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THE INFLUENCE OF MALE INTERFERENCE ON FEMALE PERCHING BEHAVIOUR BEFORE AND DURING OVIPOSITION IN LIBELLULID DRAGONFLIES (ANISOPTERA)

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The female perching behaviour in *Orthetrum coerulescens, Crocothemis erythraea* and *Sympetrum vulgatum* in high density situations can be explained by habitat and situation. In *O. coerulescens* 86.2% of the females perched immediately after copulation. After disturbance of the preceding copulation and in the presence of rival males, the perching duration (PD) was longer. In *C.erythraea* at sites without perches all females immediately started to oviposit whereas at sites with emergent vegetation 75.8% remained perched. PD was longer in cases of male interference with the preceding copulation. In *S. vulgatum* after tandem oviposition at sites with emergent vegetation, 24.2% of all females settled on a perch site. This behaviour occurred more often after disturbance of the preceding tandem oviposition and in the presence of rival males. In all species PD did not change with multiple matings. Perching before the start of oviposition may serve as a tactic to evade male interference or to assess predator pressure at the oviposition site.

INTRODUCTION

In many species of libellulid dragonflies, females remain perched after copulation before they start to oviposit. In species with long copulation duration females mostly perch on the sites where copulation has occurred (e.g. *Orthetrum* spp.: HEYMER, 1969; MILLER & MILLER, 1989). In species with short copulations in flight females may settle afterwards on the vegetation or on the ground before oviposition commences (e.g. *Pachydiplax longipennis:* ROBEY, 1975; *Libellula luctuosa:* MOORE, 1989). However, females may perch also during oviposition (KRÜNER, 1977; WAAGE, 1984, 1986). In species which oviposit in tandem the female may settle on a perch site after separation of the pair and may continue to oviposit alone (UEDA, 1979).

MILLER & MILLER (1989) have recorded perching duration of the female after copulation in *Orthetrum coerulescens* and they observed the behaviour of the guarding male. They discuss as possible functions of perching the assessment by females of predator pressure at the oviposition site, or of a male's guarding capacity. Perched females may "handle" sperm either to mobilise it for fertilisation or in connection with the need to use it economically.

In their study MILLER & MILLER (1989) have not investigated the influence of other males on the post-copulatory behaviour of females. However, JACOBS (1955) in *Perithemis*, PAJUNEN (1963, 1966) and HILTON (1984) in *Leucorrhinia* and WAAGE (1986) in *Erythemis* found that females may settle on perch sites near or on the oviposition substrate to avoid attacks of approaching males.

Here, I report on the influence of male interference on the perching behaviour of female libellulid dragonflies in three species with different copulation and oviposition behaviour. In *Orthetrum coerulescens* (Fabr.) copulations last longer and are completed on a perch site (HEYMER, 1969; PARR, 1983; MILLER & MILLER, 1989). *Crocothemis erythraea* (Brullé) shows short copulations mostly in flight (AGUESSE, 1959). At habitats with emergent vegetation copulation may be completed on a perch site. In both species females oviposit with non-contact guarding by the male. In *Sympetrum vulgatum* (L.) oviposition is conducted in tandem (ROBERT, 1958). After separation females may continue oviposition with non-contact guarding by the male.

MATERIAL AND METHODS

Orthetrum coerulescens was studied at a stream in southern France (Dept. Bouche du Rhône, France) in August 1987. *Crocothemis erythraea* was observed in July and August 1987 at shallow ponds near Aigues Mortes and at rice fields and small waters covered with dense emergent vegetation near Arles (Dept. Gard, France). *Sympetrum vulgatum* was observed at gravel pits in August 1987 near Braunschweig and in July and August 1988 near Salzgitter (Lower Saxony, F.R. Germany).

The temperature at noon varied from 25 to 32° C in France and from 23 to 28° C in Germany. All species were investigated in situations with high population densities. The observations started when a female or tandem pair approached the water near potential oviposition sites and ended when the female left the water. Most of the ovipositions and copulations were filmed with a video-tape recorder. This method allowed simultaneous analysis of several behavioural parameters: copulation duration, perching duration (PD) of the female, oviposition duration, changes of the perching and oviposition sites, flight behaviour, intraspecific interactions of the males and the number of successive copulations. Means ± S.E. are given. Any non-significant results ($P > 0.05$) are denoted as NS in the text and tables.

RESULTS

OBSERVATIONS ON *ORTHETRUM COERULESCENS*

All females approaching the stream were interfered with by conspecific males. Most of the females either mated or escaped, pursued by males. Copulations were observed on perch sites on low emergent vegetation (*Juncus*) and on the embankment (*Rubus*). The duration of copulations varied from 10 s to 29 min 55 s (mean 436.7±48.7 s, N=75). After separation of the wheel, 86.2% of all females immediately perched or landed on the perch site after a few s (56/65). The duration of perching ranged from 5 s to 6 min 20 s (mean 61.8±6.7 s, N=48). Only 3 females started to oviposit immediately after copulation. Males normally perched close to the females and patrolled or took off in pursuit of rival males.

