

FURTHER OBSERVATIONS ON INTRA-MALE SPERM TRANSLOCATION BEHAVIOUR IN ANISOPTERA

C. UTZERI¹ and C. OTTOLENGHI²

¹ Dipartimento di Biologia Animale e dell'Uomo, Università "La Sapienza", Viale dell'Università 32, I-00185 Roma, Italy

² Via Mure 5, I-37011 Bardolino, Verona, Italy

Abstract

The male of *Libellula depressa* translocates sperm after each successive seizure even if the copulation does not always follow. In contrast, the male of *Aeshna cyanea* does not translocate sperm to the penis again if it has not copulated after doing this on the preceding occasion. In *Brachythemis contaminata* the sperm translocated in one act can be used for several copulations. In *B. contaminata* and *Nannothemis bella* sperm translocation seems to normally occur in the male alone. It is suggested that while in-tandem sperm translocation might imply the advantage for the male of fertilizing eggs with fresh sperm, selection for shortening the duration of the mating sequence in some species may have caused the shift of sperm translocation before the tandem formation.

Introduction

Prior to copulation, the dragonfly male flexes its abdomen to bring the genital opening (urite IX) to contact the penis (urites II and III). By this

behaviour it is assumed to translocate sperm to its accessory genitalia (BICK & BICK's, 1970 "intra-male sperm translocation") (ST in the following). Since in the Zygoptera ST lasts several seconds, it is easily observed and is reported as a rule after tandem formation (BICK, 1972). Apparently this mode does not occur if the male has performed ST while in tandem with another female, with which he has not copulated (UTZERI, 1985; CORDERO, 1989) and in a few other cases (JOHNSON, 1961; WAAGE, 1973; KUMAR & PRASAD, 1977). In the Anisoptera, ST is mostly reported in the tandem male, but in some species it is reported either for the male while alone or in tandem, and in a few others only in the male while alone. In a great number of species, ST is neither reported nor observed, in the latter case being presumed to take place in the unpaired male (review by UTZERI, 1985 and this paper). Apparently males of some species perform ST before each copulation (UTZERI, 1985; UTZERI & DELL'ANNA, 1989), but this observation is not of general value.

Since in the last few years we have recorded ST behaviour in several dragonflies and new literature is now available concerning this topic, we herewith present and discuss information to improve the knowledge of ST behaviour in the Anisoptera.

Observations

We have observed ST behaviour in tandem males of the following species (numbers of observations are reported before dates):

Aeshna mixta (1; Oct. 13, 1985). Tandem formation with the female perched; ST without the male stretching forward immediately after clasping, according to the pattern observed in *A. affinis* (UTZERI & RAFFI, 1983).

A. cyanea (13; Oct. 21 - Nov. 10, 1984; Sep. 20 and Oct. 26, 1985; Oct. 20-23, 1986). Female either captured in flight, and then pulled to the ground or water, where she was actually seized, as in *A. affinis* (UTZERI & RAFFI, 1983), or during perched oviposition. In four instances, each of three males performed very brief ST behaviour only after clasping the first of 3-4 tethered dead females that were presented to them and with which they could not mate.

A. isosceles (1; June 17, 1986). Tandem capture and very short ST behaviour in flight.

Onychogomphus forcipatus (1; June 10, 1985). Tandem capture and ST behaviour in flight; ST duration 5 seconds; ST not observed in two other pairs.

Tholymis tillarga (1; Jan. 23, 1988); *Libellula fulva* (1; June 10, 1984); *Pachydiplax longipennis* (2; Aug. 16, 1989); *Sympetrum fonscolombei* (1; May 23, 1986); *S. meridionale* (2; Sep. 9, 1985); *Orthetrum anceps* (1; July 6, 1987); *O. albistylum* (5; June 12, 1987). In all these libellulids, female capture and ST took place in flight, the ST behaviour probably lasting less than 1 second. In all the species reported above, the mating sequence follows one or more of the patterns reported by UTZERI (1985) and, except in *O. forcipatus*, ST is such an inconspicuous behaviour that it is not easily identified if the pair is in an unfavourable position to the observer. In these species, we have never observed ST behaviour in the male while alone.

