Trade-offs in female signal apparency to males offer alternative anti-harassment strategies for colour polymorphic females

O. M. FINCKE

Ecology and Evolutionary Biology Graduate Program, Department of Biology, University of Oklahoma Norman, Norman, OK, USA

Abstract

Colour polymorphisms are known to influence receiver behaviour, but how they affect a receiver's ability to detect and recognize individuals in nature is usually unknown. I hypothesized that polymorphic female damselflies represent an evolutionary stable strategy, maintained by trade-offs between the relative apparency of morphs to male receivers. Using field experiments on *Enallagma hageni* and focal studies of *E. hageni* and *Enallagma boreale*, I tested for the first time the predictions that (i) green heteromorphs and blue andromorphs gain differential protection from sexual harassment via background crypsis and sexual mimicry, respectively, and (ii) female morphs behaviourally optimize their signal apparency to mate-searching males. First, based on male reactions elicited by females, against a high-contrast background, the two morphs did not differ in being detected by males, and once detected, they did not differ in being recognized (eliciting sexual reactions). However, on green ferns, heteromorphs were less likely to be detected (elicited only fly-bys) than andromorphs, but once detected, the morphs did not differ in being recognized. In contrast, when perched on a dowel with two male signal distractors, andromorphs were detected less often, and once detected, they were recognized less often than heteromorphs. Second, in fields where females foraged, andromorphs perched higher on vegetation than heteromorphs and were more often in the vicinity of males. Neither harassment rates nor evasive behaviours differed between morphs. Males aggregated in high density near shore where solitary females were rare. Equilibrium frequencies of these and other colour morphs should reflect the relative ease with which receivers detect and recognize them in the context where they are encountered.

Introduction

As Darwin (1871) astutely noted, for species whose major sensory channel is visual, coloration is often an evolved compromise between being conspicuous to potential mates and avoiding visual predators (e.g. Morehouse & Rutowski, 2010; Garcia *et al.*, 2013). Fitness trade-offs in coloration often differ between the sexes, leading to the common phenomenon of bright males and drab females (e.g. Endler, 1983; Andersson, 1994). The evolution of sexual dimorphism in turn sets the stage for the evolution of sex-specific colour polymorphisms, maintained as an evolutionary stable strategy (ESS, Maynard Smith, 1982). For example, males of many species exhibit alternative mating strategies in which a relatively more conspicuous majority male type displays to females and/or defends a territory, whereas other males mimic females and gain context-dependent fitness advantages (e.g. Dominey, 1980; Sætre & Slagsvold, 1995; Gross, 1996; Plaistow & Tsubaki, 2000). In contrast with male mating strategies, we know relatively little about the selective pressures that favour and maintain alternative female phenotypes (Van Gossum *et al.*, 2008; Kunte, 2009; Limeri & Morehouse, 2014).

Because females are typically the sex that limits male mating opportunities, the optimum mating rate for

Correspondence: Ola M. Fincke, Ecology and Evolutionary Biology Graduate Program, Department of Biology, University of Oklahoma Norman, Norman, OK 73019, USA.
Tel.: 405 325 5514; fax: 405 325 7560; e-mail: fincke@ou.edu

males is often considerably greater than that for females (Bateman, 1948). Hence, in contrast to sex-specific competition among males, alternative mating strategies of females are expected to often ameliorate sexual conflict over mating rate (Arnqvist & Rowe, 2006; Chapman, 2006). If so, then we would expect alternative female phenotypes to evolve in response to sexual harassment, here defined as unwanted sexual attention. Harassment most commonly is exhibited by males towards females of their own species, where it can impose considerable fitness costs such as predation mortality, and/or lowered foraging efficiency and egg production (e.g. Rowe *et al.*, 1994; Jormalainen *et al.*, 2001; Sirot & Brockmann, 2001).

For mate-searching species, signal variation among females may represent alternative female strategies to reduce sexual harassment by presenting perceptual challenges to males, not unlike the difficulties that colour variation of prey present to visual predators (Greenwood, 1986; Bond & Kamil, 2002; Skelhorn *et al.*, 2011). In both cases, a receiver must detect an individual of interest that is 'encountered' (present within the receiver's perceptual range, whether or not it is detected). Once 'detected' (sensed), the receiver must then 'recognize' the individual (identify it correctly as a potential mate or prey item). The latter two tasks determine the 'apparency' of the signal for the receiver, here defined as the ease of detecting and correctly recognizing individuals as potential mates or prey, where they naturally occur in the field and are at risk of harassment or predation, respectively (Schultz & Fincke, 2013).

Visual signal variation specific to females is widespread in the damselfly family Coenagrionidae, in which 65% of the species have males of a single colour but whose sexually mature females exhibit two or more distinct colour morphs (Fincke *et al.*, 2005), traits known to reflect genetic polymorphisms (reviewed by Van Gossum *et al.*, 2008). Female 'andromorphs' resemble males in coloration and are thought to benefit from signal similarity with males ('sexual mimicry') such that upon detecting an andromorph, a male may not recognize her as a potential mate (e.g. Robertson, 1985; Sherratt, 2001). The typically green or brown 'heteromorphs' differ distinctly from males in coloration (Johnson, 1975). Heteromorphs present a second type of difficulty for males caused by their signal similarity with the vegetative background ('crypsis'), which should make it relatively difficult for males to detect them. Although Robertson (1985) proposed that such crypsis could protect heteromorphs from predation, the role of background crypsis in reducing sexual harassment has usually been ignored (but see Fincke, 2004; Schultz & Fincke, 2013). Surprisingly, whether these potential male perceptual problems in signal detection and recognition actually decrease sexual harassment towards heteromorphs and andromorphs under field conditions has never been tested.

Signal apparency depends on the visual perception abilities and the central processing ability of the receiver (Endler, 1978; Stevens, 2007; Théry & Gomez, 2010). The apparency of female colour morphs to conspecific male damselflies and visual predators in terms of the sensory physiology of the receivers has only recently been quantified. To a male damselfly as well as to birds and dragonfly predators, green heteromorphs exhibit lower chromatic and achromatic (brightness) contrast against background vegetation, compared to the brighter blue males and andromorphs. In contrast, the reflectance properties of the blue andromorphs are more similar to those of conspecific males than are those of heteromorphs (Schultz & Fincke, 2013; see also Huang *et al.*, 2014).

Thus, I first hypothesize that the female colour morphs exhibit context-dependent apparency to males that functions as a female ESS. I then hypothesize that solitary heteromorphs and andromorphs should behaviourally optimize their crypsis and sexual mimicry, respectively. My first goal here is to test two predictions arising from the crypsis/mimicry trade-off hypothesis about the ease with which mate-searching males detect and recognize female morphs: (i) when females are perched against the prevailing vegetation within their habitats, heteromorphs are less likely than andromorphs to be detected (elicit nonsexual and/or sexual responses) and (ii) when females are perched in the presence of conspecific males ('distractor signals'), andromorphs are less likely than heteromorphs to be recognized as potential mates (elicit sexual responses). My second goal is to test whether under natural conditions where solitary females forage, (iii) female morphs differ in their behaviour in ways that optimize their signal apparency, and (iv) harassment rates towards morphs are equal, as expected with balanced apparency trade-offs. I also indirectly test the underlying assumption that males rely primarily on visual cues to detect and recognize individuals, and predict that (v) males more readily detect females in sun than in shade.

