



Evening up the score: sexual selection favours both alternatives in the colour-polymorphic ornate rainbowfish

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Sympatry of multiple, interbreeding colour morphs within a single population requires equilibrium between the various agents of selection acting on alternative colour morphs. This colour polymorphism is an area of growing interest in evolutionary biology as it contradicts many assumptions of natural and sexual selection. Owing to the strong role of colour in intraspecific communication, sexual selection is a primary candidate for balancing selection and its potential is supported by a growing body of both empirical and theoretical evidence. We examined patterns of mate choice in the ornate rainbowfish, *Rhadinocentrus ornatus*, a small freshwater fish species from the wallum habitat of east coast Australia, to see whether nonrandom mating contributes to colour polymorphism maintenance in this system. Populations from Fraser Island and the adjacent mainland comprise a common blue morph and a rare red morph. These colour morphs are present in both males and females, with red individuals accounting for approximately 18% of the individuals in our focal population from Fraser Island. In dichotomous laboratory mate choice experiments, we found that female *R. ornatus* preferred males of the opposite colour morph to themselves, a mating pattern known as negative assortative mating, which may provide indirect benefits to females through the generation of outbred offspring. In contrast, males preferred red females irrespective of their own colour morph, suggesting females may possess red morph-specific traits that are the target of sexual selection by males. Our findings support an emerging pattern that suggests that multiple selection pressures may interact to maintain alternative colour morphs.

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Colour ornamentation is often a key element in intraspecific communication (Brooks & Endler 2001; Maan et al. 2006; Kokko et al. 2007), with behavioural processes such as mate recognition and mate choice frequently relying upon the information provided by colour signals (Alexander & Breden 2004; Dijkstra et al. 2007). In particular, sexual selection based on colour ornamentation can result in the fixation of a single phenotype, or colour morph, leading to monomorphic populations comprised entirely of an optimal phenotype. Colour polymorphism, where more than one colour morph persists within a population, is not predicted under traditional selection theory and is a rare occurrence in natural populations (Gray & McKinnon 2007; Roulin & Bize 2007). However, sexual selection has the potential to maintain within-population colour polymorphism by equalizing the fitness of different colour morphs (Galeotti et al. 2003; Gray & McKinnon 2007; Roulin & Bize

2007). Nonrandom mating through linear sexual selection, positive assortative mating and negative assortative mating have strong potential to maintain colour polymorphism (Gray & McKinnon 2007; Roulin & Bize 2007).

Traditional sexual selection theory has focused on linear selection, where all individuals prefer the same phenotype (Roulin 2004; Gray & McKinnon 2007; Roulin & Bize 2007). In this instance, we use linear selection to refer to a pattern of nonrandom mating where selection favours one colour morph where alternative morphs are present. This is intended to distance this idea conceptually from that of directional selection, which typically refers to selection for exaggeration of individual traits in a specific direction. In colour-polymorphic species, linear selection is most likely to act as a compensatory mechanism for the relative infrequency of that phenotype in the population (Gray & McKinnon 2007). Known as negative frequency-dependent selection or the 'rare male effect', this type of linear selection is yet to receive empirical support (Gray & McKinnon 2007; Roulin & Bize 2007), with the closest known process being a preference for novel males in the guppy, *Poecilia reticulata* (Brooks & Endler 2001; Eakley & Houde 2004; Kokko et al. 2007). The assumed benefit of mating with rare partners is the production of outbred or heterozygous offspring, which may outweigh the cost of finding the rare morph and securing

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mating opportunities (Roulin & Bize 2007). Alternatively, individuals may select rare partners not for complementary genes but for other beneficial traits associated with the morph itself (Roulin & Bize 2007), in which case its rarity does not itself predict mate choice. Preference for common morphs, however, is not undocumented. For example, males of several species within the dragonfly order Odonata adjust their mating preference to male-like or female-specific colour morphs, whichever is more common (Van Gossum et al. 1999, 2007).

Circumstances in which the colour-polymorphic trait is exhibited by both sexes may foster more complex patterns of sexual selection. The role of colour in mate recognition has led to strong support for positive assortative mating as a mechanism for the maintenance of within-population colour polymorphism. Assortative mating occurs through pairing of similarly coloured individuals and may occur where there is selection against intermorph hybrid inferiority (if colour morphs are adapted to different conditions e.g. visual habitats) or where genetic compatibility between morphs is reduced (Gray & McKinnon 2007). Positive assortative mating is well documented in avian species, with strong evidence in the case of the Gouldian finch, *Erythrura gouldiae*. Pryke & Griffith (2007) demonstrated strong assortative pairing in ca. 80% of breeding pairs in field and aviary observations, reinforced by their subsequent finding that partial reproductive isolation reduces hybrid viability, particularly in females (Pryke & Griffith 2008).

