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Condition dependence of female-specific UV-induced fluorescence in a jumping spider

Christina J. Painting [a, b, *, 1], Chia-chen Chang [a, 1], Jia Fen Seah [a], Daiqin Li [a, *]

[a] *Department of Biological Sciences, National University of Singapore, Singapore*
[b] *School of Biological Sciences, University of Auckland, Auckland, New Zealand*

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Male ornaments, commonly explained as being a result of sexual selection, are typically more elaborate than female ornaments. Interestingly, the bright and showy sexually selected traits of some female ornaments, like those of males, might be variable and condition dependent, and hence relate to individual quality. Ultraviolet (UV)-induced fluorescence is one such ornament known to be intricately involved in intraspecific communication in several animals; however, the role of fluorescence in signalling individual quality is unknown. The ornate jumping spider, *Cosmophasis umbratica*, exhibits female-specific UV-induced fluorescence on its palps to facilitate effective intersex communication but whether the fluorescence informs males of the female's condition and individual quality is unknown. We tested the prediction that UV-induced fluorescence in adult female *C. umbratica* depended on postmaturation age, mating status and feeding regime. We found that postmaturation age and feeding regime, but not mating status, affected female fluorescence. Middle-aged females were brighter than younger and older females, but the older females had a greener hue; well-fed females were brighter than starved females. We conclude that the UV-induced fluorescence of female *C. umbratica* is highly condition dependent, highlighting the importance of considering female as well as male ornamentation, particularly when this may have implications for mate choice and the maintenance of coloration in animals.

Conspicuous and showy male ornaments are commonly explained as being a result of sexual selection (Bateman, 1948; Darwin, 1871; Trivers, 1972), with their exaggeration the subject of a myriad of studies (reviewed in Andersson, 1994). Under indicator models of sexual selection, an exaggerated trait can be considered a good gauge of an individual's quality because only the fittest can display the biggest or most attractive forms (Andersson, 1994; Zahavi, 1975) and numerous studies have shown that females choose mates based on condition-dependent male ornamentations in a wide range of taxa (e.g. Boughman, 2007; Kemp, 2008; Punzalan, Cooray, Helen Rodd, & Rowe, 2008). Sexually selected traits are often underpinned by factors such as age (Kemp, 2006; Lim & Li, 2007; Siefferman, Hill, & Dobson, 2005), mating status (Hawkins, Hill, & Mercadante, 2012; Ruiz, Davis, & Martins, 2008) and feeding history (Cotton, Fowler, & Pomiankowaki, 2004; Lim & Li, 2007; Taylor, Clark, & McGraw, 2011; Uetz, Papke, & Kilinc, 2002).

Females in some species with conventional sex roles are also adorned with elaborate ornaments, and there is increasing evidence that female ornaments may be subjected to direct selection through male mate choice and/or female–female competition (Amundsen, 2000a; Edward & Chapman, 2011; Hegyi, Garamszegi, Eens, & Török, 2008; Heinsohn, 2008; South & Arnqvist, 2011; Tobias, Montgomerie, & Lyon, 2012). However, honest signalling of an individual's quality using ornamentation is more complex in females than in males. If the ornament is costly to produce, it might pose the problem of conflicting resource allocation between the ornament production and reproduction (Fitzpatrick, Berglund, & Rosenqvist, 1995). As such, male mating preference will not select for individuals that trade off resource allocation in reproduction for ornament production, and may select for average ornament quality (Chenoweth & Blows, 2005; Wheeler, Gwynne, & Bussiere, 2012). Furthermore, female ornaments may be a genetically nonadaptive by-product of male ornaments in some species, although this does not explain the evolution of ornamental traits displayed only by females (Amundsen, 2000a, 2000b).

Bright coloration has been the focus of numerous studies as a costly, condition-dependent trait in animals that may signal quality (reviewed in Andersson, 1994; Hill, 2006). Many species use either

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* Correspondence: D. Li, Department of Biological Sciences, National University of Singapore 14 Science Drive 4, 117543, Singapore; C. J. Painting, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland Mail Centre 1142, Auckland, New Zealand.

E-mail addresses: chrissiepainting@gmail.com (C. J. Painting), dbslidq@nus.edu.sg (D. Li).

[1] Both authors contributed equally to this manuscript.

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pigmentary (red, orange, yellow, brown and black; Hill, 1991; Minias, Kaczmarek, Włodarczyk, & Janiszewski, 2014) or structural (ultraviolet, blue, green and iridescent) colours (Doucet & Montgomerie, 2003; Kemp & Rutowski, 2007; Siefferman & Hill, 2003) to signal their quality. Ultraviolet (UV)-induced fluorescence is unique as short wavelengths of light are absorbed and re-emitted at longer wavelengths. Unlike UV light, UV-induced fluorescence is visible to animals that do not see in the UV spectrum, such as humans (Arnold, Owens, & Marshall, 2002). Although fluorescence has been documented in many animals (Barreira, Lagorio, Lijtmaer, Lougheed, & Tubaro, 2012; Lagorio, Cordon, & Iriel, 2015), including spiders (Andrews, Reed, & Masta, 2007; Lim, Land, & Li, 2007), its adaptive function is poorly known. In fact, fluorescence in animals has been proposed to be a nonadaptive by-product of atypical pigments that is negligible under natural viewing conditions (Pearn, Bennett, & Cuthill, 2003). Alternatively, it may be used (1) in intraspecific signalling to facilitate identification of colour signals and enhance discrimination of visual signals during threat displays (Mazel, Cronin, Caldwell, & Marshall, 2004), (2) as a sexual signal in mate choice (Arnold et al., 2002; Guillermo-Ferreira, Therézio, Gehlen, Bispo, & Marletta, 2014) or (3) to enhance the contrast with nearby UV-reflecting patches to increase conspicuousness in the UV wavelength (Pearn et al., 2003).

