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Territorial males have larger wing spots than non-territorial males in the damselfly *Calopteryx splendens* (Zygoptera: Calopterygidae)

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Abstract. Males of *Calopteryx splendens* use two alternative mating tactics, territoriality, and non-territoriality. These different mating tactics are shown to vary between males within the same population and previous studies have shown that territorial males have considerably higher fitness than non-territorial males. In this paper, we tested whether the wing spot size as sexual ornament, wing length, relative wing spot size, asymmetry in wing length, asymmetry in wing spot size, or asymmetry in relative wing spot size differed between the territorial and non-territorial males. We sampled *C. splendens* males, representing both mating tactics, from a river system in south-west Finland. According to our results, territorial males have larger wing spot than non-territorial males. In contrast, there were no differences in the other tested traits between the territorial and non-territorial males. In conclusion, our data show that the size of pigmented wing spots may predict the alternative mating tactic of *C. splendens* males.

Key words. Odonata, damselfly, *Calopteryx*, mating strategy, wing spot

Research Article

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All relevant data are within the paper.

Introduction

Territorial behavior over mating sites is very common in the mating systems of odonates (Corbet, 1999). It is commonly predicted that natural selection will favor male territoriality and the traits that facilitate successful territory defense (Suhonen et al., 2008). In general, male mating success is shown to be higher in territorial than non-territorial males within species (e.g. Plaistow & Siva-Jothy, 1996). However, alternative mating tactics have evolved because ecological and social environments often favor more than one mating tactic (e.g. Suhonen et al., 2008).

Previous studies have found that several male traits, such as muscular fat reserves, immunocompetence, intestinal parasite load, and wing pigmentation, are correlated with territoriality contest outcomes (Contreras-Garduno et al., 2007; Suhonen et al., 2008; Tynkkynen et al. 2005, 2006). These findings suggest that only males in good condition can occupy and defend territories. However, generalizations are difficult because published results from traits, associated with territorial behavior, are contradictory both within species and between species (Suhonen et al., 2008). Thus, there is still large gaps in our knowledge on how these complex alternative mating tactics function in the wild, and more research is needed on the traits associated with territorial and non-territorial behavior.

Territorial *Calopteryx* males are shown to have considerably higher reproductive success because of female preference for territorial individuals (Cordoba-Aguilar, 2000; Plaistow & Siva-Jothy, 1996; Waage, 1973). Even if territorial males do achieve the vast majority of copulations and consequently have more offspring, certain ecological and social environment may occasionally favor alternative reproduction behavior (Suhonen et al., 2008). For example, non-territorial males commonly try to intercept females arriving at ovipositing territory, before the resident owner detects them, and occasionally succeed without a complex courtship behavior. This gain considerable energy and time advantages these males with alternative mating tactics over the territorial individuals (Pajunen, 1966; Waage, 1973).

The size of wing spots varies across the geographical distribution of the *C. splendens* (Honkavaara et al., 2011; Sadeghi & Dumont, 2014), and in general *Calopteryx* females prefer males with large wing spots (e.g. Siva-Jothy, 1999). This is perhaps because e.g., larger wing spots indicate better parasite resistance via phenoloxidase cascade (Rantala et al., 2000; Siva-Jothy, 2000), and males with larger wing spots are shown to provide females more likely with the oviposition resource (for *Calopteryx* species in general, Cordoba-Aguilar, 2000; Plaistow & Siva-Jothy, 1996; Siva-Jothy, 2000; Waage, 1973). The supply of oviposition resources is particularly important in *Calopteryx* damselflies, and consequently, most males try to defend riparian territories, which include patches of floating vegetation, used by females as oviposition sites (Suhonen et al., 2008).