Materials and methods

Relevant natural history of *Enallagma* damselflies

Female *Enallagma* of both colour morphs have a black abdominal dorsum, which differs from the male's striped abdomen (Fig. 1a,b), traits that enable trained observers to distinguish andromorphs from males in the field. Sexually immature males and females vary between pale tan, pale blue and deeper browns, distinct from mature adults (Xu *et al.*, 2014). Like most nonterritorial coenagrionids, *Enallagma hageni* and *Enallagma boreale* males do not defend oviposition resources (Fincke, 2004; Fincke *et al.*, 2005). Instead of waiting for receptive females to come to them, males search areas away from shore early in the day (~1000
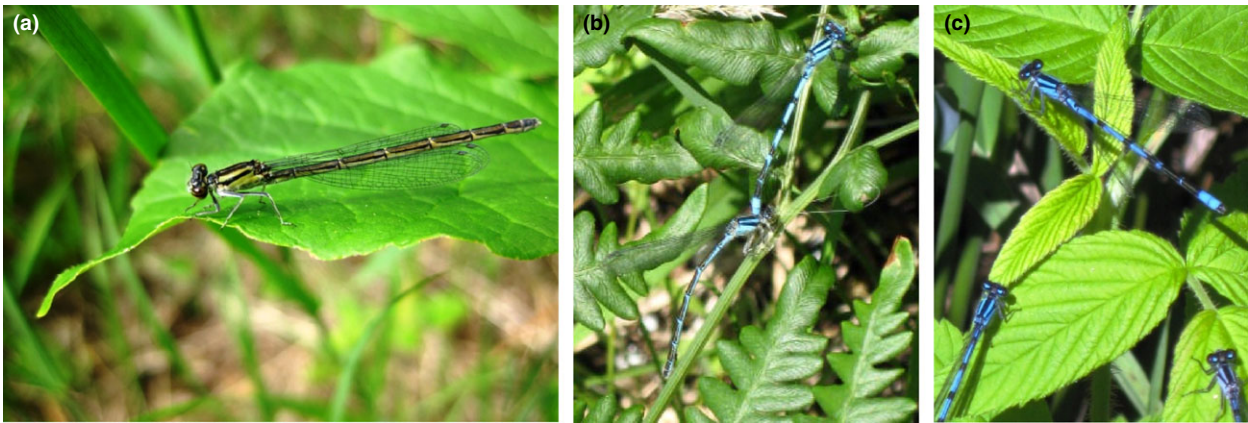
Fig. 1 *Enallagma hageni* (a) heteromorph on typical green vegetation (b) glued andromorph in medium position on fern that elicited a tandem (c) males clumped on the bank.

–1230 h) for receptive females among sexually mature and immature individuals (conditions in the focal study below). By 1200 h, males receptive to mating on a given day begin to accumulate along the shore where they search for arriving, solitary, receptive females (Fincke, 1982; free-flying males in experiments below). Males cue readily to motion and can detect flying andromorphs at greater distances (range = 11.4–85.6 cm) than heteromorphs (range = 12.7–67.8 cm, Schultz & Fincke, 2013). Males often 'inspect' each other using short-distance chases after which both individuals perch, often close together (Fig. 1c). Agonistic, male–male interactions are rare, limited to darting 'hits' by males that briefly defend fly-ways used by females arriving on shore.

Tests of context-dependent apparency of female morphs to male receivers

The signal apparency part of my study comprised three field experiments using *E. hageni*. These were conducted between 1200 and 1630 h on sunny days between 15 June and 30 July 2010–2014 at Lark's Lake, Emmet County, MI (45.1°N, 84.2°W; see Grant *et al.*, 2014 for site and species details). Here, the frequency of *E. hageni* andromorphs varied from 25% to 30%.

The three experimental protocols used modifications of the damsel-on-a-dowel technique (Fincke *et al.*, 2007), designed to measure the reactions by free-flying, mate-searching males to perched conspecifics of the three colour types (heteromorph, andromorph, male). A live, sexually mature focal individual was glued by its legs in a perched position to a dowel or fern, which was centered in a 1-m^2 plot of green vegetation on the bank (1–4 m from the water) where males actively search for females. During 10-min trials, the most extreme reaction by a passing male that was elicited by a glued individual was scored as a 'fly-by' (passing within an estimated 10 cm of an individual), 'hover', 'grab', 'tandem attempt' or 'tandem'. Hover was considered a 'nonsexual' reaction, whereas grab, tandem attempt and tandem were considered 'sexual' reactions (Robertson, 1985; Sirot & Brockmann, 2001; Fincke *et al.*, 2007). Here, failure to detect an encountered individual was inferred if a glued individual elicited only fly-by reactions from males. Whereas flying males are commonly seen to orient (deviate from a horizontal flight path) to a perched female at distances of ≤10 cm, males rarely orient to one at 15 cm. Hence, I conservatively assumed that a male passing within 10 cm of a glued individual was sufficiently close to permit detection of it. Thus, I quantified total encounters of a glued individual as the sum of fly-bys plus nonsexual and sexual reactions that it elicited, and total detections as the sum of nonsexual and sexual reactions it elicited. For a detected individual, total recognitions were the sum of sexual responses it elicited. Throughout, male–male reactions provided a comparison for male-andromorph (model-mimic) reactions. A male's sexual reaction to a glued male was interpreted as a perceptual mistake. A fly-by reaction elicited by a glued male was interpreted as a lack of detection or interest, whereas one elicited by a glued female was interpreted simply as a lack of detection. A mate-searching male should always be interested in a female that it detects; 40% of males fail to mate in their lifetime (Fincke, 1982).

To provide a comparative baseline, I used a 'high-contrast experiment' to quantify male reactions to each of the three colour types on a noncryptic, distractor-free background. A single individual was glued to a relatively wide (9.5 mm diameter), light tan dowel similar in coloration to dry grass, providing a realistic, relatively high-contrast background for each type (Schultz & Fincke, 2013). I analysed male reactions elicited by a total of 26 heteromorphs, 21 andromorphs and 27 males.

I used a 'fern crypsis experiment' to test whether when perched on green vegetation, relative to andromorphs, heteromorphs were less likely to be detected by males (elicit a higher frequency of only fly-bys). For perches, I used bracken ferns (*Pteridium aquilinum*), which are uniformly green and common around northern Michigan lakes. The reflectance properties of bracken ferns and other green vegetation are similar to those of green *E. hageni* heteromorphs (Schultz & Fincke, 2013). A single individual was glued by its legs to the top of a fern blade, either on the outer quarter of a top blade or within the first quarter of the blade near its attachment to the stalk, the position providing maximal green background against which a glued individual was viewed by approaching males. To test the assumption that male perception relied primarily on visual cues, for a subset of replicates, I also glued individuals in a 'low' position ~5 cm below the node of the blades, where individuals were in partial shade (Fig. 2a).

For each position, each of the three colour types was run separately in the same position on the same blade (one glued individual per trial). The original replicate consisted of six trials (3 colour types × 2 sunny positions). A new fern was used for each replicate. All glued individuals were used only once. In total, I analysed the reactions of free-flying males that were elicited by 28 heteromorphs, 28 andromorphs and 29 males in the high position and 23 heteromorphs, 23 andromorphs and 24 males in the medium position treatment. Late in the experiment, I included five replicates of each colour type in the low, shady position.

I used a 'male distractor experiment' to test whether, when perched in proximity of male distractor signals, andromorphs were less likely to be recognized (elicit fewer sexual responses) by mate-searching males than heteromorphs. Control and experimental treatments consisted of three individuals that were glued ~2.5–3 cm apart on a narrow (4.7 mm diameter), tan dowel (Fig. 2b). Heteromorph, andromorph and male controls consisted of three glued green females, three blue females and three males, respectively. The heteromorph experimental treatment consisted of a green female and two distractor males glued on a dowel, whereas the andromorph experimental treatment had a blue female and two males glued on a dowel. Relative to the positions of the two males, the position of the glued female varied from top, middle or bottom. There was no male experimental treatment because the question of how well females act as distractor signals for males was not of interest. Thus, a complete replicate set consisted of nine trials (heteromorph, andromorph and male controls, plus two female morph experimental treatments, each with three female positions relative to the two males). Each trial used a single dowel. Nine complete replicates plus one extra andromorph experimental were analysed (male reactions elicited by a total of 54 heteromorphs, 56 andromorphs and 137 males). Dowel individuals were used only once except in four cases (2.9%, a control heteromorph and three male control dowels); deleting the second use of the 12 individuals did not change conclusions.

