

# Why are female color polymorphisms rare in territorial damselflies?

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**Abstract**

In nonterritorial damselflies, females often come in multiple color morphs, perhaps because females with rare colors experience reduced sexual harassment, and thus have a frequency-dependent fitness advantage, compared to females of the most common color morph, but such polymorphisms are rare in territorial species. We consider three hypotheses to explain the rarity of female color polymorphisms in territorial species: (a) misdirected male aggression, (b) poor male mate recognition, and (c) low mating harassment rates. The first hypothesis has some empirical support, and can account for the absence of andromorphs (i.e., females that resemble males), but does not explain the absence of multiple heteromorphs. We tested the second hypothesis by presenting females of two novel color morphs (green- or red-banded abdomens) to territorial male *Hetaerina capitalis*. Females of both novel color morphs elicited fewer sexual responses than control females, and the red morph occasionally elicited aggressive responses. These results indicate that novel female color morphs would experience reduced mating harassment in this species, contradicting the hypothesis that male mate recognition is too poorly developed to reduce harassment of novel female morphs. By process of elimination, the third hypothesis, that harassment rates are too low in territorial species to provide rare female morphs a fitness advantage, is favored, but remains untested. Our findings also suggest that the common practice of color-marking odonates for behavioral research is likely to interfere with mate choice, as has long been known to be the case in birds.

**KEYWORDS**

color marking, learned mate recognition, male mimicry, mating harassment, misdirected aggression, sexual harassment

## 1 | INTRODUCTION

The traditional explanation for color polymorphisms in prey species is frequency-dependent predation, where common prey types are attacked more frequently than rare prey types (Allen, 1988; Bond & Kamil, 2002; Reznick, Butler, & Rodd, 2001; Stamps & Gonn, 1983). Predators are hypothesized to focus on conspicuous features of the most frequently encountered prey type and to switch prey types when the relative frequency of prey types

changes. This frequency-dependent prey switching prevents the elimination of rare morphs while regulating the abundance of common morphs (Bond & Kamil, 2002). Female-limited color polymorphisms, in which females occur in multiple morphs but males are monomorphic, have also been attributed to frequency-dependent predation in combination with genetic or selective factors that limit the polymorphism to females (e.g., heterogamy and sexual selection; Calsbeek & Cox, 2012; Herrell & Hazel, 1995; Kunte, 2008; Stamps & Gonn, 1983).

A different but analogous selective mechanism has emerged as the leading hypothesis for female-limited color polymorphisms in damselflies (Odonata: Zygoptera): frequency-dependent male mating harassment (Fincke, 2004; Fincke, Jödicke, Paulson, & Schultz, 2005; Gosden & Svensson, 2009; Takahashi, Yoshimura, Morita, & Watanabe, 2010). In damselfly species that exhibit female color polymorphisms, usually one morph resembles the conspicuously colored males (andromorph) while the other morph or morphs are cryptic in coloration (heteromorphs or gynomorphs; (Cordero & Andrés, 1996; Fincke, 2004; Fincke et al., 2005; Hammers & Van Gossum, 2008; Van Gossum, Stoks, & De Bruyn, 2005). The general hypothesis is that males predominately attempt to mate with the most common female morph, which reduces harassment of rarer morphs, and the resulting negative frequency-dependent selection maintains the polymorphism (Gosden & Svensson, 2007, 2009; Hammers & Van Gossum, 2008; Le Rouzic, Hansen, Gosden, & Svensson, 2015; Svensson, Abbott, Gosden, & Coreau, 2009; Svensson, Abbott, & Härdling, 2005; Takahashi, Kagawa, Svensson, & Kawata, 2014; Van Gossum, Stoks, & De Bruyn, 2001). Multiple versions of this hypothesis have been proposed. Under the learned mate recognition (LMR) model, males are most likely to respond sexually to females of the morph they encounter most frequently, and the morph ratio drives frequency-dependent selection (Gosden & Svensson, 2009; Hammers & Van Gossum, 2008; Miller & Fincke, 1999; Takahashi et al., 2010). Most versions of the male mimicry model also assume that male mate recognition is learned, but under this model, andromorphs benefit from their resemblance to males and the ratio of andromorphs to males drives frequency-dependent selection (reviewed in Fincke et al., 2005; Ting, Bots, Jvostov, Van Gossum, & Sherratt, 2009). These hypotheses are not mutually exclusive, and some species appear to exhibit both types of frequency dependence (e.g., Ting et al., 2009). Negative frequency-dependent selection could also arise from innate (i.e., unlearned) male mate recognition, with or without a bias against andromorphic females, but the available evidence suggests that male mate recognition in polymorphic species is at least partially learned (Fincke, Fargevieille, & Schultz, 2007; Miller & Fincke, 1999; Sánchez-Guillén et al., 2013; Takahashi & Watanabe, 2011).

