



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



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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

experiments were done using the nontoxic acrylic paint colours (DecoArt, Stanford, KY, U.S.A.) ‘Lamp Black’, ‘Ocean Blue’, ‘Mistletoe’ (green), ‘Bright Orange’, or ‘Dragon Fruit’ (pink). In the experiments below, we collected only sexually mature individuals found in tandem pairs as control or manipulated individuals. We glued the tips of legs of a live *E. hageni* to the end of a wooden dowel with either Beacon Quick Grip adhesive (Beacon Adhesive Inc., Mount Vernon, NY, U.S.A.) or Duco Cement household glue (Duco Technology Inc., Henderson, NV, U.S.A.), such that the damselfly was perched in a natural posture and was able to move its head and wings. All individuals remained alive throughout a test. Except where noted, each individual was used for only one trial, after which it was released by gently separating the tips of legs from the glue; most flew away, although sometimes one or more legs were autotomized at the joint. Occasionally, we found painted individuals in tandem within minutes of being released. In field experiments, individuals on the dowels were placed at the level of the top of surrounding vegetation. Only the most sexually extreme reaction for each reacting male was recorded. In field tests, to prevent reacting males from being counted twice, they were collected, marked on the wing, and held for the duration of the trial. All trials were conducted in full sun.

Experiment 1a and 1b: Use of Colour and Pattern in Sex Recognition: Arena and Field

Presentations of live individuals to focal males were conducted in a white plastic arena placed in a forest gap in the Chase Osborn Preserve, Sugar Island, MI, U.S.A. (46.4°N, 84.2°W) between June and July 2010. The arena was cylindrical, 110 cm in diameter, 60 cm in height, and had an observation window of 10 cm diameter near the top. The white wall and top of the arena (a white sheet) provided standard background that eliminated the confounding effect of the conspicuousness of the colour types against vegetation background in the field. A small blueberry bush in the arena served as a perch site for focal males.

Focal males were collected early in the morning before they started to fly and randomly assigned to one of the three colour type treatments (Fig. 1). We presented to a total of 30, 36 and 30 focal males a pair of either males, andromorphs or heteromorphs, respectively (i.e. 192 total trials). In the male treatment, the focal male was sequentially presented with a control male and a male

whose abdominal dorsum was painted uniformly black (i.e. the female pattern). We used natural controls in 19 of those trials and sham controls painted with male coloration in 11 trials. In the andromorph treatment, the focal male was presented with a control female (natural control in 24 trials and black-sham-painted controls in 12 trials) and a blue female that was painted with blue paint to create the male blue-and-black striped dorsal pattern (Fig. 2a). The corresponding heteromorph treatment used either a natural (19 trials) or black-sham-painted control female (11 trials) and a female painted with the male abdominal pattern. The presentation sequence of female or male pattern was randomized among focal males. The individual on the dowel was slowly moved towards a perching focal male from behind until the presented individual was in front of, and approximately 3 cm below the focal male's head. Such a presentation position has been shown to be most likely to elicit a focal male's reaction (Gorb, 1998). A focal male's reaction towards a presented individual was noted as either no response within 1 min, switch perch, hover, grab, tandem attempt, or tandem. ‘No response’ and ‘switch perch’ were treated as a male's lack of interest in mating and were excluded from the analyses. Hover was regarded as a nonsexual reaction, whereas grab, tandem attempt and tandem were regarded as sexual reactions. The presentation ended if the focal male grabbed, attempted tandem or formed tandem with the presented specimen; otherwise, the presentation was repeated three times and the most extreme sexual reaction was used for analysis.

To determine whether the results from the arena were consistent with male behaviour under more natural conditions of sex ratio, male–male competition for mates and the presence of males as andromorph distractors, we measured the reactions of free-flying males to the six types of individuals on dowels (i.e. male, andromorph and heteromorph with either male or female dorsal pattern) in the field over 3 days in July 2010. A total of six replicates were conducted for each type: three in grass close to the lakeshore and three in forest light gaps. We ran trials at these two locations because males search for mates at both sites (Fincke, 1986). Three observers recorded the reactions of the first 10 males (but the first 15 in two trials and the first 12 in one trial) that reacted to the individual on the dowel. In summary, we observed reactions of a total of 391 mate-searching males to 36 focal individuals on the dowels. The observers, blind to the purpose of this experiment, stood 1 m away from the dowels. At this distance, the type of the individual on the dowel was not easily discernible (e.g. a natural

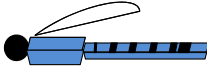
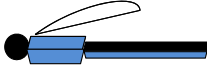
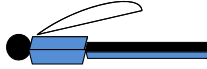
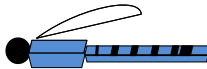




Colour type	Pattern		Predictions: % Sexual reaction
	Control (C)	Manipulated (M)	
Male			C < M
Andromorph			C > M
Heteromorph			C = M
Orange			C = M

Figure 1. Designs and predictions of experiments 1 and 2 for the control and pattern-altered individuals of *Enallagma hageni* in the arena and field. C: control individuals; M: pattern-manipulated individuals. Control individuals had natural coloration (males and andromorphic females were blue, heteromorph females were green). The black parts show the natural melanin or black-painted abdominal dorsal pattern.



