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WANDERING MALES ARE SMALLER THAN TERRITORIAL MALES IN THE DAMSELFLY *CALOPTERYX VIRGO* (L.) (ZYGOPTERA: CALOPTERYGIDAE)

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In territorial Odonata, adult ♂♂ may use 2 mating tactics that may be genetically or environmentally determined: territoriality and non-territoriality. The non-territorial tactic has been sometimes found to include 2 additional males: sneaking and wandering. The non-territorial ♂♂, however, often have lower reproductive success than territorial ♂♂. Studies on various *Calopteryx* spp. have repeatedly shown that territorial and non-territorial behaviours are conditional mating tactics and that body size does not predict ♂ resource-holding potential and territorial behaviour. Instead, the resource holding potential seems to depend on the amount of ♂ fat resources. Here, both territorial and wandering *C. virgo* ♂♂ were collected from a creek in central Finland. It was found that territorial ♂♂ were larger and heavier than wandering ♂♂. The data show that the size of the individual may predict the reproductive tactic of some odon. ♂♂ to a greater degree than previously thought.

INTRODUCTION

Alternative mating strategies and tactics evolve because ecological and social environments often favour more than one phenotype (GROSS, 1996; SUHONEN et al., 2008). However, not all males are able to obtain a territory. In territorial odonate species, adult males may use two or three mating tactics or strategies that may be genetically (SIVA-JOTHY & TSUBAKI, 1989a, 1989b; WATANABE & TAGUCHI, 1990; TSUBAKI, 2003) or environmentally determined, for example being territorial or not (FORSYTH & MONTGOMERIE, 1987; PLAISTOW & SIVA-JOTHY, 1996; TYNKKYNEN et al., 2006; SERRANO-MENESES et

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al., 2007; RAIHANI et al., 2008). Some Calopterygidae males may also actively move and search for females, without defending any territory during their life time (RAIHANI et al., 2008). This non-territorial tactic has been occasionally mentioned to take two additional modes: sneaking and wandering (WATANABE & TAGUCHI, 1990; CORDOBA-AGUILAR, 1995). In the former, non-territorial males consistently stay in the same places while in the latter, males cross many territories and do not show any sort of site fidelity. Males may adopt alternative mating tactics and behave as sneakers, trying to intercept females arriving at attractive territorial sites before being detected by the resident males (PAJUNEN, 1966). In *Hetaerina americana* males were found to use three mating tactics: territorial, non-territorial and switcher (individuals with both territorial and non-territorial periods during their life-span) and all three tactics have similar mating success (RAIHANI et al., 2008). The non-territorial tactic, however, is usually not as successful as the territorial one (SUHONEN et al., 2008). For example, it was shown that the mating success of territorial *Calopteryx splendens xanthostoma* males may be thousand times higher than that of non-territorial males (PLAISTOW & SIVA-JOTHY, 1996). Male fitness is also affected by territory quality. For example, *C. s. xanthostoma* females prefer males with a territory in which the river flow rate enables their eggs have high hatching success (GIBBONS & P AIN, 1992, SIVA-JOTHY et al., 1995).

Our aim was to determine the effect of body size (which varies considerably between individuals) on territorial behaviour in *C. virgo* males (PAJUNEN, 1966; RANTALA et al., 2001; KOSKIMÄKI et al., 2004). They have high survival rates. The daily survival probability of an adult male is about 86%, which means that their expected longevity is 6-19 days, with the maximum life-span being over 40 days (CORDOBA-AGUILAR & CORDERO-RIVERA, 2005). Most of *C. virgo* males defend riparian territories, which include patches of floating vegetation, used by females as oviposition sites (PAJUNEN, 1966; KOSKIMÄKI et al., 2004; TYNKKYNEN et al., 2006). In this study, we compared wing length and fresh body weight measurements of territorial and wandering males during early and advanced flying season. Thus, we tested whether there were any differences in the body size between territorial and non-territorial males and whether there was any seasonal variation in this respect.

