



## Selective use of multiple cues by males reflects a decision rule for sex discrimination in a sexually mimetic damselfly



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### ARTICLE INFO

#### Article history:

Received 25 August 2013

Initial acceptance 21 November 2013

Final acceptance 24 February 2014

Published online

MS. number: A13-00702R

#### Keywords:

colour

decision rule

*Enallagma*

intraspecific sexual mimicry

novel phenotype

Odonata

pattern

polymorphism

sex recognition

Discriminating between the sexes when one sex resembles the members of the other sex may be challenging. When sexual mimicry imposes costs on signal receivers, receivers can minimize confusion by using nonmimetic cues that differ between the models and the mimics. We tested this hypothesis in a female-specific polymorphic damselfly *Enallagma hageni*, whose blue coloration of andromorphic females resembles that of males, whereas the heteromorphic females have a distinctive green colour. Both female morphs share an abdominal pattern that differs from the males'. We predicted that males selectively use both colour (the mimetic cue) and pattern (the nonmimetic cue) in sex recognition: they use the nonmimetic cue only when the encountered individual has the mimetic colour. We modified the abdominal pattern of males, andromorphs and heteromorphs to resemble that of the opposite sex, and recorded males' reactions to pattern-altered and control individuals both in an arena and in the field. Our results supported our hypothesis. We then derived and tested potential male decision rules based on the two visual cues for sex recognition. We presented focal males with unnatural, orange females possessing either a male or female abdominal pattern, and recorded the reactions of mate-searching males to individuals with a novel pink-painted phenotype. Males reacted sexually to orange- and pink-painted individuals regardless of the abdominal pattern. Collectively, our results support a male discrimination rule of 'if not blue, then female', providing insights into the origin of phenotypic novelty in colour-polymorphic species.

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An animal's life is filled with discrimination tasks, such as differentiating between its own and other species, kin and nonkin, palatable and nonpalatable prey, as well as mates of various qualities (Duncan & Sheppard, 1965; Hepper, 2008; Ryan, 1990; Walker, 1974). Among such choices, one of the most fundamental is to discriminate between one's own and the opposite sex. Individuals from a wide range of invertebrates and vertebrates are known to distinguish sex using sex-specific visual (Rutowski, 1977; Sætre & Slagsvold, 1992), acoustic (von Helversen & von Helversen, 1997) or chemical cues (Ferkin & Johnston, 1995; Tregenza & Wedell, 1997). However, the task becomes challenging when one sex of a species resembles the opposite sex or other species. Bluegill sunfish, *Lepomis macrochirus*, represent an example of intraspecific sexual mimicry where some smaller males may mimic female morphology as an alternative mating strategy while avoiding

aggression from other males during spawning (Dominey, 1980; Gross, 1982). Another well-known example is the interspecific sexual deception of orchids that attract male hymenopterans as pollinators by mimicking mating signals of the female hymenopterans (Schiestl, 2005).

Numerous studies have focused on demonstrating how sexually mimetic signals fool the signal receivers (Gaskett, 2011; Oscar, Abby, & Morris, 2010; Slagsvold & Sætre, 1991), yet it is equally important to understand how receivers respond to the mimicry beyond their initial confusion. Sexually mimetic signals can be costly for the receivers (Semple & McComb, 1996). For example, mating between a nesting female and a female-mimicking male pied flycatcher, *Ficedula hypoleuca*, can compromise the fitness of a territorial male that fails to recognize its competitor (Sætre & Slagsvold, 1995). Understanding how receivers perceive and react to sexually mimetic cues is integral to predicting the dynamics between receivers and signallers in a sexual signalling system. However, although the evolutionary responses of receivers have long been studied in the context of predator–prey and brood parasite–host interactions (Lotem, Nakamura, & Zahavi, 1995;

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Turner & Speed, 1996), we know relatively little about how receivers recognize sex in the presence of sexual mimicry (but see Wong, Salzmann, & Schiestl, 2004).

One way receivers can lower the cost of mimicry is to adjust their discrimination level in response to external cues (Holen & Johnstone, 2006). For example, superb fairy-wrens, *Malurus cyaneus*, lower their discrimination threshold for egg rejection when brood parasites are near the nest (Langmore, Cockburn, Russell, & Kilner, 2009). Alternatively, we propose that receivers can lower the cost of mimicry by increasing attention to nonmimetic cues, an addition to Arnqvist's (2006) hypothesis for receiver resistance to sensory exploitation. Furthermore, if discrimination of nonmimetic cues imposes assessment or other costs to the receivers, we propose that a receiver seeking to optimize its efficiency of discrimination should use nonmimetic cues only when the mimetic cue is insufficient to distinguish sex.

Evidence for such use of nonmimetic cues comes from egg mimicry of a brood parasite. The eggs of a cuckoo finch, *Anomalospiza imberbis*, and those of its host, *Prinia subflava*, are similar in colour and pattern proportion, but differ significantly in pattern dispersion. The host uses multiple visual cues to reject parasitic eggs, among which colour (a mimetic cue) and pattern dispersion (a nonmimetic cue) are the two most important cues (Spottiswoode & Stevens, 2010). In the context of sexual mimicry, an experiment on the Augrabies flat lizard, *Platysaurus broadleyi*, showed that female-mimicking males ('she-males') mimic visual, but not chemical, signals of females; accordingly, 'he-males' court she-males based on visual signals alone at long distance, however, at closer range where chemical signals become detectable, he-males become less likely to court she-males (Whiting, Webb, & Keogh, 2009).