The following conditions applied to all experiments. All glued individuals remained alive during a trial. Three to four observers (each in a different replicate) scored male reactions elicited by glued individuals. After an interaction, the male was caught, marked and held until after the trial. This prevented the same male from reacting multiple times and ensured sufficient time between interactions to prevent an interacting
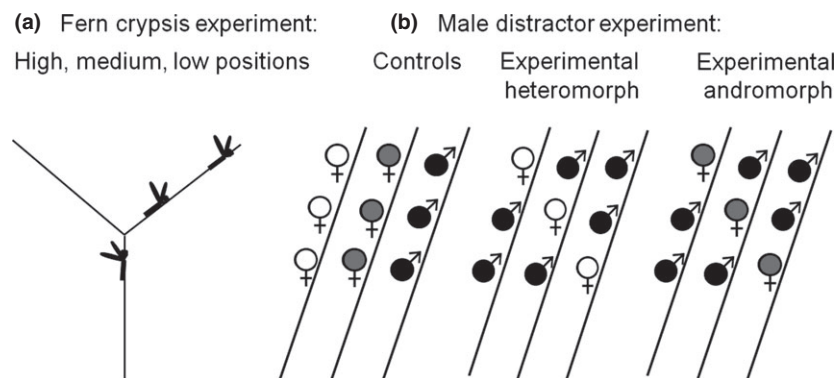

Fig. 2 Experimental design of (a) fern experiment, which tested the female evolutionary stable strategy (ESS) prediction that when perched on green vegetation, heteromorphs are less likely than andromorphs to be detected. The high position was separated by ~13–15 cm from the medium position, which provided the greatest area of green surrounding a glued individual. The low position in partial shade was used to test the assumption that males relied primarily on visual cues. If so, males should be less likely to recognize individuals in the low position. Only one glued individual was on the fern at any time; (b) male distractor experiment, which tested the ESS prediction that when in the presence of male distracters, andromorphs are less likely than heteromorphs to be recognized. Only one dowel was tested at a time.

male from cuing other males to the glued individual. Trials were randomized by colour type, and the location of the perch was changed between replicates. Nonreacting males that entered the 1-m² plot during a 10-min trial were counted to account for variation in male activity. Trials that lacked any nonreacting males in the 1-m² plot and whose glued individuals elicited no interactions were uninformative and eliminated from analyses.

Behaviours and harassment rates of free-flying females and males

To quantify harassment rates in the field and determine whether free-flying, foraging female morphs differed in their use of microhabitats and responses to male harassment, focal observations were made on solitary individuals of both sexes in *Enallagma* populations during the summers of 2008, 2010, 2012 and 2014. On sunny days between 1000 and 1230 h, observations were made on *E. hageni* in a field 150 m from Larks Lake, and on *E. boreale* in fields 20–100 m from shore at Koviak Pond (43°32′N, 84°38/W) and West Burt Lake (45°30′N, 84°38′W), in Cheboygan County, MI. The reflectance characteristics of *E. boreale* colour types are similar those of *E. hageni* (Schultz & Fincke, 2013), but its higher andromorph frequency (50–60%) made it easier to obtain data on both colour morphs. At all sites, the focal species (*E. hageni* or *E. boreale*) was the only *Enallagma* present for all or most of the study. Minority species that co-occurred briefly (*Enallagma ebrium* and *Enallagma exsulans* with *E. boreale*) were easily distinguished. In total, 76 andromorphs (48 *E. boreale* and 28 *E. hageni*), 64 heteromorphs (34 *E. boreale* and 30 *E. hageni*) and 31 males (13 *E. boreale*, 18 *E. hageni*) were followed for a total of 12.5, 9.7 and 8.8 man-hours, respectively.

A total of seven observers quantified interactions between males and solitary individuals. A 'focal' individual was captured, marked by writing a unique number on the wing and then released on a plant stem at the start of observations. Only the most extreme interaction by a given male with a focal individual was counted. Interactions were scored as hover (any approach), grab, chase, tandem or copula. The outcome of a male–focal female interaction was scored as either 'evade male', tandem or copula; all were considered 'harassment' except for copula and tandems that were not observed to separate. Focal individuals were followed until an observer lost track of the individual, copulation began, or it did not move for 10 min; durations ranged from 0.1 to 50.0 min. For comparison with harassment rates, prey capture by and predation on focal individuals was also noted.

To determine whether heteromorphs optimized their predicted context-dependent apparency by perching lower in vegetation than andromorphs, for a subset of observations, the vegetation heights at which a focal individual perched was scored as 'high' (top 1/3), 'medium' or 'low' (bottom 1/3) relative to the vegetation canopy. Perching on the same stem between foraging flights was counted as a single perch height. To test the prediction that andromorphs were more likely than heteromorphs to be found in the vicinity of male distractor signals, nonreacting males within an estimated 50 cm of a focal female were noted. To test whether andromorphs were more likely than heteromorphs to mimic male behaviour, rejection and evasive methods by which female morphs and males reacted to a male approach were noted. The least extreme rejection signal was a 'wing raise', usually accompanied by a downward 'abdomen curve' followed by 'face-off', in which an individual flew up and down vertically ~5–10 cm in front of the harassing male. Evasive behaviours were scored as 'hide', which included moving around or lower down a stem or to the underside of a leaf in the presence of a passing male, tandem separation, or 'fly', which included flying away low in shade, or up high.

To test the possibility that solitary andromorphs were more likely than heteromorphs to frequent the shoreline where the density of male distractor signals was highest, I quantified the number of *E. hageni* along 50-m transects, 2–5 m. from water. Counts were made under sunny conditions between 1200 and 1645 h at Lark's Lake and Duck Lake on Sugar Island, MI (46.4°N, 84.2°W, see Grant *et al.*, 2014 for site description). Upon sighting a solitary, perched male, I immediately counted (within ~5 s) the total number and sex of other solitary, perched individuals within a 1-m² area around the focal male.

Statistical tests

Field experiments were each analysed using two separate general linear models. I first determined the probability that a morph female was detected (sum of nonsexual and sexual reactions), using the total number of male encounters (fly-bys plus detections) as a covariate. Then, ignoring individuals that were not detected (elicited only fly-bys), I used the total number of detections by males as a covariate to determine the probability that, once detected, a morph female was recognized as a potential mate (elicited a sexual reaction). In the high-contrast experiment, the independent variable was colour type (heteromorph, andromorph, male). In the fern crypsis experiment, independent variables were colour type and fern position (high, medium, low). For the male distractor experiment, independent variables were colour type, treatment (control vs. experimental) and perch position relative to the two other glued individuals (high, middle, low). I pooled females by colour morph to compare male reactions elicited by sex.

In the field study of free-flying focal females and males, I compared the effect of female morph on the

frequency of harassments, evasions and proximity to males, using a general linear model with observation duration as a covariate. Two-tailed Fisher's exact tests were used to compare species and morphs with respect to evasive behaviours. Perch use was analysed using a general linear model with colour type as the independent variable and observation duration as a covariate. Dependent variables were the frequency of use of high, medium and low perch positions. I used a Morisita index to determine whether male distributions in the shoreline transects were clumped (> 0), random (0) or over-dispersed (< 0, Krebs, 1998). All statistics were done in SAS version 9.1, SAS Institute Inc., Cary, NC, USA. All models were first run with all interaction effects; nonsignificant interaction effects were dropped from models to gain greater power. Only significant interactions are reported in results. I used Bonferroni corrections to adjust α levels of pairwise comparisons. Throughout, means are reported with ± standard error (SEM).

Analysis of the field focal study was simplified by pooling morphs across the two *Enallagma* species (82 *E. boreale* and 56 *E. hageni*) because there was no difference between species in observation duration ($F_{1,137} = 2.74$, $P = 0.10$), total males in proximity to a focal female ($F_{1,137} = 0.81$, $P = 0.37$), the probability that a female was harassed ($F_{1,137} = 0.77$, $P = 0.38$) or that a male failed to detect a focal female ($F_{1,46} = 0.98$, $P = 0.38$). No interaction effects between species and morph were significant (all P values > 0.49). Similarly, results of male distributions in transects on shore were pooled because there was no difference between sites in the number of solitary males ($F_{2,178} = 2.34$, $P = 0.10$) or solitary females ($F_{2,178} = 0.89$, $P = 0.41$) around a focal male.

