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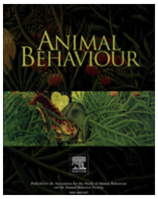

Ontogenetic colour change in females as a function of antiharassment strategy

Y. Takahashi[a,*], G. Morimoto[b,c], M. Watanabe[d]

[a] *Division of Ecology and Evolutionary Biology, Graduate School of Life Sciences, Tohoku University, Miyagi, Japan*
[b] *Department of Life Sciences, Rikkyo University, Tokyo, Japan*
[c] *Tokyo Bay Ecosystem Research Center, Toho University, Chiba, Japan*
[d] *Graduate School of Life and Environmental Sciences, University of Tsukuba, Ibaraki, Japan*

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Mate choice by females is an important component of sexual selection in many species. Theoretically, female sexual traits may be influenced by selection acting on the females via male mate choice, while the evolutionary consequences of male mate preferences are largely unknown, especially in the context of sexual conflict. We tested whether male mate choice affects the evolution of female colour in the damselfly *Ischnura senegalensis* in which females exhibit dimorphism consisting of a gynomorph that experiences ontogenetic colour change and an andromorph that does not. We first quantitatively confirmed that only gynomorphs change their body colour in relation to sexual maturation. In field experiments, males were unwilling to mate with sexually immature gynomorphs, although they attempted to mate with immature andromorphs. This is because males changed their mating preference for female colour depending on previous copulation experiences with sexually mature females. As a result, immature andromorphs received more male harassment than sexually immature gynomorphs, and then showed decreased food intake. Immature-specific colour functioned to avoid costly male harassment during female prereproductive stages, suggesting that ontogenetic colour changes in females have evolved as an antiharassment strategy of females via male mate choice.

Because males' investment in offspring is low after mating, their reproductive success must be maximized by mating with as many females as possible (Bateman 1948), resulting in males competing successfully with other males or males with qualities that increase mating opportunities. In contrast, the number of offspring of females is limited by the number of eggs that they can produce (Trivers 1972). Thus, selection favours females that choose high-quality mates to gain direct benefits, which increases egg production rate (Norris 1990; Boggs 1995) or indirect (genetic) benefits, which improve the quality of their offspring (Welch et al. 1998; Bussière et al. 2006). Such female choice appears to be a selection pressure driving the evolution of sexual ornamentation of males (Alcock 1998). Therefore, studies on intersexual selection have mainly focused on female mate choice and successfully explained the evolution of sexual dimorphism in relation to female mate choice behaviour as well as male–male competition (Andersson 1994). Nevertheless, in nature, male mate choice has also been reported in various animal taxa (Amundsen 2000). Male choice as well as female choice is suggested to be adaptive because male potential reproductive rate is restricted, and females themselves vary in quality and status (Weiss 2006). Thus, males may choose females in order to increase the number of offspring per mate, to gain indirect (genetic) benefits and to increase mating frequency (Amundsen 2000; Bonduriansky 2001; Amundsen & Forsgren 2001; Bateman & Fleming 2006; Clutton-Brock 2007; South & Arnqvist 2011).

Many studies have reported on pre- and/or postcopulatory mate choice depending on female qualities such as body size or fecundity (Rosenqvist 1990; Berglund & Rosenqvist 1993; Monaghan et al. 1996; Swenson 1997; Jones et al. 2001; Byrne & Rice 2006), symmetry (Hansen et al. 1999) and willingness to mate (Andersson et al. 2000; Van Gossum et al. 2001). Theoretically, male mate choice in these animals is suggested to drive the evolution of female ornamentation, and then to lead to the evolution of sexual dimorphism as well as female mate choice (Swenson 1997; Amundsen 2000; Amundsen & Forsgren 2001; Clutton-Brock 2007; South & Arnqvist 2011). Therefore, mutual mate choice between sexes should be explored to elucidate the evolution of sex-specific traits and sexual dimorphism in animals. Detailed properties and the adaptive consequences of male mate choice have been well studied in species with reversed sex roles and with cooperative breeding systems, such as pipefishes (Rosenqvist 1990; Berglund & Rosenqvist 1993) and birds (Amundsen 2000, 2006), but have hardly been

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[*] Correspondence: Y. Takahashi, Division of Ecology and Evolutionary Biology, Graduate School of Life Sciences, Tohoku University, Aoba, Sendai, Miyagi 890-8578, Japan.
E-mail address: takahashi.yum@gmail.com (Y. Takahashi).

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considered in species with noncooperative breeding systems (typical sex roles), that is, in the context of sexual conflict when males often negatively influence their mates (cf. Long et al. 2009).

The evolution of female-specific colour changes during an individual's life is mainly explained by the development of nuptial coloration, which increases mating opportunity by making females more attractive (Swenson 1997). Amundsen & Forsgren (2001) provided empirical evidence that male mate choice selects for female-specific ontogenetic colour changes. Note that most evidence for the evolution of colour change in females has been restricted to species with reversed sex roles or cooperative breeding because in most species with 'typical' sex roles, attractiveness is costly for females because of unrelenting courtship and repeated mating harassment (Long et al. 2009). Females should not show nuptial colours that elicit male aggression in the context of sexual conflict.