Female-specific, colour-polymorphic damselflies provide an advantageous system to test the optimal use of nonmimetic cues. In such species, there are usually two female morphs: an andromorph whose coloration is similar to that of the males and a heteromorph whose coloration distinctly differs from that of the males (Johnson, 1975). Both female morphs share traits that differ from those of males, such as body size, abdomen width, wing shape and the melanin pattern (Abbott & Svensson, 2008; Gorb, 1998). In a female colour-polymorphic damselfly, *Enallagma ebrium*, the sexually dimorphic abdominal dorsal pattern, in addition to coloration, affects sex recognition of mate-searching males (Miller & Fincke, 1999). Odonates have highly acute vision (Briscoe & Chittka, 2001; Bybee, Johnson, Gering, Whiting, & Crandall, 2012) and, even though the chemoreceptors are present in the antenna of odonates (Rebora, Salerno, Piersanti, Dell'Otto, & Gaino, 2012; Slifer & Sekhon, 1972), to date there is no evidence that damselflies use modes of communication other than vision in mate searching and sex recognition (Corbet, 1999).

Using the female-specific polymorphic damselfly *Enallagma hageni*, we tested the hypothesis that males determine the sex of the blue andromorphic females using the sexually dimorphic abdominal dorsal pattern. Here, 'colour' refers to spectral reflectance properties and 'pattern' refers to the distribution of colour patches across body parts. Throughout the paper, we refer to 'mimicry' in the sense of signal similarity in coloration between andromorphic females and males. We modified the abdominal pattern to resemble that of the opposite sex in individuals of three colour types: andromorph, heteromorph and male, and presented a control and a pattern-altered individual of the same colour type to focal males (see Fig. 1). We had two specific predictions: (1) painting the abdominal pattern of a male or an andromorphic female (i.e. the mimetic female) to resemble that of the opposite sex would change the probability of a male's sexual reaction and (2) painting the abdominal pattern of a

heteromorphic female (i.e. the nonmimetic female) to resemble that of a male would not affect the probability of sexual reactions towards her. Additionally, to further deduce how males make decisions based on information from colour and pattern, we recorded the reactions of males to unnatural, orange-painted females with either a female or male pattern both in the arena and in the field. We also recorded the reactions of mate-searching males in the field to individuals of both sexes that were painted pink (i.e. a completely novel colour in the genus) with their natural abdominal patterns (see Fig. 3). Our results suggest differential use of visual cues by males in sex recognition in the presence of female polymorphism with sexual mimicry, and a possible decision rule for sex recognition that could facilitate the origin of novel colour phenotypes in polymorphic systems.

## METHODS

### *Study Species and General Methods*

Male *Enallagma* damselflies search for mates around breeding sites on the edge of ponds and lakes but also in areas far from shore (Fincke, 1986). There is intense scramble competition for mates among males, although operational sex ratios (male:female) at lakeshores are much higher than in surrounding forests (Fincke, 1982).

Like the majority of species in the family Coenagrionidae (Fincke, Jödicke, Paulson, & Schultz, 2005), the common North American bluet damselfly, *Enallagma hageni*, shows female-specific colour polymorphism. The andromorph has blue coloration similar to that of the males, except that the andromorph's reflectance peaks at a slightly longer wavelength, and is less bright and saturated, whereas the green coloration of the heteromorph has a spectral reflectance distinct from that of the males and the andromorph (Fincke, Fargevieille, & Schultz, 2007). Whereas both sexes have a striped thorax, both female morphs have a uniformly black abdominal dorsum that is distinct from the male's striped abdominal pattern. In addition to the abdominal dorsal pattern, there are several additional visual cues that differ between the sexes, such as body size and abdomen width (Fincke, 1982; Gorb, 1998). However, the two female morphs do not differ in body size as measured by wing length (Fincke, 1994) or abdomen width; nor do andromorphic females mimic males in behaviour (Fincke, n.d.). The two female morphs do not differ in fecundity (Fincke, 1994) and thus are of equal value to mating males. Here we limited our investigations to the use of colour- and pattern-related traits by males. Hence, heteromorphic females, which do not differ from andromorphic females in other sex cues (e.g. abdominal width, body size, presence of an ovipositor), represented a within-species control for visual cues to sex other than colour and pattern. One-fourth to one-third of the females in our study populations in 2010, 2011 and 2013 were andromorphs.

Male *E. hageni* should be able to perceive orange and pink because a long-wavelength photoreceptor appears to be ancestral in damselflies (Bybee et al., 2012). Whereas the genus *Enallagma* includes an orange species, *E. signatum* that co-occurs with *E. hageni* over much of *E. hageni*'s range (Schultz, Anderson, & Symes, 2008; Schultz & Fincke, 2013), pink coloration is a novel trait for North American members of the family Coenagrionidae (i.e. the European *Ischnura elegans rufescens* may have a spattering of pink on the underside of the orange thorax), distinct in reflectance from that of red or violet damselflies (e.g. *Enallagma pictum*: Schultz et al., 2008; *Argia fumipennis violacea*: T. D. Schultz, personal communication, 20 February, 2014; see also Romney & Tarow, 2002). Colour and pattern manipulation in the

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