Figure 2. (a) An andromorphic female *Enallagma hageni* painted with the striped male abdominal dorsal pattern (above) and a natural male (below) glued to wooden dowels, and (b) an andromorphic female *E. hageni* painted with pink paint on her body where the original colour was blue.

male or a blue female painted with male pattern). As in the arena, male reactions were categorized as either hover, grab, tandem attempt, or tandem. Hover was treated as a nonsexual reaction whereas the rest were considered sexual reactions.

Experiments 2a and 2b: Deduction of Male Decision Rule from Orange-painted Individuals

In experiment 2a, we individually presented each of 35 focal males with orange-painted, heteromorphic females in the arena in August 2010 and June 2011. Each focal male was randomly assigned to either the female pattern or the male pattern treatment. Females were painted orange on their thoraces and abdomens where the natural coloration was green (Fig. 1). In addition, in experiment 2b, using the protocol as in field experiment 1b, we recorded the reactions of 80 unique mate-searching males towards orange-painted females with either a female ($N = 4$) or male ($N = 4$) pattern in late July 2011 at Cheboygan Marsh, MI (45.38°N, 84.28°W).

Experiments 3: Deduction of Male Decision Rule from Pink-painted Individuals

To determine whether a male’s decision rule could be generalized to completely novel phenotypes of both males and females in the field, on 20 sunny days between 26 June and 22 July 2013 at Larks Lake, MI (45.1°N, 84.2°W), we recorded the reactions of mate-searching males to control or pink-painted males and females of both morphs. Manipulated individuals were painted pink where their natural colours were blue or green (Fig. 2b) whereas controls were either natural (for all three colour types) or sham-painted (for andromorphs and heteromorphs only). The natural abdominal dorsal pattern was retained for all three colour types (Fig. 3). Individuals on dowels were positioned in grass 3–5 m from shore. We used six types of individuals: 17, 23 and 21 pink-painted and 13, 18 and 19 natural control andromorphs, heteromorphs and males, respectively, as well as 9 and 14 sham control andromorphs and heteromorphs (Fig. 3). Each of the six types was positioned one at a time at the same site in a random sequence; sites changed among replicates.

We recorded reactions of passing males for 10 min, scoring them as ‘fly-by’ (male passed within 5 cm of the individual on the dowel without subsequent reaction), hover, grab, tandem attempt, or tandem, as described above. Fly-by and hover were considered nonsexual reactions, whereas the remaining three were considered sexual reactions. We also recorded the number of nonreacting males passing within a 1 m² square around the dowel; the total number of males per m² per 10 min was used to control for variation in male density among trials. A few painted individuals were used in two trials; none were used more than twice.

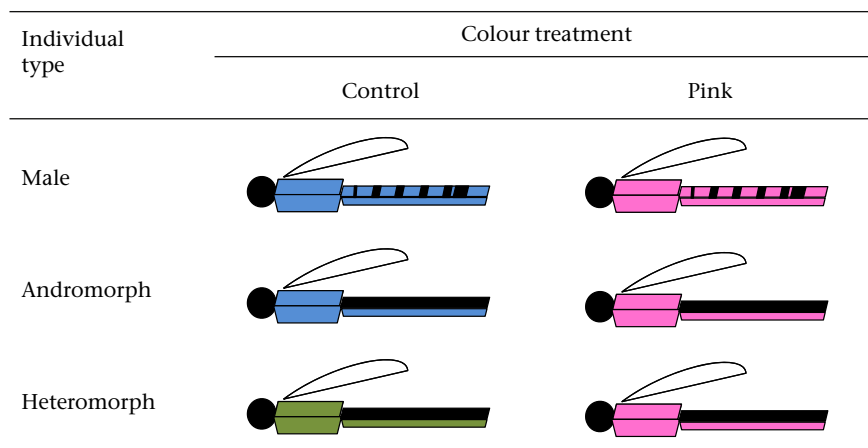


Figure 3. Design of experiment 3 for the control and pink-painted individuals of *Enallagma hageni* in the field. Control individuals had natural coloration. Abdominal dorsal patterns were unaltered in this experiment.

