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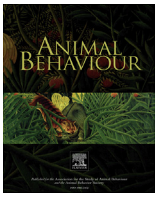

Sexual conflict does not maintain female colour polymorphism in a territorial damselfly

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Female-limited dimorphism is commonly hypothesized to be an adaptation resulting from male harassment or sexual conflict over female mating rate. We examined whether males discriminate between female colour morphs of the beautiful Hawaiian damselfly, *Megalagrion calliphya*, in order to evaluate whether male harassment could explain the existence and/or maintenance of this dimorphism. Previous studies of this species suggest that spatially varying ecological selection maintains the dimorphism, but these hypotheses are not mutually exclusive. Here, we used a common method of measuring male behaviour towards secured females at mating sites under naturally occurring conditions, using five populations that range in male-like female morph frequency from 0 to 0.86. We found very low rates of interaction in a total of 64 one-hour trials, and male behaviour towards females did not differ significantly between colour morphs. By comparing the populations that vary in female morph frequency, we found no evidence of frequency-dependent sexual selection on colour, suggesting that this polymorphism is maintained by selective forces other than sexual conflict.

Polymorphic species have long served as model systems for understanding how variation is maintained within populations (Gray & McKinnon, 2007). The coexistence of distinct heritable morphs within a population can be maintained by gene flow between populations with divergent selection or by balancing selective forces such as negative frequency-dependent selection (Endler, 1977; Fisher, 1930; Ford, 1945). In this study, we evaluated whether frequency-dependent selection could contribute to the maintenance of female-limited colour dimorphism in the Hawaiian damselfly, *Megalagrion calliphya*.

Sex-limited polymorphism, in which only one sex displays multiple morphs, is commonly attributed to sexual selection (Hammers & Van Gossum, 2008). Male-limited polymorphism in many taxa is associated with alternative mating strategies that have evolved due to intrasexual competition over access to mates (Dominey, 1981; Forsyth & Alcock, 1990; Gross, 1991; Sætre & Slagsvold, 1996), while female polymorphism is generally thought to be the result of intersexual conflict over mating rate (Wellenreuther, Svensson, & Hansson, 2014). High mating rates may increase male fitness, but because females of many species can fertilize their clutch with a single copulation, additional mating or harassment may have a fitness cost (Bateman, 1948; Sirot & Brockmann, 2001; Trivers, 1972). Female-limited dimorphism has been studied most commonly in damselflies, where it has been described in more than 100 species (Fincke, Jödicke, Paulson, & Schultz, 2005). In these species, one female morph (called the andromorph) is similar to the male in coloration, while one or more other morphs (gynomorphs) are distinct from the male coloration.

Two prominent sexual conflict hypotheses explain how selection from male mating harassment drives the evolution of such polymorphisms. The male mimicry hypothesis states that andromorphs escape harassment by mimicking the appearance of males (Cordero, 1992; Hinnekint & Dumont, 1989; Robertson, 1985). This strategy is expected to be successful when andromorphs are rare, but as mimics become more common, the benefits of mimicry become reduced as males increase harassment of all male-like individuals (Fincke et al., 2005; Ting, Bots, Jvostov, van Gossum, & Sherratt, 2009; Xu & Fincke, 2011). The learned mate recognition hypothesis predicts that harassment of both morphs will be

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frequency dependent, as males learn to recognize mates based on which female morph is most common in their population (Fincke, 2004; Miller & Fincke, 1999). Both hypotheses assume that harassment occurs and carries a fitness cost to the female.

In addition to negative frequency-dependent selection, female polymorphisms might be maintained by variation in selection both within and between populations (Endler, 1977; Galeotti, Rubolini, Dunn, & Fasola, 2003; Huxley, 1955). If morphs exploit different ecological niches within populations, both could be maintained (Van Gossum, Sherratt, & Cordero-Rivera, 2008). If selection varies between populations, with each morph having a selective advantage in some areas, gene flow could lead to a range of population morph frequencies (Endler, 1977). In some damselfly species, morph frequencies vary along environmental clines, but the role of ecological selection is often unclear (Hammers & Van Gossum, 2008; Iserbyt, Van Gossum, & Stoks, 2012; Sánchez-Guillén, Hansson, Wellenreuther, Svensson, & Cordero-Rivera, 2011; Takahashi, Morita, Yoshimura, & Watanabe, 2011). There is evidence that female polymorphism is under divergent ecological selection along an elevational cline in the Hawaiian damselfly *M. calliphya* (Cooper, 2010; Cooper, Brown, & Getty, 2016), but sexual selection on this polymorphism has not previously been measured. Since the hypotheses are not mutually exclusive, it is important to test whether both mechanisms may operate on colour in this system (Svensson, 2017).