Besides, W. Schneider (pers. comm.) on January 25, 1988, at Periyar Lake, Kerala, India,

observed some males of *Brachythemis contaminata* each performing seven STs while alone, between successive copulations. Apparently the ST was performed once between two successive copulations, but one or more copulations were between two STs, according to the following scheme: ... ST ... TAND--COP ... ST ... TAND--COP ... TAND-COP ... TAND--COP ... ST ... He did not observe the in-tandem ST.

One of us (C.O.), on July 10, 1986, recorded a male of *Libellula depressa* seizing a female nine times within two hours, with which he did not copulate, since she was not cooperative. This male performed the ST behaviour probably after each seizure (six times actually seen) even though he did not mate with other females in this period. Ten minutes later he successfully mated with another female, also performing ST after tandem seizure. Then a further non-cooperative female, probably the same as before, was seized thrice by the male, in-tandem ST being performed all three times.

The above data, except the last one, together with those from recent literature, are listed in Table I. Previous records of in-tandem ST in *L. depressa* are in UTZERI (1985) and UTZERI & DELL'ANNA (1989).

Discussion

Some points concerning ST behaviour were previously discussed (UTZERI, 1985). It is however worth to outline some new aspects emerging from the present observations, in particular:

- (1) In *Libellula depressa* ST behaviour appears highly stereotyped, taking place immediately after each tandem formation, irrespective of whether or not copulation follows, but consequently before each copulation, in accordance to what is observed in other libellulids (UTZERI, 1985).
- (2) In contrast to this, the males of *Brachythemis contaminata* can translocate sperm only once before several copulations and those of *Aeshna cyanea* do not repeat ST after seizing the next female if they failed to copulate with the previous one. These modes, if occurring in a greater variety of species than recorded, might explain why the ST behaviour is missed by many observers.

Table I – Records of intra-male sperm translocation in Anisoptera, evidenced subsequent to UTZERI (1985)

Species	References
IN THE MALE WHILE ALONE	
Odonata	DUNN, 1984 (general statement)
Aeshnidae	
<i>Aeshna juncea</i>	JURZITZA, 1988 (picture)
Corduliidae	
<i>Cordulia aenea amurensis</i>	UBUKATA, 1984 (presumed)
Libellulidae	
<i>Brachythemis contaminata</i>	this paper
<i>Nannothemis bella</i>	HILDER & COLGAN, 1985
<i>Leucorrhinia hudsonica</i>	HILTON, 1985
<i>Erythemis simplicicollis</i>	WAAGE, 1986 (presumed)
<i>Sympetrum obtrusum</i>	SAVARD, 1986 (picture)
<i>Orthemis ferruginea</i>	NOVELO GUTIERREZ & GONZALEZ SORIANO, 1984 (presumed)
<i>Libellula croceipennis</i>	NOVELO GUTIERREZ & GONZALEZ SORIANO, 1984 (presumed)
AFTER TANDEM FORMATION	
Odonata	VAN TOL, 1985 (general statement)
Anisoptera	DONATH & RADESTOCK, undated (general statement and drawing)
Aeshnidae	
<i>Aeshna isosceles</i>	this paper
<i>A. mixta</i>	this paper
<i>A. cyanea</i>	this paper
<i>A. juncea</i>	SCHMIDT, 1984 (in JURZITZA, 1988) DREYER, 1986 (in JURZITZA, 1988)
Gomphidae	
<i>Onychogomphus forcipatus</i>	this paper
Libellulidae	
<i>Tholymis tillarga</i>	this paper
<i>Perithemis tenera</i>	RÜPPELL, 1988 (film projection)
<i>Pachydiplax longipennis</i>	this paper
<i>Libellula fulva</i>	this paper
<i>L. depressa</i>	UTZERI & DELL'ANNA, 1989
<i>Selysiothemis nigra</i>	DELL'ANNA, 1991
<i>Trithemis annulata</i>	DELL'ANNA, 1991
<i>Orthetrum trinacria</i>	UTZERI, 1990
<i>O. anceps</i>	this paper
<i>O. albistylum</i>	this paper
<i>O. a. speciosum</i>	MIYAKAWA & SUGIMURA, 1985 (picture)
<i>O. cancellatum</i>	RÜPPELL, 1984 (drawing)
<i>Erythemis simplicicollis</i>	WAAGE, 1986 (sometimes)
<i>Sympetrum croceolum</i>	ARAI, 1983
<i>S. striolatum</i>	OTTOLENGHI, 1987
<i>S. fonscolombi</i>	this paper
<i>S. meridionale</i>	this paper
<i>S. danae</i>	MICHIELS & DHONDT, 1988
<i>Orthemis ferruginea</i>	NOVELO GUTIERREZ & GONZALEZ SORIANO, 1984

