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FIELD OBSERVATIONS ON SPERM TRANSLOCATION BEHAVIOUR IN THE MALES OF *CROCOTHEMIS ERYTHRAEA* (BRULLÉ) AND *ORTHETRUM CANCELLATUM* (L.) (LIBELLULIDAE), WITH A REVIEW OF THE SAME IN THE ANISOPTERA

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The main question about the little-known process of sperm translocation in anisopteran males, is whether sperm translocation is performed by the male alone and/or "in tandem". Systematic observations of the pairing in *C. erythraea* and *O. cancellatum*, from male-female seizure till starting of copulation, revealed that sperm translocation always occurred following tandem formation. The sequence (tandem seizure — sperm translocation — copulation) is suggested to be a behavioural chain in which each phase takes a rigid position. On this basis, the "in tandem" sperm translocation is considered to be the normal behaviour, while sperm translocation in the male alone is suggested to be anomalous.

INTRODUCTION

Within the Anisoptera, sperm translocation (hereafter referred to as ST) is reported to be performed after tandem formation in the males of several species. The species concerned are: *Aeshna juncea, A. subarctica, A. affinis, Boyeria irene* and *B. vinosa* (SCHMIDT, 1964; HEYMER, 1967 (in BICK, 1972); 1968; JURZITZA, 1971; UTZERI & RAFFI, 1983), *Oxygastra curtisi* and *Somatochlora metallica* (HEYMER, 1964 (in BICK, 1972); 1968; JURZITZA, 1966a), *Cordulegaster boltoni* (HEYMER, 1968), *Uropetala carovei* (WOLFE, 1953), *Orthetrum coerulescens, O. brunneum, O. cancellatum, Aethriamantha rezia, Urothemis assignata, Erythrodiplax connata, Libellula quadrimaculata* and *Sympetrum* sp. (HEYMER, 1969; JURZITZA, 1966a, 1966b, 1975, KRÜNER, 1977; HASSAN, 1981).

WESENBERG-LUND (1913, in ROBERT, 1958; 1943), KENNEDY (1915), MAYER (1957) and ROBERT (1958) suggest that males possibly perform ST at the instant immediately before actual clasping of the female's head.

However, some authors report ST to be performed by the male while alone, before pairing: *Aeshna* sp., KENNEDY (1915); *A. juncea*, CORBET (1962); *Cordulia aenea*, UBUKATA (1975); *Uropetala carovei*, WOLFE (1953); *Orthetrum cancellatum*, KRÜNER (1977); *Libellula quadrimaculata*, MOORE (1960); *L. pulchella*, PEZALLA (1977, in BICK, 1983, in litteris); *L. julia*, HILTON (1983); *Brachythemis lacustris* and/or *Nesciothemis farinosa*, MILLER (1982).

ROBEY (1975) observed ST in *Pachydiplax longipennis* during the short postmating flight.

CARLE (1982) reports to have observed ST in Anisoptera either before or after pairing, but species are not stated.

A third set of authors who studied the reproductive behaviour of anisopteran dragonflies either were not able to observe ST, or do not expressly report to have

Table I

Reports of intra-male sperm translocation in the Anisoptera (? = unclear statement)

