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SITE FIDELITY, SATELLITE TACTICS AND MATING SUCCESS IN *LIBELLULA FULVA* (MÜLLER) (ANISOPTERA: LIBELLULIDAE)

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The site fidelity and satellite behaviour in relation to mating success were investigated in *L. fulva* ♂♂ during 2 reproductive seasons (2002-2003) in eastern Hungary. There was no difference in mating success in ♂♂ that were faithful to 1, 2 or 3 independent territories. Those that were site-faithful had a higher mating success than non site-faithful ♂♂. Site-faithful ♂♂ showed satellite behaviour more frequently than non site-faithful ones. ♂♂ used both of the 2 tactics and this switching ability was independent of ♂ body size. The better mate-rewarding tactic appears to show site fidelity and satellite behaviour alternatively.

INTRODUCTION

In many dragonfly species mature males are characterized by their overt territorial behaviour (CORBET, 1999). The territory is a space where the resident male has priority of access over conspecifics (KAUFMANN, 1983). The dragonfly male may choose its territory on the basis of habitat quality (TSUBAKI & ONO, 1986; KOENIG, 1990), which can be characterised by relevant variables like safety from predators (SWITZER, 1997), sunny resting places (CORBET, 1999), oviposition sites (e.g. ALCOCK, 1987) and, more importantly, mating success (e.g. TSUBAKI & ONO, 1995). The effect of past reproductive success and experience on a single territory was studied in *Perithemis tenera* (SWITZER, 1997a) and it was found that manipulated males (with no access to matings) left

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their territories with higher probability than the non-manipulated ones.

A high number of studies regarding territoriality in dragonflies have focused on male site fidelity or residentiality (SWITZER, 1997a, 1997b, 2002; ALCOCK, 1993, 2000). Site fidelity is the propensity to return to a previously occupied location, which reduces the risk of not finding a new site (JAKOB, PORTER & UETZ, 2001). Site fidelity periods can range from a few minutes to several consecutive days (CORBET, 1999) and depend on site quality (defined as the number of matings occurring in the site in a certain time window; SWITZER, 1997).

There is a substantial variation in mating tactics used by dragonflies (CAMPANELLA, 1975). Alternative mating tactics may arise when mating success is influenced by age (e.g. TSUBAKI & ONO, 1987év), size (e.g. SERRANO-MENESES et al., 2007), population density (e.g. PAJUNEN, 1966; FINCKE, 1985), muscular fat reserves (e.g. MARDEN & WAAGE, 1990; PLAISTOW & SIVA-JOTHY, 1996), or parasitism (e.g. MARDEN & COBB, 2004). The mating pattern in dragonflies is focused on the method how the males compete for fertilizations by controlling females (FINCKE, 1997). The mating pattern is influenced by such variables like male density (CORBET, 1999), and male size (ALCOCK, 1979; FINCKE, 1984; TSUBAKI & ONO, 1987). Any departure from the mating pattern used by the majority of males in a dragonfly population can be taken as an alternative reproductive behaviour (CORBET, 1999).

Males of some odonate species often use alternative reproductive tactics to obtain a mate. For example, satellite males do not defend a territory, but exploit the resources defended by resident males (CONVEY, 1989; SANDELL & LIBERG, 1992). In *Calopteryx maculata* older males often use the sneaker alternative tactic while younger ones defend mating territories (FORSYTH & MONTGOMERY, 1987). Males of non-territorial *Enallagma hageni* use two alternative tactics to find mates: they actively search for females, or wait at oviposition sites for females which come up to the surface from underwater oviposition (FINCKE, 1985). After loosing a dispute on his territory, an *Erythemis simplicicollis* male usually remained there as a satellite (McVEY, 1988). An ousted resident *Nannophya pygmaea* occupied a vacant site elsewhere (42%), became sneaker (33%), or disappeared (25%) (TSUBAKI & ONO, 1986).

Several odonate studies have discussed the role of male body size in relation to fitness components (THOMPSON & FINCKE, 2000). Some of them have reported positive correlations (e.g. ALCOCK, 1979; FINCKE, 1984; TSUBAKI & ONO, 1987), while others have documented weak negative effects or no effect at all (e.g. FINCKE, 1988; ANHOLT, 1991). Large size can be an advantage in territorial species where the fighting ability is extremely important (e.g. FINCKE, 1984; TSUBAKI & ONO, 1987; SERRANO-MENESES et al., 2007), while small size is advantageous in non-territorial species where manoeuvrability is essential (FINCKE, 1988). There is a physiological basis for large size during male-male competition in territorial species. A field-based study on *Hetaerina americana* demonstrated that fat load increased with body length in territorial males but it was unrelated to body length in non-territorial males. At the same time, territory tenure and the male fighting rate increased with body length (SERRANO--MENESES et al., 2007).

