

**THE STRUCTURE OF THE GENITALIA AND THE VOLUMES OF
SPERM STORED IN MALE AND FEMALE *NESCIOTHEMIS
FARINOSA* (FOERSTER) AND *ORTHETRUM CHRYSOSTIGMA*
(BURMEISTER) (ANISOPTERA: LIBELLULIDAE)**

P.L. MILLER

Department of Zoology, University of Oxford, South Parks Road,
Oxford OX1 3PS, United Kingdom

Received July 14, 1983 / Accepted November 6, 1983

Female *O. chrysostigma* possess a very small bursa able to hold only about 26% of the sperm stored in this species, the remainder being contained in the long, narrow spermathecae. The male has a penis with a long barbed flagellum which may be able to enter and reach the distal ends of the spermathecae. It may hook out the sperm of other males from the storage organs of the female during the long copulations sometimes seen in this species. In contrast, in *N. farinosa*, a sympatric species of similar size and colour, the female storage organs can contain over a hundred times more sperm than in *O. chrysostigma*; about 83% of it being kept in the bursa. This species makes relatively short copulations, and the male has a penis whose structure suggests that it compresses pre-existing sperm in the bursa but cannot enter the spermathecae. One male *O. chrysostigma* carries enough sperm in the secondary genitalia to furnish about 6 females, whereas one female *N. farinosa* has stores large enough to contain the contributions of about 6 males. In both species, towards the end of copulation new sperm is probably injected through a bursal valve, whereas during fertilisation sperm leaves the bursa through a small posterior pore under muscular control.

INTRODUCTION

Morphological evidence has suggested that some libellulids achieve sperm precedence mainly by packing down sperm already present in the female genital stores before inserting their own, while others remove foreign sperm partly or completely before they inseminate the female (WAAGE, 1984; MILLER 1982b). Sperm removal has been shown to occur in several species of damselfly and in two dragonflies, *Celithemis elisa* and *Erythemis simplicicollis* (WAAGE, 1979a, 1982, 1984). Sperm precedence has been demonstrated directly by the use of irradiated

males in a damselfly (FINCKE, 1984) and in a dragonfly (McVEY & SMITTLE 1984). Males which pack down sperm may gain precedence only during the immediately ensuing bout of oviposition (last in, first out), since, at least by the following day, sperm mixing may have abolished their advantage. Replacement of all sperm by his own, on the other hand, would allow a male to continue to fertilise all the eggs laid in subsequent clutches on following days until another male mated with the female. The males of some species, however, remove only a proportion of the sperm present in a female (WAAGE, 1984). Females of *Erythemis simplicicollis* store enough sperm for at least six clutches, but, as in other libellulids, they seldom have the chance in the wild of laying more than one clutch without a fresh mating (McVEY 1981; McVEY & SMITTLE, 1984).

Nesciothemis farinosa and *Orthetrum chrysostigma* are libellulids of similar size and colour which both occur commonly at a stream at Hunter's Lodge in Kenya (MILLER, 1982a, 1982b). In spite of these similarities their reproductive behaviour differs in a number of ways, as does their genital morphology. Individual male *N. farinosa* spend relatively short periods each day holding territories at the stream, and the duration of their copulation has a mean of 28 s. In contrast, some male *O. chrysostigma* spend many hours holding a territory at the stream on each of several successive days, and copulation is longer lasting, sometimes extending for up to an hour in satellite males. The penis of *N. farinosa* bears broad inflatable sacs but it has no structure capable of entering the spermathecal stores of the female. That of *O. chrysostigma*, on the other hand, bears a long and barbed flagellum which may be able to enter the spermathecae and withdraw sperm from them as well as from the bursa. Measurements described here show that a female *N. farinosa* can store over a hundred times more sperm than a female *O. chrysostigma*, and that it probably requires contributions from about six males to fill the stores of a female *N. farinosa*. A male *O. chrysostigma*, however, carries enough sperm in the secondary genitalia to fill the stores of about six of its females. The possible adaptive significance of these differences is considered.

METHODS

Nesciothemis farinosa and *Orthetrum chrysostigma* were both obtained from the neighbourhood of a stream at Hunter's Lodge in Kenya during July, 1982 (MILLER, 1983). After capture they were preserved in 90% alcohol or in 2.5% glutaraldehyde. In the laboratory, stored sperm, in the form of solid plugs, was dissected from the bursae and spermathecae of alcohol-preserved females, and from the secondary genitalia of preserved males. Sperm plugs were measured in situ in the spermathecae of *O. chrysostigma*. Sperm volumes were calculated from accurate drawings of the plugs which were then approximated to regular figures (spheres, cones, cylinders etc.). In addition, plasticene models were made from the drawings, scaled up 6.8×10^6 times, and the volume of plasticene used was then determined by weighing it or by forming it into a cylinder. Each plug was modelled up to four times and a mean taken. No allowance for shrinkage of the sperm in alcohol was made, and the values are

therefore reliable mainly for comparisons. No account has been taken of possible differences of sperm densities between or within species.

