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REPRODUCTIVE BEHAVIOUR OF *SYMPETRUM STRIOLATUM* (CHARP.) AT AN ARTIFICIAL POND IN NORTHERN ITALY (ANISOPTERA: LIBELLULIDAE)

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Observations were carried out at an artifical pond, where the larvae cannot survive but imagines exhibit reproductive behaviour (incl. oviposition). The males attempt to perch at the pond, but only the "pond owner" does so, excluding the others which perch around the pond according to a hierarchy; those most successful in contest remaining closer to the water. Receptive females are usually present only above water. For this reason the pond owner has the greatest probability of finding a mate. After copulation he remains in tandem during oviposition. Meanwhile the second most aggressively successful male takes his place, and after oviposition the dominant male is usually excluded by the former, which becomes the new owner. Copulatory behaviour is described, and the factors inducing and limiting oviposition are discussed.

INTRODUCTION

After a four-year period of field observations on *Sympetrum striolatum* (Charp.) at an artificial pond in northern Italy, I discovered that some aspects of the behaviour of this species differ significantly from those recorded in the literature. Moreover the individuals composing the "population" of this pond have not emerged "in loco". A description of their behaviour is given, and the causes of the peculiarities of the behaviour are tentatively discussed.

STUDY SITE AND METHODS

The pond where most observations were made is located in the Verona province (Veneto), Bardolino commune: Mure (45°34'N, 10°43'E). The pond is made of cement (surface about 25 m^2;

depth 80 cm). All the western and northwestern border of the pond is constituted by a house. The northern and northwestern borders (5 m long) are bounded by a meadow (about 5x5 m), hereafter called "little meadow", bordered by the house and a scarp (both 3 m high), except on the southeastern side. The southeastern and southern sides of the pond are adjacent to another meadow, hereafter called "big meadow". The only aquatic plant is *Nymphaea alba*. The pond is periodically drained and cleaned, so that no dragonfly larvae can permanently survive. However, some species were observed to be reproductively active at the pond (*Ceriagrion tenellum, Coenagrion puella, Erythromma viridulum, Ischnura elegans, Aeshna cyanea, Anax imperator, Libellula depressa, Orthetrum cancellatum, Crocothemis erythraea, Sympetrum striolatum*) while several other species seemed to be attraced by the water.

Adults of *S. striolatum* (all sexually mature) were present from middle August to November, each year of the study period (31 days, 1983-1986). In 1985 and 1986, respectively 10 males and 2 females and 5 males and 4 females were individually marked, but with poor results, because few individuals seemed to be present for more than one day at the pond. Those marked left on the day of marking and many did not return. However, the usually low number of males often allowed one to recognize individuals without recourse to marking. On 20 and 21 September 1986, the activities of 6 males were accurately registered from their arrival at the pond until their departure; records were kept at approximately 2-second intervals of the flight performed as well as of the presence of other dragonflies or moving objects at the pond, of their distance from the male, and of the time spent perching (cf. KAISER, 1979).

OBSERVATIONS

PRESENCE AT THE POND

Males were observed at the pond from 09:15 to 15:06 h (solar time), and the male density was highest between 10:00 and 12:00. The maximal male density was 3 to 5 individuals.

The number of ovipositing females visiting the pond per day varied from 1-3.

MALE PRECOPULATORY BEHAVIOUR

Males coming to the pond fly for a few seconds above water, making dipping movements as described for other libellulid species (cf. e.g. JACOBS, 1955). Usually the first male to arrive perches near the area where leaves of *Nymphaea alba* float (about 1.5 x 1.5 m wide), at the northwestern side of the pond. Most males seem to prefer plant stems for perching, but they may perch on the cement embankment, especially if no stems are available near the pond. Each male coming to water after the first is attacked by the latter (hereafter called the "pond owner", or "male A"), and excluded from the pond after a chase. Very rarely, in about 2% of observations, a second male is tolerated at the opposite side of the pond. These males perch around the pond according to a hierarchy, such that the male winning over all the others except the pond owner, hereafter called "male B", perches in the little meadow, whereas the others perch on the roof of the house or in the scarp. No male was ever seen perching in the remaining area, i.e. in the big meadow. All subordinate males sometimes fly over the pond, but they are usually attacked and pursued by male A. In one case, the male B excluded the male A from the pond for a few minutes.