Results

Male reactions to individuals on high-contrast background

On a high-contrast background, solitary heteromorphs and andromorphs were equally likely to be detected (elicit nonsexual and/or sexual reactions) by passing males ($F_{1,44} = 0.08$, $P = 0.78$, Fig. 3). Once detected, morph females were equally likely to be recognized by males (elicit sexual reactions; $F_{1,38} = 0.59$, $P = 0.45$).

Compared to females, perched males were more likely to be overlooked (elicited only fly-bys) by mate-searching males ($F_{1,71} = 48.3$, $P < 0.0001$). And once detected, males elicited fewer sexual reactions than females ($F_{1,47} = 20.1$, $P < 0.0001$).

Male reactions to individuals perched on vegetation

The probability that a passing male detected a female perched on a fern depended on her morph and position
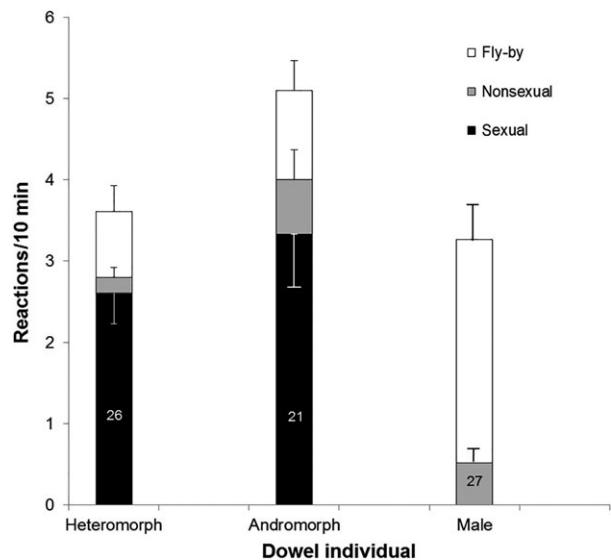

Fig. 3 Results of the high-contrast experiment. Mean ± SEM frequency with which single individuals each glued to a wide, tan dowel were encountered but not detected (elicited only fly-bys), detected (elicited nonsexual and/or sexual reactions) and recognized (females elicited sexual reactions, males elicited nonsexual reactions) by passing males. Numbers refer to sample sizes.
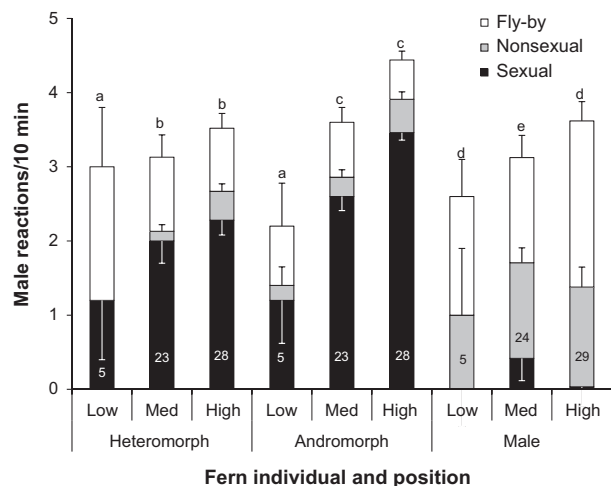

Fig. 4 Results from fern crypsis experiment. Mean ± SEM frequency with which single individuals glued on a fern blade were encountered but not detected (elicited only fly-bys), detected (elicited nonsexual and/or sexual reactions) and recognized (females elicited sexual reactions, males elicited nonsexual reactions). Letters above bars indicate significantly different means with respect to detection only, adjusted for total encounters. Numbers refer to sample sizes.

(Fig. 4). As predicted, a blue andromorph perched on a green fern was more likely to be detected than a green heteromorph ($F_{1,107} = 8.76$, $P = 0.004$). Females

perched in sun (high and medium positions) were more likely to be detected than those perched in the low, shady position ($F_{2,107} = 4.71$, $P = 0.01$). Once detected, however, andromorphs and heteromorphs were equally likely to be recognized (elicit sexual responses from males, $F_{1,89} = 0.20$, $P = 0.66$), regardless of their position ($F_{2,89} = 1.30$, $P = 0.28$). All interaction effects were insignificant ($P > 0.60$).

A male perched in the medium position on the fern blade was more likely to be detected than one perched in the high, sunny or the low, shady position ($F_{2,54} = 3.25$, $P = 0.05$) and if detected was more likely to elicit sexual responses from passing males ($F_{2,35} = 4.87$, $P = 0.01$, Fig. 4).

Male reactions to individuals perched near males

In the male distractor experiment, a total of eight dowel females (3.7%, three andromorphs, five heteromorphs) and 73 dowel males (38.2%) failed to elicit any reaction from mate-searching males. Once encountered, the probability that a female was detected depended on morph and treatment (Fig. 5). Relative to heteromorphs, andromorphs were less likely to be detected (elicit only fly-bys; $F_{1,103} = 13.61$, $P < 0.0004$). A control female perched with two other females was
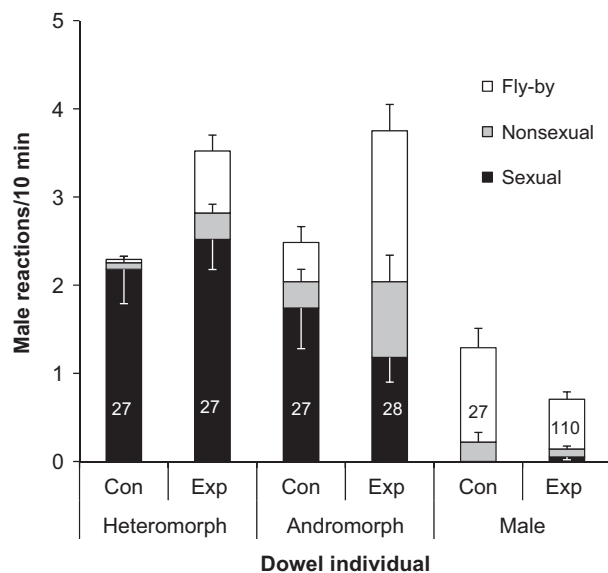
more likely to be detected than an experimental female perched with two males ($F_{2,103} = 2.75$, $P < 0.0004$). A female perched in the middle position between two individuals was marginally less likely to be detected than a female in the high or low position ($F_{2,103} = 2.75$, $P < 0.07$). All interaction effects were insignificant ($P \geq 0.10$).

Once detected, the probability that a female was recognized (elicited sexual responses) depended on morph, treatment and position, but there was also a significant morph by treatment interaction effect. Specifically, andromorphs elicited fewer sexual reactions than heteromorphs ($F_{1,84} = 13.0$, $P = 0.0005$), and relative to controls, morph females perched with two distractor males were less likely to elicit sexual reactions from passing males ($F_{1,84} = 11.48$, $P = 0.001$). However, once detected, an andromorph perched with two males was significantly less likely than a heteromorph to be recognized (elicit sexual reactions) by males ($F_{1,84} = 4.25$, $P = 0.04$). Thus, in close vicinity with males, andromorphs enjoyed a proportionally lower signal apparency (detection plus recognition) and hence enjoyed disproportionately lower sexual harassment than heteromorphs (treatment by morph interaction effect with respect to total apparency ($F_{1,102} = 4.65$, $P = 0.03$; Fig. 6, $X^2 = 32.3$, d.f. = 1, $P < 0.0001$). This result occurred despite the fact that when perched with two males, females were encountered more often (elicited more total fly-bys plus detections), compared to control females ($F_{1,107} = 8.7$, $P < 0.004$, Fig. 5). Finally, morph females that were perched in the middle position between two males were less often recognized (elicited fewer sexual reactions) relative to the other positions ($F_{1,84} = 3.18$, $P = 0.04$).
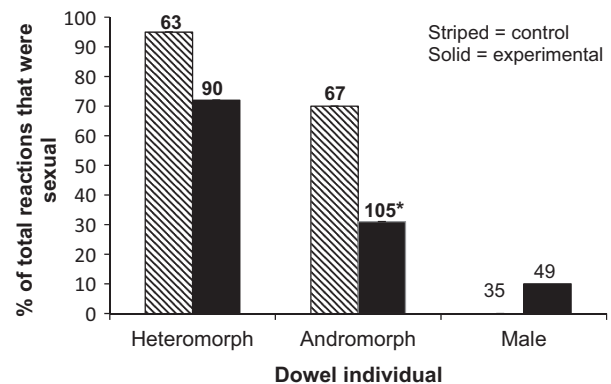