In the male while alone	Connected with tandem formation
Before pairing	**Before seizure (supposed)**
Actually observed	Odonata, undet. (WESENBERG-LUND, 1913; 1943)
	Anisoptera, undet. (KENNEDY, 1915; ROBERT, 1958)
Anisoptera, undet. (CARLE, 1982)	*Aeshna cyanea* (MAYER, 1957)
Aeshna sp. (KENNEDY, 1915)	*A. mixta* (MAYER, 1957)
Aeshna juncea (CORBET, 1962)	*A. grandis* (MAYER, 1957)
Cordulia aenea amurensis (UBUKATA, 1975)	
Uropetala carovei (WOLFE, 1953)	**After seizure (observed)**
Orthetrum cancellatum (KRÜNER, 1977)	Anisoptera, undet. (CARLE, 1982)
Libellula quadrimaculata (MOORE, 1960)	*Boyeria irene* (HEYMER, 1968)
L. pulchella (PEZALLA, 1977)	*B. vinosa* (JURZITZA, 1971)
L. julia (HILTON, 1983)	*Aeshna subarctica* (SCHMIDT, 1964)
(?) *Brachythemis lacustris* (MILLER, 1982)	*A. juncea* (HEYMER, 1967; 1968)
(?) *Nesciothemis farinosa* (MILLER, 1982)	*A. affinis* (UTZERI & RAFFI, 1983)
	Anax parthenope (this paper)
Assumed but not observed	*Oxygastra curtisi* (HEYMER, 1964)
	Somatochlora metallica (JURZITZA, 1966a; HEYMER, 1968)
Aeshna sp. (GARDNER, 1956)	*Cordulegaster boltoni* (HEYMER, 1968)
Tetragoneuria spp. (KORMONDY, 1959)	*Uropetala carovei* (WOLFE, 1953)
Cordulegaster boltoni (MÜNCHBERG, 1964)	*Orthetrum coerulescens* (HEYMER, 1969)
Hagenius brevistylus (JOHNSON, 1972)	*O. brunneum* (HEYMER, 1969; this paper)
Pachydiplax longipennis (JOHNSON, 1962)	*O. cancellatum* (KRÜNER, 1977; this paper)
Leucorrhinia dubia (PAJUNEN, 1963)	*Aethriamantha rezia* (HASSAN, 1981)
L. rubicunda (PAJUNEN, 1963)	*Urothemis assignata* (HASSAN, 1981)
L. pectoralis (KIAUTA, 1964)	*Erythrodiplax connata* (JURZITZA, 1975)
Acisoma panorpoides inflatum (HASSAN, 1978)	*Leucorrhinia* sp. (PAJUNEN, 1963, doubtful)
	Libellula quadrimaculata (JURZITZA, 1966a)
After pairing	*L. depressa* (this paper)
Pachydiplax longipennis (ROBEY, 1975)	*Crocothemis erythraea* (this paper)
	Sympetrum sp. (JURZITZA, 1966b)
	Sympetrum striolatum (this paper)

observed it. However, they believe that this behaviour is performed by the male alone, before pairing (e.g. KORMONDY (1959); JOHNSON (1962); MÜNCHBERG (1964); HASSAN (1978)). GARDNER (1956) and JOHNSON (1972) do not state this explicitly, but give drawings of males adopting the ST position while alone. PAJUNEN (1963) and KIAUTA (1964) analyzed the amount of sperm in the sperm vesicles of males of *Leucorrhinia* caught before pairing, during copulation and after the release of the females. Though these authors did not find differences in the content of the sperm vesicles they assumed that ST took place when the male was alone. PAJUNEN (1963), however, reports with some doubt to have observed a male of *Leucorrhinia* performing ST while in tandem.

During the last five years the author of the present paper recorded ST performed in tandem by *Aeshna affinis, Anax parthenope, Libellula depressa, Orthetrum cancellatum, O. brunneum, Crocothemis erythraea* and *Sympetrum striolatum.* These records, however, show an excess of copulations in respect to the STs observed.

The above data are synoptically gathered in Table I.

From the above data, two main questions concerning ST in anisopteran males arise: (1) is ST performed after or before tandem seizure, or does this vary within and among families, species and individuals, and (2) when ST is performed in tandem, is it performed each time seizure occurs, or can it be sometimes omitted.

This paper presents the results of systematic observations on ST behaviour of *C. erythraea* and *O. cancellatum,* with the objective of gathering material to discuss the above questions.

Observation of mating in both species is easily carried out, as distinct wing rustling of the partners occurring at the moment of tandem formation enables the observer to quickly identify mating couples.