Jumping spiders (Salticidae), the largest and most diverse family of spiders (World Spider Catalog, 2016), provide an ideal model system to study condition-dependent coloration, female ornamentation and male mate choice involving UV-induced fluorescence. All salticids have acute eyesight assisted by two large principal eyes that possess colour vision (Blest, Hardie, McIntyre, & Williams, 1981; Harland, Li, & Jackson, 2012; Land, 1969, 1985; Land & Nilsson, 2012; Zurek et al., 2015) extending into the UV (Blest et al., 1981; De Voe, 1975; Yamashita & Tateda, 1976). Many salticids are also known to exhibit extreme sexual colour dimorphism. Adult *Cosmophasis umbratica* males have several body parts such as their carapace and abdomen that exclusively reflect UV, while females exhibit UV-induced fluorescence only on their palps, the second pair of appendages attached to the cephalothorax that are held in front of the face (Fig. 1; Lim et al., 2007). Male *C. umbratica* will court females under full-spectrum light, but ignore females that lack UV, suggesting that palp fluorescence may be an important signal for species recognition or mate choice that could indicate female quality (Lim et al., 2007) or attract the attention of males (Clutton-Brock, 2009). In Singapore, males are sometimes more abundant than females but at other times of the year there are more females than males inhabiting the leaves and flowers of tropical ‘sun-loving’ flowering shrubs in open areas (Li, n.d.; Lim & Li, 2004). This suggests that the sex ratio is dynamic, making mutual mate choice possible in this species. In the laboratory, male *C. umbratica* can mate multiple times (Li, n.d., Lim & Li, 2004) and males often copulate by engaging one of both or their palps for insemination (Lim & Li, 2004). These behaviours suggest that sperm supplies may be depleted by frequent mating, driving selection on males to be choosy of condition-variable females (Wong & McCarthy, 2009). Although currently unknown, palp fluorescence may also be used as a signal during female–female competition, as has been shown for collared flycatchers, *Ficedula albicollis* (Hegyi et al., 2008).

In this study, we investigated the condition dependence of the UV-induced fluorescence of females in *C. umbratica*. Previous studies on other animals have shown that aspects of coloration such as brightness and hue vary in relation to an individual's condition, although these patterns are not ubiquitous among species (Delhey, Peters, Johnsen, & Kempenaers, 2006; Jacot & Kempenaers, 2007; Siefferman et al., 2005; Taylor et al., 2011). We hypothesized that the UV-induced fluorescence on the palps of adult females is dependent on age, mating status and/or feeding history. We thus predicted that young, unmated or well-fed females would have brighter fluorescing palps and may exhibit a shift in wavelength (hue) compared to old, mated or starved females. To test these predictions we conducted three experiments to test for the effect of female condition on palp fluorescence: (1) we determined the relationship between a female's age and palp colour by measuring palp fluorescence of virgin females 3–99 days after maturation; (2) we compared the change in palp fluorescence of mated versus unmated females; and (3) we tested for the effect of short-term feeding history by comparing palp fluorescence of virgin adult females that were well fed or starved.

METHODS

Study Species and Maintenance

We collected *C. umbratica* as juveniles, subadult males and females (i.e. one moult away from becoming adults), in Singapore and

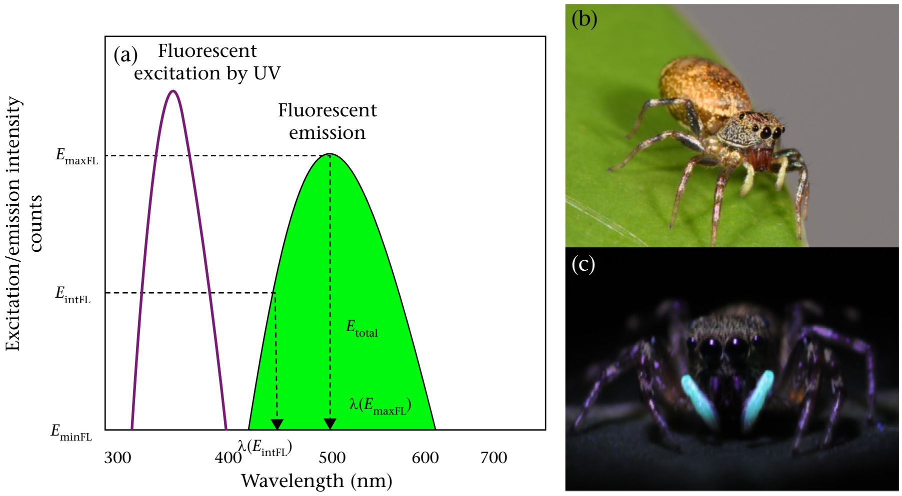

Figure 1. (a) Colour variables of UV-induced fluorescent green palps of female *Cosmophasis umbratica*. E_{maxFL}, E_{minFL}, E_{intFL}: maximum, minimum and intermediate fluorescence intensity counts, respectively; $\lambda(E_{maxFL})$, $\lambda(E_{intFL})$: wavelength (nm) at maximal and intermediate fluorescent emission, respectively; E_{total}, total brightness: total intensity counts of fluorescent spectrum (400–700 nm). (b) Adult *C. umbratica* female (Photo: Caleb Nicholson) and (c) fluorescing palps of *C. umbratica* female under UV light (Photo: Daiqin Li).