

**SPERM COMPETITION IN THE FAMILY  
LIBELLULIDAE (ANISOPTERA)  
WITH SPECIAL REFERENCE TO  
*CROCOTHEMIS ERYTHRAEA* (BRULLE) AND  
*ORTHETRUM CANCELLATUM* (L.)**

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Examination of the behavior and of the male and female genital structure of a number of libellulid dragonflies has suggested that some may be defined as "removers" while others are probably "repositioners". The latter are those species which are believed to gain sperm precedence mainly by repositioning sperm already present in the female before inserting their own, thereby gaining a last-in-first-out precedence. The former, on the other hand, tend to spend longer in copulation and possess penes armed with barbed flagella and/or processes. They are thought to remove sperm from females before introducing their own. Some species probably depend on a strategy which may combine repositioning with removing. *Crocotthemis erythraea* and *Orthetrum cancellatum* are examined in this context.

### INTRODUCTION

In any mating system where a female may mate with several males prior to the fertilization of her ova (or per fertilization event) there is a potential for competition between the sperm of different males within a female. This occurs in many insects and the potential is further enhanced by the facts that 1) sperm may live in the female for a long time, so the ejaculates from different males may mix, and 2) there is efficient utilization of sperm for fertilization with the result that the female maintains the maximum number of sperm from the maximum number of ejaculates thereby increasing the chances of ejaculate overlap (PARKER, 1970).

The resultant intense intra-sexual selection pressures on males have probably led to the development of the two major types of sperm competition mechanisms found within the insects: 1) those which allow males to gain sperm precedence by displacing rival gametes during copulation and 2) those which reduce the "effectiveness" of subsequent copulations or copulation attempts (PARKER, 1970).

There is good evidence to suggest that sperm competition by the removal of rival sperm from the female prior to insemination occurs in three zygopteran families: the Calopterygidae (WAAGE, 1979), the Coenagrionidae (MILLER & MILLER, 1981; WAAGE, 1984) and the Lestidae (WAAGE, 1982). Within the Anisoptera, examples of possible mechanisms of sperm competition come from the family Libellulidae. Evidence so far stems from the study of the structures associated with the fourth segment of the secondary genitalia (the penis) of the male, the structure of the female genitalia and, in both *Erythemis simplicicollis* (Say), (WAAGE, 1984 and WAAGE, pers. comm.) and *Celithemis elisa* Hagen (WAAGE, pers. comm.) measurements of sperm volumes before, during and after copulation, and sperm precedence studies involving irradiated males (MCVEY & SMITTLE, 1984).

### **Penis morphology**

The fourth segment (Fig. 1) of the libellulid penis consists of a number of rigid structures as well as non-rigid inflatable sacs or lobes. The occurrence, size and shape of these structures vary among species but they usually consist of: 1) the medial process — a highly variable structure in close association with the medial lobe (e.g. Fig. 2E — the two large hemispherical spiny lobes on the apex of this penis); 2) the medial lobe — a single inflatable dorso-medial structure; 3) the apical lobe — usually a single ventral lobe that varies in its degree of inflatability; 4) the lateral lobes — not usually inflatable, or only slightly so (Fig. 1B).

These structures change their orientation during inflation and are thought to play an important part in the mechanism of sperm competition. Inflation is caused by the action of muscles which are associated with the first segment (PFAU, 1971). These increase the pressure in a closed hydrostatic system within the penis and this causes the apical and medial lobes to move in the dorso-ventral plane around what is probably a hinge of resilin (MILLER, 1982). The medial lobe moves dorsally, whilst the apical lobe travels ventrally. The lateral lobes move out at right angles to these, probably as a result of a similar mechanism (Fig. 1A and B). On the basis of the morphology of the fourth segment it is possible to categorize a number of libellulid species into three penis types:

Type 1 libellulids show only the structures described above, *i.e.*, they possess apical, medial and lateral lobes with the associated inflatable sacs. Examples of species that fall into this category are *Trithemis arteriosa* (Burmeister), *Crocothemis erythraea* and *Nesciothemis farinosa* (Foerster) (Fig. 2).

The distinguishing feature of type 2 libellulids is that they possess paired cornua in addition to the type 1 features. The cornua are rigid, uninflatable structures that arise from the median process and may or may not be associated