The precopulatory activities of the males at or near the pond include perching (most of the time) and some kinds of flight. The males do not seem to spontaneously take to flight, but solely do so when an object is moving in the surroundings. This may induce the male to exhibit avoidance or direct flight. The former is performed by disturbed males, which take rapidly to flight and, after a stationary hovering for about 1-2 seconds, about 1 m above water, fly away. The direct flight is directed towards small moving objects. In this case, the following kinds of flight may occur: (1) feeding flight (the male catches a flying insect and immediately returns to perch), (2) investigatory flight (the male stops, hovering for about 1 second, facing the object being investigated; if the object is a flying dragonfly, the male pursues it from below and, if the dragonfly is a conspecific, the attack or sexual flight follow), (3) attack flight (the male tries to strike the abdomen of a conspecific male from below), (4) sexual flight (the male tries to size a conspecific female). The support-searching flight, when the male seeks the "settling base", according to CORBET (1983) characterized by a vertical zig-zag pattern, and the patrol flight (slow flight, interrupted by very frequent stationary hovering above water) occur after any of the preceding flights.

The duration of a patrol flight varies from a few seconds to 38 minutes (mostly 2-5 min). From the incidental observations and from the analysis of the behaviour of 6 males (cf. also KAISER, 1979), I obtained the impression that the duration correlates directly with intra- and interspecific encounters. Males appear to patrol longer after more encounters in rapid succession, inversely with the time already spent flying (i.e. they patrol for a few seconds only also after frequent encounters if they have already patrolled beforehand for, say at least 5-10 min), and directly with the likelihood of encountering a mate. Thus, they patrol longer when female arrival at the pond is higher, i.e. in the hottest hours.

Three of the analysed males perched at the pond and their activities included: perching (82-99.8% of the time spent at the pond, $\bar{x} = 92.2\%$), investigatory flight (1.4-6.5%, $\bar{x} = 2.7\%$), patrol flight (0-5.1%, $\bar{x} = 1.7\%$), attack flight (0-3.5%, $\bar{x} = 1.6\%$), support-searching flight (0-5%, $\bar{x} = 1.6\%$), feeding flight (0-0.1%, $\bar{x} = 0.05\%$). The remaining three analysed males did not perch at the pond but they flew above it for some seconds (10, 12 and 38). Their activities included: patrol flight (60-68.4%, $\bar{x} = 65\%$), investigatory flight (0-33.3%, $\bar{x} = 14.6\%$) and support-searching flight (0-40% $\bar{x} = 20.3\%$).

One male perched near the *Nymphaea alba* area and remained motionless, so that the A-male did not respond to him. This seems to be the situation in *Orthetrum coerulescens* where satellite males perch in the area defended by an aggressive male and wait for females without being recognized or attacked by the latter (pers. observ.). In another case, a male patrolled the pond, flying slowly along the borders, ignoring the other males which attacked him, first of all vigorously, and then less vigorously until finally they almost ignored him. This anomalous male flew over the pond for some minutes and then departed.

FEMALE PRECOPULATORY BEHAVIOUR

Females arriving at the pond may immediately either (1) try to oviposit or begin to do so or, (2) after a rapid flight around the pond, they perch in the little meadow (N=4). Females in category (1) may accept seizure and copulation by a male (many cases), or may not (one case). In the latter case, the female raised her abdomen at an angle of more than 45° from the horizontal plane and tried to fly above the male. The male flew near the female while she oviposited and sometimes attempted to seize her; finally he chased her. Only one female in category (2) was seized by a male that was perching in the little meadow and seemed to recognize her after she took to flight.

SEIZURE

With no apparent courtship, males attempt to seize any flying female, approaching from below (investigatory flight), then gaining a superior position and trying to grasp her (sexual flight). If the female is receptive, she flies slowly in the direction taken when the male approached, and the male can easily seize her. Then the couple fly for some seconds in tandem before the intra-male sperm translocation takes place (N=2) (sequence A-B-C-E- of UTZERI, 1985, fig. 1), or the translocation is performed immediately after seizure, with the male straightening his abdomen (N=1) (sequence A-C-E of UTZERI, 1985, fig. 1). Four timed translocations lasted 1, 1.3, 1.5 and 1.5 seconds. Usually, after sperm translocation, the female immediately completes the wheel position, but sometimes a further period of tandem is required before she does so (stage D of UTZERI, 1985, fig. 1).