Male genitalia were prepared for scanning electron-microscopy from glutaraldehyde-fixed material by inflating the penis and plunging it into liquid nitrogen: it was then freeze-dried, coated with gold and examined in a Philips PSEM 500.

RESULTS

MALE SECONDARY GENITALIA

When a male is viewed ventrally, the dorsal surface of the fourth segment of the penis is seen because the penis turns through 180° and faces posteriorly. It therefore has the same orientation as the body of the female during copulation since the partners are head-to-tail, and ventral side to ventral side.

The penis of *N. farinosa* has already been described (MILLER, 1982b). It possesses inflatable bristly apical and medial lobes, but no flagellum or extended cornu, and no structure with proximally directed

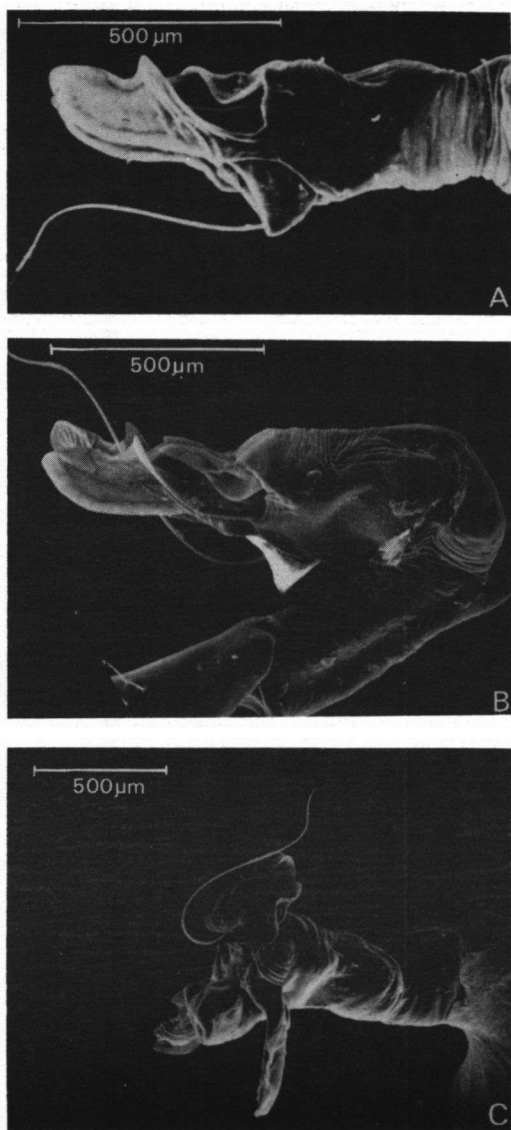


Fig. 1. Scanning electron micrographs of the fourth segment of the penis of *O. chrysostigma* (dorsal, upwards): (A) penis at rest; — (B) compression of the first segment has started to separate the lateral lobes and rotate the flagellum upwards; — (C) the completely inflated penis with the medial lobes and flagellum rotated dorsally and the lateral lobes ventrally. Compare with Fig. 2.

spines. These features suggested that it could probably not remove more than a small amount of pre-existing sperm from the female during copulation, but might pack down such sperm in the bursa.

The penis of *O. chrysostigma* is equipped with a long, single, stiff and non-retractile flagellum, possibly the equivalent of a cornu (cf. RESTIFO, 1972). The flagellum is attached to the median process, and in the deflated state its base passes through a cleft in the apical lobe (Figs 1A, 4A). The median process together with the pair of medial lobes join the large lateral lobes at a hinge concealed under the hood (Fig. 2). By applying pressure to the first segment of the penis, the fourth

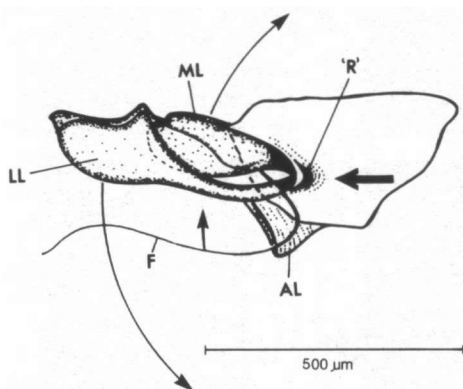


Fig. 2. Lateral view of the fourth segment of the penis of *O. chrysostigma* with the hinge shown by transparency. The thick arrow indicates the hydraulic movement of liquid which forces the elastic hinge ("R") distally. Thin arrows indicate movements of lobes which occur when the hinge opens. — AL: apical lobe; — F: flagellum; — LL: lateral lobes; — ML: medial lobes.

segment can be made to inflate hydraulically in fresh or preserved specimens by liquid displacement (MILLER, 1981; WAAGE, 1984). Inflation forces the hinge distally causing it to open widely. The median process, the attached flagellum and the medial lobes swing dorsally through about 90°, while the lateral lobes swing outwards and ventrally by a similar amount. At the same time the apical lobe inflates (Fig. 1B-C). A C-shaped region of thick translucent cuticle (possibly of resilin), close to the hinge, causes the hinge to close and the lobes and flagellum to snap back into their resting positions when the first segment is decompressed. The rotary movement of the flagellum is comparable to that described in *Brachythemis lacustris* (MILLER, 1982b), except that inflation caused the flagellum of that

species to be extruded from its housing in a ventral direction.

