Odonatologica 23(3): 291-295 *September 1, 1994*

ASPECTS OF THE REPRODUCTIVE BEHAVIOUR IN *ORTHETRUM COERULESCENS* (FABRICIUS) (ANISOPTERA: LIBELLULIDAE)

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Received February 10, 1994 / Revised and Accepted March 22, 1994

Courtship and post-copulatory resting (PCR) were examined. Courtship is known not to take place before the formation of the tandem pair. This study shows that the amount of time spent in tandem depends on the territorial status of the male involved. Pairs involving a non-territorial male remain in tandem for longer than pairs with a territorial male. This may be because the male must court the female by showing her a suitable oviposition site before she will accept copulation. Such a site is more readily available to a territorial male. In-tandem courtship has thus been demonstrated to take place in this species. Females do not start to oviposit immediately after termination of copulation. The period of time they spend perched before oviposition is variable. G.E. REHFELDT (1989, *Odonatologica* 18: 365-372) has produced evidence that this is a mechanism by which females avoid the unwanted attentions of other males who wish to mate with her. The present observations do not support this hypothesis, and no correlation between male activity and the PCR duration was found.

INTRODUCTION

Orthetrum coerulescens is locally extremely abundant at the study site. This study is an investigation into two aspects of their reproductive behaviour: courtship and post copulatory resting. Courtship may be defined as any process in which potential mates exchange information in order to allow one or other of them to make a choice about the suitability of the other. The information conveyed by courtship behaviour varies from species to species. In the Odonata this may include recognition of a potential mate, assessment of the fitness of the potential partner, or of territory quality (THORNHILL & ALCOCK, 1983; WEST-EBERHARD, 1984; EBERHARD, 1985; MILLER, 1991). Most reported courtship behaviour amongst the Odonata is to be found amongst the Zygoptera. Here it

generally takes the form of displaying before the formation of the tandem. This behaviour is rare amongst the Anisoptera, having been reported in only 5 libellulid species (JACOBS, 1955; CORBET et al., 1960; WILLIAMS, 1977; MILLER, 1982a, 1982b).

In *O. coerulescens* a tandem pair may be formed between a female and the first male she comes into close contact with over the stream site. He uses his claspers to grab the female at the back of the head, seemingly without any preliminaries. If true, this would mean that females had little or no choice in initial pair formation. It would therefore be advantageous to the female if a mechanism existed whereby she could make a choice about whether she wanted to mate after this stage. MILLER (1991) has suggested this may involve in-tandem courtship. The hypothesis is that in order to mate, a male must show a female that he can provide a suitable oviposition site for her. This is usually in a territory which he holds. MILLER (1991) has suggested that tandem lasts longer when a non-territorial male is involved because the male takes longer to convince the female. This is because the pair are chased away from potential sites by territorial males. In summary, the prediction is that on average, pairs involving males without territories should spend more time in tandem than pairs with territorial males.

The second aspect of the study is on the post-copulatory resting (PCR) of *O. coerulescens*. In this species (as in many other libellulid dragonflies) the females do not immediately start ovipositing as soon as copulation has ceased. Instead, they perch on vegetation in the territory of the male they mated with (HEYMER, 1969; MILLER & MILLER, 1989).

Potential reasons for this behaviour have been discussed by REHFELDT (1989), who has found evidence that the duration of PCR is correlated with the presence of conspecific males near the perching site. He therefore hypothesizes that PCR acts as a mechanism to allow the females to avoid disturbance (and subsequent remating) by other males. This study tests Rehfeldt's hypothesis by looking to see whether there is indeed any correlation between the level of male activity and the duration of PCR.

STUDY SITE AND METHODS

O. coerulescens was observed over a period of one week during July 1993 at the Canal de Vergières, a small stream in the Dept Bouches du Rhône, S. France. 47 odonate species are known to occur there (Frank Suhling, pers. comm.). The habitat consists of a shallow stream bordered on one side by a low bank and emergent reeds (*Juncus* spp.) and on the other by a high hedge (mainly *Rubus* spp. and *Prunus spinosa*). However, shade is provided at the downstream end of the canal by overhanging trees, including fig (*Ficus*), ash (*Fraxinus excelsior*), elm (*Ulmus*) and hazel (*Corylus avellana*). Most mating events take place in the reeds near the water. Activity was observed to be strongly dependent upon the ambient temperature, which can reach 25-32°C at noon [REHFELDT, 1989]. Therefore, care was taken to standardise the time when observations were made to a three

hour window in the mid to late afternoon when activity seemed to be at a peak.

A voice recorder was used to record four pieces of data about each mating event:

(1) The territorial status of males was ascertained by watching a small length (max. 4 m) of bank for up to 60 minutes. Territorial individuals remain within a 1 m length of stream bank. These territories are fairly static – individuals were observed to remain in the same small patch of reeds for over 30 minutes. They vigorously defended this area against intruders, fighting highly acrobatic battles, which might last several seconds. The winner settled back onto the territory. In contrast, non-territorial individuals did not stay in one place for any significant length of time. Instead, they are observed to fly along the stream. Because of their mobile habit, they frequently come into contact with territorial males, with whom they fight, as above. If the male involved in a particular event was not previously observed to hold a territory in the area, he was designated as being non-territorial. Few matings of satellite males were observed.