In previous studies we observed variation in the territorial behaviour of adult *Libellula fulva* males (NAGY et al., 2004). Every male defended a territory but only a few males showed site fidelity. There were males which, apart from the fact that they held a territory, also showed satellite behaviour (there were no individuals which used only satellite behaviour without territorial behaviour). We also observed that some site-faithful males were faithful even to two or three different territories (NAGY et al., 2004). These males were seen at least three times on the same 15 meter long section.

In the present study, our aims were to explore the differences in mating success of site-faithful and non site-faithful males. Also, we investigated whether there exists a difference in reproductive tactics of the males showing or not site fidelity, in the terms of switching between territoriality and satellite behaviour. Finally we studied the differences in abdomen length between site-faithful and non site-faithful males, and between satellite and territorial males.

MATERIAL AND METHODS

We studied a closed *L. fulva* population during two reproductive seasons (2002, 2003). Fieldwork was carried out along a small lowland creek (Kutas), near Ártánd village (47°06'N and 21°45'E) in eastern Hungary. The behaviour of males was studied along a 350 meter natural section of the creek using a multiple capture-mark-recapture method. We marked 355 males (169 in 2002 and 186 in 2003) on the right wings, using at least double characters, with a permanent marker (Edding 750). Marking had no presumable influence on male activity as there was not observed increase of predation while a high recapture rate was assessed (more than 65%). After capture, we measured the abdomen length with a digital calliper.

The movement of marked animals was followed by two observers using 8×40 binoculars. At each resighting we wrote the number of a respective male, its location on the study site, its behaviour (three categories: fighting, perching, mating), and the time of resighting. Prior to emergence, we placed marked sticks in points every five meters each along the creek to follow the behaviour and movement of marked dragonflies. Marked individuals were observed daily between 9:00-15:00, time at which mating activity was high.

To find out whether site fidelity contributes to mating success, we divided males in two groups: those which showed site fidelity, and those which did not, and we compared the mating success of them. We calculated the mating success of a group from the number of matings and the number of males belonging to that certain group as follows: the ratio of matings (in Figs 1, 3) is equal with the number of observed copulations of site-faithful males (respective non site-faithful males), divided with the number of site-faithful (respective non site-faithful) males.

While satellite behaviour can alter mating success, we calculated the ratio of satellite behaviour as well, for the males which showed site fidelity, and those which did not, and we compared them. We calculated the ratio of satellite behaviour of a group from the number of observed satellite behaviours and the number of males belonging to that certain group as follows: the ratio of satellite behaviours (Fig. 2) is equal with the number of observed satellite behaviours of site-faithful males (respective non site-faithful males), divided with the number of site-faithful (respective non site-faithful) males.

R statistical software package (R DEVELOPMENT CORE TEAM, 2005; version 2.2.1) was used for data analysis. Normal distribution of data was tested using Kolmogorov-Smirnov test. Differences between groups were calculated using Kruskal-Wallis and Wilcoxon W tests.

RESULTS

The two year data were treated together as there were no significant differences in the number of matings and number of observed satellite behaviours studying both periods (Wilcoxon rank sum test – number of matings: N1 = 128, N2 = 151, W = 9357.5, p = 0.61; – number of satellite behaviours: N1 = 153, N2 = 150, W = 11492, p = 0.97).

There were no differences in mating success of males which were faithful to one (0.97 ± 0.14), two (1 ± 0.59) or three (1.76 ± 0.41) territories and found no difference in number of matings for the three groups (Kruskal-Wallis test; N1 = 45, N2 = 10, N3 = 17, chi-squared = 3.51, df = 2, p = 0.17).

The mating success of site-faithful males was higher than for non site-faithful males (Fig. 1) (Wilcoxon W; N1 = 72, N2 = 245, W = 8917, p = 0.0068). From site-faithful males we observed only 43 males, from not site-faithful 115 males which mated at least once.

Males with site fidelity showed satellite behaviour more frequently than males without site fidelity (Fig. 2) (Wilcoxon W; N1 = 72, N2 = 245, W = 10996, $p < 0.0001$), but the frequency of satellite behaviour between satellite males with and without site fidelity showed no differences at all (Fig. 2). From site-faithful males we observed 32 males, from non site-faithful 28 males which showed satellite behaviour at least once.