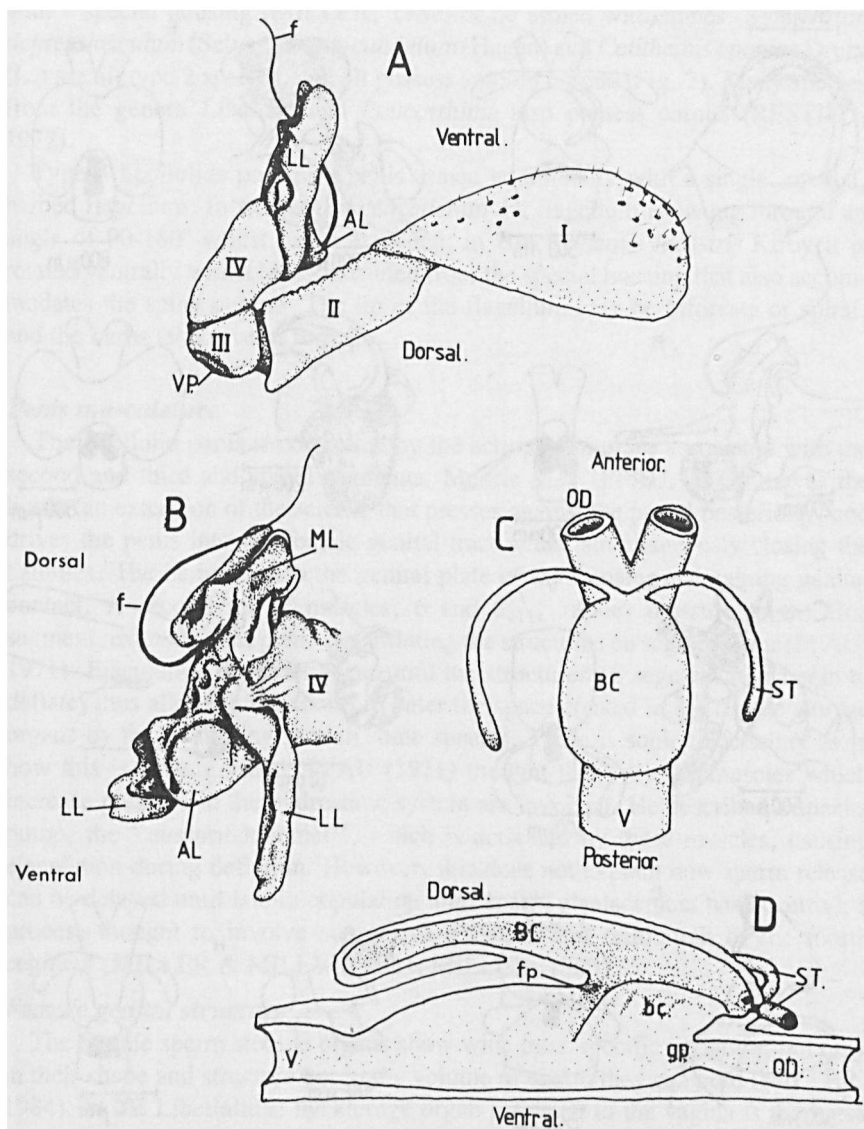


Fig. 1. (A) Lateral aspect of the uninflated secondary genitalia of *Orthetrum chrysostigma*. (B) Lateral aspect of the fourth segment of the inflated penis of *O. chrysostigma*, showing the orientation of the lobes. (C) A stylized diagram of the anisopteran female genitalia in dorsal aspect. (D) A stylized diagram of the anisopteran female genitalia in longitudinal section and viewed in lateral aspect. I = segment 1, II = segment 2, III = segment 3, IV = segment 4, AL = apical lobe, bc = bursa copulatrix, f = flagellum, fp = fertilization pore, gp = gonopore, LL = lateral lobes, ML = medial lobes, OD = oviducts, ST = spermathecae, V = vagina, VP = vesicle pore.