In *O. chrysostigma* the distal end of the flagellum is armed with many small barbs (Fig. 3A-C), as is that of some other *Orithetrum* spp. (Fig. 3D-E). In *O. cancellatum*, the flagellum also bears barbs half-way along its length (Fig. 3F). The apical lobe of *O. chrysostigma* bears numerous stout, multi-pronged spines (Fig. 4), and the outer surfaces of the lateral lobes have a scattering of smaller spines. The flagellum is about 1040 μm long and it tapers from a diameter of 10 μm near the base to 3-4 μm towards the tip.

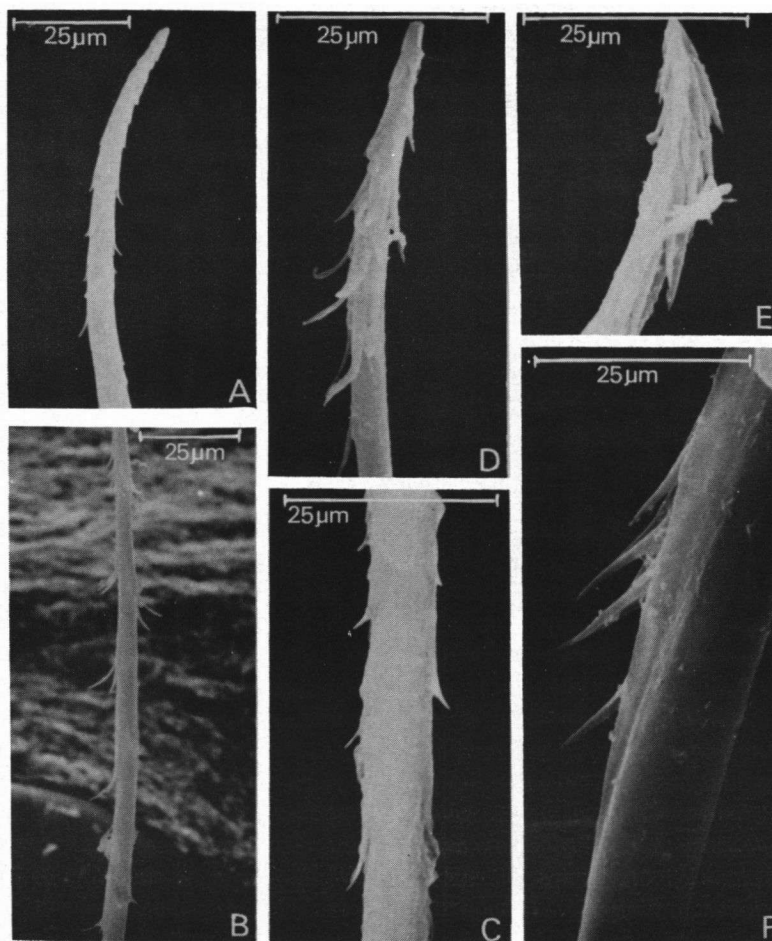


Fig. 3. Scanning electron micrographs of barbed regions of the flagella of the fourth segment of the penis in various *Orthetrum* species (distal ends upwards): (A-C) *O. chrysostigma*; — (D) *O. coerulescens*; — (E-F) *O. cancellatum* (F is taken half-way along the flagellum, and the remainder are near the distal end).

FEMALE GENITALIA

In both species the oviducts unite anteriorly before entering the vagina through a long valve. A single bursa and paired spermathecae are given off dorsally from the vagina. A thick layer of complex musculature arises from sclerites on the dorsal walls of the vagina and bursa: it surrounds the vagina and inserts at various positions on the sternites.

In *N. farinosa* the bursa and spermathecae are large structures (Fig. 5). The bursa narrows posteriorly to form a small chamber which opens into the vagina through a ventral slit about $370\text{ }\mu\text{m}$ long. The slit bears spines along its margins and more spines line the inside of the posterior chamber (Fig. 9E). The slit widens into a small rounded opening at the posterior end where it lacks spines and is

closely associated with a transverse cuticular structure. A pair of bellows-like organs, also usually containing sperm, extend on either side of the posterior chamber (Fig. 5: BO).

