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# PRE-COPULATORY GUARDING AND OTHER ASPECTS OF REPRODUCTIVE BEHAVIOUR IN *SYMPETRUM DEPRESSIUSCULUM* (SELYS) AT RICE FIELDS IN SOUTHERN FRANCE (ANISOPTERA: LIBELLULIDAE)

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Sexually mature male and female *S. depressiusculum* were observed in large swarms throughout the day at or near rice fields in the Camargue, southern France, in July, 1983. Males became active 19 min before sunrise when they formed tandems with roosting females. Tandem pairs remained perching on rice plants and adjacent grass with only occasional changes of position for 2½-3 hours, after which copulation and oviposition commenced. No territorial behaviour or other interaction between single males was observed, but on a few occasions single males were seen unsuccessfully to attempt to seize females in tandem. Many further pairs in tandem flew into the rice fields from neighbouring meadows throughout the morning: they either rested or commenced to copulate and oviposit soon after arrival. Copulations were commonly preceded by dipping movements which resembled aerial oviposition in other species but were without egg release. Dipping may enable females to verify the presence of an oviposition site before accepting copulation. Unsuccessful attempts to copulate were frequently followed by further dipping. Postcopulatory dipping may represent attempts by the male to initiate oviposition. After about 13:30 h, little or no reproductive activity was seen and both sexes joined in the immense feeding swarms which built up over the rice fields until dusk. Intense competition for females may explain the prolonged phase of pre-copulatory guarding (tandem formation) in a species in which both sexes remain abundant at or near the oviposition sites throughout the day, but in which females are willing to oviposit only during the later part of the morning.

## INTRODUCTION

In many species of Odonata tandem formation between male and female is an immediate precursor to copulation. A common pattern is that a male seizes a

female in flight, clasps her in tandem and then adopts the copulatory wheel position before settling (CORBET, 1962). In a few genera, such as *Enallagma,* tandem coupling is sometimes separated from copulation by a longer interval (MILLER & MILLER, 1981; FINCKE, 1982), and this probably represents pre--copulatory guarding, a behaviour pattern which has been thoroughly investigated in locusts, dungflies and sepsids (PARKER, 1974, 1979; WARD, 1983) but not in Odonata. We describe here tandem coupling in *Sympetrum depressiusculum* which starts at dawn and continues for at least 2½ hours until copulation occurs, allowing a male to retain a female until she is willing to copulate and to commence oviposition; it exemplifies PARKER's (1979) "passive phase".

*S. depressiusculum* is commonly found at still waters in lowland regions of central and southern Europe, sometimes in very large aggregations, and it is also found in parts of Asia (CONCI & NIELSEN, 1956; AGUESSE, 1968). ROBERT (1958) noted some aspects of its behaviour and described it as roosting in dense flocks in open grassland where tandem formation occurs as soon as the sun warms the dragonflies. He did not observe copulation before 10:00 h, but from 11:00 h he found many pairs flying to the water 10-20 cm above the ground and then ovipositing among aquatic vegetation in shady places. Our observations agree with and extend those of Robert, and we discuss the possible significance of prolonged pre-copulatory guarding in a species which occurs at a high density and which shows no territorial behaviour or intermale aggression (cf. PAJUNEN, 1966).

## OBSERVATIONS

Our observations were carried out at a rice field, 8 km north of Le Sambuc in the Camargue region of southern France (4° 38' E; 43° 35' N), during the period 22-30 July, 1983. On July 23, sunrise was at 06:23 h and sunset at 21:11 h, while on July 29 sunrise was at 06:29 h and sunset at 21:05 h (European Summer Time). The rectangular rice field (ca 100 x 200 m) was about 1 km west of the River Rhône, and was flooded to a depth of 10-20 cm. Rice plants (*Oryza sativa*) stood 30-50 cm above the water. The south flank of the field was lined with trees (ca 20 m high), and on the West and North sides there were dry grass meadows, while to the East there was another rice field. *Sympetrum depressiusculum* was extremely abundant in the vicinity of the rice fields throughout each day and there was no sign of a general migration occurring.