Fig. 5 Results from the male distractor experiment. Mean ± SEM frequency with which individuals were encountered but not detected (elicited only fly-bys), detected (elicited nonsexual and/or sexual reactions) and recognized (females elicited sexual reactions, males elicited nonsexual reactions). Con = controls, in which three individuals of the same colour type were glued to a dowel. Exp = experimental treatments, in which a single female was glued to a dowel with two males. Exp males were male distracters (two per dowel) from the two female treatments. Data pooled across positions within dowels. Numbers refer to sample sizes.

Fig. 6 The percentage of total encounters of dowel individuals that elicited sexual reactions in the male distractor experiment. Relative to controls, in the presence of two distractor males, andromorphs enjoyed disproportionately reduced recognition by passing males compared to heteromorphs (*$P < 0.05$). Numbers refer to total encounters by unique males.

Relative to females, males perched with two other individuals were more likely to elicit only fly-bys (be undetected or ignored) by passing males ($F_{1,243} = 33.8$, $P = 0.001$). Among males, neither treatment ($F_{1,149} = 0.38$, $P = 0.54$) nor position ($F_{1,149} = 0.41$, $P = 0.66$) affected the probability that a male elicited only fly-bys. Once detected, a male perched near a female was no more likely to elicit a sexual response from a passing male than a control male perched with two other males ($F_{1,149} = 0.38$, $P = 0.54$, Fig. 5).

Behaviour and harassment of free-flying female morphs in the field

When foraging in the fields, solitary females typically perched in sun, regardless of the perch height. Heteromorphs were less likely than andromorphs to use high perches ($F_{1,57} = 4.54$, $P = 0.04$), whereas female morphs did not differ in their relative use of medium ($F_{1,48} = 0.00$, $P = 0.95$) and low perches ($F_{1,39} = 2.87$, $P = 0.10$, Fig. 7). Focal males were more likely than females to use high perches ($F_{1,82} = 24.32$, $P < 0.001$).

Controlling for observation duration, focal andromorphs were more likely than heteromorphs to be found within 50 cm of males ($F_{1,137} = 5.63$, $P = 0.02$). Nevertheless, of focal females that perched within 50 cm of a male, andromorphs were no more likely
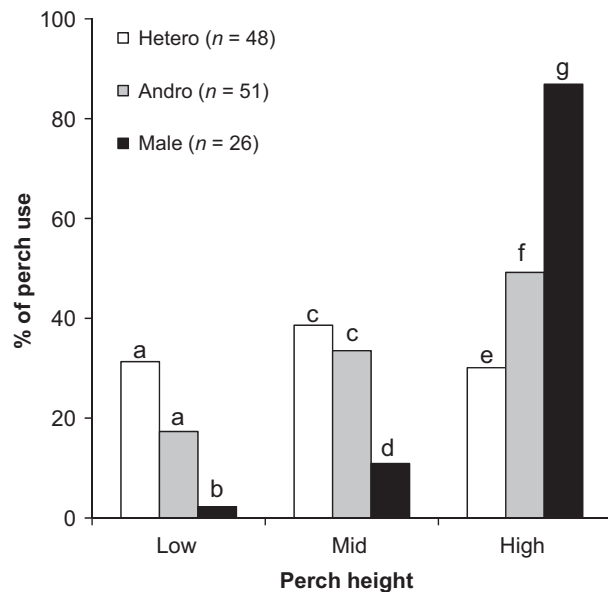

Fig. 7 Percentage of total perch use by 48 focal heteromorphs (166 unique perches), 51 focal andromorphs (179 unique perches) and 26 focal males (165 unique perches). Letters above bars indicate significantly different perch use by colour types, accounting for variation in observation duration (see text); difference between low perch use by female morphs was marginally significant ($P = 0.10$).

than heteromorphs to be recognized ($F_{1,46} = 2.82$, $P = 0.10$). More generally, andromorphs and heteromorphs did not differ in the probability of being recognized (elicit sexual reactions) by males ($F_{1,137} = 2.48$, $P = 0.12$), nor in their ability to evade harassing males ($F_{1,137} = 0.01$, $P = 0.92$).

Harassing males departed after nonfocal immatures of both sexes, and mature males used rejection behaviours. In contrast, milder rejection behaviours always led to face-offs or evasive flight for heteromorphs and andromorphs, which did not differ in their use of evasive behaviours (Table 1). Focal females typically flew away, over half of the time (56%) into shade where males rarely pursued them. Evasive behaviours did not appear to function as a way for females to choose persistent males as mates; most harassing males lost track of females once they flew, and one female that avoided detection by hiding, minutes later, accepted copula with a different male. Of the 26 (19%) focal females taken in tandem, 65% separated before copula, typically by holding onto vegetation or moving down a stem, increasing the acuteness of the angle between herself and the male until tandem was broken. Three males released the tandem female after she moved her head back and forth; one also raised her legs towards her thorax. Of the 31 focal males, four (13%) harassed females; five (16%) repeatedly inspected other males.

Prey capture ($F_{2,168} = 0.60$, $P = 0.55$) and predation ($F_{2,168} = 0.07$, $P = 0.93$) did not differ among colour types, but both events were rare. Females were seen to capture a prey item only once per 60.2 min, whereas they experienced one harassment event every 18.1 min of observations. On average, it took a female four bouts of foraging to capture a prey, which required 6.52 ± 1.38 min ($n = 9$) to consume (range = 2–12 min). Six dragonflies and six robber flies were seen within 50 cm of 12 focal individuals, three of which (25%) were captured. Robber flies caught a solo male and a heteromorph, and a dragonfly caught an andromorph resisting tandem.

In contrast with field habitats, at lakeshores, the only two solitary females found during the transect censuses were dull in colour, characteristic of females leaving the water after submerged oviposition (see Fincke, 1986). Here, males were highly clumped, as indicated by Morisita indexes that ranged from 2.0 to 4.5 at Larks Lake ($n = 3$ transects) and from 2.6 to 4.0 on Sugar Island ($n = 6$, $P < 0.005$ for all X^2 values). Of the total 135 solitary focal males, 80% were perched in groups of 2–10 per 1-m^2; 52% were in groups of three or more males per 1 m^2. Only 28 of the 1-m^2 plots contained females, of which all but two (above) were in tandem. On only two occasions over five summers at my study sites (once in a field, once near shore) did I find an andromorph perched in a cluster of 3–4 males, none of which responded to the andromorph until she flew.

Table 1 Male interactions with free-flying focal individuals by colour type. The number of evasions can total more than the number of individuals harassed because some were harassed more than once during the observation. Five focal males harassed females during the observations, whereas three of them were approached by other males.