The whole of the very small bursa in *O. chrysostigma* is equivalent in size to the posterior chamber in *N. farinosa* (Figs 6, 7). It also opens into the vagina through a slit, about $220\text{ }\mu\text{m}$ long and lined with spines. Again the posterior end of the slit widens slightly, lacks spines and is associated with a cuticular structure (Fig. 8: TCS). In one female this part was seen to contain a continuous thread of sperm leading from the bursa into the micropyle of an egg which was held up against the end of the bursa. In both species a pair of oval cuticular plates form part of the lateral walls of the vagina and they press on the

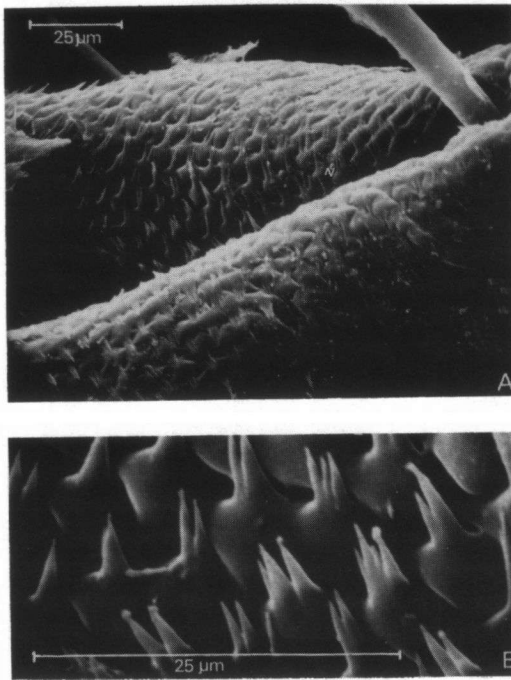
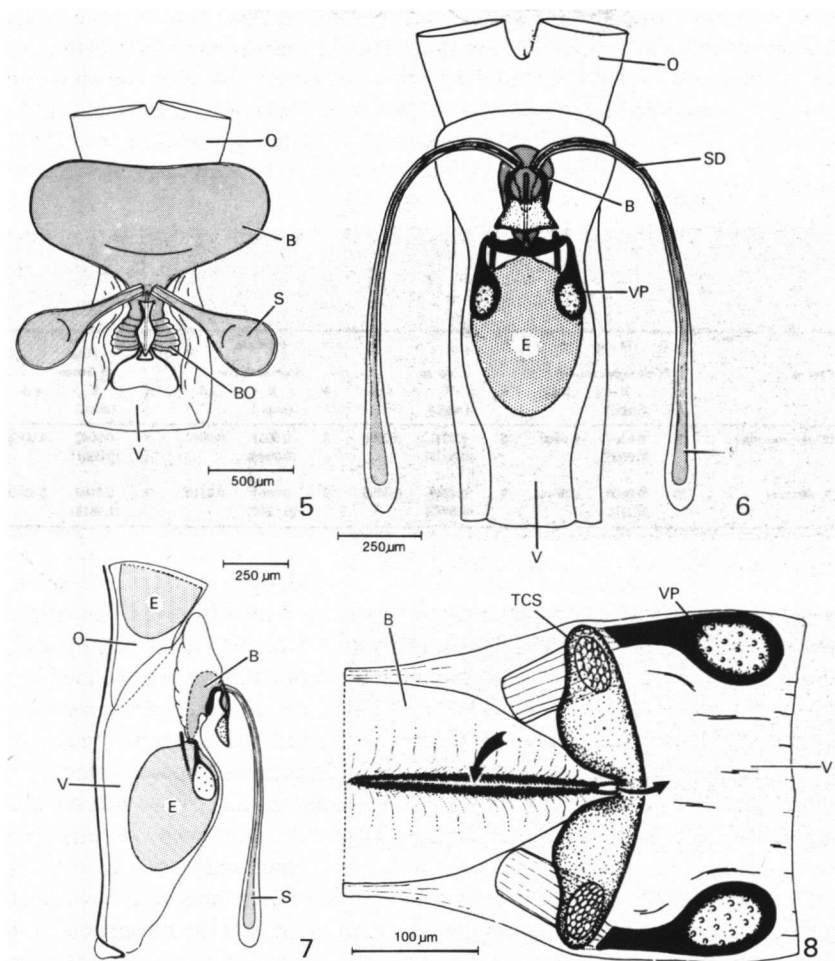


Fig. 4. Scanning electron micrographs of the apical lobe of the fourth segment of the penis of *O. chrysostigma*: (A) the base of the flagellum is shown passing through the cleft in the uninflated lobe; — (B) part of the lobe showing scales each bearing 1-5 spines.

anterior end of the egg when it is in position for fertilisation against the bursa (Figs 6-8, VP). They contain sensilla, about $20\text{ }\mu\text{m}$ in diameter.