We compared the mating success of satellite and territorial males in two groups: site-faithful males and non site-faithful males. Males with site fidelity which showed satellite behaviour had a higher mating success than those which have not used the alternative mating tactic (Fig. 3) (Wilcoxon W; N1 = 33, N2 = 39, W = 418, p = 0.008). Altogether we had N = 256 males which did not show satellite behaviour and N = 61 males which did. From males without satellite behaviour there were N = 39 which showed site fidelity, and N = 217 which did not. From males showing satellite behaviour we observed N = 33 being site-faithful and N = 28

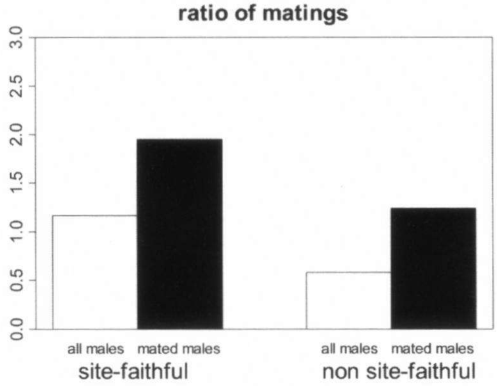

Fig. 1. *Libellula fulva*: differences in the relation of mating success of site-faithful and non site-faithful males.

being not.

There was no significant difference in the abdomen length between site-faithful (27.27 ± 0.13, N = 72) and non site-faithful males (27.49 ± 0.07, N = 245; Wilcoxon W; W = 7896.5, p = 0.177). Length of the abdomen also did not differ between satellite (27.46 ± 0.14, N = 61) and territorial males (27.43 ± 0.07, N = 256; Wilcoxon W; W = 7707, p = 0.996).

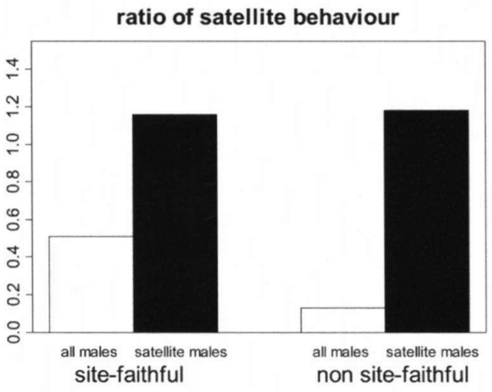

Fig. 2. *Libellula fulva*: frequency of satellite behaviour in site-faithful ad non site-faithful males.

DISCUSSION

There was no significant difference in the number of matings between the three male groups. The defended territories seemed similar on the whole research plot from the point of view of the percentage of plant-cover and water-depth. However, if we consider site-faithful males against non-faithful ones, the former showed a significantly higher mating success. Males with site fidelity showed a higher occurrence of satellite behaviour than those without.

In a previous study we found that site fidelity of males which defended only one territory was significantly higher than of those which defended two or three territories, while the territory defending ability was higher for males which defended more territories. For a male with more territories, the time spent defending each of its separate territories was less than for those with only one. Those that had only one territory invest all of their energy to the defence of that certain territory (NAGY et al., 2004). Those males which defended two or three territories were more able to occupy and keep a territory or they were chased by conspecifics from their previous territory.

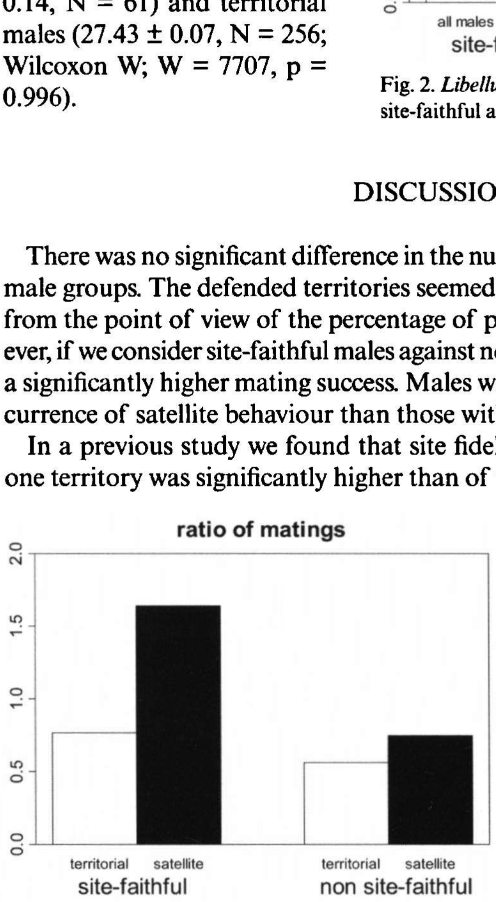

Fig. 3. *Libellula fulva*: differences in the mating success of males which use both of site fidelity and satellite behaviour and males which use only the site fidelity.

