

A preliminary study on female-limited colour polymorphism in *Lestes sponsa*

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Female-limited colour polymorphisms are widespread in Odonata, usually showing an androchrome and one or more gynochromes. Androchromes have been hypothesized to function as male mimics with a consequent decrease of male harassment, although males may also learn to recognize the different female colour morphs. In the Eurasian damselfly *Lestes sponsa*, the occurrence of two female colour morphs (androchrome and gynochrome) has been known since the beginning of the twentieth century, although this has been generally overlooked. In this work, we studied a Swedish population of *L. sponsa* by counting the number of females of each morph during nine consecutive days, as well as the number of tandems. Androchromes showed blue pruinescence at similar body parts as males, although more limited at the tip of the abdomen. Moreover, androchromes also showed bright blue coloured eyes as males. We found no indication that androchromes might be a result of age changes in female coloration. The androchrome morph accounted for 19% of the female population. Androchromes did not form tandems at a lower frequency than expected in the population, given the frequency of presence of each morph. Therefore our results suggest that either androchromes in this species do not function as male mimics, or that the population has reached equilibrium with equal fitness for each morph. Other aspects of male harassment and learned mate-recognition, as well as female morph behaviour, would shed light on the evolutionary and ecological significance of female morphs in this species.

Keywords: androchrome; dragonfly; morph frequency; Odonata; tandems

Introduction

Colour polymorphisms can be defined as two or more distinct colour morphs, genetically determined, coexisting within the same interbreeding population, where the least abundant morph is too frequent to be due solely to recurrent mutation (Huxley, 1955). Colour polymorphisms are widespread in nature, with examples in arthropods, fish, reptiles, birds and mammals (McKinnon & Pierotti, 2010). The colour polymorphism may occur in only one of the sexes, i.e. sex-limited colour polymorphism.

In Odonata, female-limited colour polymorphisms are very common and have been found in more than 130 of the Holarctic species (Fincke, Jödicke, Paulson, & Schultz, 2005). Usually, one of the morphs resembles the male coloration (androchrome), while the other(s) have a different coloration (gynochromes). Some genera have an especially high frequency of species with female-limited colour polymorphism, such as *Ischnura* Charpentier 1840 and *Enallagma* Charpentier

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1840 (Fincke et al., 2005). Several hypotheses have been suggested to explain the female-limited polymorphisms in Odonata (reviewed in Van Gossum, Sherratt, & Cordero-Rivera, 2008). One group of hypotheses states that androchromes have evolved as male mimics, leading to reduced male harassment, which presumably involves important costs for the female (Robertson, 1985; Gosden & Svensson, 2007; Van Gossum et al., 2008). Alternatively, the learned mate-recognition hypothesis states that males must learn to recognize the different conspecific female morphs (Miller & Fincke, 1999; Fincke, 2004).

In the family Lestidae, female colour polymorphisms are known in the Eurasian species *Lestes sponsa* (Hansemann, 1832) (Jödicke, 1997). This species ranges from northern Spain to Japan and, contrary to other lestids, it is not specific to ephemeral habitats (Jödicke, 1997; Dijkstra & Lewington, 2006). Although the existence of polymorphic females in this species has been known since the beginning of the twentieth century (Jödicke, 1997), this fact is not mentioned in most of the Odonata field guides (but see Sandhall, 2000). Hence, we have little knowledge about the percentage of the morphs in populations and the proportion of male reproductive attempts to each colour morph. To our knowledge, the only ecological study on *L. sponsa* in which female morphs were taken into account is from southern Japan (Uéda, 1989).

In this work, we describe the androchromic female morph of a Swedish population of *L. sponsa* and study its frequency in the female population. We also explored whether the tandem frequencies of each morph differed from the expected frequencies, given the percentage presence of each morph in the population. We used tandem as a proxy for male harassment. If the androchromes are male mimics, we would expect to find a lower tandem frequency of androchromes than predicted from unselective pairing.

Material and methods

The adults of *L. sponsa* have a metallic coloration on the body, greenish in males and more bronze in females. Males and females look morphologically quite similar. However, mature males show blue eyes and blue pruinescence covering the thorax (except the upper side between the prothorax and the wing bases) and the abdominal segments S1, S2, S9 and S10. Gynochromic females have brownish eyes and lack body pruinescence.

We studied a population of *L. sponsa* in summer 2013, located in a group of boggy wetlands surrounded by boreal forest near Uppsala, in central Sweden (59°58'33"N, 17°26'45"E, 60 m asl). We visited the wetlands on nine days from 31 July to 10 August, from 11:30 to 16:00, as part of a mark-recapture study. First-time captured females were marked with a dot on the left hind wing using a permanent marker. Each day, the number of new females (unmarked) for each morph was noted, and also whether those new females were alone or in tandem (as a measure of male harassment). Hence, we obtained the total number of females of each morph in the population during the study period, as well as the frequency of females in tandem and alone (we note that the data were independent for each day, i.e. females were not counted more than once). A chi-square test was used to explore whether the observed frequencies of tandems of each morph differed from the expected frequencies (given the frequencies of each morph in the population).