Morph	Time observed (min)	Harassed?		Ways of evading males once harassed			
		No	Yes	Fly	Face-off	Hide	Tandem separation
Heteromorph	9.09 ± 1.24	41	23	10	6	7	4
Andromorph	9.90 ± 1.17	38	38	16	6	9	13
Male	17.1 ± 2.92	28	3	2	1	–	–

Discussion

Results from the field experiments demonstrated for the first time context-dependent trade-offs between detection and recognition of signallers. Morph-specific differences in apparency to receivers resulted in context-dependent harassment of colour polymorphic females by mate-searching males. First, when solitary female *E. hageni* were perched on high-contrast dowels lacking male distractors, the two morphs did not differ in the probability of being detected (elicited nonsexual and/or sexual reactions) or recognized by males (elicited sexual reactions). In contrast, on green bracken ferns, relative to the brighter blue andromorphs, the green heteromorphs were less likely to be detected by males (elicited only fly-bys). Importantly, once detected on the fern, andromorphs were as likely as heteromorphs to be recognized as 'female'. Thus, in the context of green vegetation alone, sexual mimicry did not function to protect andromorphs from harassment. On the other hand, when perched with two males on a dowel, andromorphs were less often detected than heteromorphs, and as predicted, once detected, they were less often recognized as potential mates. Importantly, although perching with two males lowered the harassment rate to both heteromorphs and andromorphs relative to controls, andromorphs enjoyed disproportionately less sexual recognition and hence less harassment than heteromorphs (morph × treatment interaction for both recognition, Fig. 5, and overall signal apparency, Fig. 6). Whereas one might expect that a female perched with two other females (controls) would elicit more harassment by males than when perched near two males, surprisingly, the latter experimental females were encountered more often, due to an increase in fly-bys and nonsexual reactions elicited (Fig. 5). This likely resulted from the habit of males to investigate other males, as was found in the field study.

The current study is, to my knowledge, the first to test under natural conditions, the effect of perceptual trade-offs of receivers (Schultz & Fincke, 2013) on signallers. Thus, my results provide broad insights for understanding equilibrium frequencies of polymorphisms and their maintenance more generally. First,

although reflectance patterns have been quantified for species in only three genera (*Enallagma*, Fincke *et al.*, 2007; Schultz & Fincke, 2013; *Ischnura*, Van Gossum *et al.*, 2011; Huang *et al.*, 2014; *Argia*, T.D. Schultz, unpublished data), the crypsis/mimicry trade-off in signal apparency that I found in female *E. hageni* should be common among colour polymorphic female Odonata. Heteromorphs typically vary between green and brown, across and sometimes within species (Lam, 2004; Paulson, 2009) and hence are relatively cryptic against local vegetation compared to the brighter, typically blue andromorphs (Schultz & Fincke, 2013). As a female ESS, the crypsis/mimicry trade-off suggests that the number and type of colour morphs occurring within species are constrained by the perceptual and cognitive abilities of males and visual predators, making it difficult for a noncryptic or nonsexually mimetic mutant morph to invade. Colour polymorphic species that have two types of heteromorphs but no andromorph (reviewed by Fincke *et al.*, 2005) challenge the above scenario if a heteromorph is common but not cryptic and lacks any other morph-specific fitness benefit to off-set its apparency cost. For example, *Ischnura senegalensis* males are green with a blue abdominal tip, whereas females are either uniformly brown or blue with a blue tip. Given a high apparency against background vegetation coupled with low sexual mimicry (limited to its blue abdominal tip), the blue morph would be expected to be relatively rare. Curiously, at equilibrium its frequency is ~50% (Takahashi *et al.*, 2010). Developmental colour morphs offer an example of how either high or low female apparency can lower sexual harassment when females behaviourally optimize the context in which they encounter males. The conspicuously orange immature *Ischnura verticalis* females frequent areas away from the mature green males and receive sexual reactions from them only after the orange colour starts turning black, signalling the on-set of sexual receptivity, prior to turning the characteristic dull grey-blue (Fincke, 1987). In contrast, the blue immature *Ischnura heterosticta* sexual mimics frequent areas with mature blue males before turning green at sexual maturity, when they should benefit from background crypsis (Huang *et al.*, 2014). An

adaptive function of signal similarity for females is less clear when it occurs between heterospecific females whose female signals are confusing to males (Fincke *et al.*, 2007; Limeri & Morehouse, 2014). Then, any harassment protection gained must be weighed against the cost of sexual interference for both sexes, which, in damselflies, may have driven congeneric species to diverge in signalling space (Fincke, 2004).

Although models of female-specific colour polymorphisms indicate that they can be maintained by negative frequency-dependent selection (Svensson *et al.*, 2005; Kunte, 2009; Takahashi *et al.*, 2014), the proximate mechanisms that give rise to such selection have been unclear (Ajuria Ibarra & Reader, 2013). Harassment by male *E. hageni* receivers depended on the immediate context in which a male encountered a female morph, and not on frequency-dependent perception. Thus, my results offer a more parsimonious driver for sexual harassment than either 'search image formation' (short-term perceptional bias towards the morph recognized most recently, within the temporal limits of a male's memory) predicted by the learned mate recognition hypothesis (LMR, Fincke, 2004) or associative learning by copulating males (Takahashi & Watanabe, 2009). Moreover, my results are consistent with the recent discovery of the male's 'decision rule' for sex recognition in *E. hageni*, which explains why novel colour types of both sexes elicit sexual responses from male *Enallagma* (Xu *et al.*, 2014; Barnard *et al.*, 2015), and learned mate recognition by males that occurs at an early age. In *Enallagma* (Fincke *et al.*, 2007) and *Ischnura* (Sánchez-Guillén *et al.*, 2013), naïve males learn to distinguish females from males, and likely the decision rule. Assuming sufficiently high rates of signal recognition by receivers, frequency-dependent perception by mate-searching males and visual predators could expedite the return of a population to its equilibrium frequency, even though context-dependent perception by receivers suffices.

The finding that andromorphs in proximity to male distractors elicited fewer sexual reactions than heteromorphs (Fig. 5) was consistent with the LMR and Sherratt's (2001) ground-breaking signal detection model of male mimicry (MM), as well as all other mimicry-based hypotheses (Johnson, 1975; Robertson, 1985; Hinnekint, 1987). However, other results were contrary to MM but consistent with LMR. Heteromorphs were not invariably detected more often than andromorphs (Fig. 5), and once detected, they were not invariably recognized by males (Fig. 4). Fincke's (2004) verbal application of signal detection theory to damselfly systems predicted that sexual harassment towards females was a function of morph–environment interactions, specifically those arising from background crypsis and signal similarity with males. Thus, a modified LMR whose learned mate recognition occurs in young adult males offers a broad, apparency-dependent model whose equilibrium frequencies depend largely on the relative apparency of heteromorphs and andromorphs to males (Fig. 5 of Fincke, 2004; Fincke *et al.*, 2005) and perhaps visual predators (Schultz & Fincke, 2013) in areas where females are encountered.

The sequential receiver steps of encounter, detect and recognize as defined here illustrate the heuristic value of noting relevant components of context-dependent apparency when comparing studies of receiver perception. For example, Sherratt (2001) used 'encounter' to mean detect, thus focusing on recognition, while ignoring undetected individuals. Fincke (2004) used 'detect' synonymously with recognize, focusing more broadly on both components of signal apparency as a type of morph–environment interaction. Conclusions about male perception that are based solely on male sexual reactions elicited by females presented to them directly (e.g. Forbes *et al.*, 1997; Rivera & Sanchez-Guillen, 2007; Iserbyt & Van Gossum, 2011; Takahashi *et al.*, 2014) pertain only to a male's ability to recognize females. The presentation method circumvents a male's detection problem. Similarly, conclusions about male harassment and morph fitness based on caged individuals (e.g. Sirot & Brockmann, 2001; Takahashi *et al.*, 2014) are likely valid only for the cage context. Even when vegetation is provided, both sexes often perch on cage screening, where heteromorphs lose their anti-harassment apparency advantage, but andromorphs may not (Xu & Fincke, 2011). Similarly, the only direct evidence for search image formation by damselfly males (Miller & Fincke, 1999; Van Gossum *et al.*, 2001; Fincke *et al.*, 2007) and by visual predators (Bond & Kamil, 2002) is limited to cage and laboratory contexts, respectively. There, rates of recognition by receivers may exceed those under natural conditions. Finally and more generally, due to the logistical challenges of following individuals in the field, direct measures of harassment rates towards females have typically had to rely on laboratory environments (e.g. Krupa & Sih, 1993; Makowicz & Schlupp, 2013).