COPULATORY BEHAVIOUR

The duration was estimated of five wheel positions (all started in the air and completed perching): 7 min 54 s, about 8 min, about 7 min (1 min flying + 6 min perching), 7 min and about 4 min. The start of the last copula was not observed. AGUESSE (1959) recorded copulation durations of 10-15 minutes in the species.

The copulatory movements performed by the male in the three 4, 7 and 7 minute copulations were accurately observed. In the first copulation, the 2nd male abdominal segment was depressed and the 1st stimultaneously raised upward during 3 minutes. This movement was performed 0.5-1 s^{-1}, while the body was otherwise motionless. During the 4th minute the male was motionless. In the second and third copulations, during the 1st minute, 1-1.5 s^{-1} movements were exhibited. During a second stage, lasting 3 and 5 minutes respectively, the male raised his 2nd segment twice in quick succession after 1 second periods of inactivity. During the last two minutes (third stage) in both copulations the male was motionless.

Probably the 4 minute copulation was observed during a stage corresponding to the second stage of the other (7 min) ones.

The postcopulatory pause lasted 5 and 31 seconds in two pairs, and it was less than one minute in the three others.

POSTCOPULATORY BEHAVIOUR

After a postcopulatory pause the pair takes to flight and moves to the pond in tandem. First, the pair makes dipping movements in various places for about 1 minute, without the female contacting water. At this stage, oviposition presumably does not take place. After such a period the pair continuously hovers over one point, gradually descending until the female touches the water during dipping. Then the pair may dip in a few selected points, near *Nymphaea* leaves or near the pond margins, or along an elliptical course, gradually advancing, in the middle of the pond, where no plants are present. Some couples oviposited in both ways. Oviposition was usually performed at a rate of 1-1.5 s^{-1}. The inclination of a hovering pair, before dipping, was oblique and about 10-20° below the horizontal plane, with the male head up and the female abdomen, down, and the dipping movements change the inclination to about 90° below the horizontal, i.e. to a vertical or forward oblique position. Oviposition movements were performed into water or against the cement borders, but only once were eggs seen adhering to the cement at water level.

It seems that water must be touched in order for eggs to be extruded. When three females (held by the wings) were dipped into water, their eggs accumulated in a drop adhering to the vulvar lamina after the first touch, and then dispersed in the water after contact. Then another drop adhered to the lamina, the eggs accumulated in it and were then released when water was again contacted, and so on. Three other hand-held females, dipped without contacting water, did not release the eggs. If the vulvar lamina touched water at least twice, eggs accumulated in the drop adhering to the lamina (except in one case), and were not released if water was again touched.

This shows that water touching is necessary in order to release the eggs. On average, free-flying females touched the water about 104 times (range: 55-194) during each oviposition bout.

The ovipositing pair separates in either of two ways: (1) the female exhibits refusal display, raising the abdomen up to more than 45°, and struggles until the male releases her, then she flies upwards, with the male following, and at a height of about 10 m chooses a direction and leaves the pond, or (2) the male releases the female before she has finished ovipositing and flies about 30 cm above her and about 50 cm behind her, dashing at approaching males. However in 4 out of 5 observations, the male did not find the female again after the first pursuit. In one case the male released the female before she had finished laying and flew away.

Each male, whether an A-male or not, after having guarded a female in tandem until she has finished laying, is expelled by any male (usually the B-male) occupying the pond. Tandem oviposition usually lasts more than 3 minutes (5 complete ovipositions lasted 3-6 min, x = 4.4, (not including the exploratory water-touching tandem flight, which lasts 1-2 min).

In two cases the female was released after 2 minutes of true oviposition and, respectively, 1 and 1.5 minutes of exploratory water-touching tandem. One male was disturbed by another while non-contact guarding the ovipositing mate and chased him from the pond. The latter perched in the little meadow, returned when the female had left, and successfully drove out the original pond owner. The male of the other couple successfully expelled other males also after his mate had left.

It seems, from the above, that if a male shows contact guarding only during the first part of oviposition, he may be able to successfully attack and exclude from the pond any other male.

Some females oviposited unattended and it was observed that they made dipping movements about once every 1-1.5s, i.e. less frequently than during tandem oviposition, and two of them almost immersed the whole body while dipping.