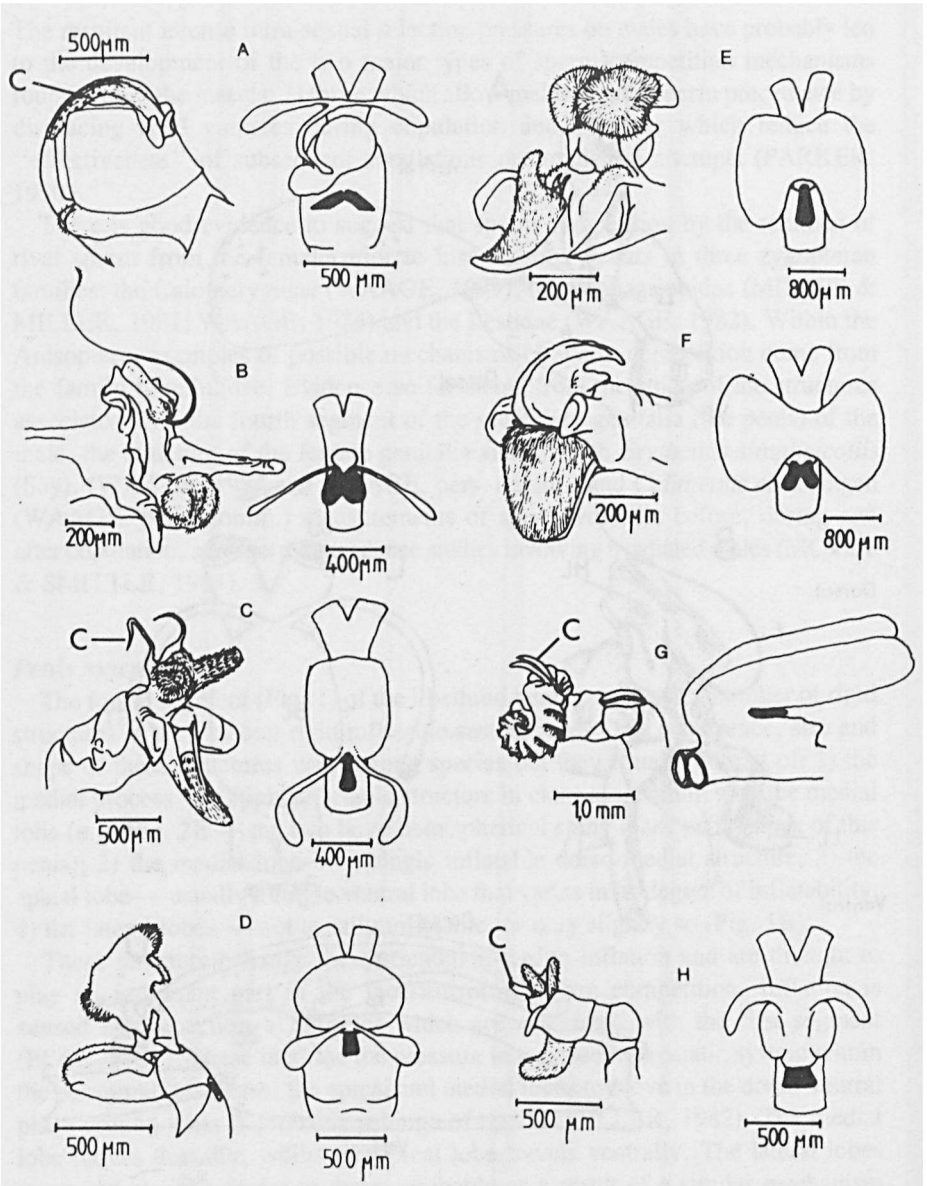


Fig. 2. The fourth segment of the male secondary genitalia and the female genitalia in eight species of Libellulidae. (A) *Brachythemis lacustris* (after MILLER, 1982), male uninflated. (B) *Orthetrum cancellatum*, male inflated. (C) *Sympetrum depressiusculum*, male inflated. (D) *Nesciothemis farinosa* (after MILLER, 1982), male inflated. (E) *Trithemis arteriosa*, male inflated. (F) *Crocothemis erythraea*, male partially inflated. (G) *Sympetrum rubicundulum* (after WAAGE, 1984), male uninflated, female in lateral view. (H) *Celithemis eponina* (male after MILLER, 1981), male inflated. All males in lateral view; all females except (G) are in dorsal view with the two oviducts lying anterior to the sperm storage organs. C = cornua.

with a special housing (MILLER, 1982) or be armed with spines. *Sympetrum depressiusculum* (Selys), *S. rubicundulum* (Hagen) and *Celithemis eponina* Drury (L.) are all type 2 species, and all possess smooth cornua (Fig. 2). Many species from the genera *Libellula* and *Leucorrhinia* also possess cornua (RESTIFO, 1972).

Type 3 libellulids possess a penis armed additionally with a single, medial, barbed flagellum. In *Orthetrum cancellatum* the flagellum is swung through an angle of 90-180° whilst being extended; in *Brachythemis lacustris* Kirby it is rotated ventrally whilst being extruded from the special housing that also accommodates the spiny cornua. The tip of the flagellum may be bifurcate or spiral, and the barbs take several forms.

### ***Penis musculature***

The libellulid penis is controlled by the action of muscles associated with the second and third abdominal segments. Muscle M11 (PFAU, 1971) moves the ligula (an extension of the sclerite that presses against the penis) posteriorly, and drives the penis into the female genital tract whilst simultaneously closing the hamules. The hamules grip the genital plate of the female, maintaining genital contact. A second set of muscles, 6 and 8<sub>111</sub>, applies pressure to the first segment, extending the penis and inflating the structures on segment four (PFAU, 1971). Ejaculation does not occur until the structures on segment four begin to deflate, thus allowing the sperm to enter the space created in the female storage organs by the collapsing sacs in some species. There is some uncertainty as to how this is accomplished. PFAU (1971) thought that only the muscles which increase pressure in the hydrostatic system are involved. He described a special pump, the "ausspritzkammer", which is activated by these muscles, causing ejaculation during deflation. However, this does not explain how sperm release can be delayed until late in copulation after sperm displacement has occurred, a process thought to involve successive deflation and re-inflation of the fourth segment (MILLER & MILLER, 1981; MILLER, 1982).