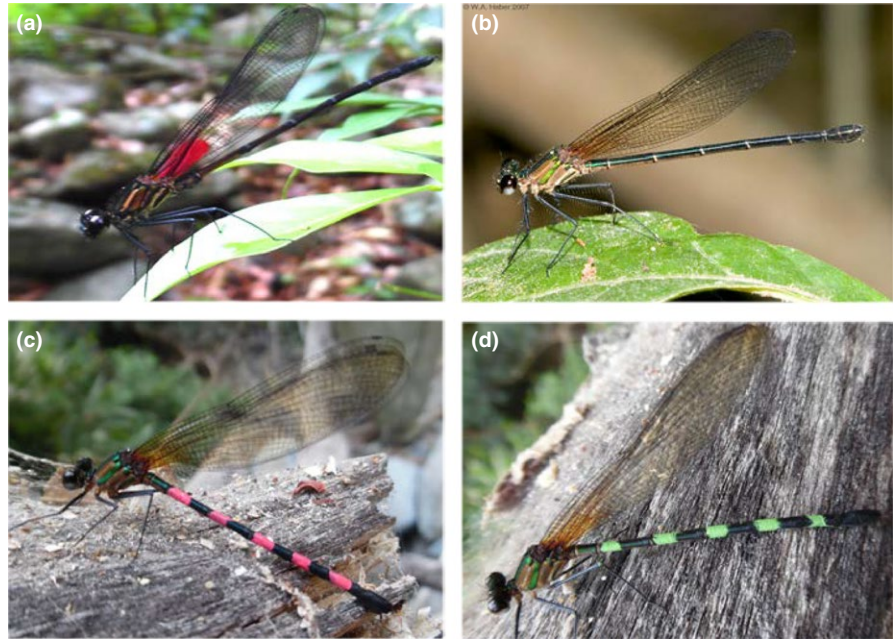
Many studies have tested assumptions and predictions of the frequency-dependent male mating harassment hypotheses in polymorphic damselflies (e.g., Cordero-Rivera & Sánchez-Guillén, 2007; Fincke et al., 2005, 2007; Gosden & Svensson, 2009; Hammers & Van Gossum, 2008; Sánchez-Guillén et al., 2017; Svensson et al., 2005; Takahashi et al., 2010, 2014; Ting et al., 2009), but studies of nonpolymorphic species are needed to understand the conditions that favor the evolution of polymorphisms. One incompletely understood pattern is that in the vast majority of species with female polymorphisms, males engage in a type of mate-searching scramble competition; polymorphic females are rarely found in species with oviposition site-based male territoriality (Fincke, 2004). This pattern has been interpreted as consistent with the LMR model, on the grounds that females in territorial species can avoid mating harassment by staying away from

oviposition sites (Cooper, Brown, & Getty, 2016; Fincke, 2004). To the best of our knowledge, however, no studies have been carried out to compare mating harassment rates between territorial and nonterritorial species. Furthermore, even if mating harassment rates are indeed low in territorial species, females might still benefit from being able to use stored sperm to fertilize their eggs and thereby avoid costs associated with re-mating (Córdoba-Aguilar, Uhía, & Rivera, 2003).