The second possibility seems to be suggested by the fact that abdomen length of males which defended one territory was significantly higher than in those which defended three territories (NAGY et al., 2004). The fact that abdomen length of males which defended one single territory was significantly larger than in those which defended three territories (NAGY et al., 2004) suggests a possible second explication of the problem. This should mean that smaller males try to enhance their mating success by increasing number of defended territories, but the results show that this tactic has no positive consequences. While satellite behaviour increases mating success, the increase of territorial holding ability does not.

The increase of mating success by site fidelity is not surprising, because site fidelity in Odonata in most cases requires territorial behaviour. Territoriality increased mating success may be the consequence of increased body size which can lead to superiority in intraspecific struggles (FINCKE, 1992). The bigger body size can be – via territorial behaviour – an advantage in intraspecific competition. This phenomenon was described a *Libellula luctuosa* where the territorial males had higher body size than the satellite males (MOORE, 1989).

It is surprising that in *Libellula fulva* there is no difference in body size between site-faithful and non site-faithful males. Therefore site fidelity cannot be the result of the body size caused advantage in intraspecific competitions. If site fidelity is the result of superiority in intraspecific competitions, the superiority must be influenced by other factors than body size. Other factors than abdomen size could be the fat storage, muscle mass, age, site quality or the previous reproductive success (MARDEN & WAAGE, 1990; PLAISTOW & SIVA-JOTHY, 1996; CONTRERAS-GARDUÑO et al., 2006; SERRANO-MENESES et al., 2007; SWITZER, 1997; NEWTON & MARQUISS, 1982). Since *L. fulva* males are characterized by strong intraspecific competition, the most relevant of these could be the fat storage and the muscle mass. Because these are localized in the thorax it would be more appropriate to measure the whole body length rather than the abdominal length only.

Satellite males showed no differences between the ratio of satellite behaviour in site-faithful and non site-faithful males. The site-faithful males showed a higher number of satellite behaviours than the non-site faithful ones. This means that male site fidelity in *L. fulva* is combined with the satellite behaviour. This strategy was also found in non-territorial *Enallagma hageni*, where males mated by using both waiting and searching tactics, sometimes within the same day (FINCKE, 1985). This behaviour was described as a single, conditional strategy, reflecting behavioural plasticity within individuals. FINCKE (1985) also concluded that the use of the tactics was independent of age, size, and the previously successfully used tactics. This switching ability was described in *Plathemis lydia*, where males are able to switch the territorial and the satellite behaviour (KOENIG & ALBANO, 1985). In *Libellula luctuosa*, males do not show this behavioural plasticity, a satellite male never becomes territorial (MOORE, 1989).

The difference between our results and the previous studies, is that most of the latter demonstrate that the territorial behaviour has higher mating success than the satellite behaviour, e.g. in *Libellula luctuosa* (MOORE, 1989), and in *Plathemis lydia* (CAMPANELLA & WOLF, 1974; KOENIG & ALBANO, 1985), while in *L. fulva*, where the males are not only territorial but show even site fidelity, their mating success can increase by switching to satellite behaviour. We hypothesize that a site-faithful male may become satellite when it encounters a stronger conspecific individual.

A quite similar behavioural plasticity was found in a cactus fly, *Odontoloxosus longicornis*, which shows both territorial and satellite behaviour. The satellite behaviour occurs in the presence of territorial males and when no males can held a territory (MANGAN, 1979). An explanation could be that males using the two tactics would have equal or greater fitness than those using only the territorial tactics because the secondary tactics could be used successfully at times when the main tactics is inefficient. This behavioural plasticity, which allows responses to the present environment, can be responsible for many of the alternative mating behaviours. A simulation used by WALKER (2003) demonstrated that calling males of field crickets have higher mating success than satellite ones under most conditions, but if parasitoid flies were present, satellite males had similar or higher mating success than calling males, which shows that satellite behaviour contributes to the increase of mating success which was also found in *Libellula fulva*.

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