METHODS

The study was conducted on the Mustajoki creek, close to the city of Jyväskylä (62°16'N, 25°30'E) in central Finland. The creek is ca 400 m long, has a gravelly/sandy bottom and abundant aquatic vegetation.

In order to facilitate the recording of the *Calopteryx* positions, fiber-tapes were put out on the trees at 5 m intervals. Several days prior to the actual study, all *C. virgo* males were collected, their left and right hindwings measured (0.01 mm) with a digital calliper, dragonflies were marked with a silver marking pen, and subsequently released back into the habitat (RANTALA et al., 2001). The same

procedure was followed with the new males that turned up in the study section during the study.

On the 18th and 28th of July 1998, the behaviour and the positions of males were recorded hourly. Based on the observations of PAJUNEN (1966), WAAGE (1973), FORSYTH & MONTGOMERIE (1987), TYNKKYNEN et al. (2006) males that defended a territory within a distance not exceeding 2 m and during at least 3 consecutive hours were considered territorial. Since territorial males are known to perch close to the water surface (PAJUNEN, 1966), a male was accepted as territorial only if it was always observed within 50 cm of the water surface. Males that were not defending a territory during the days of our study were designated as non-territorial. The non-territorial males that moved at least 100 m during a day were classified as wanderers.

In this study, only mature males, with unflexible wing edge, were considered. In all, we collected 11 wanderers and 28 territorial males. They were placed individually in a cooler, transferred to the laboratory where their wet body mass was measured with an accuracy of 0.1 mg, whereupon they were returned back to the stream.

We tested proportion of wanderer males on study days with chi square test, and analyzed the differences in mean wing lengths and body mass of territorial and wanderer males with two-way ANOVA in which the male status (territorial or wanderer) and study days (18 and 28 July) are factors. All the analyses were performed with SPSS for Windows (Version 14.0).

RESULTS

On the 18th of July there were seven wanderers out of a total of 18 males (39 %) and on the 28th of July four wanderers out of a total of 21 males (19 %). There was no significant difference between the two days in proportion of wanderer males in the Mustajoki creek ($\chi^2 = 1.88$, df = 1, $p = 0.17$). The mean wing lengths (Two-way ANOVA, $F_{1,34} = 0.10$, $p = 0.76$) and wet body mass (Two-way ANOVA, $F_{1,35} = 2.02$, $p = 0.16$) did not differ between days. Wanderers were smaller than territorial males as estimated by their wing length ($F_{1,34}$ = 15.35, $p < 0.001$) and wet body mass ($F_{1,35}$ = 15.25, $p < 0.001$, Fig. 1). The mean wet body mass of wanderers was 99 mg (SD = 11 mg) and of territorial males was 112 mg (SD = 9.4 mg). The mean length of left hindwing of territorial males was 30.9 mm (SD = 1.0 mm) while that of wanderers was

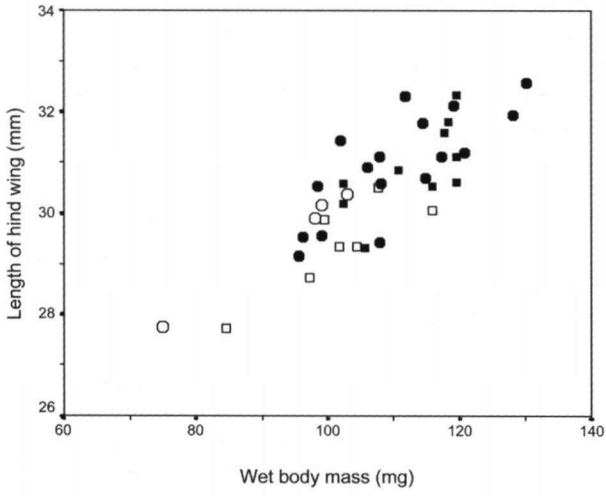

Fig. 1. Wing length and wet weight of wanderers (open symbols) and territorial males (black symbols). Squares indicate the first day of capture (18 July) and dots indicate the second day of capture (28 July) at the Mustajoki creek.