The spermathecal ducts in *N. farinosa* are $50\text{--}100\text{ }\mu\text{m}$ in diameter near the junction with the bursa, whereas those of *O. chrysostigma* are only $10\text{--}15\text{ }\mu\text{m}$. In both species, a continuous thread of sperm was found between the bursal and spermathecal stores (Fig. 10A).



Figs 5-8. Female genitalia of *N. farinosa* (Fig. 5) and *O. chrysostigma* (Figs 6-8): (5) Dorsal view of the genital tract of *N. farinosa* (anterior, upwards); — (6) Dorsal view of the genital tract of *O. chrysostigma* (anterior upwards); — (7) Lateral view of the genital tract of *O. chrysostigma* (anterior upwards); — (8) Ventral view of the bursa and adjoining parts of the vagina of *O. chrysostigma*, showing the longitudinal spiny slit through which sperm may enter the bursa (larger arrow), and the posterior opening from which sperm may leave the bursa (smaller arrow). (B): bursa; BO: bellows-like organ (an extension of the posterior chamber of the bursa); E: egg; O: oviduct; S: spermatheca; SD: spermathecal duct; TCS: transverse cuticular structure and muscles; V: vagina; VP: vaginal plate which bears sensilla.

VOLUMES OF STORED SPERM

Measurements of the sperm volumes carried by both sexes in the two species are summarised in Table I. Considerable variations in the values were found, partly because the storage organs themselves varied, but mainly because of differences in the amounts they contained. Variable filling may depend on the recency and duration of copulation, and/or on the amount of oviposition carried out.

Table I
Mean and maximum volumes of sperm stored by male and female *Orthetrum chrysostigma* and *Nesciothemis farinosa* (mm³)

Species	Male				Female			
	Penis segments 1-3		n	Bursa	Spermathecae	Total in female	n	s.d.
	n	\bar{x} (max.)		\bar{x} (max.)	\bar{x} (max.)	\bar{x} (max.)		
<i>O. chrysostigma</i>	8	0.0267 (0.0605)	8	0.0011 (0.0020)	8	0.0031 (0.0049)	8	0.0012 (0.0061)
<i>N. farinosa</i>	20	0.0800 (0.2192)	9	0.4247 (1.5472)	9	0.0861 (0.1216)	9	0.5108 (1.6618)

All mature females caught at or near the stream carried substantial volumes of stored sperm (Tab. I). The totals in *O. chrysostigma* varied from 0.0026 to 0.0061 mm³ (i.e. X 2.3) (cf. Fig. 10A), whereas those in *N. farinosa* varied from 0.1052 to 1.6618 mm³ (i.e. X 16). The totals included three *N. farinosa* females caught in copulation whose mean was 0.3973 ± 0.1933 , and four *O. chrysostigma* in copulation whose mean was 0.0042 ± 0.0008 mm³. The sample sizes from copulating females are too small for conclusions about sperm removal or compaction to be reached, but one *O. chrysostigma* female caught in copulation with a satellite in the field (after an unknown duration) contained no sperm in the bursa although its spermathecae were well filled, containing 0.0047 mm³.

All mature males of both species caught either in the field nearby or at the stream contained substantial amounts of sperm in the first three segments of the penis. Segment I carried the greatest but also the most variable amount, whereas segments II and III carried smaller but more constant amounts, and none was found in segment IV (Fig. 10B). In *N. farinosa* the volume varied from 0.0197 to 0.2192 mm³ (i.e. X 11), while in *O. chrysostigma* it varied from 0.0096 to 0.0605 mm³ (i.e. X 6.3). The samples included six *N. farinosa* and four *O. chrysostigma* males caught in copulation, but their values did not differ significantly from those of non-copulating males and they may have broken off before insemination had occurred. The samples also included four *N. farinosa* males behaving territorially at the stream, four caught in the field at 1745 h when they were preparing to roost, and six caught at 1000 h before they had visited the stream. In none of these sub-samples did the volume differ significantly.