We measured male behaviour towards secured *M. calliphya* gynomorphs, andromorphs and males at mating sites under naturally occurring conditions, similar to tests of male harassment in other studies (e.g. Andrés & Sánchez-Guillén, 2002; Cordero, Carbone, & Utzeri, 1998; Miller & Fincke, 1999; Ting et al., 2009). We observed male behaviour in five populations that range in andromorph frequency from 0 to 0.86. The sexual selection hypotheses predict that harassment of females occurs and that male behaviour towards females differs between the morphs, with greater attention either to gynomorphs (expected under the male mimicry hypothesis) or the more common morph in population (the learned mate recognition hypothesis). Previous research on this system found no difference in the frequency at which gynomorphs and andromorphs are found in tandem and in copulo in the field, regardless of their frequency in the population (Cooper, 2010). Harassment may be low in this species because *M. calliphya* males are territorial. Territorial behaviour has not been measured in this species, but males display male–male aggression and expulsion behaviours, similar to other *Megalagrion* species described as territorial (Moore, 1983). Females may avoid attention from males by leaving the mating site, and therefore this type of mating system seems unlikely to contain the high levels of harassment seen in damselfly species with mate-searching behaviour by males (Fincke, Fargevieille, & Schultz, 2007; Xu & Fincke, 2011). The previous measures of sexual behaviour in this species (Cooper, 2010), however, included only tandem and in copulo behaviours, not other types of interactions that might lower female fitness. Additionally, that study did not manipulate female presence at the mating habitat. If females escape unwanted interactions by leaving the area, observational studies can underestimate harassment and its costs (Bots, Iserbyt, Van Gossum, Hammers, & Sherratt, 2015; Fincke et al., 2007; Van Gossum, Stoks, & De Bruyn, 2001). This study, therefore, was designed to measure the levels of harassment experienced by female morphs at the mating habitat.

METHODS

Natural History

The endemic Hawaiian damselfly *M. calliphya* lives near intermittent streams and upland bogs. Males defend territories around open water where females oviposit, while females spend most of their time away from the water and are usually found near the water only when mating and ovipositing. Males initiate mating by clasping the female by the thorax using abdominal appendages. The pair may stay in this position, called tandem formation, for some time before the female chooses to copulate by moving the tip of her abdomen forward to make contact with the accessory genitalia of the male. The pair will then perch just above open water and the female will oviposit in submerged vegetation. Other males may approach the pair and attempt to drive off the male.

In *M. calliphya*, males and andromorphs are red, and gynomorphs are green (Cooper, 2010). The genetic basis of this variation is unknown, but in other damselfly species female-limited colour polymorphisms are determined by one or two autosomal loci (Cordero, 1990; Cordero Rivera & Andrés, 1999; Johnson, 1964, 1966; Sánchez-Guillen et al., 2011; Sanmartín-Villar & Cordero-Rivera, 2016; Takahashi et al., 2011). In *M. calliphya*, morph is fixed; colour does not change between red and green over the life span of individual adults (Cook, Brown, & Cooper, n.d.). A previous study found that the frequency of andromorphs in populations on Hawaii Island ranged from almost 0% to 100% (Cooper, 2010).

Sex and Morph Ratios

We conducted all observations of *M. calliphya* populations on the windward slope of Mauna Loa on Hawaii Island. We measured sex and morph ratios for each of the five populations between 18 June and 8 August 2015 (Table 1). Unmarked adults were netted in multiple passes through the mating habitat between 0800 and 1400 hours on days that it was not raining. Damselflies are rarely encountered outside of the mating habitat, so our measurements of sex and morph ratios are limited to that area. Captured individuals were identified as male, andromorphic female, or gynomorphic female and marked on the wing with a unique number in indelible ink to prevent recounting the same individuals.

Behaviour Trials

We measured male behaviour experienced by focal individuals at the five populations during a total of 64 trials between 28 June

Table 1
Elevation and demographic information for the five populations, including the total number (*N*) of gynomorph females (G), andromorph females (A) and males (M) captured

Population	GPS	Elevation (m)	*N* G, A, M	Andro. freq. A/(G+A)	Male freq. M/(M+A+G)	*N* trials
Ninole	19°10.58′N, 155°33.61′W	646	11, 0, 101	0.00	0.90	12
Portuguese	19 5.863′N, 155°36.727′W	792	63, 6, 380	0.09	0.85	12
Waiaele	19°06.96′N, 155°36.68′W	853	91, 70, 451	0.43	0.74	16
UMHR	19°8.15′N, 155°36.77′W	1036	50, 28, 426	0.36	0.85	14
Kulani	19°35.69′N, 155°20.73′W	1676	5, 31, 289	0.86	0.89	10

UMHR: Upper Mountain House Road.