Fluctuating asymmetry may affect the fitness and behavior (Leung & Forbes, 1997; Rantala et al., 2000; Schultz & Fincke, 2009). By definition, fluctuating asymmetry is nondirectional variation between the left and right sides of a bilateral character, which may originate either from genetic or environmental stress (Møller & Swaddler, 1997; Palmer & Strobeck, 1986). In damselfly *C. splendens*, this fluctuating asymmetry has been shown to correlate negatively with the size of the wing spots and males with asymmetrical wing spots also had lower encapsulation rates than the males with more symmetrical wings (Rantala et al., 2000). Here, encapsulation means the ability to form a capsule of hemocytes around a multicellular pathogen as a part of immune reaction. Furthermore, fluctuating asymmetry has been shown to predict e.g., mating status in closely related *C. maculata,* so that mating males showed significantly lower levels of forewing asymmetry than non-mating males (Beck & Pruett-Jones, 2002).

In this study, we aimed to determine the association between the wing length, wing asymmetry, and the wing spot size of territorial and non-territorial *C. splendens* males. We hypothesized that territorial individuals of *C. splendens* have larger wing spots, since the size of these sexual ornaments is sexually selected. Additionally, we predicted that territorial individuals are larger (longer wing length), and have more symmetrical wings, to defend their territories more successfully.

Methods

The study was conducted between 15 and 22 June 2013, in the Tarvasjoki creek, close to the city of Turku (60°32′ N, 22°45′ E) in south-west Finland. For the sampling site, we chose a short section of river that was characterized by a 90-m long rocky and rapidly flowing section and a 350-m smooth-flowing section. The total length of the river section under study was densely populated by *C. splendens,* and the study area also harbors a few individuals of closely related damselfly *C. virgo*. The study section is relatively isolated because the river immediately up- or downstream does not provide suitable habitat for *Calopteryx* species.

In the first part of the study, we collected all sexually mature *C. splendens* males present in the study area between 15 and 18 July 2013 using a butterfly net. Since the age of the individual is shown to affect the territoriality of the *Calopteryx* males so that older males may switch to a non-territorial tactics (e.g. Forsyth & Montgomerie, 1987), the age of the focal individuals was determined by the stiffness and wear on the leading edge of the wings as described in Plaistow & Siva-Jothy (1996), in order to exclude all immature and old individuals. In other words, the age of the individuals was determined between classes 1 to 4, so that the class 1 includes newly hatched tenerals and class 4 the oldest individuals with worn wings, and only individuals in the classes 2 and 3 were included into this study. Altogether we were able to mark 336 *C. splendens* males. We measured both the left and right hindwing length, as well as the length of the wing spots from both hindwings of each damselfly to the nearest 0.01 mm using digital calipers (Fig. 1). Wing spots of the *C. splendens* males are located in the central parts of the wing and

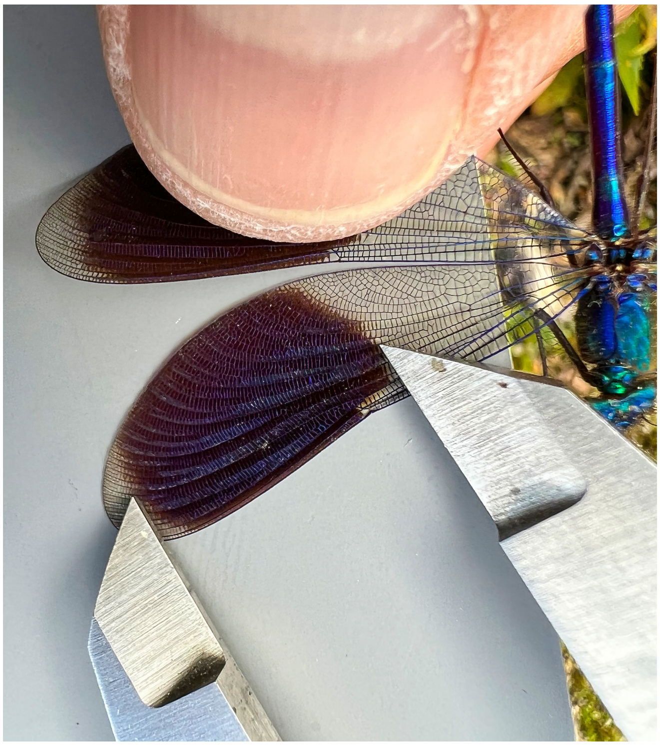

Figure 1. The size of the wing spot of focal *C. splendens* individuals were measured to the nearest 0.01 mm using digital calipers.