However, in coenagrionid damselflies, which are organisms with typical sex roles, ontogenetic colour changes are distinct in females (Corbet 1999; Hammers et al. 2009; Takahashi & Watanabe 2010b; Van Gossum et al. 2011). Female body colour is typically showy in prereproductive states and drab in reproductive ones. Because body colour is the most important visual cue for males in mate choice in Odonata (Gorb 1998; Van Gossum et al. 2001), a difference in body colour between sexually immature and mature females might help males identify the degree of sexual maturity of females. In some damselflies, males change their mating preference depending on previous mating experience with sexually mature females (Takahashi & Watanabe 2008, 2011). As a result, males regard mature females as potential mates (Takahashi & Watanabe 2008, 2010a) and tend to attempt to mate with mature females rather than immature ones that are not sexually receptive (Hammers et al. 2009). Such mate choice behaviour in relation to female willingness to mate is adaptive in terms of mate-searching efficiency (McLennan 1995; Andersson et al. 2000).

The damselfly *Ischnura senegalensis* is ideal for examining the adaptive significance of ontogenetic colour change in females from the perspective of male mate choice. While the males are monomorphic, the females exhibit colour dimorphism (andromorph and gynomorph). The gynomorph (i.e. typical female morph) experiences ontogenetic colour change from orange to dark brown in relation to sexual maturation, while the andromorph (i.e. male-like morph) shows little change in body colour throughout its life. According to preliminary experiments in the laboratory, males discriminate between sexually immature and mature gynomorph individuals, but cannot do so between sexually immature and mature andromorphs (Takahashi & Watanabe 2011). This predicts that immature andromorphs are not distinguished from mature ones, and thus receive mating attempts of males more frequently than immature gynomorphs. Because male mating harassment decreases the amount of food intake in females (Takahashi & Watanabe 2010b), immature-specific body colour in gynomorphs may function to reduce costs of harassment throughout immature stages. Therefore, it is possible to confirm the adaptive significance of immature-specific colour in females by intermorph comparisons in *I. senegalensis*. In the present study, to reveal the adaptive significance of ontogenetic colour changes in females in species with typical sex roles, the effect of ontogenetic colour changes on avoidance of harassment was quantified in the field. We (1) quantified the ontogenetic colour change in males and both female morphs, (2) examined male mating preference for sexually mature and immature females, and (3) compared the amount of food intake of sexually mature and immature females of both female morphs. As stated by Van Gossum et al. 2008, testing selection on immature females was also important to understand fully the evolution and maintenance of female polymorphisms in damselflies.

METHODS

Species and Study Sites

Ischnura senegalensis is a nonterritorial damselfly that inhabits pond edges, where individuals feed, mate and oviposit. Both males and females emerge from early May to late September in the warm-temperate zone of Japan. Morph frequency varies among local populations and changes with generation (Takahashi & Watanabe 2009, 2010b; Takahashi et al. 2010).

Sexually mature males actively fly about throughout the day, searching for mates at the water's edge. They attempt to mate with females without courtship behaviour (Takahashi & Watanabe 2009, 2010b). Since the acceptance of copulation in females is restricted to early morning, copulations begin around 0800 hours and terminate around 1200 hours. Oviposition and foraging activities follow mating activity. Although very few females accept mating attempts in the afternoon, during this time males continuously search for females and attack them for the purpose of mating because they sometimes achieve matings (Takahashi & Watanabe 2009). Because males change their mating preference in accordance with daily mating experience, and lose their memory of mating experiences overnight (Takahashi & Watanabe 2008, 2010a), they show different mating preferences between, before and after mating activities. That is, while in the morning each male has no mating preference, the majority of males in the afternoon try to mate with sexually mature gynomorphs (the common morph) because most males have experienced copulation with the common morph in the morning as a result of random mating (Takahashi & Watanabe 2009, 2010b; Takahashi et al. 2010).

The study site was a pond located in the city of Tsuchiura, Ibaraki Prefecture, in the warm-temperature zone of Japan. Emergent plants, such as *Phragmites australis*, *Schoenoplectus* spp. and *Typha* spp., which provide perching sites and oviposition substrates for *I. senegalensis*, were found along the edges of the pond. All field experiments and surveys were performed on a sunny day.

Previous experiments indicated that females of both morphs achieve sexual maturation at the same age (Takahashi & Watanabe 2010c). They started egg production (Takahashi & Watanabe 2010c) and mating (Takahashi & Watanabe 2012) at 4 days old after emergence. For both morphs, just emerged (0-day-old) individuals show shiny thorax and wing, and pre-mature individuals (4–5 days old) have a bloated abdomen like mature females in the laboratory. Thus, in the present study we used typical immature females (1–3 days old) as immature females, and then there was no difference in average age between immature andromorph and immature gynomorphs tested. Likewise, to eliminate the effect of age, older mature females, which have dull wings and body, were not used as mature females.

Measurements of Body Colour

Reflectance spectra were measured using a USB2000 spectrometer and a PX-2 full-spectrum light source (Ocean Optics, Inc., Dunedin, FL, U.S.A.). Measurements were taken at a 90° angle to the sample. The sampling of females except just-emerged and muddy individuals was carried out on 17 June 2009. For each individual, maturation stage (sexually immature or sexually mature) was recorded according to the degree of worn wing condition and the colour of the ventral side of the abdomen. Three to seven individuals were tested for each category (three immature males, four mature males, four immature andromorphs, seven mature andromorphs, three immature gynomorphs and five mature gynomorphs). For both female morphs, the ventral side of the abdomen