During the night males and females roosted close to each other on the rice plants, on the grass in neighbouring meadows and on surrounding bushes. Many males and females were seen to be caught in the webs of *Argiope bruennichi* among the rice plants, perhaps during the night. On July 29 many dew-laden males and females were observed by torchlight at 05:30 h roosting separately and motionless, but by 06:10 h (19 minutes before sunrise, when there was a heavy mist) males started to become active. They flexed their wings forwards and then commenced wing-whirring, making an audible rustling; there was, as noted by ROBERT (1958), "...de tout part le bruissement de leur ailes, secouant la rosée".

Males then took off and flew low among vegetation searching for females which remained inactive. Most males quickly found females, settled on them and clasped them in tandem without further activity. By 06:40 h most females had been found and coupled in tandem and many hundreds of pairs were seen among the rice, on the grass and on bushes as far as 280 m from the water. There was now less activity than earlier although unsuccessful males continued searching, using a slow steady flight with frequent yawing movements close to rice or grass stems, and sometimes flying vertically up and down the length of a stalk. Later in the morning searching males flew with the last 4 segments of the abdomen strongly depressed, but this was not noted during the dawn flights.

Between 06:40 and 09:00 h most tandem pairs rested or made occasional short flights. Single males normally ignored tandem pairs while searching, but they pounced on solitary females. Thirteen males were found in tandem with teneral male and female *Orthetrum cancellatum* which were emerging from the rice field, and two with female *Crocothemis erythraea*. Copulations were first noted at 09:00 h, although on those days when the mist lingered they were not seen until 10:30 h. They continued in increasing numbers during the morning, and Figure 1 shows their number, together with numbers of tandem pairs, counted at intervals within a 40 x 5 m strip of rice on the western edge of the field on July 29. Counts were also made on 27 and 28 July and they gave similar figures. The number of pairs in tandem remained approximately constant until about 09:30 h when it began to rise rapidly as further pairs started to immigrate from the surrounding meadows, supplementing the population which had roosted and then formed tandems on the rice. Figure 2 shows the rate of arrival of immigrants across 40 m of the western margin of the rice field, the number of tandem pairs in flight being counted during 5 min every 30 min. It shows that immigration peaked at about 10:30 h, and probably over a thousand pairs arrived at the rice field during the morning. Immigrant pairs settled on the rice immediately or they flew further in to the field before settling. Observations at the east of the field showed that only very few pairs continued to fly eastwards beyond the first rice field.

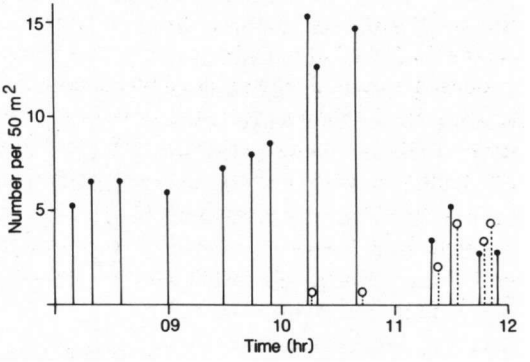


Fig. 1. Histogram of the number of pairs of *S. depressiusculum* in tandem (●) and in copulation (○) counted in a 40 x 5 m strip at various times, and expressed per 50 m², on the western margin of the rice field on 29th July, 1983, between 08:00 and 12:00 h.

The majority of dragonflies at the rice field were in tandem or copulation throughout the morning. In a total of 14 counts of dragonflies at the rice field in the 40 x 5 m strip on July 28 between 08:00 and 12:00 h, 17% of the males (83) were single and the remainder were either in tandem or in copulation. The proportion of single males changed during the morning: at 09:00 h it was 22%, but by 09:30 h it had dropped to 10%, perhaps as some males left the rice to search elsewhere. By 10:40 h it had risen to 29%, and by 12:22 h it was 74%, as pairs split up after oviposition. No single female was seen between 08:45 and 09:50 h. One was seen at 10:40 h and 9 at 12:22 h. Only those sitting on the rice were counted. Most single females therefore left the immediate vicinity of the water after oviposition.