### ***Female genital structure***

The female sperm storage organs show wide inter-specific variation, not only in their shape and structure but in the volume of sperm they can hold (MILLER, 1984). In the Libellulidae the storage organ proximal to the vagina is the bursa copulatrix. This communicates with the vagina through a large slit-like valve thought to be under muscular control, called the bursa communis, and through a small posterior opening, the fertilization pore.

Associated with the bursa copulatrix are the spermathecae, which are usually smaller than the bursa and in some species have long narrow ducts through which they communicate with it (Fig. 1C and D).

There are generally two recognizable types of female genital morphology; 1) those with separate spermathecae that communicate with the bursa through narrow ducts (e.g. Fig. 2A, B, C, D and H) and, 2) those with a large, lobed, sac-like storage organ usually derived from the spermathecae (Fig. 2E, F and G) and sometimes confluent with the bursa.

### ***Mechanisms for sperm competition***

The structure and proposed operation of the male genitalia and the form of the female genitalia suggest three possible mechanisms by which sperm competition may occur.

**Mechanism 1:** The males in this category are of penis type 1, that is, they possess only the basic complement of lobes; however, the dorso-medial structures are capable of large volume changes during inflation. The females have sac-like sperm storage organs. While in *Crocothemis erythraea* and *Trithemis arteriosa* the spermathecae appear as one large sac, in *Sympetrum rubicundulum* the spermathecae are more distinct but still sac-like (Fig. 2G).

In these species the large, inflatable male structures may displace sperm within the female stores. In *T. arteriosa* (Fig. 2E) the two large, spiny sacs of the male probably thrust upwards in the region of the bursa during inflation and may push sperm aside; in *C. erythraea* the smooth medial lobe rotates through 180° to lie with its tip touching the dorsum of the fourth segment. In *S. rubicundulum* the bifid median process probably uncurls to fill the spermathecae possibly pushing sperm to their distal ends (WAAGE, 1984).

**Mechanism 2:** In *Nesciothemis farinosa*, *Sympetrum depressiusculum* and *Celithemis eponina* the female has a bursa capable of storing a large volume of sperm, as well as spermathecae with narrow ducts, which store less. The penis in these species has no structure that can enter the spermathecae. However, measurements of the fourth segment of the penis, the female genital tract and the bursa suggest that the medial lobe and the median process of the fourth segment could enter the bursa during copulation. Measurements of sperm volumes in the bursa and spermathecae, and in the secondary genitalia of the male in *N. farinosa* (MILLER, 1984) show that the female can store sperm from more than one ejaculate, and the same may be true for *S. depressiusculum* (pers. obs.). Males may therefore use the medial lobes and median process to move or compress existing sperm within the female storage organs. Some of the spines on these structures which point distally or are orientated perpendicularly to the surface in *N. farinosa* and *S. depressiusculum* could act as a sieve, compressing sperm and so allowing fluid to drain past.

The species considered here may be able to remove sperm in addition to repositioning it; in *N. farinosa* there is the so-called "snapping zone" that could entrap sperm as it deflates (MILLER, 1982), and both the other species have spines that could trap and so remove sperm.

**Mechanism 3:** Males of species utilizing this strategy generally possess the type 3 penis. Their flagellum is of the right length and diameter to pass through the long narrow spermathecal ducts that are present in the female. *Brachythemis lacustris* and *Orthetrum cancellatum* (Fig. 2A and B) fall into this group. The males of *B. lacustris* also have long extensible cornua armed with backwardly pointing spines. MILLER (1982) suggests that these remove sperm from the bursa whilst the flagellum enters one of the spermathecal ducts. *O. cancellatum* has no such cornua; in this species the flagellum might remove sperm from the bursa and spermathecae.

So far the suggestion that sperm competition exists in the Libellulidae is based on morphological studies. The exceptions are *Erythemis simplicicollis*, and *Celithemis elisa*. For *E. simplicicollis* MCVEY & SMITTLE (1984) provide direct evidence for a sperm competitive strategy. By using irradiated males, they showed that on average the last male to mate replaced 60-66% of the female's sperm stored from previous matings, and fertilized 97.3% or more of the eggs laid immediately afterwards. From measurements of sperm volumes in the females of both species WAAGE (pers. comm.) found that there was about a 43-50% decrease in total sperm volume from pre- to interrupted-copula specimens in *E. simplicicollis* and a 46% decrease in total sperm volume from pre- to interrupted-copula in *C. elisa*.

The aim of this paper is to provide quantitative evidence for mechanisms I and III by using a technique that assesses the absolute numbers and density of sperm in the female storage organs.

## MATERIALS AND METHODS

*Crocothemis erythraea* and *Orthetrum cancellatum* were studied on a small, shallow, permanent pond of about 50 m<sup>2</sup> surface area, surrounded by sparse *Juncus* scrub, on the Tour du Valat nature reserve in the Camargue, France (43°30'N, 04°30'E), between the 1st and 30th July 1983.

