009; Seehausen & Schluter, 2004). These three forces (female mate preferences, male mate preferences and male–male competition) may all interact to shape the form of selection on sexually dimorphic traits and behavioural isolation, and ideally all three should be considered when examining how sexual selection can drive speciation.

Darters (Percidae: Etheostomatinae) are a group of North American freshwater fishes that show high diversity (approximately 250 species) and widespread sexual dichromatism (Near et al., 2011; Page, 1983). Behavioural isolation appears to be the most important reproductive barrier between darter species, evolving faster and farther towards completion than other isolating mechanisms such as postzygotic hybrid inviability (Mendelson, 2003). Previous research suggests that behavioural isolation may

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be based on preferences for species-specific male coloration; both male and female *Etheostoma zonale* and *Etheostoma barrenense* prefer to associate with fish models painted in conspecific colours (Williams & Mendelson, 2011, 2013). Darters thus represent potentially fruitful subjects for understanding how the diversification of male coloration may facilitate speciation.

The orangethroat darter, *Etheostoma spectabile*, and the rainbow darter, *Etheostoma caeruleum*, are members of the subgenus *Oligocephalus* and are similar in morphology, behaviour and ecology. Males of both species show blue-green and orange-red breeding coloration. The most obvious visual difference between male *E. spectabile* and *E. caeruleum* is the presence of an orange-red colour patch on the anal fin of the latter. They have widely overlapping ranges in the eastern United States and often co-occur in close proximity (Kuehne & Barbour, 1983; Page, 1983). Both species spawn during the spring and lack parental care; males are non-territorial and follow gravid females while attempting to drive away conspecific rivals. Females that are ready to spawn bury themselves shallowly in the substrate; with the arrival of one or more males, the fish release eggs and sperm (Winn, 1958). There is little evidence for inviability in *E. spectabile*–*E. caeruleum* hybrids, at least in the F1 generation (Hubbs & Strawn, 1957; Linder, 1958). Nevertheless, reproductive isolation between these species is heightened to near-completion in sympatry relative to allopatry, suggesting that there is selective pressure against heterospecific mating (Zhou & Fuller, 2014). Female *E. spectabile* show no preference for more colourful males or for conspecific males in dichotomous choice trials (Pyron, 1995; Zhou & Fuller, 2012). Sexual selection on male coloration, and any resultant effects on behavioural isolation, may therefore occur via alternative processes to female preference, such as male–male competition.

## METHODS

We conducted a series of behavioural observation trials to assess (1) the relative contributions to sexual selection and behavioural isolation by male and female *E. spectabile*, and (2) the signalling role of male coloration in within- and across-species interactions. To determine whether male coloration encodes behaviourally relevant information, we used coloured lighting to disrupt colour perception by the fish. Similar behavioural experiments using lighting manipulation have been conducted in guppies, *Poecilia reticulata* (Long & Houde, 1989), threespine sticklebacks, *Gasterosteus aculeatus* (Brooks & Endler, 2001; Milinski & Bakker, 1990) and cichlids (*Haplochromis nyererei* complex; Seehausen & van Alphen, 1998), wherein female preferences for a particular colour expressed by the males could be eliminated using lighting conditions that impeded the perception of that colour. As a prerequisite step for informing our lighting treatments, we investigated the visual pigments of *E. spectabile* and *E. caeruleum* via microspectrophotometry.

### Microspectrophotometry

Adult *E. spectabile* ( $N = 2$  females) and *E. caeruleum* ( $N = 1$  female, 2 males) were collected by seine net from a tributary of the Embarras River (Douglas Co., IL, U.S.A.) in June 2009 and transported to Cornell University (Ithaca, NY, U.S.A.). Microspectrophotometry was performed following the methods described in Loew (1994). The fish were dark-adapted for at least 12 h and then euthanized by cervical transection under infrared light. The eyes were enucleated, hemisected and placed in Sorensen's phosphate buffer (pH 7.2) with 6% sucrose, whereupon the retinas were separated from the pigment epithelium with razor blades and tungsten needles. Pieces of retina were sandwiched between two

coverslips sealed with grease and transferred to the microspectrophotometer.

The measurement of absorbance has been described in detail elsewhere (Loew, 1994; Provencio, Loew, & Foster, 1992). Briefly: absorbance was recorded from single cone and rod cells in 1 nm increments from 750 to 300 nm and then back to 750 nm. The data were smoothed using the 'smooft' digital filtering routine (Press, Flannery, Teukolsky, & Vetterling, 1987) and the smoothed spectrum was then overlaid with the unsmoothed spectrum and inspected by eye to ensure no shift in the apparent maximum. The absorbance maximum ( $\lambda_{\max}$ ) was determined by fitting vitamin A<sub>1</sub> and A<sub>2</sub> template curves from Lipitz and Cronin (1988), using the Mansfield's method as described in MacNichol (1986). Data that did not meet the selection criteria given in Loew (1994) were disregarded. We averaged the  $\lambda_{\max}$  values of the three cell types from each individual.

### Experimental Observations

Adult *E. spectabile* and *E. caeruleum* were collected by seine net (dimensions 106 × 122 cm) from three adjacent tributaries of the Salt Fork River, Illinois in April and May of 2013, during the breeding season of these species. Both species were encountered at all three sites during the collection period. The fish were maintained in group tanks segregated by species and sex, at a temperature of 20 °C and a 13:11 h light:dark cycle. Fish were fed frozen bloodworms (chironomid larvae) daily; behavioural observations were performed prior to feeding on that day.

Behavioural trials took place in a 38-litre aquarium (bottom area 25 × 50 cm) with naturalistically coloured gravel substrate. Illumination was provided by six 15 W 'daylight' fluorescent tubes (Damar F15t/8d) positioned directly above the tank. Three light quality treatments were used: control (no filter), grey and blue. The grey treatment was achieved by passing the overhead light through four 0.6 'Neutral Density' filter sheets (LEE Filters). Similarly, the blue lighting treatment was achieved via a single 'Winter Blue' colour filter sheet (LEE Filters). The blue lighting treatment was designed to suppress stimulation of the long-wavelength-sensitive cones in the retina (see Results), and thus interfere with the fish's ability to discern the orange and red components of male breeding coloration.

To assess the effectiveness of the lighting filters, we measured the downwelling irradiance using an Ocean Optics USB 2000 spectrophotometer connected to a 400 µm diameter patch cord connected to a cosine corrector. A calibrated deuterium-halogen 2000 lamp (Ocean Optics) was used to calibrate the spectrophotometer, and data were taken using SpectraSuite software. The grey filter yielded light with a similar profile to the control at much lower intensity, whereas the blue filter virtually eliminated wavelengths above 530 nm while allowing through blue light of 400–530 nm (Fig. 1). We multiplied the irradiance and the absorbance of the two cone types from 400 to 600 nm, and summed the area beneath the two curves to obtain a rough estimate of the total light available to the fish's eye in the different light quality treatments. The amount of available light under the grey filter was approximately 0.3% that of the control, whereas the available light under the blue filter was approximately 4% that of the control. Hence, the grey filter allowed through much less light overall than the blue filter, but with similar spectral characteristics to the control.

To further verify that the blue filter selectively obscured the orange-red components of male mating coloration, we used the Ocean Optics spectrophotometer to measure the coloration of a single male *E. spectabile*. The fish was first anaesthetized in a 0.03% tricaine methanesulfonate (MS-222) solution, which has been used

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