METHODS

Observations were carried out at Castel Porziano (Roma) during August 8 and September 1, 1983, at a permanent pond of about 15 m in diameter, where the two species coexist. Males were observed while alone, both when perched and in flight, as well as while in tandem. Ovipositing females were also observed, since they were soon taken in tandem.

All copulations were recorded, and for each, whether or not tandem seizure and ST had been observed. The distance of each pair from the observer was also recorded to determine if this affected the observation of ST.

Timings were taken of the wing rustlings heard during the tandem formation, of the STs and of the interval between the first contact of the male and female of the pair when forming the tandem and the start of copulation. The latter were taken to determine if couplings where ST was not observed were of shorter duration than couplings where ST was observed.

It is to be emphasized that the timing data reported below are to be considered as indicative of their relative duration class rather than as representative of real durations. In consideration of this, when timing very brief events such as wing rustlings and STs, a delayed-timing method was sometimes used, as follows: the time spent for the behaviour concerned was memorized by the observer, and then timed closely after. It is the belief of the author that this method gives reliable enough timings as direct timing, when used for very short intervals. The timings obtained by this method will be indicated below.

A pair of each species from the studied populations were delivered to the Museo di Zoologia, Dipartimento di Biologia Animale e dell'Uomo, Università di Roma.

BEHAVIOUR OF TANDEM MALES

The following description of the behavioural events that the author assumes to be ST in *O. cancellatum* and *C. erythraea*, is based on 78 and 192 observations respectively.

As soon as the male seizes the female he stretches forward and the pair flies very briefly in tandem. Then the male curves his abdomen and brings its IInd and IXth urites in contact for a time generally not exceeding one second. After ending this contact the male stretches forward again and soon afterwards the copulation position is assumed while in flight (Fig. 1).

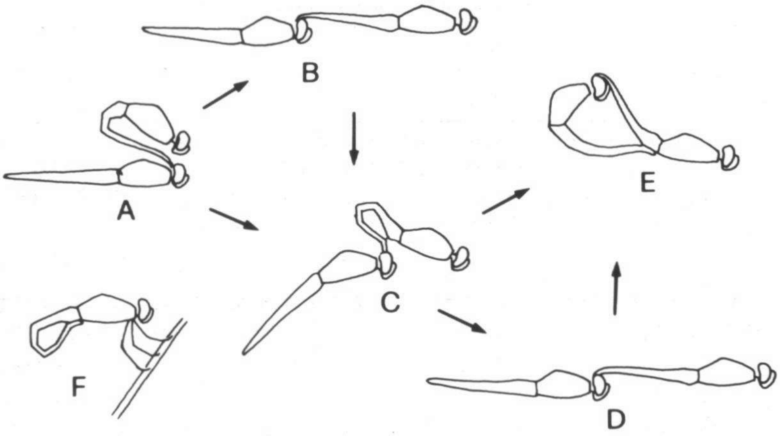

Fig. 1. Sequences in the reproductive behaviour of *Crocothemis erythraea* and *Orthetrum cancellatum*. A = tandem seizure; B, D = tandem flight; C = sperm translocation; E = copulation; F = male contacting accessory genitalia with abdomen tip. Observed sequences: A-B-C-D-E: *O. cancellatum* (common), *C. erythraea* (rare); A-C-D-E: *C. erythraea* (infrequent); A-C-E: *C. erythraea* (common).

The above pattern was always observed in *O. cancellatum*, but in *C. erythraea* the male after clasping the head of the female with his cerci, usually does not stretch his abdomen but directly brings his IXth urite to contact the IInd. Following this, the wheel position is quickly assumed (Fig. 1).

In both species, ST closely follows tandem seizure, and if the pair shifts to avoid disturbance by other males this shifting almost always occurs after ST has been performed.