Ethical Note

We chose the kind of paints and glues, as well as our protocol to minimize adverse impacts from the manipulations on the damselflies. In the experiment in the enclosure, we provided food for damselflies at all times and arranged the interior environment as natural as possible to reduce stress. All our experimental procedures were approved by University of Michigan Biological Station (UMBS) and complied with the legal requirements of U.S.A.

Spectrum Analysis of the Paints

To assess how closely the paints matched the natural colours of the damselflies, we measured the relative reflectance of nine males, 12 andromorph females, 11 heteromorph females, as well as five samples of each paint with an OceanOptics SD 2000 spectrometer and a PX-2 xenon light source (OceanOptic, Dunedin, FL, U.S.A.). We compared the hue (wavelength at the maximum reflectance) and brightness of the blue paint to those of andromorph females and males, and the green paint to those of the heteromorph females in Avicol version 6 (Gomez, 2006). We also calculated colour contrasts in the unit of 'just noticeable differences' (JNDs; Vorobyev & Osorio, 1998) with a tetrachromatic model of odonate colour vision (for details, see Schultz & Fincke, 2013) to examine whether males could detect the difference between the paints and the damselfly colours. A colour contrast value of 1 JND is usually considered detectable by the signal receivers.

Statistical Analyses

The presentation sequence (painted individual first or control individual first) and the type of control (i.e. natural control or sham control) had no effect on the reactions of focal males in experiment 1a (generalized linear mixed model: sequence: $\chi^2_1 = 0.001$, $P = 0.97$; control type: $\chi^2_1 = 0.002$, $P = 0.99$). Hence, data from the two presentation sequences and the two control types were pooled in the analyses below. Using data from all three treatments, we first used a generalized linear mixed model (GLMM) with binomial error distribution to investigate the general effects of colour and pattern on sex recognition by focal males. In this model, focal male reaction (i.e. sexual versus nonsexual) was used as a binary dependent variable; focal male was treated as a random effect, and pattern was nested within focal male. We performed two additional tests to further examine the relationship between colour and pattern cues. First, we used a Fisher's exact test to investigate whether the effect of pattern on sex recognition was contingent on colour. Second, we used a generalized linear model (GLM) to investigate whether the effect of pattern differed in magnitude among the three colour types. In this model, we used 'difference in response' as the dependent variable. This variable was scored '0' if a focal male's reaction towards the pattern-altered individual was the same as towards the control individual, and '1' if a focal male changed his reactions. The dependent variable was colour type (i.e. andromorph, heteromorph, or male). Both tests required excluding two focal males that did not react sexually to control heteromorph females and a male that reacted sexually to a control male. We interpret the former two cases as a focal male lacking an interest in mating, and the latter as a mistake in male sex recognition. These cases provided no information on how males recognize sex using colour or pattern cues. Within each colour type, we used Wilcoxon signed-ranks test to investigate whether the abdominal pattern modification changed the focal males' reactions. In this test, zeros and ties were handled according to Pratt's (1959) modification of the original Wilcoxon test, and the exact P values were calculated. In field experiment 1b, male reactions towards individuals on the

dowel did not differ between the two field locations (grass near water or forest light gap; GLM: $\chi^2_1 = 0.001$, $P = 0.98$). Hence, data from the two locations were pooled in the analyses. We used GLM with binomial error distribution to examine male reactions (i.e. sexual or nonsexual) to the control and the pattern-altered individuals in experiment 1b.

In the arena presentations of orange females in experiment 2a, each focal male was presented only one individual; thus, we used a Fisher's exact test to investigate the effect of abdominal dorsal pattern on focal males' reaction. We also used a GLM similar to the above to examine the reaction of mate-searching males towards orange-painted individuals. To examine male reactions to the control and the pink-painted individuals in the field in experiment 3, we used generalized linear models (GLM) with the number of sexual and nonsexual reactions by males as dependent variables, and total number of males in the 1 m² area as a covariate. Because males were less likely to react sexually towards andromorphic sham control females than towards natural control females ($\chi^2_1 = 6.68$, $P = 0.01$), we excluded andromorphic sham control females from analyses; including them did not change the results.

We used Bonferroni correction to adjust the α levels for our planned pairwise comparisons. All statistical tests were performed in R (version 2.15.1, R Development Core Team, 2012). Throughout, means are shown with standard errors.