There are at least two other plausible reasons for the negative association between female polymorphism and male territoriality. First, in territorial species, females with andromorphic coloration are likely to elicit aggressive responses from males, which might counteract any benefits of reduced mating harassment. This "misdirected aggression" hypothesis cannot explain the absence of multiple heteromorphs but might account for the rarity of andromorphs in territorial species. Second, males can only refine their conspecific female search image when they encounter females in a mating context (Fincke, 2004), which probably happens less frequently in territorial species in which males have a sit-and-wait mating strategy than in nonterritorial species in which males actively search for females. In nonterritorial species, males that fail to develop an efficient search image would be selected against, but in territorial species, selection might favor males that react immediately to anything remotely resembling a conspecific female entering their territory. Thus, even if females would benefit from being less recognizable, males of territorial species might respond too indiscriminately for negative frequency-dependent selection on female coloration to arise.

To advance our understanding of why female polymorphisms are rare in territorial species, we tested whether novel female color morphs would experience reduced sexual interest from conspecific males in the damselfly *Hetaerina capitalis* (Odonata: Zygoptera: Calopterygidae). This species is sexually dichromatic but monochromatic within the sexes, which appears to be the ancestral state of the genus and the family (Fincke et al., 2005). Males have reddish-brown body coloration and red wing patches (Figure 1a), while females have greenish-brown body coloration and amber wing patches (Figure 1b). Previous research on a similar species, *Hetaerina americana*, showed that putting artificial red patches on female wings reduced sexual responses and triggered aggressive responses from territorial males (Greyer, Drury, Berlin, & Anderson, 2015), as predicted by the misdirected aggression hypothesis. This might explain the absence of andromorphic females in *Hetaerina*, but does not help account for the absence of multiple heteromorphs.

It is possible that the fitness costs of mating harassment are too low in *Hetaerina* to favor the evolution of female polymorphism under the LMR model (Fincke, 2004). The goal of our experiment was to test the alternative hypothesis that males respond too indiscriminately for frequency-dependent male mating harassment to arise in the first place. There is ample evidence for indiscriminate male mate recognition in *Hetaerina*; males of most species tested do not discriminate between conspecific females and females of sympatric congeners (Drury, Anderson, & Greyer, 2015). However, the differences in coloration between the females of most sympatric



**FIGURE 1** Photographs of *Hetaerina capitalis* showing (a) mature male, (b) natural female, (c) experimental red female morph, and (d) experimental green female morph. Photograph (b) courtesy of W.A. Haber. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

*Hetaerina* species are subtler than the differences between the morphs of species with female polymorphisms.

Our results show that conspicuous changes in female coloration do reduce male sexual responses in *H. capitalis*, thereby eliminating one alternative hypothesis for the absence of female polymorphisms in this species.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

We carried out the experiment at two sites in Costa Rica, Quebrada Socorro, near San Luis, Puntarenas (10.2783, -84.81894, elev. 780 m) and Rio Tempisque near Maritza in the Guanacaste Conservation Area, Guanacaste (10.9283, -85.5297, elev. 290 m). These rivers are tributaries of Rio Guacimal and Rio Tempisque, respectively, and enter the Pacific Ocean separately in the Gulf of Nicoya.

### 2.2 | Study species

Mature adult male *H. capitalis* compete for small mating territories close to the surface of rivers in areas with flowing water and submerged vegetation, where females come to oviposit, as in most other species in this genus (Córdoba-Aguilar, Raihani, Serrano-Meneses, & Contreras-Garduño, 2009; Grether, 1996; Weichsel, 1987). Females evidently store sperm and can oviposit without re-mating if circumstances allow, but generally, they are pursued by one or more males and clasped as soon as they arrive to oviposit (there is no preclasping courtship). Clasping is usually followed by copulation, which includes several minutes of sperm removal, and then, the pair flies in tandem while the female searches for a site to submerge and oviposit (Córdoba-Aguilar et al., 2009; Grether, 1996; Weichsel, 1987).