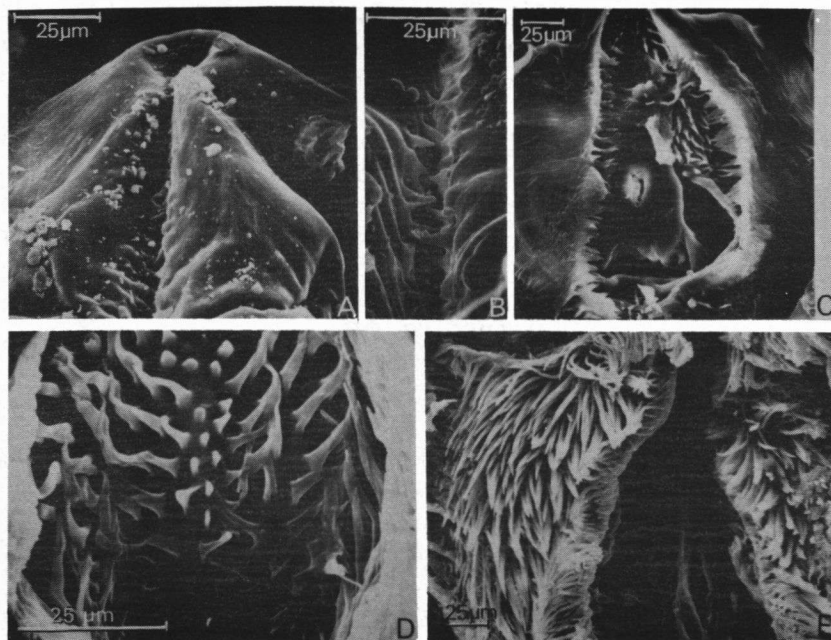


Fig. 9. Scanning electron micrographs of bursae: (A-C) *O. chrysostigma*, showing the longitudinal ventral slit, guarded by spines, and the posterior rounded opening (top of A), which lacks spines; in C the slit has been forced open and a clump of sperm is seen within the bursa; — (D) *O. cancellatum*, forced open and with sperm removed to show the large spines which line the inside; — (E) *N. farinosa*, seen from inside, with the slit opened to show the vagina.

CONCLUSIONS

The following conclusions can be reached from the means of the measurements of sperm volumes (values in brackets are based on the maximum measured sperm volumes):

- (1) A female *N. farinosa* can store up to 122 (272) times more sperm than a female *O. chrysostigma*.
- (2) A female *N. farinosa* stores 17% (7%) of the total sperm in the spermathecae and the remainder in the bursa.
- (3) A female *O. chrysostigma* stores 74% (80%) in the spermathecae and the remainder in the bursa.
- (4) A female *N. farinosa* can store 5-6 (7-8) times more sperm than a male can carry in the secondary genitalia. A well-filled female may therefore carry contributions from 5-6 (7-8) males.

- (5) A female *O. chrysostigma* can store only about 0.16 (0.10) times the amount of sperm carried in the secondary genitalia of a male. A single male may therefore be able to carry enough sperm in the secondary genitalia to fill the stores of 6 (10) females.
- (6) All mature males examined in both species were found to have some sperm in the secondary genitalia. A male *N. farinosa* can carry 3.0 (3.6) times more sperm in the secondary genitalia than a male *O. chrysostigma*. In both species, males are probably able to inseminate females with a fraction of their total store.

DISCUSSION

POSSIBLE COPULATORY MECHANISMS

Only the fourth segment of the penis enters the female vagina during copulation (PFAU, 1971; MILLER, 1982b). In *O. chrysostigma* the fourth segment is about 840 μm long whereas the total length of the vagina is about 1.0 mm in this species. By manually inserting the fourth segment into female and compressing the first segment to inflate the fourth, the flagellum can be seen to become appropriately positioned to enter the bursa through the ventral slit which is about 220 μm long. The distal ends of the medial lobes are of an appropriate breadth also to do so. Compression of the first segment inflates the apical lobe and causes the lateral lobes to swing ventrally, both of which force the penis dorsally towards the bursa. The abdominal rocking movements, observed during copulation in this species (MILLER, 1983), may inflate and deflate the fourth segment causing the flagellum to make thrusting movements upwards in the vicinity of the spermathecal openings (cf. Fig. 1B), without unlocking the grip of the hamules on the female's genital plate (cf. MILLER, 1981). The length and diameter of the flagellum are compatible with its entry into the spermathecae from where it might withdraw sperm on the proximally directed barbs. The flagellum could also be used to pull out sperm from the bursa; the lateral lobes might then trap a sperm ball in the vagina and withdraw it as they closed during decompression. Sperm clumps have been found

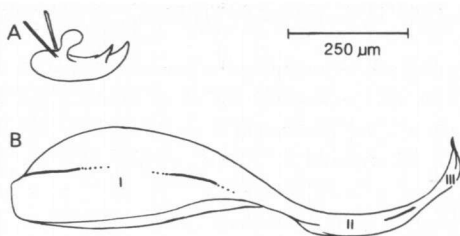


Fig. 10. Sperm clumps of *O. chrysostigma*: (A) dissected from the bursa (note the extensions into the spermathecal ducts); — (B) dissected from the penis (I, II and III represent parts of the clump in the first, second and third segments of the penis respectively).

on the flagella of two males caught in copulation. PFAU (1971) has shown that decompression of the penis of *Orthetrum* releases sperm previously stored in the fourth segment. Insemination may occur therefore only towards the end of copulation when the penis is presumed to be decompressed prior to withdrawal (cf. WAAGE, 1979a, 1984).

In contrast, the fourth segment of the penis of *N. farinosa*, with its large inflatable lobes bearing perpendicular spines and its lateral clicking mechanism (described in MILLER, 1982b), may be used to compress pre-existing sperm during copulation. The medial lobe is appropriately sized to be thrust through the valve into the bursa where it might make room for the male's own sperm, allowing it to be positioned advantageously for fertilising the next batch of eggs.