- (3) The males of at least two species, *B. contaminata* (this paper) and *Nannothemis bella* (HILDER & COLGAN, 1985), perform ST while alone according to an apparently fixed pattern. In the latter, the ST behaviour lasts almost 60 seconds, thus it would have been improbable to miss it if also performed in tandem.

In the Anisoptera, the fact that more numerous reports exist of in-tandem ST, than of ST in the male alone (UTZERI, 1985; this note), might be due to a greater difficulty to observe this behaviour in the unpaired male. This however does not exclude that in-tandem ST be really the most common. For several zygopteran species ROBERTSON & TENNESSEN (1984) pointed out the possibility that ST occurs immediately before copulation to prevent sperm coagulation in the penis, in case copulation fails. Apparently, sperm coagulation is unlikely to occur in *L. depressa* and other species (cf. UTZERI, 1985) that translocate sperm each time after seizure, whether copulation actually follows or not. However, there is still the possibility that sperm viability in the penis is lower than in the primary reservoir, so it is of advantage for the male to load its penis with fresh sperm each time and shortly before copulation, viz. after securing the female.

In the Anisoptera, the sequence [TANDEM - ST - COPULATION] lasts from a few seconds to several minutes, however ST is usually accomplished in a second or less (UTZERI, 1985; this paper). A short mating time in dragonflies is generally associated with territorial defense (WAAGE, 1984), thus permitting the male both to remain dominant in the territory and to possibly mate again in a brief interval (ALCOCK, 1979; SHERMAN, 1983; WAAGE, 1984), and also reduces male-pair interference. A short in-tandem ST is coherent with this view: within the Zygoptera, in which ST generally lasts several seconds, the calopterygids, which show the most developed territoriality, have not only copulation durations but also ST durations amongst the shortest in the suborder (e.g. BICK & SULZBACH, 1966; HEYMER, 1973; ROBERTSON & TENNESSEN, 1984). On the other hand, selection for shorter mating might have led to shifting of the ST behaviour before pair formation in *B. contaminata* and *N. bella*, particularly so in the latter,

which needs a relatively long time to translocate sperm. However, why in long-copulating species (e.g. Libellulidae, Aeshnidae) the ST behaviour is also very brief remains unclear. PARKER (1970), for dungflies, has shown that long copulations function both in removing more sperm from the female's ducts and fertilizing more eggs and MILLER (1983) suggests the same for *Orthetrum chrysostigma*. In the light of sperm competition, we are tempted to speculate that in these species long copulation may be a relatively recent acquisition, while there is no need to change either the length of the ST or its position in the mating sequence.

Acknowledgements — Contributi C.N.R. e stanziamenti M.U.R.S.T., quote 40% e 60%.