RESULTS

Experiments 1a, b: Use of Colour and Pattern in Sex Recognition: Arena and Field

In the arena, except for two focal males from the heteromorph treatment and one male from the male treatment, the focal males all reacted sexually to control females and nonsexually to control males as expected (Fig. 4). No male reacted nonsexually to the model with the female pattern and sexually to the model with the male pattern. Both colour and pattern had significant effects on focal male reaction (GLMM: colour: $\chi^2_2 = 9.55$, $P = 0.01$; pattern: $\chi^2_1 = 10.39$, $P = 0.001$). Because the pattern-colour interaction was not significant, we dropped it from the final model to recover power. When analysed within each treatment, focal males were less likely to react sexually to the blue andromorphic females painted

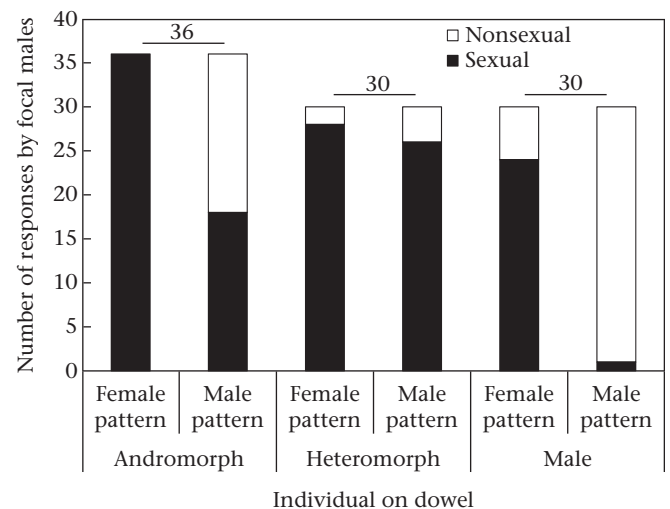


Figure 4. Number of responses by focal male *Enallagma hageni* in paired presentations of control and pattern-altered individuals in the arena. Responses in the female pattern and the male pattern treatments from each colour type on the dowel (i.e. andromorph, heteromorph and male) are from the same focal males. Numbers above bars show numbers of focal males.

with the male-like striped abdominal dorsal pattern than to the control blue females (Wilcoxon signed-ranks test: $\alpha' = 0.017$, $W = 4.24$, $N = 36$, $P < 0.001$; Fig. 4). Similarly, focal males were more likely to react sexually to males painted with the female uniform black abdominal pattern than to control males ($W = 4.80$, $N = 30$, $P < 0.001$). Finally, as expected, there was no difference between the focal males' sexual reactions to green heteromorphic females painted with a green-and-black striped male pattern and their sexual reactions to control females ($W = 1.41$, $N = 30$, $P = 0.50$).

Excluding the three focal males that did not react to control individuals in the expected way, the effect of abdominal dorsal pattern on male sex recognition was contingent on colour (Fisher's exact test: $P = 0.007$). Additionally, the magnitude of the pattern effect depended on colour type (GLM: $\chi^2_2 = 34.51$, $P < 0.001$). The post hoc comparisons revealed a significant gradient in the magnitude of response to the pattern alteration among three treatments with the most drastic change in the male treatment and the least change in the heteromorph treatment (Tukey test: andromorph–heteromorph: $P = 0.004$; andromorph–male: $P = 0.045$, heteromorph–male: $P < 0.001$; Fig. 4).

Reactions by males in the field experiment 1b were similar to those of males in the arena presentations (Fig. 5). Overall, the probability of male sexual reactions differed between the two pattern treatments ($\chi^2_1 = 12.91$, $P = 0.0003$) and among the three colour types ($\chi^2_2 = 37.41$, $P < 0.001$), but the pattern-treatment interaction was not significant ($\chi^2_2 = 2.45$, $P = 0.29$). When analysed within each treatment, males were more likely to react sexually to the control andromorphic females than to andromorphic females painted with the male abdominal pattern (GLM: $\alpha' = 0.017$, $\chi^2_1 = 12.91$, $P = 0.0003$). Similarly, males were more likely to react sexually to males painted with the female abdominal pattern than to control males ($\chi^2_1 = 9.47$, $P = 0.002$). In contrast, the probability of male sexual reactions towards heteromorphic females with female or male patterns did not differ ($\chi^2_1 = 0.27$, $P = 0.60$).

Experiment 2a, b: Deduction of Male Decision Rule from Orange-painted Individuals

In the arena experiment 2a, six out of 19 (32%) focal males reacted sexually to orange-painted females with the female

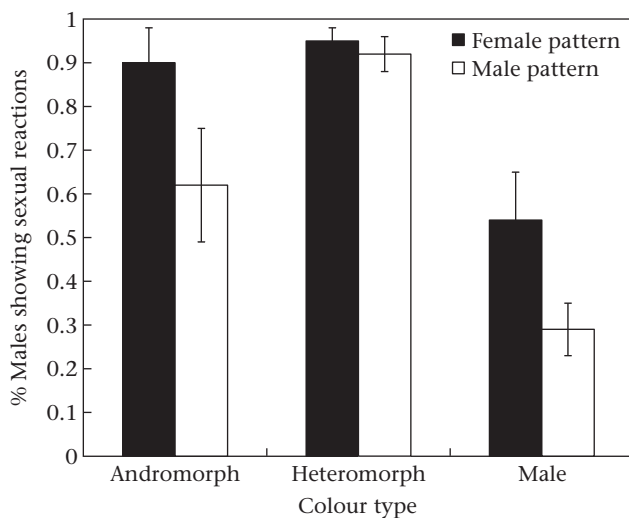


Figure 5. Mean \pm SE proportion of male *Enallagma hageni* showing sexual reactions towards six control and six abdominal dorsal pattern-altered andromorphic, heteromorphic and male *E. hageni* in the field.