Table 1. Mean hindwing length (mm), mean hindwing spot size (mm), relative wing spot size (%), fluctuating asymmetry in hindwing length (mm), fluctuating asymmetry in wing spot size (mm) and fluctuating asymmetry in relative wing spot size in creek Tarvasjoki in south-west Finland of territorial and non-territorial *Calopteryx splendens* males. Differences were tested with t-test and test power is presented.

	Territorial			Non-territorial			*t*-test			
Trait	Mean	SD	n	Mean	SD	n	*t*	df	*p*	Power
Wing length	30.0	0.79	20	29.7	0.56	20	1.33	38	0.192	0.25
Wing spot	16.3	1.05	20	15.5	1.11	20	2.53	38	0.016	0.70
Relative wing spot	54.4	3.25	20	52.1	4.34	20	1.94	38	0.060	0.47
Asymmetry in wing length	0.15	0.17	20	0.15	0.15	20	0.01	38	0.992	0.05
Asymmetry in wing spot size	0.28	0.29	20	0.22	0.25	20	0.69	38	0.492	0.104
Asymmetry in relative wing spot size	0.91	0.97	20	0.67	0.86	20	0.83	38	0.411	0.128

the size of these spots varies between every individual. Consequently, it is not possible to measure wing spot of these damselflies from a specific marker, for example from the tip of the wing onwards, as with many other odonates with wing spots. However, this method of measuring the size of wing spot in *C. splendens* has been shown to be accurate and reproducible even without specific "marker locations" in many previous papers (e.g. Aromaa et al., 2019; Corbet, 1999; Honkavaara et al., 2011; Rantala et al., 2010). The mean length of both wings was used in further analyses, except in asymmetry estimations, where both wings were compared. Thereafter, we marked the males with unique code on the wings with permanent marker (Sharpie non-toxic fine marker silver 0.5 mm), for later identification in categorizing them into territorials and non-territorials as described below.

In the second part of the study, between 19 and 22 July 2013, the behavior of the marked *C. splendens* males were recorded. Here we categorized the males into territorial group, if they defended a territory at least one hour from their conspecifics. During monitoring, individuals were identified with binoculars by the unique code markings on their wings. Furthermore, before netting, they were approached by the researcher until they flew away and if they returned to their putative territory, they were designated as territorial individuals. Males that were further than 10 m away from a potential territory and did not return to their original perch when approached, were designated as non-territorial. Eventually, we were able to categorize 20 individuals of the previously marked individuals (n = 336) as non-territorials. Since we aimed at the balanced data design with equal amount of territorial and non-territorial individuals, we included these 20 non-territorial males and the firstly captured 20 territorial males for further measurements. We used six traits: mean hindwing lengths, mean wing spot size, relative wing spot size, asymmetry of relative wing spot, asymmetry of hindwing length and asymmetry of wing spot size in our comparison between the territorial and non-territorial males (Table 1).

Relative wing spot size was calculated using the following formula (1)

(1) Relative wing spot size = wing spot size (mm) / length of hind wing (mm)

The fluctuating asymmetry between the hind wing length and size of wing spot was calculated using the following formula (2):

(2) Asymmetry of a trait = | right trait – left trait |

We used *t*-test to compare measured traits of territorial and non-territorial males of *C. splendens*. Before the *t*-test, relative wing spot size values were arcsin-transformed. We tested the association between mean wing length and mean wing spot size with correlation coefficient. All the statistical analyses were performed with IBM SPSS Statistics for Windows version 26.

Results

Mean size of wing spot was larger in territorial males than non-territorial males (Fig 2a; Table 1). Moreover, there was tendency that relative wing spot size was larger in territorial males than non-territorial males (Fig 2b, Table 1). Furthermore, we neither found statistically significant difference in the wing length between the territorial and non-territorial, nor there was asymmetry of hindwing length, asymmetry in wing spot size nor in relative wing spot size (Table 1).