References — ALCOCK, J., 1979, *J. nat. Hist.* 13(4): 439-446; — ARAI, Y., 1983, *Nature & Insects* 18(14): 29-30; — BICK, G.H., 1972, *ContactBr. ned. LibellenOnderz.* 10(suppl.): 1-14; — BICK, G.H. & D. SULZBACH, 1966, *Anim. Behav.* 14: 156-158; — BICK, G.H. & J.C. BICK, 1970, *Ent. News* 81: 157-163; — CORDERO, A., 1989, *Odonatologica* 18(3): 237-244; — DELL'ANNA, L., 1991, *Notul. odonatol.* 3(7): 110-111; — DONATH, H. & K. RADESTOCK, undated, *Umweltschutzinformation* 21; — DREYER, W., 1986, *Die Libellen*, Gerstenberg, Hildesheim; — DUNN, R.H., 1984, *Derbyshire dragonflies*. Derbyshire Naturalists' Trust, Derby; — HEYMER, A., 1973, *Verhaltensstudien an Prachtlibellen. Beiträge zur Ethologie und Evolution der Calopterygidae Selys, 1850 (Odonata: Zygoptera)*, [Fortschr. Verhaltensf. 11], Parey, Berlin; — HILDER, B.E. & P.W. COLGAN, 1985, *Can. J. Zool.* 63(5): 1010-1016; — HILTON, D.F.J., 1985, *J. Kansas ent. Soc.* 57(4): 580-590; — INOUE, K., 1989, *Insectarium* 26: 10-11; — JOHNSON, C., 1961, *Can. Ent.* 93: 260-266; — JURZITZA, G., 1988, *Ent. Z., Frankfurt/Main* 98(9): 127-128; — KUMAR, A. & M. PRASAD, 1977, *Odonatologica* 6(3): 163-167; — MICHIELS, N.K. & A.A. DHONDT, 1988, *Behav. Ecol. Sociobiol.* 23: 257-263; — MILLER, P.L., 1983, *Odonatologica* 12(3): 227-238; — MIYAKAWA, K. & S. SUGIMURA, 1985, *Shiokara-tombo. [orthetrum albistylum speciosum]*. Shūeisha, Tokyo; — NO-

- VELO GUTIERREZ, R. & E. GONZALEZ SO-
RIANO, 1984, *Folia ent. mex.*, 59: 11-24; –
OTTOLENGHI, C., 1987, *Odonatologica* 16(3):
297-306; – PARKER, G.A., 1970, *J. Insect Phy-*
siol. 16: 1301-1328; – ROBERTSON, H.M. &
K.J. TENNESSEN, 1984, *Odonatologica* 13(4):
591-595; – RÜPPELL, G., 1984, *Publ. wiss.*
Filmen (Biol.) (16)36: 1-12; – RÜPPELL, G.,
1988, *Abstr. Pap. IXth Int. Symp. Odonatol., Ma-*
durai, p. 37 (film); – SAVARD, M., 1986, *Notul.*
odonatol. 2(8): 125-127; – SCHMIDT, E.,
1984, *Libellula* 3(1/2): 53-54; – SHERMAN,
K.J., 1983, *Anim. Behav.* 31: 1107-1115; –
UBUKATA, H., 1984, *J. Hokkaido Univ. Educ.*
(II) 35(1): 43-52; – UTZERI, C., 1985, *Odon-*
atologica 14(3): 227-237; – 1990, *Ann. Mus. civ.*
St. nat. "G. Doria" 88: 331-335; – UTZERI,
C. & R. RAFFI, 1983, *Odonatologica* 12(2): 141-
151; – UTZERI, C. & DELL'ANNA, 1989, *Adv.*
Odonatol. 4: 133-147; – VAN TOL, J., 1985,
Naturopa 49: 15-19; – WAAGE, J.K., 1973,
Behaviour 47(3-4): 240-256; – 1984, in: Smith,
R.L. [Ed.], *Sperm competition and the evolution*
of animal mating systems, pp. 251-290, Acad.
Press, N.Y.-London; – 1986, *Odonatologica*
15(4): 429-444.

Received November 27, 1991