EGG HATCHING

Observations were made on eggs obtained from females, made to oviposit in the laboratory. Eggs laid on 5 September 1985 (about 600) began to hatch after 15 days. Those laid on 21 September 1985 (1038) hatched after 10-16 days, (the number hatching on successive days being 118, 549, 330, 34, 2, 2, and 3). In both cases eggs were held in a sunny place, but the temperature was not recorded. Those laid on 26 October 1985 (497) hatched between 22 January and 7 February 1986, i.e. after 88-104 days. They were kept unfrozen, though air temperature was often below 0° C.

FEMALE REFUSAL DISPLAY

When some females were seized by subordinate males, they exhibited a refusal display like the unreceptive ovipositing females or those which have already oviposited, i.e. they raised the abdomen up to more than 45° and often struggled.

In two cases the behaviour of such pairs was recorded: the male coming from the surroundings of the pond already in tandem, flew above the water, while the female exhibited refusal display. The male pushed the female forwards, so that the tip of her abdomen came close to his hind legs, which then grasped the tip of her abdomen and rubbed it.

HEYMER (1966) described a similar behaviour in males of *Platycnemis* when females do not cooperate in attaining the wheel position. Indeed, one of the two pairs copulated after about one minute, whereas the other after 2.5 minutes began to make dipping movements, until the female touched the water, whereupon the male immediately flew upwards, rubbed his mate's abdomen two or three times and perched. When he tried to take to flight, the females refused, remaining firmly perched, and the male released her. MOORE (1952) observed a *S. striolatum* male making dipping movements with a dead female with which he had not copulated. Perhaps the male, making the female touch water, signals to her that the site is suitable for oviposition. If so, this could be regarded as a kind of courtship, resembling that found in Calopterygidae (e.g. HEYMER, 1973) and in *Perithemis tenera* (Libellulidae) (JACOBS, 1955), males of which attract females to sites which females may or may not then accept as suitable for ovipositing. In the former case the females accept copulation; in the latter they refuse it and fly away. But the "courtship" of *S. striolatum* differs in that it is performed after seizure and only if the female refuses to copulate. To designate the behaviour of that single male as a "courtship" would be premature.

Many other males were observed in tandem with struggling females. The seizure was not observed, therefore it is impossible to say whether or not they had copulated before coming to the pond. They made dipping movements above the water, without touching it. One seemed not yet to have copulated, since the male held the female with the abdomen bent as in the copulatory position, while perching and flying. MILLER et al. (1984) observed an apparently identical behaviour in *Sympetrum depressiusculum*, in which paired males commonly exhibit aerial dipping movements above water, before copulation. It is, however, interesting to note that JURZITZA (1963) observed an *Enallagma cyathigerum* male that, after having seized an *Erythromma viridulum* male, performed the movements usually adopted to induce the female to copulate ("copulation invitation"). Then the pair perched on a *Nymphaea* leaf, "wo das *Enallagma*-Männchen sich auf dem Nacken des vermeintlichen Weibchens aufrichtete wie bei der Eiablage".

DISCUSSION

These observations reveal some interesting points, particularly the hierarchical organization of males. Subordinate and dominant males occupying the same area have previously been observed in Calopterygidae, e.g. *Mnais pruinosa* (HIGASHI, 1981; NOMAKUCHI & HIGASHI, 1985; NOMAKUCHI et al., 1984) and Libellulidae, e.g. *Plathemis lydia* (CAMPANELLA & WOLF, 1974), *Libellula luctuosa* (CAMPANELLA, 1975), *Crocothemis erythraea* (FALCHETTI & UTZERI, 1974), *Orthetrum chrysostigma* (MILLER, 1983) and *O. coerulescens* (pers. observ.). Whereas in Calopterygidae and *Orthetrum* dominant males exhibit full-time or nearly full-time territoriality (sensu PARR, 1983), so that subordinate males act as "satellites" of the former, perching around the territory of the dominant male and making incursions into it, *P. lydia, L. luctuosa* and *C. erythraea* males occupy an area intermittently during the day, alternating with each other according to a hierarchy such that the "dominant" male occupies the territory when most females arrive at water. A feature common to all these species is the postcopulatory non-contact guarding of the female. In *S. striolatum* the postcopulatory contact guarding (tandem) is always adopted. Although this species is reproductively almost continuously ("full-time") active, like Calopterygidae and *Orthetrum*, the hierarchy is of an intermediate type between these two groups: the dominant male excludes the subordinate ones from the pond until he copulates (spatial hierarchy like Calopterygidae and *O. chrysostigma*), and then, after oviposition, he is replaced by the first subordinate male, who then acts as a new dominant male, probably until he copulates. In this way, a temporal hierarchy, rather similar to that in *Plathemis, Libellula* and *C. erythraea,* is involved.