Arriving females were continuously observed and caught after a number of observed copulations; these females were restrained in paper envelopes and placed in a cool box for transportation to the laboratory (ca. 10 mins after capture). Each female was decapitated and the abdomen was dissected under saline to reveal the bursa, the spermathecae and their stored sperm. Accurate drawings were made of the stored sperm mass. Plasticene models were then constructed which allowed the volume of the sperm and seminal fluid contained in these structures to be calculated. The constituent organs were then individually "nipped" off by gently pulling with watch-maker's forceps; care was taken to avoid leakage of sperm. They were then transferred into separate micro tissue-homogenisers that contained from 1 ml to 5 ml of saline depending on the estimated quantity of stored sperm in the organ. The organ was ruptured with a few careful strokes of the plunger which also served to mix the sperm thoroughly in the saline. A sample of this suspension was then introduced onto a standard haemocytometer, and the sperm in a known volume counted. Data collected were used to assess the number and density of sperm in the various parts of the female storage organs.

Male secondary genitalia were prepared for scanning electron microscopy (SEM) by plunging the inflated penis into liquid nitrogen and then freeze-drying it. The penis was inflated by gently squeezing the first segment with blunt forceps. When dry, the penis was mounted and coated with gold in the standard way. Drawings were then made of the inflated penis from the SEM photographs.

Drawings of the female genitalia were made using a binocular dissecting microscope fitted with an eye-piece graticule. Results are given as means  $\pm$  standard deviations.

## RESULTS

*Crocothemis erythraea* is a medium-sized libellulid about 43 mm long and with a wingspan of about 65 mm. Reproductively active males show two main types of behavior when at water — they either guard a territory around a perch site, which is usually a reed near the bank, or they patrol central regions of the pond. Males that show patrolling behavior periodically leave the rendezvous (mating) site, perhaps to thermoregulate on or near the bank (K. WILSON, per. comm. and pers. obs.).

Arriving females attempt to oviposit without mating, but are usually quickly seized by males. There is no apparent courtship; copulation begins immediately, usually occurring in flight and lasting  $7.0 \pm 3.3$  sec ( $n = 44$ ). After the genitalia are disengaged the female flies down to the water surface and begins to oviposit, although she sometimes sits on emergent vegetation for a few seconds before commencing oviposition. The male hovers about 0.5 m behind her, occasionally moving from side to side in an arc about 200 cm above the water. He will attempt to fend off males by displays which may be followed by chases or clashes (FALCHETTI & UTZERI, 1974).

Females that were observed continuously since their arrival at the pond were captured after a known number of observed copulations. The interval between successive copulations was short, the female usually being caught by another male in a matter of seconds after beginning oviposition. However, in some cases, the female was able to oviposit for longer periods; if she did so for more than about 30 seconds she was not examined. Data from measurements of the absolute numbers and density of sperm in the female sperm storage organs are represented in Fig. 3A and B. The absolute number of sperm in the female sperm storage organs (Fig. 3A) increases stepwise with successive copulations ( $r = 0.999$ ). However, the data point for one copulation shows a noticeably small "step" compared to the others; this is probably due to the small sample sizes and the difficulty in accurately measuring the small sperm numbers for this point. The average size of the step between copulations is a possible indication of the size of the ejaculate; this has a value of  $7.9 \times 10^6$  sperm. The increase in sperm numbers with successive copulations suggests that males of *C. erythraea* are adding their sperm to that of previous males, although they might be removing a constant, small quantity of rival sperm at each copulation. The repositioning of rival sperm is the strategy predicted for this species on the basis of morphological studies of the male and female genitalia. As the male has no obvious structures that appear to be capable of sperm removal it is likely that sperm repositioning is the important mechanism in this species.