pattern, whereas two out of 16 (13%) focal males reacted sexually to orange-painted females with the male pattern. There was, however, no difference in male sexual reactions towards the two types of orange females (Fisher's exact test: $P = 0.24$).

The overall sexual response ratios towards orange individuals in the arena were low. Nevertheless, two previously unreacting males did take an orange female with female pattern and an orange female with male pattern in tandem as the females were withdrawn from the arena, respectively, even though these could not be included in the analysis. Including these two cases does not change the conclusion above. Focal males were more likely to react sexually to orange-painted individuals with a female pattern than to control males (Fisher's exact test: $\alpha' = 0.025$, $P = 0.01$). However, male sexual responses towards orange-painted females with a male pattern were not significantly different from those towards control males ($P = 0.27$).

In the field experiment 2b, males readily reacted sexually to orange-painted females regardless of the abdominal pattern. The probability of a sexual reaction by a mate-searching male towards an orange individual with a female pattern (0.95 ± 0.03) did not differ from that towards an orange individual with a male pattern (0.85 ± 0.06 ; GLM: $\chi^2_1 = 2.32$, $P = 0.13$).

Experiment 3: Deduction of Male Decision Rule from Novel, Pink Individuals: Field

In the field experiment using pink-painted individuals and the controls, the probability of sexual reactions by males decreased with total number of males in the 1 m^2 area ($\chi^2_1 = 15.47$, $P < 0.001$). However, controlling for total number of males in the area, the total number of reactions (i.e. sexual plus nonsexual reactions) did not differ between controls and pink-painted individuals for any colour type (andromorph: $\chi^2_1 = 1.01$, $P = 0.32$; heteromorph: $\chi^2_1 = 1.81$, $P = 0.18$; males: $\chi^2_1 = 2.44$, $P = 0.12$).

Overall, controlling for total number of males, the probability of sexual reactions by mate-searching males differed between the three colour types (GLM: $\chi^2_2 = 93.82$, $P < 0.001$; Fig. 6); there was no significant effect of the pink paint treatment ($\chi^2_1 = 0.38$, $P = 0.54$) on the probability of sexual reactions, but colour type \times pink paint treatment interaction was significant ($\chi^2_2 = 31.52$, $P < 0.001$). More specifically, controlling for total number of males, the probability of a male's sexual reaction did not differ between control andromorphic females and the pink-painted andromorphic females (GLM: $\alpha' = 0.017$, $\chi^2_1 = 0.48$, $P = 0.49$), or between control heteromorphic females and the pink-painted heteromorphic females ($\chi^2_1 = 3.12$, $P = 0.08$). In contrast, males were more likely to react sexually to pink-painted males than to control males ($\chi^2_1 = 28.28$, $P < 0.001$). The probability of sexual reactions did not differ between the three types of pink individuals, two of which had the female pattern and one of which had the male pattern (GLM: $\alpha' = 0.025$, $\chi^2_2 = 4.45$, $P = 0.11$).

Colour Contrasts of Damselflies and Paint as Perceived by an Odonate

The green paint matched the heteromorph colour in both hue (green paint: $540.0 \pm 0.0 \text{ nm}$; heteromorph: $543.6 \pm 2.1 \text{ nm}$; Welch t test: $t_{5.55} = 1.80$, $P = 0.13$; Fig. 7a) and relative brightness (green paint: $10.41 \pm 0.53\%$; heteromorph: $9.37 \pm 0.23\%$; $t_{10.0} = 1.70$, $P = 0.12$). Using the visual physiology model, the chromatic (colour) and achromatic (brightness) contrasts between green-painted and natural heteromorphic females were not likely noticeable by a male damselfly in the field (chromatic: 0.63 JND; achromatic: 0.36 JND). The blue paint peaked at a shorter wavelength ($459.0 \pm 0.4 \text{ nm}$) than the naturally andromorphic blue