The behaviour of immigrant pairs was watched after their arrival. Three principal behaviour patterns were distinguished, all being carried out without breaking the tandem connection: (1) settling in tandem and remaining inactive; (2) making dipping movements while hovering, which sometimes led to oviposition. Dipping started near the top of the rice plants and comprised a series of small downward swings resembling oviposition but with no egg release. Aerial oviposition is known in *S. sanguineum* and other *Sympetrum* spp. (EDA, 1975), but examination of dipping pairs through binoculars failed to produce evidence for aerial oviposition in *S. depressiusculum*. The dipping pair sometimes descended between the rice plants and the female then made brief contact with the water whereupon they flew up again. On other occasions dipping led into a more prolonged sequence of contacts with the water, presumed to be oviposition. Females were sometimes abandoned by males at this stage, and they continued ovipositing alone with males guarding them from above (cf. ROBERT, 1958); (3) copulations, which included short bouts with only brief genital contact, and prolonged engagements of many minutes duration (see below).

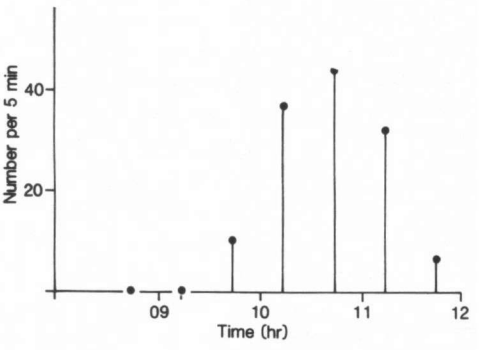


Fig. 2. Histogram of the number of pairs of *S. depressiusculum* immigrating in tandem in 5-minute periods across 40 m of the western margin of the rice field. Counts were made every half-hour between 08:30 and 12:00 h on July 29th, 1983.

Figure 3 summarises the behaviour of 52 pairs of immigrants which arrived on the wing between 09:30 and 12:30 h. Of 49 pairs which arrived in tandem, 51% (25

pairs) settled immediately and 49% (24 pairs) commenced dipping without settling; a further 3 pairs arrived in the copulatory wheel position and then continued to copulate after settling. Dipping led to copulation in 65% of the cases (37 times) whereas it led to settling in 35% (20 times). Copulation led to dipping in 72% of cases (18 times) and to settling in 28% (7 times). Finally, settling led to copulation in only 17% of cases (3 times) and to dipping in 83% (15 times). Thus copulations were commonly preceded by dipping, and in turn they often led to further bouts of dipping. Some pairs performed long, alternating sequences of the two activities: one such sequence was -C-D-C-D-C*-S-D* (where C = a brief copulatory attempt and C* = a full copulation; D = dipping and D* = oviposition; S = settling in tandem). Many similar sequences were noted and they further emphasize that dipping normally preceded copulation or attempts to copulate, and that unsuccessful attempts to copulate (presumed female rejection) were often followed by further dipping.

Copulations always started in flight and they were continued after settling on rice or grass, or rarely on the ground, with occasional changes of position. During copulation, vigorous rocking movements of the male's second and third abdominal segments could be seen at up to 3 $sec^{-1}$. There were also occasional violent jerks which swung the female upwards, and at intervals the male made a strong, slow wing depression. At the end of copulation he sometimes fluttered his wings and then disengaged the genitalia. The mean duration of 9 copulations was 15 min (max. 35, and minimum, 7 min). Sometimes a second copulation followed shortly after a first with a brief intervening period of oviposition, and this made estimations of the true duration of a copulation difficult to make.

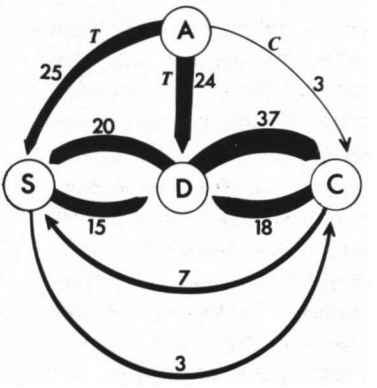


Fig. 3. Summary of the behaviour of immigrant pairs of *S. depressiusculum* after arrival at the rice field between 09:30 and 12:30 h on July 27th — 29th, 1983. (A), arriving pairs, of which 49 arrived in tandem (T) and 3 arrived in copulation (C). They then either settled (S), or commenced to dip (D), or they copulated (C). The numbers of transitions between these three major behaviour patterns are also shown.