29.4 mm (SD = 1.0 mm). The interaction between these two main effects did not account for significant variation in wing length ($F_{1,34} = 0.03, p = 0.86$) or wet body mass ($F_{1,35} = 0.56, p = 0.45$).

DISCUSSION

We found that territorial *C. virgo* males are larger than wandering males; they have longer hindwings and are heavier than wanderers. However, several previous studies in various *Calopteryx* species have shown that territorial and non-territorial behaviours are conditional mating tactics (MARDEN & WAAGE, 1990; PLAISTOW & SIVA-JOTHY, 1996; KOSKIMÄKI et al., 2004; CONTRERAS--GARDUNO et al., 2006). For example, *C. virgo* males that were winners of staged territorial contests had more fat than losers but there was no difference in body size (KOSKIMÄKI et al., 2004). Our data contradict previous studies in calopterygids in which there was no size difference between territorial and non-territorial males (FORSYTH & MONTGOMERIE, 1987; CORDOBA-AGUILAR, 1995; PLAISTOW & SIVA-JOTHY, 1996; BECK & PRUETT-JONES, 2002; TYNKKYNEN et al., 2006; SUHONEN et al., 2008). However, in *C. maculata*, larger males are able to hold territories for longer time than smaller males (BECK & PRUETT-JONES, 2002), similarly as in the pseudostigmatid, *Megaloprepus coerulatus* (FINCKE, 1984). Moreover, recent works on *Hetearina americana* have also shown that territorial males are larger than non-territorial males, with large territorial males having high energy reserves and a capability to hold territories longer than smaller, non-territorial males (SERRANO-MENESES et al., 2007; RAIHANI et al., 2008).

Mating success is likely to be higher in territorial males than in non-territorial males (PLAISTOW & SIVA-JOTHY, 1996; SERRANO-MENESES et al., 2007; SUHONEN et al., 2008), because females prefer territorial males (WAAGE, 1973; PLAISTOW & SIVA-JOTHY, 1996; CORDOBA-AGUILAR, 2000; SERRANO--MENESES et al., 2007). However, non-territorial males are still likely to have mating opportunities. For example, non-territorial *C. virgo* and *C. maculate* can sometimes clasp females without courtship (PAJUNEN, 1966; WAAGE, 1973) but only 20% of non-courted clasped females allowed copulation (WAAGE, 1973). In a recent study on *Hetaerina americana*, the mating success of territorial males, switcher males (those that demonstrate both territorial and non-territorial behaviour) and non-territorial males did not differ significantly (RAIHANI et al., 2008). It is possible that wanderers and territorial males may be two morphs with different life-histories but equal estimated reproductive success as has been shown in the *Mnais* damselflies (WATANABE & TAGUCHI, 1990; WATANABE, 1991; NOMAKUCHI, 1992; TSUBAKI et al., 1997). For example, male *M. costalis* occur as territorial orange-winged "fighter" males or non-territorial clear-winged "sneaker" males, and the two morphs have equal reproductive suc-

cess (TSUBAKI et al., 1997; PLAISTOW & TSUBAKI, 2000). In *M. costalis*, orange-winged fighter males are larger than clear-winged sneaker males (TSUBAKI et al., 1997). Studies on this species have shown that the clear-winged, non-territorial morph lives longer (TSUBAKI et al., 1997; TSUBAKI & HOOPER, 2004). Females in this system mate preferentially with territorial males but since non-territorial males have a larger sperm displacement ability, they are able to fertilise more eggs as they can transfer more sperm to the female (SIVA-JOTHY & TSUBAKI, 1989a). The estimates of lifetime reproductive success indicate that both morphs achieve a similar fertilization success, which explains the coexistance of the two morphs in the same population (TSUBAKI et al., 1997).

In conclusion, our data show that wanderer *C. virgo* males are smaller than territorial males. However, in our study only individuals from a single population were examined. In addition to the body size of wanderers and territorial males, future studies should also measure the body size of sneakers and possible switchers (RAIHANI et al., 2008) and should investigate whether similar patterns are apparent in other *C. virgo* populations and in other species. Measuring the life time reproductive success in the different behavioural phenotypes will also be a fruitful avenue of investigation.

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