Results from the focal study of free-flying females and males supported my prediction that in locations where solitary females forage, the two morphs differ in their use of microhabitats in ways that optimize their signal apparency to males. In fields, foraging heteromorphs typically perched in sun but below the vegetation canopy, where they enjoyed a cryptic background above and below them. In contrast, andromorphs were more likely to perch at the top of vegetation and consequently were more likely than heteromorphs to perch within 50 cm of a male. Despite being more often in the vicinity of males, andromorphs were not harassed more than heteromorphs, suggesting they enjoyed some protection from male distractors at distances greater than those in the male distractor experiment. The potential for sexual mimicry in behaviour was constrained in *E. hageni* and *E. boreale* because tenerals of

both sexes, mature males and both female morphs used the same rejection behaviours. In contrast, some andromorphic *Ischnura* that are better sexual mimics in colour and pattern than those of *Enallagma* also mimic male behaviour (Robertson, 1985; Sirot *et al.*, 2003; Van Gossum *et al.*, 2011).

My focal study using *E. hageni* and *E. boreale* offers the first direct measure of harassment rates towards females in the wild for any odonate, and probably any animal. Heteromorphs and andromorphs suffered similar harassment rates, an expected result for populations at equilibrium frequency set by balanced crypsis/mimicry trade-offs. Both morphs were equally good at evading harassing males, and 74% of harassment events did not escalate to tandem. Even when unwilling females were taken in tandem, at least 65% broke tandem without mating (26% of harassment events). In contrast, indirect evidence for harassment based only on tandem separations (inferred from the transfer of fluorescent dust from males to females in the field), suggested that andromorphs of *Ischnura elegans* were harassed less often than heteromorphs (Gosden & Svensson, 2009; see also Robertson, 1985; Sirot *et al.*, 2003).

My focal study was not designed to quantify the relative fitness advantage that female morphs may enjoy by deflecting sexual harassment or predation, a goal that remains elusive for polymorphic signalling systems in the field (Ruxton *et al.*, 2004). Nevertheless, females were often interrupted in foraging activities by males searching for mates, events that occurred much more often than females' successful capture of prey. Thus, one cost of sexual harassment in *Enallagma* seems to be a reduction in a female's foraging opportunities.

My assumption that a male's encounter with individuals reflected the distance over which he perceived them visually was consistent with all but one result. Although damselflies may use olfactory cues to locate prey in a lab (Piersanti *et al.*, 2014), they did not appear to use olfaction to detect mates in the field. Males often failed to recognize either morph in the low fern position and andromorphs perched with two males on dowels, and males typically lost females flying into shade. Had males been using chemical cues, neither shade nor signal distractors should have prevented them from detecting females at distances of ≤10 cm (Figs 4 and 5). Chemical sexual mimicry is known in crickets (Maroja *et al.*, 2014). Similar, short-range cues cannot be ruled out here, because males perched low on ferns elicited fewer mistakes than those in the sunny, medium position (Fig. 4), even though low sample size provides a more parsimonious explanation.

The high apparency of the bright blue male signal appeared beneficial for both sexes. Males rarely mistook perched males for females, reducing sexual harassment of males, as predicted by Sherratt & Forbes (2001). But males also often inspected each other, a surprising behaviour given that males competing for limited females should be more evenly distributed than the resulting clumped distribution (Fretwell & Lucas, 1970). Males on shore provided 'beacon' signals for arriving solitary females, likely maximizing encounter rates with receptive individuals for both sexes. Indeed, the speed at which females were taken in tandem at the shore suggested a constraint on sexual mimicry for andromorphs. Perching among males might be an effective ruse, but only as long as a female remained still; as soon as she started to forage, she would be pursued.

Background crypsis offered heteromorphs a more general way to deceive male receivers than sexual mimicry, which required andromorphs to be in a more specific context to deceive males and likely visual predators, especially ones with a blue colour bias (Taylor *et al.*, 2014). Although context-dependent receiver perception appears sufficient for the maintenance of odonate colour polymorphisms, its role in driving negative frequency-dependent selection more generally requires further testing, particularly in butterflies, the other insect group with abundant female-specific colour polymorphisms (Kunte, 2009).

Acknowledgments

References

Ajuria Ibarra, H. & Reader, T. 2013. Reasons to be different: do conspicuous polymorphisms in invertebrates persist because rare forms are fitter? *J. Zool.* **290**: 81–95.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.

Arnqvist, G. & Rowe, L. 2006. *Sexual Conflict*. Princeton University Press, Princeton.

Barnard, A., Fincke, O.M., Shields, M. & Xu, M. 2015. Melanic individuals in color polymorphic *Enallagma* damselflies result from phenotypic, not genetic, variation. *Int. J. Odonatol* (in press).

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* **2**: 349–368.

Bond, A.B. & Kamil, A.C. 2002. Visual predators select for crypticity and polymorphism in virtual prey. *Nature* **415**: 609–613.

Chapman, T. 2006. Evolutionary conflicts of interest between males and females. *Curr. Biol.* **16**: R744–R754.

Darwin, C.R. 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London.

Dominey, W.J. 1980. Female mimicry in male bluegill sunfish —a genetic polymorphism? *Nature* **284**: 546–548.

Endler, J.A. 1978. A predator's view of animal color patterns. *Evol. Biol.* **11**: 319–364.

Endler, J.A. 1983. Natural and sexual selection on color patterns in Poeciliid fishes. *Environ. Biol. Fishes* **9**: 173–190.

Fincke, O.M. 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* **10**: 293–302.

Fincke, O.M. 1986. Underwater oviposition in a damselfly (Odonata: Coenagrionidae) favors male vigilance, and multiple mating by females. *Behav. Ecol. Sociobiol.* **18**: 405–412.

Fincke, O.M. 1987. Female monogamy in the damselfly *Ischnura verticalis* Say (Zygoptera: Coenagrionidae). *Odonatologica* **16**: 129–143.

Fincke, O.M. 2004. Polymorphic signals of harassed female odonates and the males that learn them support a novel frequency-dependent model. *Anim. Behav.* **67**: 833–845.

Fincke, O.M., Jödicke, R., Paulson, D. & Schultz, T.D. 2005. The frequency of female-specific color polymorphisms in Holarctic Odonata: why are male- like females typically the minority? *Int. J. Odonatol.* **8**: 183–212.

Fincke, O.M., Fargévielle, A. & Schultz, T.D. 2007. Lack of innate preference for morph and species identity in mate-searching *Enallagma* damselflies. *Behav. Ecol. Sociobiol.* **61**: 1121–1131.

Forbes, M., Schalk, G., Miller, J.G. & Richardson, J.M.L. 1997. Male-female morph interactions in the damselfly *Nehalennia irene* (Hagen). *Can. J. Zool.* **75**: 253–260.

Fretwell, S.D. & Lucas, H.J. Jr 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta. Biotheor.* **19**: 16–36.

Garcia, J.E., Rohr, D. & Dyer, A.G. 2013. Trade-off between camouflage and sexual dimorphism revealed by UV digital imaging: the case of Australian Mallee dragons (*Ctenophorus fordi*). *J. Exp. Biol.* **216**: 4290–4298.

Gosden, T.P. & Svensson, E.I. 2009. Density-dependent male mating harassment, female resistance, and male mimicry. *Am. Nat.* **173**: 709–721.

Grant, M., Robison, A. & Fincke, O.M. 2014. Use of stable isotopes to assess the intraspecific foraging niche of males and female color morphs of the damselfly *Enallagma hageni*. *Ecol. Entomol.* **39**: 109–117.

Greenwood, J.J.D. 1986. Crypsis, mimicry, and switching by optimal foragers. *Am. Nat.* **128**: 294–300.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**: 92–97.