Results and discussion

Description of the androchromic female

Androchromic females (Figure 1) showed blue pruinescence covering the thorax, except the upper surface between the prothorax and the wing bases, as in males. Abdominal segments S1, S2, S9



Figure 1. Photograph of an androchromic female of *Lestes sponsa* (Hansemann, 1832) showing the blue pruinescence on the thorax and abdominal segments S1, S2, S9 and S10, and the blue-coloured eyes.

and S10 had also blue pruinescence, but not in the upper side of segments S2 and S9. In segment S10, the blue pruinescence was less conspicuous compared to males. Young mature females are easily recognized by their hard, non-shiny wings, with no visible damage; old mature females, on the contrary, are recognized by their torn and dirty wings. We observed both colour morphs in both young mature and old mature females. Therefore, this suggests that the two morphs were not a result of female ageing, although a mark–recapture study would be necessary to fully address this question. The description of the androchrome is similar to that reported by Jödicke (1997), but in our study population androchromes also had bright blue eyes, similar to males. Jödicke (1997) reported a lack of this trait in a German population, but Uéda (1989) reported the trait in some of the females of a Japanese population and the blue eyes are evident in the picture included in Sandhall (2000). The presence of pruinescence in females might have a role in colour recognition since the wax particles of the pruinescence reflect the ultraviolet (Hilton, 1986) which is detected by the odonate eye (reviewed in Bybee, Johnson, Gering, Whiting, & Crandall, 2012). Yet no studies have explored the role of pruinescence in sexual recognition in Lestidae. We may also speculate that the presence of pruinescence in males and females might be a vestigial trait or a by-product of some other physiological characteristics. Therefore, studies exploring the role of pruinescence in lestids are clearly needed.

The occurrence of androchromes over the distribution range of *L. sponsa* seems still unknown. We have found reports of these morphs in three publications covering populations in Germany (Jödicke, 1997), France (Sandhall, 2000) and Japan (Uéda, 1989). However, there might be other records reported in local entomological journals that we have overlooked. Moreover, we also observed androchromic females in two populations of *Lestes dryas* Kirby, 1890 in northern Spain (two females ovipositing on 30 July 2013 at Valdecarrín, 43°4'44"N, 5°14'48"W, 1638 m asl; one female in tandem on the same date at Isoba, 43°2'44"N, 5°18'58"W, 1416 m asl.). To our knowledge, this is the first report of androchromes in *L. dryas*.

Morph and tandem frequencies

During the study period, we found 176 gynochromic and 40 androchromic females. Thus, the androchromic females represented 18.5% of the female population in the study site. Of those

females, 132 gynochromic and 29 androchromic females were in tandem. The number of observed tandems did not differ from the expected frequencies of tandems, given the proportion of each colour morph in the population ($\chi^2 = 0.0002$, d.f. = 1, $p = 0.990$).

Our results on morph frequencies in the study population clearly contrast with the results reported for a Japanese population where the proportion of morphs was almost equal (Uéda, 1989). The androchromes are rarely the majority in the populations of species with female-limited colour polymorphism (reviewed in Fincke et al., 2005; but see Cordero Rivera & Sánchez-Guillén, 2007 and Takahashi, Morita, Yoshimura, & Watanabe, 2011). In fact, the maintenance of the morphs in a population has been suggested to be explained by a model of negative frequency-dependent selection: the fitness of the rarest morph is higher than that of the commonest morph, since it benefits from lower male harassment (Fincke, 2004).

We did not find support for the male mimic hypothesis in androchromes, since the frequency of tandems did not differ from expected. An alternative explanation is that our study population has reached equilibrium via negative frequency-dependent selection by male learned mate recognition (Fincke, 2004; Schultz & Fincke, 2013). In this case, the fitness of each morph would be equal (Fincke, 2004). Unfortunately, we did not run experiments on learned mate recognition in males. Therefore, further research is needed to find more evidence that might support the several possible hypotheses to explain colour polymorphism in our study species. A study of a large range of populations with different morph frequencies would be necessary to address this question. We do not know the genetic mechanisms underlying the female polymorphism of *L. sponsa*. In other species, the expression of sex-limited polymorphism is governed by simple Mendelian inheritance patterns (e.g. Andrés & Cordero, 1999). Finally, behavioural experiments are also required, since female morphs have previously been found to differ in behaviour in *Ischnura elegans* (Vander Linden, 1820) (Van Gossum, Stoks, & De Bruyn, 2001; Gosden & Svensson, 2007). Thus, different behaviours can be related not only to the ability avoiding males, but also to predation risk, since gynochromes are usually the more cryptic morph (Robertson, 1985; Schultz & Fincke, 2013).

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