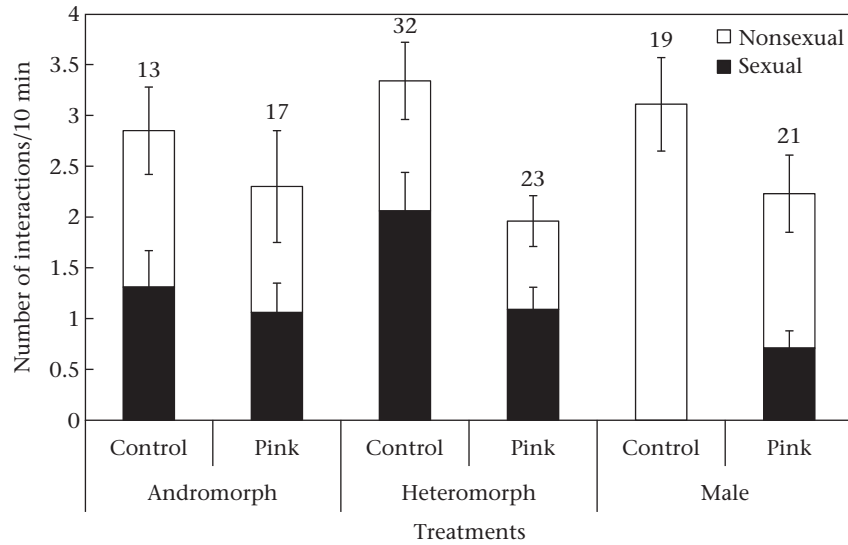


Figure 6. Mean ± SE number of sexual and nonsexual reactions per 10 min from mate-searching males towards the control and pink-painted andromorphic, heteromorphic and male *Enallagma hageni* in the field. Numbers above bars show numbers of focal males.

(486.8 ± 2.5 nm; $t_{11.68} = 10.90$, $P < 0.001$), but this difference was likely not noticeable to males (chromatic contrast = 0.70 JND). However, the relative brightness of the blue paint ($19.69 \pm 0.42\%$) was significantly greater than the natural blue of andromorphic

females ($11.95 \pm 0.47\%$; $t_{12.81} = 12.89$, $P < 0.001$; Fig. 7b). This difference may be detectable by males (achromatic contrast = 1.23 JND), although the contrast value was close to the borderline value of 1.0 JND. In fact, to a damselfly, the blue paint was probably as bright as males (male brightness = $17.02 \pm 0.62\%$; achromatic contrast = 0.53 JND). Both orange and pink paints were noticeably different from the natural blue and green colour types in both hue and brightness (Fig. 7a).

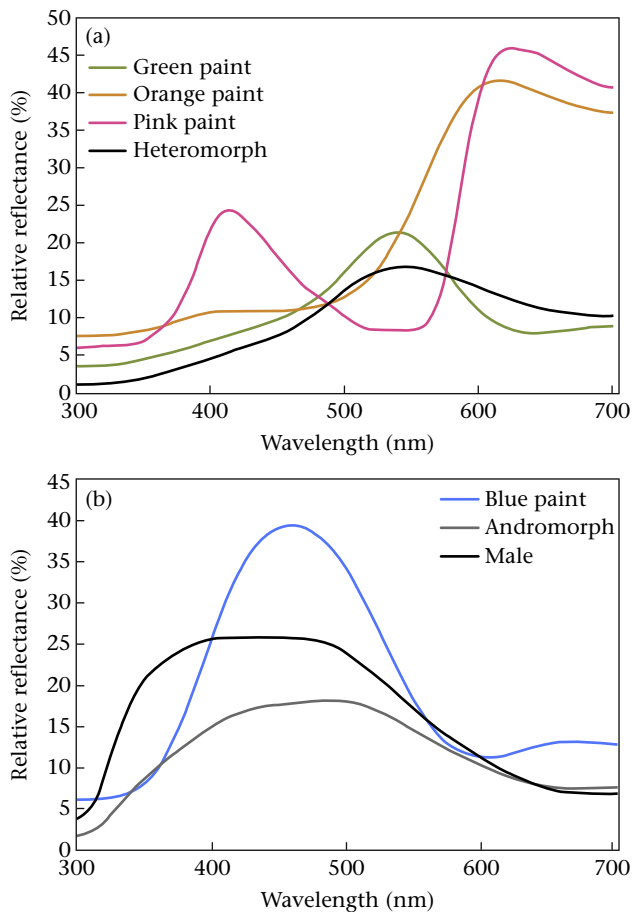


Figure 7. Relative reflectance of (a) heteromorphic female and (b) male and andromorphic female *Enallagma hageni* and the paints used to alter the abdominal dorsal pattern. Damselflies were from the study population at Duck Lake, Sugar Island, MI, U.S.A.