To explain these differences, the following hypothesis seems to be justified. The behaviour of dragonfly males is mainly conditioned by the availability of sites suitable for oviposition, the density of other males and the frequency of ovipositing females in the characteristic habitats of the species concerned. Species where reproductive sites are usually clumped and whose ovipositing-female frequency is usually high exhibit strong territoriality and non-contact guarding. Species whose reproductive sites are usually dispersed and where ovipositing female frequency is usually low, exhibit less strong territoriality and contact guarding or unattendance of the female. The mating strategies appear to be the most effective when in accordance with the local ecological situation (cf. also THORNHYLL & ALCOCK, 1983).

All the above species, except *S. striolatum,* belong to the first group. But in case of unusual ecological situations, such as when a population of one group finds itself in the situation optimal to the other, the behaviour does not change to comply with the unusual ecological conditions. Under such circumstances, therefore, the behaviour becomes less effective.

S. striolatum usually lives in habitats characterized by the dispersed oviposition sites and by the low frequency of ovipositing females, while in Bardolino the pond induces the clumping of females. Therefore contact guarding and weak territoriality are not very effective strategies there. In fact, sometimes as many as 3 females arrive at the pond in a day, but only the first may copulate with the most successful male. An example in the opposite direction is that of *Libellula quadrimaculata,* which belongs to the group with the clumped oviposition sites. In one locality (France, La Tour-d'Auvergne, Lac Chauvet; 45°55'N, 2°7'E) male density was very high in the oviposition sites, while females were not frequent and were chased by males, so that non-contact guarding was not an effective strategy and probably contact guarding could be more effective. In any case, the hierarchical behaviour of *S. striolatum* seems to occur when the number of males exceeds the number of available territorial areas and it seems, therefore to be a direct consequence of normal male behaviour: males attempt to settle in the sites where females oviposit and are receptive, and the more a male is successful in excluding the others from a territory, the greater is his probability of finding receptive females.

Copulatory male movements are similar to those observed by me in *Ceriagrion tenellum* and *Sympetrum sanguineum.* I speculate that during the first and second stages sperm removal takes place (WAAGE, 1979; SIVA-JOTHY, 1984). The last motionless stage probably corresponds to sperm transfer.

Comparing the oviposition behaviour of *S. striolatum* with that of two related species which exhibit non-contact flying oviposition, *S. sanguineum* (some tandem ovipositions observed) and *S. meridionale* (one unpaired female observed), it may be noted that: (1) the change of inclination during dipping movements is greater in *S. striolatum* (70-80° approx.) than in *S. sanguineum* and *S. meridionale* (30° approx.; pers. observ.), (2) the number of dipping movements per second is lower in *S. striolatum* (max: $3/2\ s^{-1}$) than in *S. sanguineum* and *S. meridionale* (usually $6/2\ s^{-1}$ and $4/2\ s^{-1}$, resp.; pers. observ.), and (3) *S. striolatum* needs to touch water in order to release the eggs, whereas the others do not (pers. observ.).

If the last point is true for the species, and not only for the individuals observed, the non-contact oviposition, already attributed to *S. striolatum* (WESENBERG LUND, 1913; ROBERT, 1958; EDA, 1975), may be performed only after having touched water at least some times, i.e. until a drop adheres to the lamina. Nevertheless, the eggs may be released in this way only if they accumulate in a large number, so that separated from the lamina they fall down by their own weight. This implies that the last remaining eggs cannot be released by non--contact flying oviposition, since they are neither sufficiently separated from the lamina, nor sufficiently heavy. Consequently, non-contact oviposition seems unlikely to occur in this species and the preceding observations are probably due to an interpretation error, where the dipping movements made by the male before the female touches water have been mistaken for actual oviposition. The oriental *S. s. imitoides* oviposits only by contacting the water (EDA, 1975). Perhaps the difference in oviposition behaviour results from the different shape of the lamina, which is very prominent in *S. striolatum,* but not at all in *S. sanguineum* and *S. meridionale* (cf. e.g. CONCI & NIELSEN, 1956).

Finally, it is possible that eggs deposited late in the reproductive season show delayed embryogenesis.

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