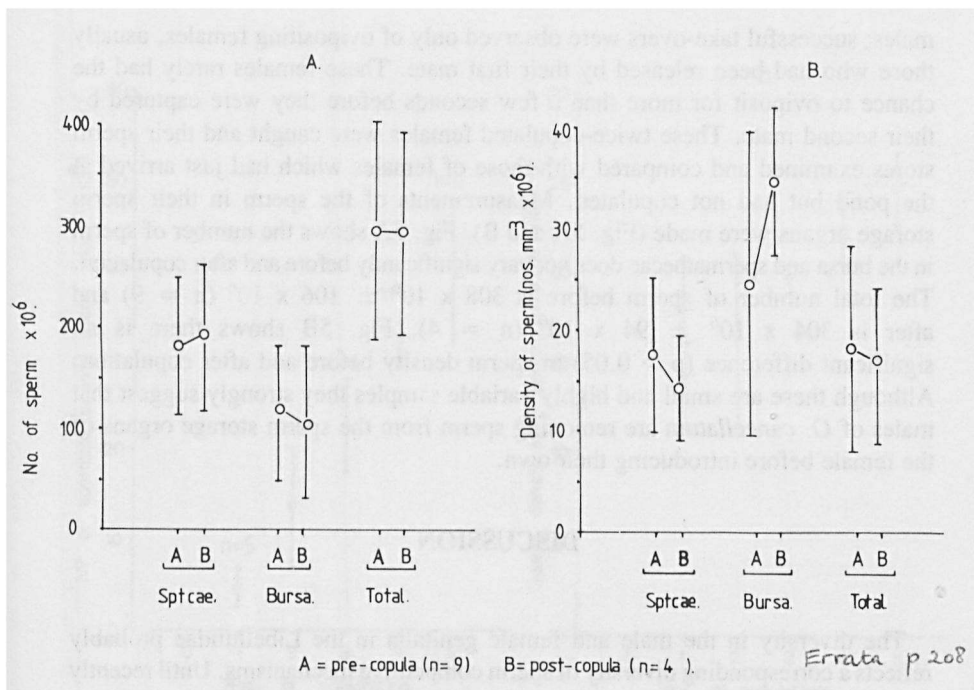


Fig. 3. (A) The relationship between the absolute number of sperm in the female sperm store and the number of times the female has copulated in *Crocothemis erythraea* ( $r = 0.999$ ). (B) The relationship between the density of sperm in the female sperm storage organs and the number of times the female has copulated in *C. erythraea*. Means  $\pm$  SD.

The density of sperm in the female sperm store (*i.e.* the numbers per unit volume) only increases after 3 copulations. The approximate point of inflection on Fig. 3B corresponds to an absolute sperm number of about  $22.4 \times 10^6$  sperm (from Fig. 3A). On average the storage organ cannot expand beyond a volume of about  $1.6 \text{ mm}^3$  (Fig. 4) and the smallest number of sperm that can fill this volume after successive copulations is between  $25 \times 10^6$  and  $30 \times 10^6$  sperm. This suggests it is mainly the inelastic properties of the storage organ wall that are responsible for the increase in sperm density. However, any decrease in density of sperm must be caused by a reduction in the volume of seminal fluid accompanying that sperm, or the sperm already in the storage organ. How this concentration is brought about is unclear.

*Orthetrum cancellatum* is a libellulid about 50 mm long with a wingspan of about 77 mm. Males wander up and down the edges of bodies of water whilst searching for females. No territorial behavior was observed. Arriving or ovipositing females are grabbed as soon as they are spotted and copulation usually begins immediately, but occasionally a pair flies off in tandem. They usually settle during copulation; this lasts much longer than in *Crocothemis erythraea*, averaging  $82.1 \pm 66.1$  sec ( $n = 11$ ). After copulation the female begins to oviposit, often after a short period of sitting, with her mate in close attendance. Pairs in copulation and ovipositing females are frequently disturbed by other

males; successful take-overs were observed only of ovipositing females, usually those who had been released by their first mate. These females rarely had the chance to oviposit for more than a few seconds before they were captured by their second mate. These twice-copulated females were caught and their sperm stores examined and compared with those of females which had just arrived at the pond but had not copulated. Measurements of the sperm in their sperm storage organs were made (Fig. 5A and B). Fig. 5A shows the number of sperm in the bursa and spermathecae does not vary significantly before and after copulation. The total number of sperm before is  $308 \times 10^6 \pm 106 \times 10^6$  ( $n = 9$ ) and after is  $304 \times 10^6 \pm 94 \times 10^6$  ( $n = 4$ ). Fig. 5B shows there is no significant difference ( $p > 0.05$ ) in sperm density before and after copulation. Although these are small and highly variable samples they strongly suggest that males of *O. cancellatum* are removing sperm from the sperm storage organs of the female before introducing their own.

## DISCUSSION

The diversity in the male and female genitalia in the Libellulidae probably reflects a corresponding diversity of sperm competitive mechanisms. Until recently there was only quantitative evidence for the mechanism in *Erythemis simplicicollis* and *Celithemis elisa*, species in which the males appear to remove sperm from the female before insemination (MCVEY & SMITTLE, 1984; WAAGE, 1984 and WAAGE, pers. comm.). The results of the present work suggest that the