PD was not correlated with the duration of the preceding copulation (Product moment correlation coefficient, r=-0.13, NS, N=45). With multiple copulations of the female (1-4) mean PD did not change (Spearmans rank correlation coefficient rs=0.067, NS, N=50).

During copulation conspecific males approached the perching wheel. When disturbed, pairs changed the perch site up to 8 times (1.9±0.35, N=21) within one copulation, often leaving the water and flying to the embankment vegetation. After interference of copulations females perched longer than without interference by rival males (Tab. I). Six out of sixty-five females were interfered with by other males immediately after copulation and they escaped without perching or oviposition. When rival males perched on the vegetation 0.1-0.9 m from the female, PD was longer. In this situation PD lasted 98.8±18.5 s (N=10), without rival males it lasted 52.4±6.5 s (N=36) (t-test, t=2.99, df=44, $p < 0.01$).

Females started to oviposit near the perch site or they flew from the embankment to the nearest part of the stream with shallow water. Males non-contact guarded their ovipositing mates. Oviposition duration varied from 3 s to 2 min 31 s (N=72). There was no correlation with the preceding PD of the female (r=0.283, NS, N=45). When females (N=59) were interfered with by other males immediately after leaving the perch site, they all mated again. However, long PD after copulation did not lead to lower intensities of disturbance by other males. PDs followed by intercepted ovipositions did not differ from PDs in which the following ovipositions were not interfered with by males (Tab. I).

OBSERVATIONS ON *CROCOTHEMIS ERYTHRAEA*

At ponds without emergent vegetation, *C. erythraea* mostly showed short copulations in flight (range 4 s-51 s, N=79). After separation of the pair females started immediately to oviposit by dipping the tips of their abdomens into the water. After male disturbance they flew rapidly off to the bank vegetation

Table I
Duration of perching in female *Orthetrum coerulescens* and *Crocothemis erythraea* with interference of preceding copulations and following ovipositions by rival males

Behaviour	*N*	Duration of perching (s) with interference	*N*	Duration of perching (s) without interference	t	df	p
ORTHETRUM COERULESCENS							
Preceding copulation	13	92.5±16.2	33	50.6±6.4	2.83	44	<0.01
Following oviposition	30	71.6±10.8	25	55.5±7.8	1.17	53	NS
CROCOTHEMIS ERYTHRAEA							
Preceding copulation	5	43.0±6.7	27	18.5±3.2	2.81	29	<0.01
Following oviposition	28	20.8±3.2	6	25.0±7.9	0.54	32	NS

pursued by the male.

At small habitats with dense emergent vegetation (*Typha, Phragmites*, rice plants) most copulations were completed after perching. Forty-seven out of 62 females remained perched for some time after separation of the pair on this site before oviposition started. PD ranged from 2 to 58 s (mean 22.03±2.9 s, N=35). During this period the guarding male hovered over the female or interacted with neighbouring males. Interference of the flying tandem wheels by these males influenced the following PD of the female (Tab. I). PD correlates with the duration of the preceding copulation ($r=0.307$, $p < 0.05$, $N=31$). With multiple copulations by the female (1-5) mean PD did not change (Spearmans rank correlation coefficient $rs=0.07$, NS, $N=20$).

Nine of 36 females were interfered with by other males immediately after leaving the perch site before the start of oviposition. Three females mated again. PD does not correlate with the following oviposition duration (range 2 s-1 min 59s, $r= -0.248$, NS, $N=31$) and PD of females in disturbed and undisturbed ovipositions is not different (Tab. 1).

OBSERVATIONS ON *SYMPETRUM VULGATUM*

Tandems in *S. vulgatum* flew from perch sites of the preceding copulation to the oviposition sites in shallow water with varying density of emergent vegetation. Here they started to oviposit (range 19 s-6 min 5 s, N=61). After this period of contact-guarding the male released the female. She continued oviposition with non-contact guarding by the male or she immediately left the oviposition site. Males showed non-contact guarding usually only for some s, hovering above the female (range 3 s-1 min 10 s, N=19); females continued oviposition alone after the male had departed (range 20 s-3 min 53 s, N=31).

At sites without reed vegetation females either continued oviposition immediately after tandem separation or they flew off (N=39). On the other hand, at sites with dense emergent vegetation (*Calamagrostis*) 24.2% of the females (31/128) perched after oviposition. If they left the site without oviposition and flew off the mean PD was 62.9±11.8 s (N=12): if oviposition followed, the PD lasted for 49.3±9.3 s (N=12). These values are not significantly different (t-test, t=0.89, NS, df=20). Three females settled after aggressive interference and separation of the ovipositing tandem by a rival male. In 7 tandem ovipositions (N=52) conspecific males perched on sites nearby and they disturbed females immediately after separation. All females escaped without oviposition.