(2) The duration of time that the pair spent in the pre-copulatory tandem position was measured using a stopwatch. Recording started when a male formed a pair with a female flying along the stream in his vicinity, and finished when the pair went into the copulatory wheel position. If however, the pair then went back into the tandem position (as happened several times when the male was non-territorial) the duration of the intercession was added to the total tandem time.

(3) The level of activity of other males in the vicinity of the copulating pair was measured by counting the number of males present in the minute immediately prior to the onset of PCR. For a male to be counted as present, it had to have passed within a two metre radius of the copulating pair. In the instance that copulation did not last one minute, the max. number of males present during the entire period was measured.

(4) The duration of PCR was measured as the period between the splitting up of the copulatory wheel and the onset of oviposition by the female.

OBSERVATIONS AND DISCUSSION

COURTSHIP BEHAVIOUR

Males were present at this site at very high densities (up to 2 territories m^{-1} of bank). However, females are relatively rare in the immediate vicinity of the stream itself. This lead to all females approaching the stream being rapidly pursued by a number of males. The duration of the tandem phase was 12.9 ± 9.94 s (N=26, min=2s, max=35s).

The data are not normally distributed, probably because factors such as time of day and condition of the individuals may skew them. Therefore, a Mann--Whitney test was used to compare the tandem duration times for non-territorial (N=13; median=20.000) and territorial (N=13, median=4.000) males.

The 95.4% confidence interval for ETA1-ETA2 is (13.998-20.999), and the test of ETA1 = ETA2 vs. ETA1 n.e. ETA2 is significant at 0.0000. Therefore, the analysis shows that the duration of the tandem phase is significantly greater for non-territorial males.

The situation seen arises because non-territorial males, once in tandem, fly the female over a series of potential oviposition sites. In all cases the pair performed a dipping motion low over the potential site. I interpret this as the male courting the female by showing her that there is a suitable site available

in which to oviposit. The dipping movement may be a mimic of the females' oviposition action. The time taken for this activity is high because they are chased away from many otherwise suitable sites by a male who holds that site as a territory. In contrast, pairs involving a territorial male spend only a very short period of time in tandem. This is because the male quickly flies the female to his territory. In all cases she accepted formation of the copulation wheel almost instantaneously, leading to the low average time for the duration of the tandem phase with territorial males. It can therefore be seen that this study supports the theory of MILLER (1991): in-tandem courtship does take place in at least one species of libellulid dragonfly.

PCR DURATION

After the termination of copulation, all females perched on or very near the mating site. The mean duration of PCR was 110s ± 26.57s. (N=28, min=55s, max=170s). During this time, the male either perched close to the female or patrolled the territory edges. The mean number of males present within a two metre radius of the mating pair was 1.169 ± 1.385, (N=28, min=0, max=4). Again, it was found that the data are not normally distributed, and a Kruskal--Wallis test was used. The null hypothesis of no differences between the population categories is tested against the alternative of at least one difference (Tab. I).

Table I

Kruskal-Wallis test; for explanation see text

Male activity	N	Median	Z value
0	6	128.50	2.30
1	7	105.00	0.90
2	7	90.00	-3.10
3	7	109.00	-0.11
4	1	113.00	0.31
	Overall 28		*Overall 14.5*

p = 0.017 (adj. for ties)

It can be seen that the p-value is significant at the 5% level. Therefore the null hypothesis that all the medians are the same can be rejected. From the z-values, it is the median duration for activity level 2 that is different from the others.

REHFELDT (1989) found that PCR duration (PD, as he calls it) increases with male activity. He explains PCR as "a tactic to evade male interference." My results do not support this. Although there are significant differences between the PCR durations for different levels of male activity, the relationship is not the same as that found by him. This can be seen if the values for the median durations of PCR at each level of male activity are referred to. PCR duration does not increase with male activity. Possible alternatives to Rehfeldt's explanation are postulated by MILLER & MILLER (1989); PCR may allow internal manipulation of sperm. The probability of this is increased by the fact that storage organs in the females of this species are unusually small. Therefore little sperm can be stored, and it is an advantage to be able to use sperm as efficiently as possible. Internal manipulation may allow this. Alternatively, PCR may allow females to

check that the vicinity is clear of predators; she is highly conspicuous whilst ovipositing and there is a very high density of frogs at the site.

However, it should be noted that these results have been found for one population at one locality. Different populations may display the behaviours in response to other adaptive pressures. For example, PCR may act as a tactic to evade male interference where there is a higher density of males, or where females can be more easily seen by other males.

ACKNOWLEDGEMENTS

I am very grateful to both Dr P. MILLER and Mrs. A.K. MILLER for their support and help with the practicalities of this study. I also thank Dr M. SIVA-JOTHY for his valuable comments. Dr G. GARNETT and Dr P. MILLER both made helpful suggestions on earlier drafts of this report. The field work for this project was partly funded from three sources: The Oxford University Biological Sciences Undergraduate Project Fund; The OU Poulton Entomological Fund; and a Travel Bursary from New College, Oxford.

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