DISCUSSION

Our study offers one of the few examples from a sexual mimicry system that demonstrates the selective use of a nonmimetic cue by receivers in sex discrimination. Male *E. hageni* used information from at least two types of visual cues, body coloration (the mimetic cue) and abdominal dorsal pattern (the nonmimetic cue) to distinguish sex. Moreover, results from experiment 1 from both the arena and the field suggested that the two cues were not used in the same manner. Although the lack of a significant interaction between pattern and colour in the models for data from experiment 1 restricted our ability to draw a definitive conclusion on the hierarchical use of colour and pattern cues, the Fisher’s exact test for data from the arena experiment showed that the effect of pattern in male sex recognition depended on colour type. Furthermore, the GLM using the difference in response as a dependent variable revealed a significant difference in the magnitude of effect of the pattern cue among three colour types. Similarly, results from the field component of experiment 1 indicated that male attention to pattern was more important in sex recognition of andromorphs relative to heteromorphs (Fig. 5).

More specifically, experiment 1 showed two distinct types of response to pattern alteration. Imposing a male abdominal pattern on the green heteromorph did not significantly diminish a male’s ability to correctly recognize her sex. However, when the individual was blue, altering its pattern from the natural one significantly increased the probability of a male’s mistake in sexual recognition. Moreover, males made more mistakes in response to the blue males with a female abdominal pattern than they did to the blue andromorphic females with a male pattern. This difference in the magnitude of the pattern effect between males and andromorphic females suggests that the males did not interpret the information

from pattern equally across the two blue colour types. Apparently, males paid more attention to other cues that differed between the sexes (e.g. reflectance of blue coloration, abdominal width, body size, or the presence of an ovipositor or penis) when they assessed andromorphic females, compared to when they assessed other males. A male's reaction to green-painted males with male and female patterns would have helped to infer the importance of a male's colour versus these other sexually dimorphic visual cues. In the pattern-altered heteromorph treatment, we do not know whether males only assessed the green colour cue or whether they assessed the pattern as well but chose to ignore it. Nevertheless, the use of the pattern cue enhanced the accuracy of a male's sex discrimination only when colour alone was insufficient to indicate sexual identity. In this sense, the sexually dimorphic abdominal pattern may act as a 'backup signal' (Johnstone, 1996) for sexual identity, and a male's selective attention to it is potentially adaptive for males.

The value of the arena experiment was that it eliminated both types of crypsis that colour morphs enjoy under natural conditions (Schultz & Fincke, 2013). Other males, which normally serve as signal distractors for blue andromorphic females (Fincke, n.d.) were absent. Similarly, against the white background of the arena, a normally cryptic green heteromorph was readily visible to a focal male. Finally, testing a single focal male at a time eliminated any confounding effect of male–male competition. Importantly, under these conditions, our results demonstrate that a focal male was equally good at distinguishing control andromorphic and heteromorphic females. Thus, in the most natural field experiment (Fig. 6), the tendency for control heteromorphs on dowels to elicit more sexual interactions relative to andromorphic females on dowels was most likely the result of the presence of male distractors, rather than some innate predisposition of males for green females. Learning experiments with naïve *Enallagma* males (Fincke et al., 2007) also support this conclusion.

An interesting question is why the use of colour appears to be higher in the decision hierarchy than abdominal pattern. Theory has predicted that differential error rates among multiple signals can affect a receiver's optimal assessment strategy (Fawcett & Johnstone, 2003). In *Enallagma* species, the sexually dimorphic abdominal pattern is a more accurate cue to sex than colour, raising the question why males do not use the pattern cue exclusively. One reason may be due to trade-offs between speed and accuracy (Abbott & Sherratt, 2013; Chittka & Osorio, 2007; Chittka, Skorupski, & Raine, 2009). Colour may be more easily discerned at a greater distance than the details of the abdominal pattern. Being able to distinguish sex from further away should be advantageous because it allows a male to react faster, especially when there is scramble competition for mates among males in this species (Fincke, 1982). Although male *E. hageni* react to blue andromorphic females at greater distances than they do to green females (Schultz & Fincke, 2013), distance at which pattern is detected has yet to be measured.

Consistent with our results, male *E. ebrium* also cue to the sexually dimorphic abdominal pattern (Miller & Fincke, 1999), which is characteristic of all female *Enallagma*. In Miller and Fincke's experiment, both andromorphic and heteromorphic females that were painted with a male-like blue tip and stripes on part of the abdomen tended to receive fewer sexual reactions than control females, although the tendency was not significant for the andromorph ($P = 0.07$). Similarly, when the abdominal dorsum of *E. ebrium* males was painted completely black, the males received more sexual reactions than control males. The latter finding was also reported for a confamilial polymorphic damselfly *Coenagrion puella* (Gorb, 1998). In addition, sexually dimorphic wing reflectance patterns have also been found to function in sex recognition in several odonates (Guillermo-Ferreira, Therézio, Gehlen, Bispo, & Marletta, 2014; reviewed by: Corbet, 1999; Schultz & Fincke, 2009).