The males in some species of Zygoptera empty their sperm vesicles completely during copulation (MILLER & MILLER, 1981; WAAGE, 1984) and this is also so in the libellulids, *Celithemis elisa* and *Sympetrum rubicundulum* (WAAGE, 1984). However, in the species described here, sperm has been found in some male's secondary genitalia shortly after copulation without further translocation. They may therefore be able to control the amount of sperm released, or alternatively sometime males may not release sperm at all during copulation, e.g. perhaps when a female's storage organs are already full. One female *N. farinosa* requires sperm from about six males to fill her stores completely. Similarly one female *Sympetrum rubicundulum* is filled by 3-5 males (WAAGE, 1984). In contrast, however, one male *O. chrysostigma* carries enough sperm in the secondary genitalia to fill the stores of up to six females. A territorial male could therefore inseminate a sequence of females in quick succession which would be advantageous if females sometimes tended to synchronize their arrivals at the water, although sperm translocation can be carried out very rapidly. These figures assume sperm density to be the same in males and females, but this may not always be the case.

SPERM ENTRY INTO AND EXIT FROM THE BURSA

Towards the end of copulation sperm is believed to be injected into the bursa through the ventral slit, and the slit probably remains closed in non-copulating females. When pressure is applied to the bursa of *O. chrysostigma* by the surrounding muscles, sperm may be forced into the spermathecae, and also into the vagina through the small posterior expansion of the slit, the aperture of which may be controlled by the transverse cuticular structure and associated muscles (Fig. 8). One preserved female was found to have a thread of sperm running from the bursa through the aperture into an egg micropyle. In *N. farinosa*, the small posterior chamber may be equivalent to the whole bursa of *O. chrysostigma*. This part, together with the two lateral bellows-like extensions could be compressed by muscular action, possibly forcing sperm anteriorly into the remainder of

the bursa, dorsally into the spermathecae and posteriorly into the vagina.

Eggs in the oviduct of *O. chrysostigma* appear to be randomly orientated. As they leave the oviduct, however, and pass through the vagina they become oriented with the micropyle facing anteriorly ready to receive sperm from the posterior end of the bursa. McVEY (1981) found that eggs could be laid at 11 s⁻¹ in *E. simplicicollis* at 38° C, and at 18-28 s⁻¹ in *Plathemis lydia* at 30-34° C. Similar high egg-laying rates are probably widespread in libellulids. They imply that fertilisation can be carried out very rapidly since the vagina is too small to hold more than two or three eggs at one time.

THE SIZE OF THE SPERM STORES

Over one hundred times more sperm can be stored by a female *N. farinosa* than by a female *O. chrysostigma*. Dissection of several other libellulids species has suggested that the amount stored in *O. chrysostigma* and in other *Orthetrum* spp. is unusually small.

Large storage organs carried by females may be beneficial in the following ways: firstly, they may allow females to derive a nutritional gain from excess sperm (cf. WAAGE, 1984). Secondly, they may allow the sperm of several males to be mixed, which may give the fertilised eggs greater genetic variability (WALKER, 1980). Thirdly, they may allow females to store enough sperm to fertilise several clutches of eggs without further mating. *Erythemis simplicicollis*, for example, stores enough sperm for a least six (and sometimes up to 13) clutches (McVEY & SMITTLE, 1984). The dispersal of adult dragonflies occurs mainly in the pre-reproductive phase (CORBET, 1962), but if some mated females made further dispersal flights and located new habitats not frequented by males, they would benefit from large sperm stores. Males in contrast would be expected to remain in regions where females were likely to be abundant, and would be unlikely to undertake solitary dispersal flights after reproductive maturation. My observations suggest that *N. farinosa* is widely distributed in East Africa and that it is found at a greater variety of habitats than *O. chrysostigma* (cf. PINHEY, 1961) which is perhaps consistent with the possession of large stores.

In contrast, small sperm stores might benefit females if they facilitated the more complete removal of sperm by copulating males and if the last male to mate was superior on average to males with which a female had mated previously (WALKER, 1980; WAAGE, 1984). Satellite male *O. chrysostigma* sometimes perch at some distance from the stream, and they occasionally capture and mate with females as they approach the water. Once at the stream such females will normally mate again with territorial males (MILLER, 1983). Hence at the stream a female may exchange the sperm of a satellite for that of a resident, but if no resident is present she can still lay fertile eggs. Females whose eggs are fertilised by residents are likely to benefit for two reasons: firstly they may gain access to

better oviposition sites (WAAGE, 1979b, 1984; FINCKE, 1984) and secondly they are more likely to be guarded during oviposition (cf. McVEY, 1981; MILLER, 1983).