### 2.3 | Behavioral observations

At each site, prior to the experiment, we captured most of the adult male *H. capitalis* along a 300-m transect using aerial nets and color marked them with unique IDs using a previously described method (Anderson, Córdoba-Aguilar, Drury, & Grether, 2011). To determine which males were active territory holders, observers surveyed the transects, recording territorial fights and the locations of males to 0.1 m in three dimensions (distance along the transect, distance from the nearest bank, and height above the water) using handheld computers, throughout the period of the day that males defended territories (about 08:00–17:00 hr). We considered males that consistently perched close to the water surface ( $\leq 0.5$  m) near the same location ( $\pm 1.5$  m) during two or more consecutive days to be territory holders eligible for testing (Anderson & Grether, 2010). These insects habituate to the presence of humans, and most territory holders could be approached closely without visibly affecting their behavior, by the time we began the experiment.

### 2.4 | Experimental design and procedure

Territorial males were presented sequentially with (a) an unmanipulated female (natural morph, Figure 1b); (b) a female with red bands on her abdomen (red morph, Figure 1c); and (c) a female with green bands on her abdomen (green morph, Figure 1d). The colored bands were added using paint pens (200-S Fine Point, Marvy Decocolor Paint Marker, Uchida of America, Torrance, CA, USA). By design, neither of the abdomen color treatments resembles the natural abdomen coloration of males or females of this or any other sympatric species. We used these unnatural color manipulations to test for an effect of novelty, per se, on male responses (see Introduction). The colored bands were placed so as not to interfere with abdomen movement (painting the entire abdomen would likely have fused

some abdominal segments together and introduced a behavioral/postural difference between control and experimental females). The order of presentation was random in the first test at each study site and then varied systematically to achieve a balanced design. One person presented the tethered female while a second person recorded the male's responses. Females were tethered with fine transparent thread (0.076 mm diameter) to a thin fiberglass pole and directed to fly within 1 m of the male for 5 s or until the male stopped interacting with her, whichever happened last (as in Drury et al., 2015). We used unmanipulated females as the control group, for lack of a suitable sham manipulation treatment (any paint added to a female's abdomen could affect her appearance). However, because the females were tethered and presented to males in a standardized way, it is very unlikely that any effects of the color treatments on a female's behavior or flight performance could have influenced the results. Individual females were used in a maximum of four tests (range: 1-4, median 2 tests,  $n = 101$  females), and there was no difference between treatments in the number of times females were used (Kruskal-Wallis test,  $\chi^2 = 0.12$ ,  $df = 2$ ,  $p = 0.94$ ,  $n = 34$  natural,  $n = 33$  red,  $n = 34$  green). Tests were carried out on nonrainy days between 09:00 and 17:00 hr from Mar. 31, 2016 to Apr. 8, 2016 at Quebrada Socorro and from May 12, 2016 to May 25, 2016 at Rio Tempisquito. It was impossible for observers to be blind to the experimental treatments, but the behaviors recorded were unambiguous.

The possible responses of males were as follows: no response (remained perched); approach (flew toward the female); clasp (clapped the female with his cerci); attempted clasp (approached the female with abdomen curled into a clasping position but did not clasp the female); slam (rammed into the female headfirst); and grab (grasped the female with his legs). Slams and grabs are aggressive responses, frequently seen in male territorial fights (Anderson & Grether, 2010), while clasps and attempted clasps are sexual responses (Drury et al., 2015). Approaches are a necessary prelude to both kinds of physical interactions and were not classified as aggressive or sexual.

A "successful" test was defined, a priori, as one in which the male responded sexually to at least one of the three females presented, regardless of the female's treatment group (Drury et al., 2015). At Quebrada Socorro, 31 of 50 tests were successful; at Rio Tempisquito, 39 of 53 tests were successful. Males were retested if their first test was unsuccessful (range: 1-5, median 2 repeat tests,  $n = 24$  males), and eleven males responded sexually when retested. Only successful tests were included in the analysis.