By 12:30 h the number of tandem pairs was much reduced, and copulation was also seen less commonly (cf. Fig. 1). Most dragonflies now perched on bushes or high on trees, or they flew slowly and separately 10-20 m above the ground, feeding intermittently. Females flew with the abdomen slightly elevated and they rejected males when they were occasionally approached. No tandem or copulating pair was seen after 15:00 h and by this time many hundreds of individuals were flying over the rice and other fields. By 20:15 h a very large feeding swarm had built up in the neighbourhood

and it continued to fly until at least 20:45 h.

## DISCUSSION

The most striking feature of the behaviour of *S. depressiusculum* at the rice field was the prolonged precopulatory tandem phase which in most pairs lasted for at least 2½ h, and in some for probably 4-5 h (Fig. 4). ROBERT (1958) also described the occurrence of prolonged precopulatory tandems in a densely aggregated population of this species. We noted that tandem pairs were seldom challenged by single males, although a female relinquished by one male was sometimes soon captured by another, indicating that such females might mate more than once during a morning. Although dragonflies remained present at the rice fields throughout the afternoon and evening in large numbers, very little sexual interaction was seen after 13:00 h, and none after 15:00 h. Similarly in *Celithemis eponina* and in *Brachythemis lacustris,* sexual activity is limited to one part of the day, but males and females remain together without interacting during the remainder of the day (MILLER, 1981, 1982).

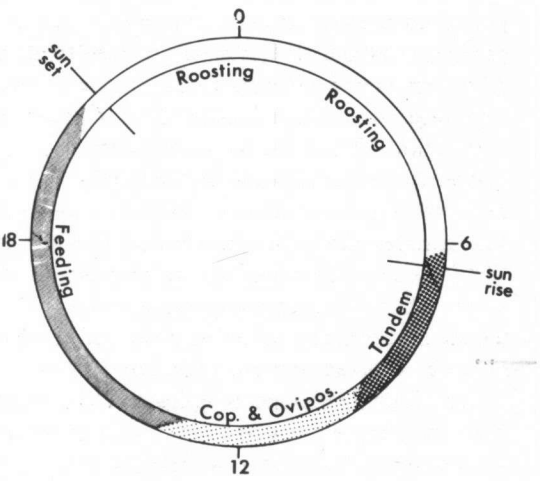


Fig. 4. Summary of the behaviour of *S. depressiusculum* during 24 hours. Pre-copulatory tandem guarding is shown as lasting about 3 hours; copulation and oviposition (Cop & Ovipos), about 4 hours; feeding, 7 hours, and the remainder is spent roosting.

In *S. depressiusculum* the widespread occurrence of tandem pairs at dawn probably reflected intense competition for females, even though copulation did not follow for some hours. The long delay may have arisen because a high temperature was required for copulation, or more likely because females were unwilling or unable to oviposit until the temperature rose. Had a male copulated early and then abandoned the female, his sperm might have been displaced by a later male. Had he copulated and then remained in tandem until the female was ready to oviposit, he would still risk sperm displacement if another male had taken over the female (but we saw no take-over of a female in tandem). Were he to search for single females later in the morning when they might be ready to

oviposit, he would risk finding none. We observed single males searching persistently during the morning, but most searches were fruitless. Thus when both sexes are present at the oviposition site continuously and at high density, and oviposition is possible only later in the morning, the best strategy for a male may be to commandeer a female early and to wait until she can oviposit before copulating. Were competition for females to be still more intense males might even form tandem pairs at dusk and remain in tandem all night, but this was not observed. The behaviour is strikingly different from that of other libellulids at lower densities, in which males adopt territories at oviposition sites and greatly outnumber females at them, the females often making only brief visits to the water (CORBET, 1980).