Far less common is the process of negative assortative mating, where individuals preferentially mate with colour morphs that are different from their own (Gray & McKinnon 2007; Roulin & Bize 2007). Still poorly understood, negative assortative mating has strong potential to maintain within-population colour polymorphism. Heterozygote advantage has long been touted as a mechanism for the maintenance of within-population genetic diversity. If hybrid offspring have increased fitness because of heterozygosity, the most beneficial strategy of mate choice would be to select partners based on genetic complementarity. If colour is a reliable signal of underlying genotype, this may provide strong selection for negative assortative mating. However, the preference of one morph for partners of the opposite morph is still yet to be empirically demonstrated, and this may be because of the focus of previous studies on systems that have the potential for gene flow or introgression between populations (see Gray & McKinnon 2007; Roulin & Bize 2007 for examples), or where spatial segregation is facilitated. Conversely, individuals from isolated populations may be more likely to encounter close relatives when searching for potential mating partners, whereby selection of partners based on phenotypic similarity would further increase this risk.

Freshwater fish species are ideal for examining sexual selection (Hughes et al. 1999; Brooks & Endler 2001; Alexander & Breden 2004; Eakley & Houde 2004; Wong et al. 2004; Kokko et al. 2007), often displaying strong preference for secondary sexual characters, including colour ornamentation. Furthermore, obligate freshwater species often represent discrete populations, being restricted to drainages or even to specific sites with little chance for migration and introduction of new alleles (McGlashan & Hughes 2002). This places great importance on within-population processes. To date, studies of colour-polymorphic freshwater fish species have been largely restricted to examining the maintenance of male polymorphism, owing to sexual dimorphism in the trait among the majority of these species (Fuller 2002; Eakley & Houde 2004). This restricts the role that assortative mating, either positive or negative, can play in these systems. Where colour polymorphism is expressed in both sexes, study systems represent sympatric sister or incipient species where polymorphism is partitioned between subspecies. As a result, empirical support is overwhelmingly in favour of positive assortative mating in freshwater fish.

The ornate rainbowfish, *Rhadinocentrus ornatus*, is a unique freshwater fish species in that it displays a within-population colour polymorphism that is expressed in males and females. Populations of *R. ornatus* from Fraser Island, Queensland possess a known colour polymorphism comprising a common blue morph and a rare red morph (Fig. 1; Allen & Cross 1982; Allen et al. 2002; Pusey et al. 2004). This colour polymorphism provides an ideal system for examining the pattern of sexual selection in both sexes, and how this may differ between colour morphs. Using a focal population, we assessed the relative frequency of red and blue morphs in each sex and the proportion of red coloration expressed within the red morph, which is known to vary among individuals. We then conducted dichotomous mate choice experiments to test competing hypotheses of nonrandom mating, and examine mating preferences between male and female ornate rainbowfish.

METHODS

Study System

Habitat

The ornate rainbowfish is a small, obligate freshwater fish species restricted to the coastal wallum habitat of eastern Australia (Page et al. 2004). The streams and lakes inhabited by *R. ornatus* are situated in coastal scrub and heath and are generally fed by natural springs, making their water soft and acidic (pH 3.5–6; D. Hancox, C. J. Hoskin & R. S. Wilson, unpublished data). Individual sites also vary in the level of tannin stain that remains after filtration by aluminium compounds as the water is drawn to the surface. This results in

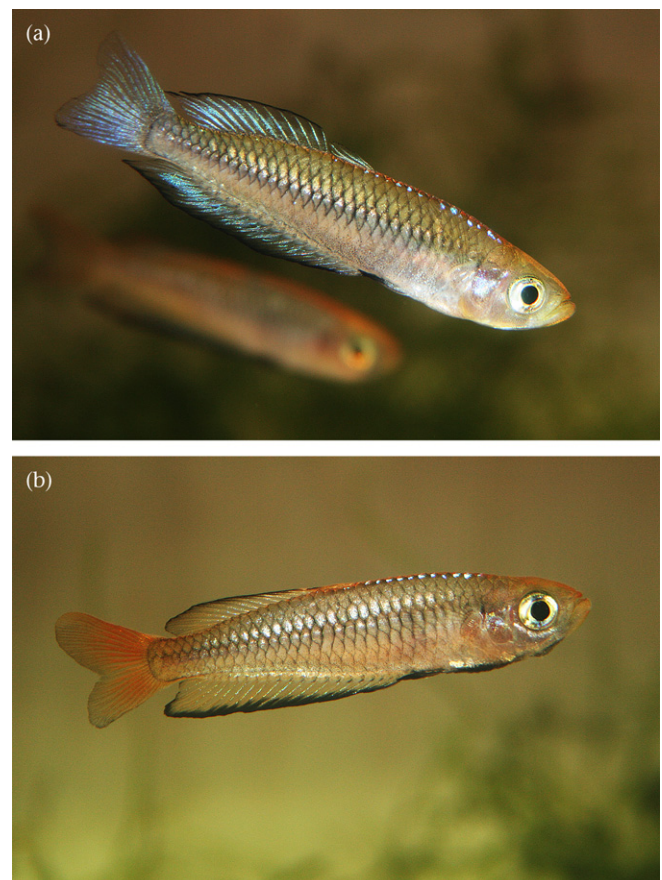


Figure 1. (a) Blue and (b) red male ornate rainbowfish from Gerowweea Creek, Fraser Island.

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