Hinnekint, B.O.N. 1987. Population dynamics of *Ischnura e. elegans* (Vander Linden) (Insecta: Odonata) with special reference to morphological colour changes, female polymorphism, multiannual cycles and their influence on behaviour. *Hydrobiologia* **146**: 3–31.

Huang, S.-C., Chiou, T.-H., Marshall, J. & Reinhard, J. 2014. Spectral sensitivities and color signals in a polymorphic damselfly. *PLoS One* **9**: 1–8.

Iserbyt, A. & Van Gossum, H. 2011. Show your true colour: cues for male mate preference in an intra-specific mimicry system. *Ecol. Entomol.* **36**: 544–548.

Johnson, C. 1975. Polymorphism and natural selection in ischnuran damselflies. *Evol. Theory* **1**: 81–90.

Jormalainen, V., Merilaita, S. & Riihimäe, K.I. 2001. Costs of intersexual conflict in the isopod *Idotea baltica*. *J. Evol. Biol.* **14**: 763–772.

Krebs, C.J. 1998. *Ecological Methodology*, 2nd edn. Benjamin/ Cummings, Menlo Park.

Krupa, J.J. & Sih, A. 1993. Experimental studies on water strider mating dynamics: spatial variation in density and sex ratio. *Behav. Ecol. Sociobiol.* **33**: 107–120.

Kunte, K. 2009. Female-limited mimetic polymorphism: a review of theories. *Anim. Behav.* **78**: 1029–1036.

Lam, E. 2004. *Damselflies of the Northeast: A Guide to the Species for Eastern Canada and the Northeastern United States*. Biodiversity Books, Forest Hills.

Limeri, L.B. & Morehouse, N.I. 2014. Sensory limitations and the maintenance of colour polymorphisms: viewing the 'alba' female polymorphism through the visual system of male *Colias* butterflies. *Funct. Ecol.* **28**: 1197–1207.

Makowicz, A.M. & Schlupp, I. 2013. The direct costs of living in a sexually harassing environment. *Anim. Behav.* **85**: 569–577.

Maroja, L.S., McKenzie, Z.M., Hart, E., Jing, J., Larson, E.L. & Richardson, D.P. 2014. Barriers to gene exchange in hybridizing field crickets: the role of male courtship effort and cuticular hydrocarbons. *BMC Evol. Biol.* **14**: 65.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Miller, M.N. & Fincke, O.M. 1999. Cues for mate recognition and the effect of prior experience on mate recognition in *Enallagma* damselflies. *J. Insect Behav.* **12**: 801–814.

Morehouse, N.I. & Rutowski, R.L. 2010. In the eyes of the beholders: female choice and avian predation risk associated with an exaggerated male butterfly color. *Am. Nat.* **176**: 768–784.

Paulson, D. 2009. *Dragonflies and Damselflies of the West*. Princeton University Press, Princeton.

Piersanti, S., Frati, F., Conti, E., Gaino, E., Rebora, M. & Salerno, G. 2014. First evidence of the use of olfaction in Odonata behaviour. *J. Insect Physiol.* **62**: 26–31.

Plaistow, S. & Tsubaki, Y. 2000. A selective trade-off for territoriality and non- territoriality in the polymorphic damselfly *Mnais costalis*. *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 969–975.

Rivera, A. & Sanchez-Guillen, R.A. 2007. Male-like females of a damselfly are not preferred by males even if they are the majority morph. *Anim. Behav.* **74**: 247–252.

Robertson, H.M. 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.* **33**: 805–809.

Rowe, L., Arnqvist, G., Sih, A. & Krupa, J.J. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol. Evol.* **9**: 289–293.

Ruxton, G.D., Sherratt, T.N. & Speed, M. 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry*. Oxford University Press, Oxford.

Sætre, G. & Slagsvold, T. 1995. The significance of female mimicry in male contests. *Am. Nat.* **147**: 981–995.

Sánchez-Guillén, R.-A., Hammers, M., Hansson, B., VanGossum, H., Cordero- Rivera, A., Mendoza, D.J.G. *et al.* 2013. Ontogenetic shifts in male mating preference and morph-specific polyandry in a female colour polymorphic insect. *BMC Evol. Biol.* **13**: 116–127.

Schultz, T.D. & Fincke, O.M. 2013. Lost in the crowd or hidden in the grass: signal apparency of female polymorphic damselflies in alternative habitats. *Anim. Behav.* **86**: 923–931.

Sherratt, T.N. 2001. The evolution of female-limited polymorphisms in damselflies: a signal detection model. *Ecol. Lett.* **4**: 22–29.

Sherratt, T.N. & Forbes, M.R. 2001. Sexual differences in coloration of Coenagrionid damselflies (Odonata): a case of intra-specific aposematism. *Anim. Behav.* **62**: 653–660.

Sirot, L.K. & Brockmann, H.J. 2001. Costs of sexual interactions to females in Rambur's forktail damselfly, *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Anim. Behav.* **61**: 415–424.

Sirot, L.K., Brockmann, H.J., Marnis, C. & Muschett, G. 2003. Maintenance of a female-limited polymorphism in *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Anim. Behav.* **66**: 763–775.

Skelhorn, J., Rowland, H.R., Delf, J., Speed, M.P. & Ruxton, G.D. 2011. Density-dependent predation influences the evolution and behavior of masquerading prey. *Proc. Natl. Acad. Sci. USA* **16**: 6532–6536.

Stevens, M. 2007. Predator perception and the interrelation between different forms of protective coloration. *Proc. R. Soc. B* **274**: 1457–1464.

Svensson, E.I., Abbott, J. & Hardling, R. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *Am. Nat.* **165**: 567–576.

Takahashi, Y. & Watanabe, M. 2009. Diurnal changes and frequency-dependence in male mating preference for female morphs in the damselfly *Ischnura senegalensis* (Rambur) (Odonata: Coenagrionidae). *Entomol. Sci.* **12**: 219–226.

Takahashi, Y., Yoshimura, J., Morita, S. & Watanabe, M. 2010. Negative frequency-dependent selection in female color polymorphism of a damselfly. *Evolution* **64**: 3602–3628.

Takahashi, Y., Kagawa, K., Svensson, E.I. & Kawata, M. 2014. Evolution of increased phenotypic diversity enhances population performance by reducing sexual harassment in damselflies. *Nat. Commun.* **5**: 4468.

Taylor, L., Maier, E., Byrne, K., Amin, Z. & Morehouse, N. 2014. Colour use by tiny predators: jumping spiders show colour biases during foraging. *Anim. Behav.* **90**: 149–157.

Théry, M. & Gomez, D. 2010. Insect colours and visual appearance in the eyes of their predators. In: *Advances in Insect Physiology*, Vol. 38 (J. Casa & S.J. Simpson, eds), pp. 267–353. Academic Press, London.

Van Gossum, H., Stoks, R. & De Bruyn, L. 2001. Reversible frequency-dependent switches in male mate choice. *Proc. R. Soc. Lond. B* **268**: 83–85.

Van Gossum, H., Sherratt, T.N. & Cordero-Rivera, A. 2008. The evolution of sex-limited colour polymorphism. In: *Dragonflies and Damselflies: Model Organisms for Evolutionary Research* (A. Cordoba-Aguilar, ed.), pp. 219–229. Oxford University Press, Oxford.

Van Gossum, H., Bots, J., Van Heusden, J., Hammers, M., Katleen, H. & Morehouse, N.I. 2011. Reflectance spectra and morph mating frequencies support intraspecific mimicry in the female colour polymorphic damselfly *Ischnura elegans*. *Evol. Ecol.* **25**: 139–154.

Xu, M. & Fincke, O.M. 2011. Tests of the harassment-reduction function and frequency-dependent maintenance of a female-specific color polymorphism in a damselfly. *Behav. Ecol. Sociobiol.* **65**: 1215–1227.

Xu, M., Cerreta, A., Schultz, T.D. & Fincke, O.M. 2014. Selective use of multiple cues by males reflects a decision rule for sex discrimination in a sexually mimetic damselfly. *Anim. Behav.* **92**: 9–18.