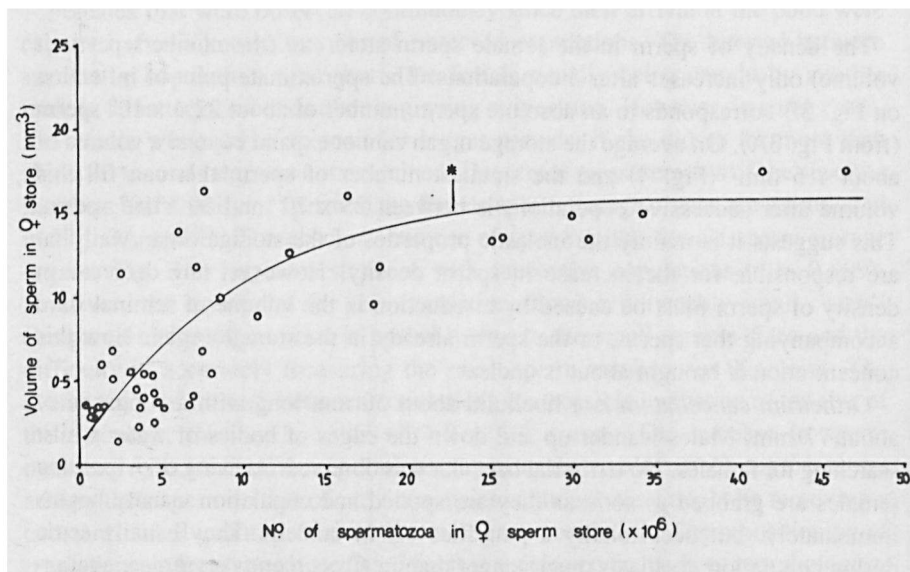


Fig. 4. The relationship between the volume of stored ejaculate in the female and the number of sperm in that store in *Crocothemis erythraea*. The vertical bar corresponds to the average number of sperm after three copulations (see text for explanation).

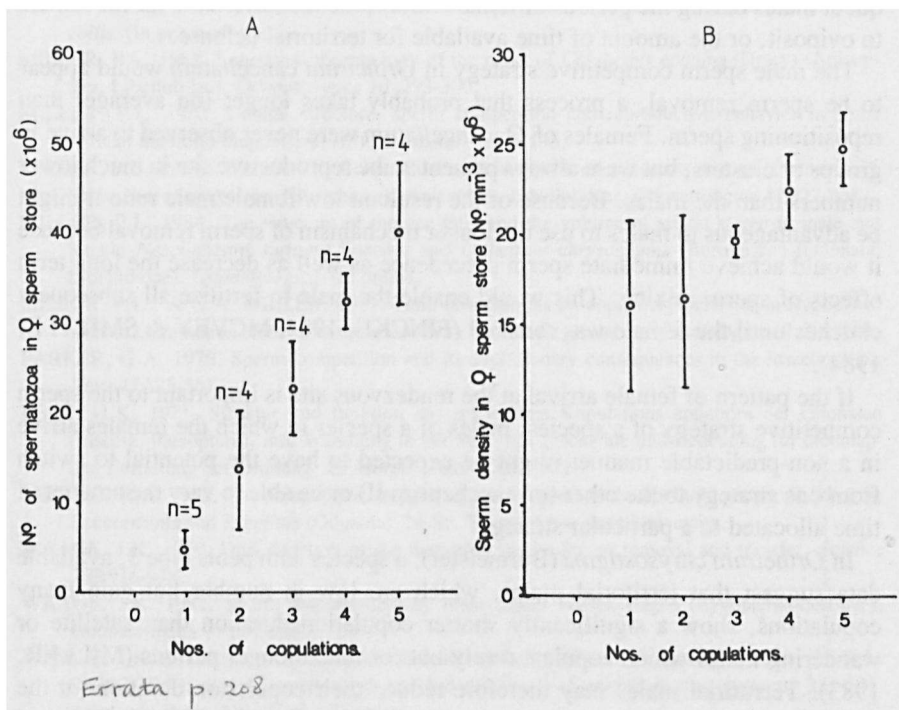


Fig. 5. (A) The relationship between the number of sperm in the female sperm storage organs before copulation and after two successive copulations in *Orthetrum cancellatum*. (B) The relationship between the density of sperm in the female sperm storage organs before copulation and after two successive copulations in *O. cancellatum*. Means  $\pm$  SD.

males of *Crocothemis erythraea* add their sperm to that of rival males. These males are possibly repositioning rival sperm whilst placing their own in a position that enables the latter to fertilize most of the clutch laid soon after copulation. However, the possibility that males may remove a small but constant quantity of sperm at each successive copulation cannot be excluded on the basis of the data presented. The large medial lobe may be responsible for displacing sperm as it swings upwards (Fig. 2F).

Data from *Orthetrum cancellatum* suggest that males of this species remove rival sperm before introducing their own. The long thin flagellum is of the right dimensions to enter the bursa and spermathecae, and is well equipped to "hook" sperm out of these structures with its terminal barbs.

These different genital structures are therefore probably responsible for different mechanisms of sperm displacement. It is possible that these different mechanisms are in some way related to the arrival pattern of the reproductively active female population at the reproductive site. Females of *C. erythraea* arrive at the rendezvous site in what appear to be synchronized groups (pers. obs.); the result is a sudden increase in the female/male ratio at the pond. By repositioning rather than removing sperm, the males of this species can spend a relatively short time in copulation, thereby increasing either the rate at which they encounter subse-

quent mates during the periods of female influx, the time available for the female to oviposit, or the amount of time available for territorial defense.