There was neither association between the mean length of hind wing and mean size of wing spot in pooled data (r = 0.07, n = 40, p = 0.689) nor in territorial males (r = 0.40, n = 20, p = 0.080), but in non-territorial males this relationship was negative (r = -0.57, n = 20, p = 0.009).

Discussion

In this study, we found that territorial *C. splendens* males have larger wing spots than non-territorial males

(Table 1, Fig. 2a) and there was strong tendency that territorial males had larger wing spot size also in relation to wing length (Table 1, Fig. 2b). Other traits measured, the length of wing, asymmetry of wing, and asymmetry of wing spot, did not differ between the non-territorial and territorial males. Finally, wing spot size did not increase with increasing wing length. However, we found negative correlation between the wing length wing spot size in non-territorial males.

In previous literature, the results on association between wing morphology and other fitness-related traits of *Calopteryx* damselflies are somewhat contradictory. For example, contrary to our prediction, Outomuro et al. (2014) found that territorial *C. splendens* males had shorter wings and wing spot size did not differ between the territorial and non-territorial individuals. On another front, Tynkkynen et al. (2006) found that territoriality in presence of closely related *C. virgo* may favor smaller wing spot size. The contradiction may at least partly be age-related confusion, since the older males may switch to a non-territorial tactics (e.g. Forsyth & Montgomerie, 1987), highlighting the importance of ageing the individuals carefully for these comparisons.

Several factors are shown to contribute to the wing spot size of *Calopteryx* damselflies, and large wing spot size has been linked to a better body condition of the *C. splendens* males. For example, it has been shown in previous studies that males with larger wing spots have higher immunocompetence than males with smaller spots, indicating better physiological condition (Rantala et al., 2000; Siva-Jothy, 2000). Larger wing spots might also help individuals to maintain higher body temperatures (Laakso et al., 2021). Additionally, individuals with larger wing spots are better in evasion of predators (Rantala et al., 2010, 2011; Svensson & Friberg, 2007).

In *Calopteryx* damselfly species, the wing spots also serve as secondary sexual characters, and they play a particularly important role in intra- and interspecific interactions. *Calopteryx* species are territorial, resulting males to fight over the optimal ovipositing areas against other males, in order to increase their chances of copulation (Plaistow & Siva-Jothy, 1996; Serrano-Meneses et al., 2007). Highest quality males are the ones that can obtain the best territories, which provides them with more matings, and wing spot size is a likely determinant of these males (Rantala et al., 2010). Moreover, it seems that individuals with larger wing spots activated quicker than smaller wing spotted males, due to thermoregulatory advantage resulting from dark color (Laakso et al., 2021). Faster activation can lead to longer foraging times, more efficient prey capture and, subsequently, larger fat reserves. Actually, several previous researchers have observed that males with larger wing ornaments have more fat reserves (Contreras-Garduno