I analysed for a possible influence of other males on the perching behaviour only in those females which continued oviposition after tandem separation. If preceding ovipositions were disturbed by other males, females perched significantly more often (disturbed/undisturbed, with perching, 12/7 vs without perching, 16/53, $\chi^2 = 10.97$, $p < 0.01$). With perching females other males more often perched 0.1-0.8 from the site of separation after tandem oviposition (male present/male absent with perching 14/5 vs. without perching 32/37, $\chi^2 = 4.45$, $p < 0.05$).

PDs of females do not correlate with the duration of the preceding tandem oviposition (r=0.491, NS, N=10) or with the following single oviposition (r=–0.677, NS, N=5). One solitary ovipositing female resettled after interference by an approaching male and another after disturbance by a frog. Two females remained perched as a frog was present and left the site without oviposition. Perching females were not interfered with by other males.

DISCUSSION

In the 3 species studied, rival males have a significant influence on the perching behaviour of females. With disturbance of copulation in *Orthetrum coerulescens* and *Crocothemis erythraea*, and of tandem oviposition in *Sympetrum vulgatum*, females perched longer and more often after separation of the pairs. In these females I regard settling on a perch site near the oviposition site as a tactic to evade male interference.

In dragonflies, females have several effective behaviours for evading disturbance or take-overs (see WAAGE, 1984, for a review). Perching after copulation or during oviposition is common in female libellulids which oviposit with non-contact guarding by the male (MILLER & MILLER, 1989). These species can occur at high population densities at limited oviposition sites. Oviposition by females at hidden sites as in some other Anisoptera (UBUKATA, 1974; KAISER, 1975) is not possible. After separation of the copulation wheel or the oviposition tandem, guarding males seem to have a lower chance of protecting females from takeover as indicated by the high number of chases and rematings with other males in these situations. Thus, in the presence of other males females have a better chance of evading male disturbance by perching immediately near the site of separation of the copulation wheel or of tandem oviposition, than by flying off. In the species studied, interference of perching females by other males did not occur or was rare.

The perching behaviour of females in high-density situations before the start of single ovipositions can be explained by habitat and situation. At oviposition sites without emergent vegetation females mostly leave the site immediately after separation from the male without oviposition (*C. erythraea, S. vulgatum*). At sites with perches, motionless settling may protect females from male disturbance. Thus, in spite of a temporal delay perching may increase reproductive success. In the 3 species studied the temporal delay due to perching was relatively highest in *C. erythraea* (Fig. 1). PD lasted 44.1 % of the mean total female visit at the water. As in *O. coerulescens* at sites with perches females re-settled regularly after copulation.

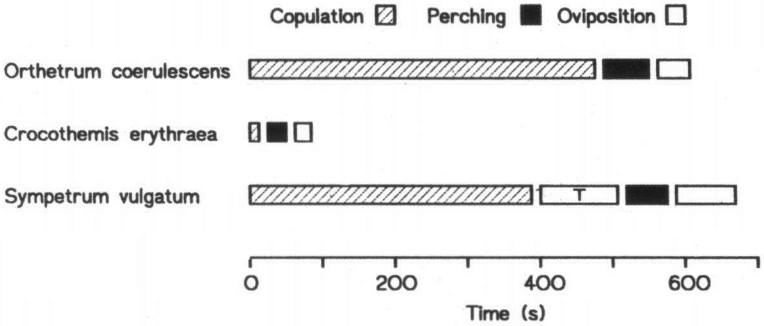

Fig. 1. Mean duration of copulation, perching of the female and tandem (T) and single oviposition in *Orthetrum coerulescens* (N=48), *Crocothemis erythraea* (N=47) and *Sympetrum vulgatum* (N=24).

However, oviposition duration with perching does not differ from that without perching. During the following oviposition, which may last several min with changes of the oviposition site, other males may disturb the female again. Especially in *C. erythraea* and *O. coerulescens* copulations and oviposition females were disturbed frequently by other males often resulting in multiple matings (SIVA-JOTHY, 1984, 1988; Rehfeldt, in prep.). Long PDs in *O. coerulescens* and *S. vulgatum* may increase the risk of loosing the guarding male before the start of oviposition. However, in both species the likelihood of take-overs was reduced as females oviposited at hidden sites within dense emergent vegetation.

MILLER & MILLER (1989) discuss some more possible functions of perching in female libellulids. It may allow females to assess predator pressure at the oviposition site before the start of oviposition. In my study two females of *S. vulgatum* remained perched as a frog was present; another female escaped from a sneaking frog to a nearby perch site.

However, it seems unlikely that perching may allow a female to test the current male's willingness to act as a guard. In *O. coerulescens* and regularly in *S. vulgatum* males departed before the end of oviposition. MOORE (1989) in *Libellula luctuosa* also found no relation between female perching and male guarding behaviour. Females may wait for the appearance of other ovipositing females and then share a male guard. However, in my study synchronous oviposition of two females could be observed only in *S. vulgatum*. In the other studied species the structure of the habitats and the high population densities prevented females from ovipositing close together or from flights along the shoreline of the waters.

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