The male sperm competitive strategy in *Orthetrum cancellatum* would appear to be sperm removal, a process that probably takes longer (on average) than repositioning sperm. Females of *O. cancellatum* were never observed to arrive in groups or clusters, but were always present at the reproductive site in much lower numbers than the males. Because of the resultant low female/male ratio it might be advantageous to males to use the longer mechanism of sperm removal because it would achieve immediate sperm precedence as well as decrease the long term effects of sperm mixing. This would enable the male to fertilize all subsequent clutches until the female was remated (FINCKE, 1984; MCVEY & SMITTLE, 1984).

If the pattern of female arrival at the rendezvous site is important to the sperm competitive strategy of a species, males of a species in which the females arrive in a non-predictable manner might be expected to have the potential to switch from one strategy to the other (*cf.* mechanism II) or be able to vary the amount of time allocated to a particular strategy.

In *Orthetrum chrysostigma* (Burmeister), a species with penis type 3, available data suggest that territorial males, which are low in number but gain many copulations, show a significantly shorter copulation duration than satellite or wandering males which copulate rarely but for much longer periods (MILLER, 1983). Territorial males may therefore reduce their copulation duration (at the expense of thorough removal) and thereby increase their female encounter rate and/or their defense of territory. The less successful wandering and satellite males, on the other hand, may copulate for a long time in order to maximize their sperm's precedence by thoroughly removing the sperm of other males.

In conclusion there appear to be several mechanisms of sperm competition within the Libellulidae and these mechanisms can be predicted to some extent by examination of the male and female genitalia. There may also be a correlation between the mechanisms employed and the timing of female arrival in *Crocothemis erythraea* and *Orthetrum cancellatum*.

#### ACKNOWLEDGEMENTS

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#### REFERENCES

- FALCHETTI, E., & C. UTZERI. 1974. Preliminary observations on the behavior of *Crocothemis erythraea* (Brulle). *Fragm. ent.* 10 :295-300.
- FINCKE, O.M. 1984. Sperm competition in *Enallagma hageni*. *Behav. Ecol. Sociobiol.* (in press).

- MCVEY, M.E., & B. SMITTLE. 1984. Sperm competition in the libellulid *Erythemis simplicicollis*. (In preparation).
- MILLER, P.L. 1981. Functional morphology of the penis of *Celithemis eponina* (Drury) (Anisoptera: Libellulidae). *Odonatologica* 10 :293-300.
- MILLER, P.L. 1982. Genital structure, sperm competition and reproductive behavior in some African libellulid dragonflies. *Adv. Odonatol.* 1:175-193.
- MILLER, P.L. 1983. The duration of copulation correlates with other aspects of mating behavior in *Orthetrum chrysostigma* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 12:227-238.
- MILLER, P.L. 1984. The structure of the genitalia and the volume of sperm stored in male and female *Nesciothemis farinosa* Foerster and *Orthetrum chrysostigma* (Burmeister) (Odonata: Libellulidae). *Odonatologica*. (In press).
- MILLER, P.L., & C.A. MILLER. 1981. Field observations on copulatory behavior in Zygoptera, with an examination of the structure and activity of the male genitalia. *Odonatologica* 10 :201-218.
- PARKER, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45:525-567.
- 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.
- RESTIFO, R.A. 1972. The comparative morphology of the penis in the libellulid genera *Celithemis*, *Leucorrhinia* and *Libellula* (Odonata). M.Sc. Thesis, Ohio State University.
- WAAGE, J.K. 1979. Dual function of the damselfly penis: Sperm removal and transfer. *Science* 203:916-918.
- 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*. 251-290. Academic Press, New York. (In press).

## ERRATA

Page 17. Replace figure captions as follows:

*Upper figure:*

Fig. 2. Size of female and male *Mecistogaster linearis*. Correlations of wing length and abdomen length are 0.97 for females and 0.56 for males.

*Lower figure:*

Fig. 1. Size of male and female *Megaloprepus coerulatus*. Correlations of wing length and abdomen length are 0.96 for females and 0.95 for all males. Sample sizes are  $n = 10$  for territorial males,  $n = 25$  for non-territorial males, and  $n = 19$  for females. Mean sizes are shown with 95% confidence intervals.

Page 203. Replace figure caption with:

Fig. 5. (A) The relationship between the number of sperm in the female storage organs before copulation and after two successive copulations in *Orthetrum cancellatum*. (B) The relationship between the density of sperm in the female sperm storage organs before copulation and after two successive copulations in *O. cancellatum*. Means  $\pm$  SD.

Page 205. Replace figure caption with:

Fig. 3. (A) The relationship between the absolute number of sperm in the female sperm store and the number of times the female has copulated in *Crocothemis erythraea* ( $r = 0.999$ ). (B) The relationship between the density of sperm in the female sperm storage organs and the number of times the female has copulated in *C. erythraea*. Means  $\pm$  SD.