## 2.5 | Data analysis

To examine how the female color treatments affected male sexual responses, we used logistic regression with sexual response (0/1) as the dependent binary outcome variable, female body color treatment, study site, and trial order (i.e., the order in which females were presented) as categorical predictor variables, male ID as a random effects panel variable (to account for the repeated measures design), and all possible two-way interactions (Table 1). We also ran the model with female ID as a random effects panel

**TABLE 1** Logistic regression results for male sexual responses to tethered females of three abdomen color treatments (natural, red, and green), with male ID as a random effects panel variable

Term	df	Chi-square	p
Female color treatment	2	34.79	<0.0001
Study site	1	0.08	0.77
Treatment × study site	2	2.26	0.32
Trial	2	6.70	0.03
Treatment × trial	4	2.94	0.56
Study site × trial	2	0.11	0.94

This analysis is based on 210 trials (three per male), clustered in 70 groups (males). Wald  $\chi^2 = 44.97$ ,  $df = 13$ ,  $p < 0.0001$ .

variable and obtained very similar results (Supporting Information Table S2). In neither case did the panel-level variance component differ significantly different from zero (likelihood ratio test,  $p = 0.5$ ), indicating that it is not essential to include male or female ID in the model. To compare levels of the categorical variables, we used the Bonferroni multiple pairwise comparisons procedure (which reduces the probability of Type I errors). We were not able to use logistic regression to analyze male aggression because the model would not converge. We therefore used Fisher's exact tests to compare the frequency of aggressive responses between treatments. All statistical analyses were carried out in STATA 14.2 (StataCorp, College Station, Texas USA).

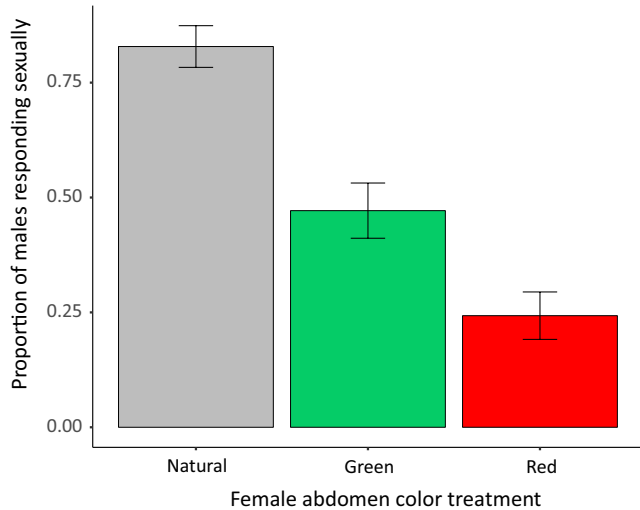
## 3 | RESULTS

### 3.1 | Sexual responses

The probability of males responding sexually to the tethered female was highest for the natural morph, intermediate for the green morph, and lowest for the red morph (Table 1 and Supporting Information Table S1, Figure 2; pairwise comparisons with Bonferroni corrections: natural vs. green  $z = -4.08$ ,  $p < 0.001$ ; natural vs. red  $z = -5.90$ ,  $p < 0.001$ ; green vs. red  $z = -2.71$ ,  $p = 0.02$ ). There was no difference in overall sexual responsiveness between study sites and no interaction between color treatment and study site (Table 1). There was a trial-order effect but no interaction between treatment and trial or between study site and trial (Table 1). The direction of the trial-order effect is that males were less likely to respond sexually to the third female than to the first or second female presented (pairwise comparisons: first vs. second  $z = 0.18$ ,  $p = 1.00$ ; first vs. third  $z = -2.32$ ,  $p = 0.076$ ; second vs. third  $z = -2.02$ ,  $p = 0.13$ ).