Results from our system were not consistent with a similar discrimination problem for avian predators learning to recognize Batesian mimics with different colours and patterns. Domestic chicks that were trained to distinguish palatable and unpalatable prey did not learn the difference between the two kinds of prey that had the same colour but differed in pattern (Aronsson & Camberale-Stille, 2008, 2012). Whether such differences generally occur between the two types of mimicry systems is unknown.

Our results from novel-coloured individuals provide insights, for the first time, on a decision rule that males seem to use in sex discrimination. Results from experiment 1 suggested that colour seemed to be higher in the hierarchy than pattern in male sex discrimination. Based on that result, we deduced two possible binary decision rules used by males to recognize sex. Males may use the following decision rules: (1) 'if green, then female; otherwise, consider pattern'; or (2) 'if not blue, then female; otherwise, consider pattern'. Results from experiment 1 were consistent with both scenarios for *E. hageni*, which has only two naturally existing female colour morphs. The two seemingly similar decision rules can be differentiated by measuring male reactions to novel-coloured individuals. If males consider novel-coloured individuals as conspecifics, rule 1 predicts that the abdominal pattern of orange and pink individuals should affect a male's reaction. In contrast, rule 2 predicts that orange or pink-painted individuals should be recognized as 'female' regardless of their abdominal pattern.

Three pieces of evidence from male reactions to both orange- and pink-painted females in the field suggest that mate-searching males use the more general rule 2 of 'if not blue, then female'. First, males readily reacted sexually to orange females, even to those with a male abdominal pattern. Second, not only did mate-searching males treat pink females with female patterns as 'female', but surprisingly, males were more likely to react sexually to pink-painted males with male abdominal pattern than to control males. Finally, the probability of males reacting sexually towards pink-painted andromorphic and heteromorphic females did not differ from that towards the respective control females, further supporting the use of rule 2. Indeed, male sexual reactions towards the three kinds of pink-painted individuals, two of which had the female pattern and one of which had the male pattern, did not differ, suggesting that males did not use the abdominal dorsal pattern as a cue when the individual was pink. However, relatively few males reacted sexually to the orange-painted individuals in the arena, and as a result, the sexual reactions towards orange individuals with male pattern were not significantly different from that of control males, contradicting rule 2. While we cannot give an explanation for this, we do know that males sometimes behave differently in enclosures than they do in the field (Xu & Fincke, 2011). In addition, one focal male sexually reacted towards a control male, an event usually much rarer in enclosures (Xu, 2013).

In contrast with our study, a previous one on another polymorphic species, *Nehalennia irene*, found that male mating attempts towards control males did not differ from that towards pink or black-painted males (Iserbyt & van Gossum, 2011). These results indicated that males were not using the decision rule, 'if not andromorphic coloration, then female'. However, unlike *E. hageni* males, in that study male *N. irene* often reacted sexually to control males, even more than they did to heteromorphic females, and we think this may have been one reason for the discrepancy in the findings. Compared to *Enallagma* males, males of both *Nehalennia* and many *Ischnura*, which are more similar to andromorphic females in both colour and pattern, more often mistake males for females (e.g. Cordero & Andrés, 1996; Rivera & Sánchez-Guillén, 2007). Hence, in such species, we expect that the male decision rule 'if not andromorph, then consider nonmimetic cues' should

still apply, although instead of pattern, the traits would more likely be body size, abdomen width and/or the presence of an ovipositor.

Although the decision rule for *E. hageni* male sex recognition deduced in our study was based on only two visual cues (i.e. colour and pattern), and hence, may not be a complete one, the rule has important implications for the evolution of polymorphic systems. First, the specific decision rule ‘if not blue, then female’ differed from Sherratt’s (2001) key assumption in his signal detection model for the maintenance of female colour polymorphism, namely, that the heteromorph is always recognized by males as ‘female’. Surprisingly, in our field experiments, males often reacted to novel-coloured conspecifics as if they were females even without any prior experience with them. Although that result contradicted the prediction that males learn to recognize females as potential mates (Fincke, 2004), we do not know the effect of experience in the formation of a male’s decision rule. Moreover, males made lots of mistakes in sexual recognition of pink individuals; our results would still be consistent with male learning if more experience with pink individuals enabled males to form search images and reduce mistakes when pink females increased in the population. Comparative studies that contrast the behaviour of sexually mature, naïve and experienced males to novel morphs should offer promising insights into the evolution and development of male decision rules.

Finally and most importantly, our study provides the first empirical evidence that a general rule ‘if not andromorphic colour, then female’ could permit a novel female colour morph to invade a population because the mutant females would still be able to find mates. Hence, such a rule may offer a proximate, behavioural mechanism for the origin of female-specific colour polymorphisms, and perhaps more generally, other types of polymorphisms.

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