In 309 copulations of *C. erythraea* and 80 of *O. cancellatum*, tandem seizure was seen respectively 125 and 45 times, and ST 97 and 40 times. In those cases when tandem formation was recorded but ST was not seen (28 of 125 and 5 of 45 respectively) this was related to reflections of light from water, quick shifting of the pair and unfavourable position of the pair in respect to the observer, that prevented him from identifying the behaviour. The author never had evidence of copulation directly following tandem seizure with ST being omitted.

The distances at which observations occurred were between two and 17 m (N = 110) for *C. erythraea*, and between two and 15 m (N = 44) for *O. cancellatum*. The seizures after which ST was not observed took place between three and 13 m (N = 25) and between four and 15 m (N = 5) for the two species respectively.

The duration of the wing rustling heard during tandem formation, estimated by the delayed-timing method, was 0.28, 0.65 and 1.07 s in *C. erythraea*, and 0.54 and 0.94 s in *O. cancellatum*.

Table II
Sperm translocation durations (sec)

Species	Timing method adopted	Duration
Crocothemis erythraea	actual	0.41 0.52 0.90 0.93
	delayed	0.27 0.38 0.54 0.59 1.66
Orthetrum cancellatum	actual	0.37 0.51 0.69 0.82 0.89 0.94 0.94 1.07 1.19
	delayed	0.46 0.52 0.54 0.72 0.74

The duration of ST behaviour in *C. erythraea* was between 0.27 and 1.66 s (N = 9; $\bar{x}$ = 0.69; SE = 0.15). In *O. cancellatum*, ST duration was between 0.37 and 1.19 s (N = 14; $\bar{x}$ = 0.74; SE = 0.07). In Table II, the durations of ST are reported.

The duration of the interval between the male seizing the female (= start of the wing rustling) and the beginning of copulation in *C. erythraea* was between 1.2 s and 5.6 s (N = 134; $\bar{x}$ = 2.1; SE = 0.06); in *O. cancellatum* it was between 1.3 and 14.8 s (N = 49; $\bar{x}$ = 3.8; SE = 0.31). Figure 2 gives the frequencies of the recorded durations related to half-second intervals. Failure to detect ST was related to timings between 1.3 and 5.6 s (N = 16; $\bar{x}$ = 2.2; SE = 0.26) in *C. erythraea*, and to timings between 3.2 and 6.7 s (N = 6; $\bar{x}$ = 4.9; SE = 0.68) in *O. cancellatum*. In comparison with these, timings when ST was seen were between 1.2 and 3.9 s (N = 118; $\bar{x}$ = 2.1; SE = 0.06) and between 1.3 and 14.8 s (N = 43; $\bar{x}$ = 3.7; SE = 0.34) in the two species respectively.

Two marked males of *C. erythraea* which mated respectively three times within 10 minutes and two times within two minutes performed ST before each copulation. Even though males of *O. cancellatum* were not marked individually 33 STs were recorded for the 10 males that were active at the pond on August 10,

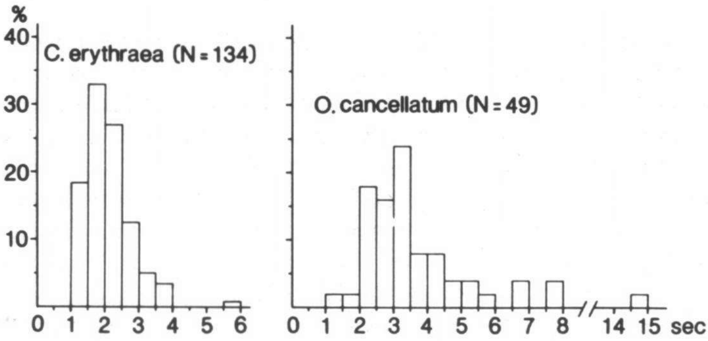

Fig. 2. Frequencies of the intervals between tandem formation and copulation in half-second intervals.

each male averaging 3.3 STs.