### 3.2 | Aggressive responses

Territory holders were more likely to respond aggressively to the red morph than to the natural morph (Fisher's exact test,  $p = 0.001$ ,  $n = 70$ ) and green morph ( $p = 0.004$ ), but they did not respond differently to the green and natural morphs ( $p = 1.0$ ). Overall, 11 of 70 males were aggressive to the red morph, one was aggressive to



**FIGURE 2** Proportion ( $\pm$ SE) of male *Hetaerina capitalis* territory holders responding sexually to conspecific females of three body coloration treatment groups. For logistic regression results, see Table 1 and text. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the green morph, and none was aggressive to the natural morph (Supporting Information Table S1).

## 4 | DISCUSSION

A basic assumption of the LMR model is that females of novel (or rare) color morphs are less likely to elicit male sexual responses than females of the common color morph (Fincke et al., 2007; Miller & Fincke, 1999). Our study appears to be the first to confirm this assumption in a species with monomorphic females. We found that putting red or green bands on the abdomens of female *H. capitalis* reduced, but did not eliminate, male sexual responses. The red bands caused a larger reduction in sexual responses than did the green bands, and aggressive responses were elicited almost exclusively by females with red bands. The primary significance of this finding is that it contradicts one hypothesis for the rarity of female polymorphisms in territorial species, namely that male mate recognition is too poorly developed in territorial species to give rare female color morphs a fitness advantage. The alternative hypothesis that females in territorial species would not benefit from a reduction in mating harassment (Cooper et al., 2016; Fincke, 2004) is strengthened by process of elimination, but still remains to be tested.

The difference in how males responded to females with red and green bands suggests that body coloration plays a role in sex recognition in *Hetaerina*, as it does in other odonates (reviewed in Xu, Cerreta, Schultz, & Fincke, 2014), although aggressive responses to red-banded females were much less consistent and intense than responses to male intruders (Drury et al., 2015). By contrast, putting red wing patches on female *H. americana* eliminated sexual responses and caused the females to be attacked almost as aggressively as male intruders (Grether et al., 2015). In combination, these

studies indicate that any fitness benefits of andromorphic coloration through reduced male mating harassment would likely be offset by costs of misdirected aggression in *Hetaerina*. This prediction could be tested by manipulating the coloration of free-flying females and monitoring survival and reproduction, as in previous phenotype manipulation experiments with *Hetaerina* (e.g., Drury & Grether, 2014; Grether, 1996, 1997).

Female color polymorphisms are common in Odonata, and appear to have evolved multiple times, but are rare in calopterygid damselflies generally (Fincke et al., 2005; Gallesi, Sacchi, & Hardersen, 2015). The only documented female polymorphism in Calopterygidae appears to be a case in which andromorphs of one species (*Calopteryx splendens*) avoid interspecific reproductive interference by resembling males of a sympatric species (*C. haemorrhoidalis*); conspecific males apparently do not distinguish between the morphs (De Marchi, 1990). Female color polymorphisms have been reported in territorial *Megalagrion* damselflies (Coenagrionidae; Cooper et al., 2016), but whether conspecific males distinguish between the color morphs remain to be investigated.

Our experiment was only designed to mimic the initial appearance of a color polymorphism, and the results have no bearing on the learning mechanism that is hypothesized to result in negative frequency dependence and maintenance of polymorphisms. However, experiments in which color-manipulated females were presented repeatedly to the same male could be used to assess whether males can learn to recognize novel female morphs, and if so, whether this interferes with their ability to recognize females of the natural morph, as predicted by the LMR hypothesis, and whether repeated exposure to andromorphs causes males to respond sexually to males, as predicted by the male mimicry hypothesis (Gering, 2017; Ting et al., 2009).

The results of this study also have methodological implications. The common practice of color-marking odonates for behavioral studies (Álvarez-Covelli, Álvarez-Covelli, & Palacino-Rodríguez, 2015; Anderson et al., 2011) might have the unintended side effect of reducing mating rates. This could be especially problematic in studies of male mate choice or mate recognition, if females are color marked. Whether color-marking males reduce female sexual responses should also be investigated. It has long been known that color marking can affect mate preferences in birds (Burley, Krantzberg, & Radman, 1982).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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