As already explained, male *N. farinosa* are thought to be mainly sperm packers, whereas male *O. chrysostigma* may hook out sperm from females during copulation (MILLER, 1982b). The prolonged copulations of satellite *O. chrysostigma* (mean 1999 s) compared to those of resident males (mean 191 s) might allow satellites to remove more sperm from females (MILLER, 1983), but alternatively it might reflect some resistance to sperm removal on the part of the female (M. Siva-Jothy, pers. comm.). Female *N. farinosa* store about 17% of the sperm in the spermathecae and the remainder in the bursa, and *E. simplicicollis* stores about 10% in the spermathecae (WAAGE, 1984). However, *O. chrysostigma* stores as much as 74% in the spermathecae. In *Brachythemis lacustris* I suggested that the asymmetry of the spermathecal ducts obstructed sperm removal from one spermatheca (MILLER, 1982b); similarly the long narrow spermathecal ducts of *O. chrysostigma* might impede sperm removal. Thus females of this species seem to offer a small readily exchangeable sperm store in the bursa, but retain most of their stored sperm in the spermathecae from which it is withdrawn perhaps with difficulty, possibly only in prolonged copulations with satellites. In contrast the spermathecal store of some other Anisoptera species such as *Sympetrum rubicundulum* (WAAGE, 1984) and *Trithemis arteriosa* (M. Siva-Jothy, pers. comm.) may be more readily accessible to copulating males, and in these the pre-existing sperm may be packed down by the penis before fresh sperm is introduced. Comparisons with other libellulid species can now be made to see if the postulated sperm removal by males generally correlates with the possession of small storage organs in females.

ACKNOWLEDGEMENTS

I am most grateful to OLA FINCKE, MEG McVEY, MICHAEL SIVA-JOTHY and JON WAAGE, all of whom made many valuable comments on an earlier version of this paper. I am also grateful to BARBARA LUKE who took the scanning electronmicrographs.

REFERENCES

- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- FINCKE, O.M., 1984. Sperm competition in the damselfly *Enallagma hageni* Walsh (Odonata: Coenagrionidae): benefits of multiple mating to males and females. *Behav. Ecol. Sociobiol.* 14: 235-240.
- McVEY, M.E., 1981. *Lifetime reproductive tactics in a territorial dragonfly Erythemis simplicicollis*. PhD thesis, Rockefeller Univ., New York.
- McVEY, M.E. & B.J. SMITTLE, 1984. Sperm precedence in the dragonfly *Erythemis simplicicollis* (Say) (Odonata: Libellulidae). *J. Insect Physiol.* (In press).

- MILLER, P.L., 1981. Functional morphology of the penis of *Celithemis eponina* (Drury) (Anisoptera: Libellulidae). *Odonatologica* 10: 293-300.
- MILLER, P.L., 1982a. Temporal partitioning and other aspects of reproductive behaviour in two African libellulid dragonflies. *Ent. mon. Mag.* 118: 177-188.
- MILLER, P.L., 1982b. Genital structure, sperm competition and reproductive behaviour in some African libellulid dragonflies. *Adv. Odonatol.* 1: 175-192.
- MILLER, P.L., 1983. The duration of copulation correlates with other aspects of mating behaviour in *Orthetrum chrysostigma* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 12: 227-238.
- MILLER, P.L. & C.A. MILLER, 1981. Field observations on copulatory behaviour in *Zygoptera*, with an examination of the structure and activity of the male genitalia. *Odonatologica* 10: 201-218.
- PFAU, H.K., 1971. Struktur und Funktion des sekundären Kopulationsapparates der Odonaten (Insecta, Palaeoptera), ihre Wandlung in der Stammesgeschichte und Bedeutung für die adaptive Entfaltung der Ordnung. *Z. Morph. Tiere* 70: 281-371.
- PINHEY, E.C.G., 1961. *A survey of the dragonflies (order Odonata) of eastern Africa*. Brit. Mus., London.
- RESTIFO, R.A., 1972. *The comparative morphology of the penis in the libellulid genera Celithemis, Leucorrhinia and Libellula (Odonata)*. M. Sc. thesis, Ohio St. Univ., Columbus.
- WAAGE, J.K., 1979a. Dual function of the damselfly penis: sperm removal and sperm transfer. *Science* 203: 916-918.
- WAAGE, J.K., 1979b. Adaptive significance of post-copulatory guarding of mates and non-mates by male *Calopteryx maculata* (Odonata). *Behav. Ecol. Sociobiol.* 6: 147-154.
- WAAGE, J.K., 1982. Sperm displacement by male *Lestes vigilax* Hagen (Zygoptera: Lestidae). *Odonatologica* 11: 201-209.
- WAAGE, J.K., 1984. Sperm competition and the evolution of odonate mating systems. In: R.L. Smith, [Ed.], *Sperm competition and the evolution of animal mating systems*. Academic Press, New York-London. (In press).
- WALKER, W.F., 1980. Sperm utilization strategies in nonsocial insects. *Am. Nat.* 115: 780-799.