The other libellulids in which the author observed ST (cf. above) show the same behaviour as described for *C. erythraea* and *O. cancellatum*. In all those species the duration of ST was very short and was timed at 0.92 and 1.11 s for *Libellula depressa*.

BEHAVIOUR OF SINGLE MALES

Males of *C. erythraea* may curve their abdomens ventrally, up to tap the proximal urites with the distal ones. The position assumed in this behaviour resembles that in which ST is performed except that the abdomen is kept lower (Fig. 1, F). The author recorded one male making such a contact for much shorter time than that made by males in tandem, and K. Lorenzi (personal communication) saw a male performing such tapping three times in close succession, for a total duration of 0.66 s (delayed timing). On both occasions the distal urites were not held at the proximal ones.

DISCUSSION

Even though mating pairs were easily identified on account of wing rustlings of the partners, yet the time that elapsed from hearing the wing rustling to the detection of the pair was generally long enough to prevent the observer from recording the behaviour preceding copulation. However, the data reported above indicate that: (1) ST in tandem was recorded every time the tandem formation was clearly seen; (2) observation of ST was not affected by the distance of the observer from the site of tandem formation and (3) the durations of the intervals between tandem seizure and start of copulation when ST was seen do not exceed those when ST was not seen, indeed, they are slightly lower. However, these differences do not bear any significance at the t-test ($t = 0.512$; $p > 0.50$ for *C.*

erythraea; $t = -1.339$; $p > 0.10$ for *O. cancellatum*). As a consequence it can be assumed that in the species concerned ST is always performed after tandem formation. It also appears that in *C. erythraea* and *O. cancellatum*, the same male may translocate the sperm to his accessory genitalia each time mating occurs.

The behavioural chain (seizure in tandem — ST — copulation), in the species concerned, appears to be very rigid (cf. HEYMER, 1968), and it is possible that the consummatory act of each phase acts as a releaser for the following one (cf. BAERENDS, 1941 [in EIBL-EIBESFELDT, 1967] for the behaviour of *Ammophila* wasps, and TINBERGEN, 1969). This seems to apply to the Zygoptera (cf. BICK, 1972) and *Epiophlebia* (ISHIDA, 1959) as well.

The very short duration and the relatively inconspicuous behaviour pattern of ST as observed in *C. erythraea* make ST very difficult to identify. This may explain why, for the same species, AGUESSE (1959, p. 178) stated: "Malgré de nombreuses observations, il m'est impossible de dire à quel moment précis les mâles remplissent de sperme leurs pièces accessoires". Assuming that ST duration is very short also in other anisopteran species (cf. the author's records reported above) it is not unlikely that many observers have failed to detect it.

The experiments of PAJUNEN (1963) and KIAUTA (1964) support the above conclusions as well. In fact as their males did not have different amounts of sperm either before or after copulation, the assumption that ST must have occurred between tandem seizure and copulation seems to be valid, since, if the sperm vesicles were filled before mating one would expect the males taken before pairing to show a greater amount of sperm in their sperm vesicles, compared with those taken after copulation. The conclusion of PAJUNEN (1963) and KIAUTA (1964) may have been influenced by the fact that, in the 1960s, ST duration in the Anisoptera was expected to be similar to that of the Zygoptera (Pajunen, pers. comm.) that is of the order of several seconds, and that the observers missed the ST in tandem.

Comparison between different amounts of sperm in consistent samples of males taken before pairing, at the instant preceding copulation and after copulation, might give clearer indications, unless volume and density of sperm vary among males of the same sample, as in *Erythemis simplicicollis* (Waage, pers. comm.). On the other hand, it would be impossible to check *C. erythraea* males between tandem seizure and copulation due to the very brief time elapsing between these two events.