Copulation was commonly seen to be preceded by bouts of dipping, a behaviour pattern which resembled oviposition but which started well above the water, and was not seen to be accompanied by egg release. *S. depressiusculum* prefers to oviposit in large bodies of water in which there is abundant surface vegetation (ROBERT, 1958), and rice fields appear to offer favourable sites. Although a few pairs were seen to copulate away from the water in the meadows, we suggest that most females do not accept copulation before inspecting the oviposition site. Dipping movements, which in tandem pairs are probably performed by the male (MOORE, 1952), may indicate to the female the presence of a site and they may also sometimes allow her to test it. This behaviour may therefore resemble courtship known in some other Odonata, where a male must first locate and then indicate an oviposition site to a female before she accepts tandem formation and copulation (WAAGE, 1973), but it differs in that the female *S. depressiusculum* is already in tandem from which she cannot escape although perhaps she can resist copulation.

The dipping movements which follow a copulation may be different in nature. They may represent efforts by the male to encourage a female to oviposit. A female might be expected to delay oviposition until she had found an optimum site for her eggs, but a male should attempt to hasten it and thus be able to release the female the sooner and to search for new females. Perhaps this conflict of interests also explains why a copulation was occasionally seen to be resumed after a bout of dipping, if the female was still unwilling to oviposit.

Collections in the water of the rice field showed that the larvae of *Orthetrum cancellatum, Crocothemis erythraea, Ischnura* spp. and unidentified aeshnids were abundant, but we found no *Sympetrum* larva. Thus although we saw much oviposition behaviour, we have no firm evidence that *S. depressiusculum* bred in the rice field. However, since the population seemed to be well synchronised and we saw very few tenerals, possibly all larvae had emerged. The rice field clearly provided a very rich habitat for dragonflies and damselflies, and by far the commonest adults at it were *S. depressiusculum, Ischnura elegans* and *I. pumilio.*

## ACKNOWLEDGEMENT

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## REFERENCES

AGUESSE, P., 1968. *Les Odonates de l'Europe Occidentale, du Nord de l'Afrique et des îles Atlantiques.* Masson et Cie, Paris.

CONCI, C. & C. NIELSEN, 1956. *Fauna d'Italia, Vol. I, Odonata.* Calderini, Bologna.

CORBET, P.S., 1962. *A biology of dragonflies.* Witherby, London.

CORBET, P.S., 1980. Biology of Odonata. *A. Rev. Ent.* 25: 189-217.

EDA, S., 1975. On the oviposition behaviour of dragonflies of the genus Sympetrum. *Tombo* 18: 2-9.

FINCKE, O.M., 1982. Lifetime mating success in a natural population of the damselfly Enallagma hageni (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 10: 293-302.

MILLER, P.L., 1981. Observations on the reproductive behaviour of Celithemis eponina Drury (Libellulidae, Odonata). *Ent. mon. Mag.* 117: 209-212.

MILLER, P.L., 1982. Temporal partitioning and other aspects of reproductive behaviour in two African libellulid dragonflies. *Ent. mon. Mag.* 118: 177-188.

MILLER, P.L. & C.A. MILLER, 1981. Field observations on copulatory behaviour in Zygoptera together with an examination of the structure and activity of the male genitalia. *Odonatologica* 10: 201-218.

MOORE, N.W., 1952. Notes on the oviposition behaviour of Sympetrum striolatum Charpentier. *Behaviour* 4: 101-103.

PAJUNEN, V.I., 1966. The influence of population density on the territorial behaviour of Leucorrhinia rubicunda. *Ann. zool. fenn.* 3: 40-52.

PARKER, G.A., 1974. Courtship persistence and female guarding as male-time investment strategies. *Behaviour* 48: 157-184.

PARKER, G.A., 1979. Sexual selection and sexual conflict. *In:* M.S. Blum & N.A. Blum, Eds, Sexual selection and reproductive competition in insects, pp. 123-166. Academic Press, New York.

ROBERT, P.-A., 1958. *Les Libellules (Odonates).* Delachaux & Niestlé, Paris.

WAAGE, J.K., 1973. Reproductive behaviour and its relation to territoriality in Calopteryx maculata (Beauvois) (Odon.; Calopterygidae). *Behaviour* 47: 240-256.

WARD, P.I., 1953. The effects of size on the mating behaviour of the dungfly Sepsis cynipsea. *Behav. Ecol. Sociobiol.* 13: 75.