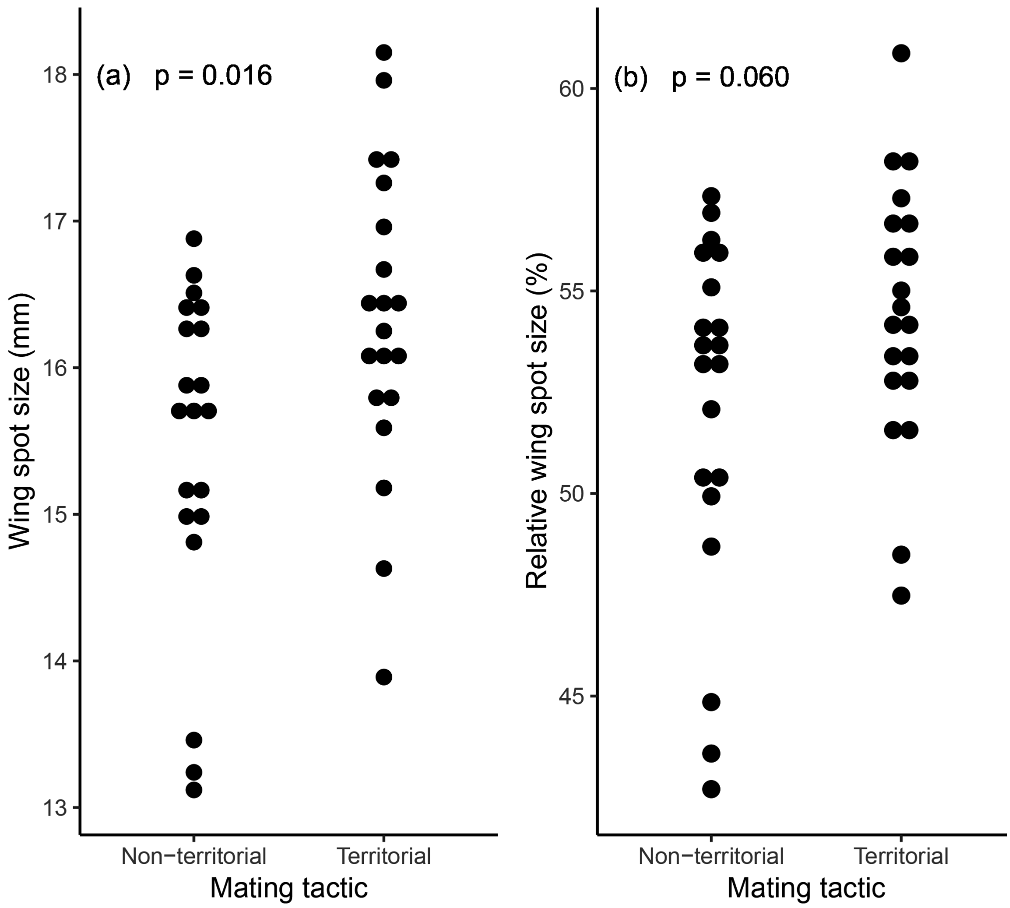

Figure 2. a – Wing spot size of territorial and non-territorial males of *C. splendens*. b – Relative wing spot size of territorial and non-territorial males of *C. splendens*. *P*-values indicates statistical significance of the results between the territorial and non-territorial males (see more details in Table 1).

et al., 2006; Cordoba-Aguilar et al., 2007, 2009), which in turn is shown to increase their ability to obtain territories (Contreras-Garduno et al., 2006; Koskimäki et al., 2004; Marden & Rollins, 1994; Marden & Waage, 1990). Furthermore, *C. virgo* males that were winners of staged territorial contests had more fat than losers (Koskimäki et al., 2004).

In several previous studies in various *Calopteryx* species have shown that territorial and non-territorial behaviors are conditional mating tactics, meaning that they are not genetically fixed (Contreras-Garduno et al., 2006; Koskimäki et al., 2004; Marden & Waage, 1990; Plaistow & Siva-Jothy, 1996). Our data support most studies of *Calopteryx* damselflies, which found no difference between territorial and non-territorial males in body size or wing length asymmetry (e.g. Beck & Pruett-Jones, 2002; Cordoba-Aguilar, 1995; Forsyth & Montgomerie, 1987; Plaistow & Siva-Jothy, 1996; Tynkkynen et al., 2006; but see Koskimäki et al., 2009, for *C. virgo*). In contrast, Schultz and Fincke (2009) found that in a tropical damselfly *Megaloprepus caerulatus,* territorial males had more symmetrical wings and larger relative size of white wing patches than non-territorial males.

According to our data, wing spot size was not associated with wing length. In other words, this means that there are individuals with large wing spots but short wings and individuals with small wing spots but long wings. This contrasts with previous studies on calopterygids (Cordoba-Aguilar et al., 2009; Hardersen, 2010; Rodriguez-Escobar et al., 2020; Schultz & Fincke, 2009), where wing spot size was positively associated with wing length. However, a recent study on *C. splendens* males also found no association between the wing spot size and wing length (Laakso et al., 2021).

In conclusion, our data show that non-territorial *C. splendens* males have smaller wing spots than territorial males. Future studies that included more spatially and temporally variable data, while covering multiple species to further explore the effects of territoriality behavior on the fitness of odonates, would be highly welcomed.

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