The reports of ST behaviour by solitary males (cf. above), on one hand, can be matched with the following statement of MOORE (1952, p. 102, footnote): "Bending the abdomen beneath the thorax, as when adopting the tandem position, appears as an apparent overflow activity. This movement is easily confused with that of the transfer of sperm to the accessory genitalia". On the other hand, observations of unpaired males assuming the ST position, raise the question as to whether or not in these occasions sperm is actually translocated to the accessory genitalia and what the significance of this behaviour is, if it represents an additional ST or if ST actually does not occur.

The author of this paper recorded a *Lestes virens* male, forcedly separated from the female he had just seized, contacting his IInd and IXth urites immediately after for a brief time. This indicates possibly that the stimulation perceived by the male after contacting the female had activated the behaviour that follows capture (namely ST). In this respect, KENNEDY's (1915) report of an *Aeshna* male performing ST closely after having failed to capture a female is of some interest. It can be speculated whether the sight of the female raised the male sexual drive to make it express as an overflow ST activity. Anomalous behaviour of this kind is known to occur in anisopteran males: *Plathemis lydia* adopt the copulation position on the shadows or wing spots of perched females they have apparently lost from sight while pursuing them (JACOBS, 1955) and *Sympetrum striolatum* bend their abdomens beneath the thorax as when adopting the tandem position (MOORE, 1952, cf. above).

HEYMER (1968) interpreted the ventral bending of the abdomen in the male *Aeshna juncea* as a "mise en état d'alerte" (p. 894), and stated: "De toute évidence, le recourbement de l'abdomen est déclenché par la vue d'une ♀...".

In *C. erythraea*, the author does not believe that ST behaviour, when performed by the male alone, is functionally comparable to that of the tandem male, for the following reasons: (1) the contact of the concerned urites lasts much too briefly in the male alone to be comparable to that in tandem; (2) it is unlikely that ST, which appears rigidly tied in the chain (tandem — ST — copulation), is also performed by the unpaired male at other times. The latter consideration applies to all those species in which ST has been reported both in the male alone and in tandem (cf. CORBET (1962) and HEYMER (1967; 1968) for *Aeshna juncea*, WOLFE (1953) for *Uropetala carovei*, MOORE (1960) and JURZITZA (1966a) for *Libellula quadrimaculata* and KRÜNER (1977) for *Orthetrum cancellatum*).

Further studies could perhaps indicate whether the stimulus eliciting the performance of functional ST depends on the internal status of the male or whether ST is elicited by the contact of the cerci with the female's head. The number of species in which evidence was obtained of ST being released after tandem seizure (six aeshnids, two corduliids, one cordulegastrid, one petalurid and 10 libellulids) is much greater than the number of species in which ST is reported only in the unpaired male, viz. *Cordulia aenea* (UBUKATA, 1975), *Pachydiplax longipennis* (ROBEY, 1975), *Libellula pulchella* (PEZALLA, 1977), *Brachythemis lacustris* and/or *Nesciothemis farinosa* (MILLER, 1982) and *L. julia* (HILTON, 1983). This consideration, along with the above, tends to suggest, as a working hypothesis, that the chain (tandem — ST — copulation) might be valid for the whole Anisoptera (cf. BICK, 1972).

PAJUNEN (1963), KIAUTA (1964), MILLER (1982) and Waage (pers.

comm.) find remainders of sperm in the penis after copulation. This possibly involves more prompt insèmination of the female, in case additional ST was to take place before next copulations, but may also indicate that the sperm translocated by the male each time is not fully utilized. Basing on this, one might expect the amount of sperm in the penis to increase with number of matings, this eventually leading the male to omit the tandem ST in the following. The author of this paper doubtfully recorded a *Coenagrion lindeni* male (Zygoptera) assuming the copulation position without previous ST, having performed ST closely before while in tandem with another female, afterwards released without any attempt to copulate (cf. UTZERI & RAFFI, 1980). In this respect it will be of particular interest to investigate whether in the anisopteran species in which ST is repeated before each copulation, a male, after performing ST movements while unpaired, would repeat ST on the next instance he happens to mate.

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