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GENITAL STRUCTURE, SPERM COMPETITION AND REPRODUCTIVE BEHAVIOUR IN SOME AFRICAN LIBELLULID DRAGONFLIES

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The structure of the penis (vesica spermalis) and of the female genital tract are described in two African libellulids. The 4th segment of the penis of *Brachythemis lacustris* possesses a flagellum and paired cornua which are retracted inside a specialized chamber at rest. On inflation they are shot abruptly out of the chamber, and the flagellum is seen to possess a pair of large barbs while the cornua have complex laterally- and proximally-directed bristles. The female genital tract has an asymmetrically disposed spermathecal system which may permit the flagellum to reach only one spermatheca and withdraw sperm from it during copulation. In *Nesciothemis farinosa* the penis bears large inflatable sacs armed with numerous bristles some of which are serrated and dentate. In the female the spermathecae are inaccessible to the penis, but sperm from previous males may be packed down or removed from the bursa during copulation. *B. lacustris* copulates rapidly on the wing and the male guards the female closely during oviposition. *N. farinosa* also copulates rapidly but on the ground and guarding during oviposition is weak and short-lived. The possible relationships between copulation duration, intensity of guarding and sperm competition are discussed.

INTRODUCTION

WAAGE (1979a, 1982) has shown that during copulation males of *Calopteryx maculata* and *C. dimidiata* remove the sperm of previous males from the female's reproductive tract before they introduce their own, and similar behaviour may occur in many other damselflies (e.g. MILLER & MILLER, 1981). The ligula, a development of the second abdominal sternite forms the penis in Zygoptera, and it is armed with various proximally directed bristles, hooks and barbed horns which probably aid in sperm extraction from the bursa copulatrix and spermatheca. The anisopteran penis is not homologous with that of Zygoptera, and it has evolved as an anterior extension of the vesica spermalis on the third sternite. It is a complex, four-segmented structure dependent on muscular and hydrostatic mechanisms for its functioning (PFAU, 1971; MILLER, 1982), and in Libellulidae, the distal or fourth segment of the penis bears hooks, bristles and inflatable structures. WAAGE (1982) has discussed the possible occurrence of sperm competition in Anisoptera by sperm extraction, as in Zygoptera, or by packing down previously deposited sperm, either of which would allow a copulating male's sperm to fertilize most of a current batch of eggs (cf. PARKER, 1970, 1979).

The genital structure and copulatory activity of two African libellulids are described here, and tentative conclusions are discussed about the types of sperm competition which may occur in each. The functional morphology and evolution of the male secondary genitalia of Odonata have been discussed by PFAU (1971) who has surveyed the older literature, but anisopteran genital structure and reproductive behaviour merit a fresh examination in the light of recent appreciation of sperm competition in many insects (cf. BLUM & BLUM, 1979; WAAGE, 1982).

STUDY AREA

Dragonflies were observed and collected at Hunter's Lodge, 160 km S.E. of Nairobi, Kenya, between April and June, 1981. The site was visited on 17 non-consecutive days, on ten of which observations were maintained from dawn to dusk. Sunset on 11th May was at 18:25 hr, and sunrise at 06:26 hr. The site consists of a number of springs from which a stream ca. 2 m wide, arises and flows along the margin of a small patch of *Acacia xanthophloea* forest. One side of the stream is open with long grass and scattered bushes of *Commiphora* and *Acacia tortilis* growing nearby. Less than 1 km from the springs, the stream is dammed to form a lake, ca. 300 X 80 m in extent.

SPECIES EXAMINED

Nesciothemis farinosa Foerster was one of the commonest libellulids present. It occurred in all parts of the habitat, but was most abundant along the stream where its behaviour was observed. *Brachythemis lacustris* Kirby was found to be common only along a 40 m strip of lake side bordered by short grass, and in an area immediately inland. Counts of perched *B. lacustris* suggested that the total population in this part was ca. 100 individuals, and only a few solitary individuals were seen elsewhere. Some other species present are mentioned below. Behaviour was observed with field glasses and photographed, while field notes were made with the aid of a pocket tape recorder. Genital structure was examined in fresh specimens, and scanning electron-micrographs were made with a Philips PSEM 500. The terminology of the penis follows that given in RESTIFO (1972), (see also PFAU, 1971), but the homologies of some parts are uncertain. Further details of reproductive behaviour and daily cycles of activity will be given elsewhere.

THE STRUCTURE OF THE MALE SECONDARY GENITALIA

The fourth, most distal, segment of the libellulid penis is flexed through 180° and thus faces posteriorly with its dorsal surface occupying the lowest position, both at rest and when in action. It therefore has the same orientation as the female during copulation. In the following account, the terms dorsal and ventral are used in their strict anatomical sense.

Segment 1 of the penis is a swollen structure containing the sperm store and a separate hydrostatic reservoir (part of the Schwellkörper of PFAU, 1971). The fluid contained in the reservoir is not in immediate contact with the haemolymph, and it can maintain a pressure different from that of the rest of the body cavity. However, when Rhodamine B was added to the haemolymph of *Libellula quadrimaculata*, it was found to permeate the penis rapidly, indicating a ready exchange of materials between the two compartments. Pressure applied to segment 1 extends segments 3 and 4 on 2, inflates structures in segment 4, and sometimes expels sperm from the sperm opening in segment 4 (WAAGE, 1982; MILLER, 1982). Compression and decompression of segment 1 are brought about in life by the antagonistic actions of muscles 6 and 8_{III} which cause a hardened posterior sclerite (part of sternite III) to swing anteriorly into the compressible part of segment 1 of the penis (Fig. 1) (PFAU, 1971). Segment 2 of the penis bears a distal blunt spur on which the ligula engages causing that segment to be flexed ventrally and the distal part of the penis to be driven posteriorly into the vagina during copulation. The ligula is controlled by muscles 11 acting between the anterior and posterior frames. Segment 3, which in *Brachythemis* is fused to 2, contains a valved slit through which sperm are introduced from the primary genitalia at the posterior end of the abdomen (sperm translocation). Segment 4 has a specialized sperm pump (Ausspritzkammer) which, according to PFAU (1971), ejects sperm

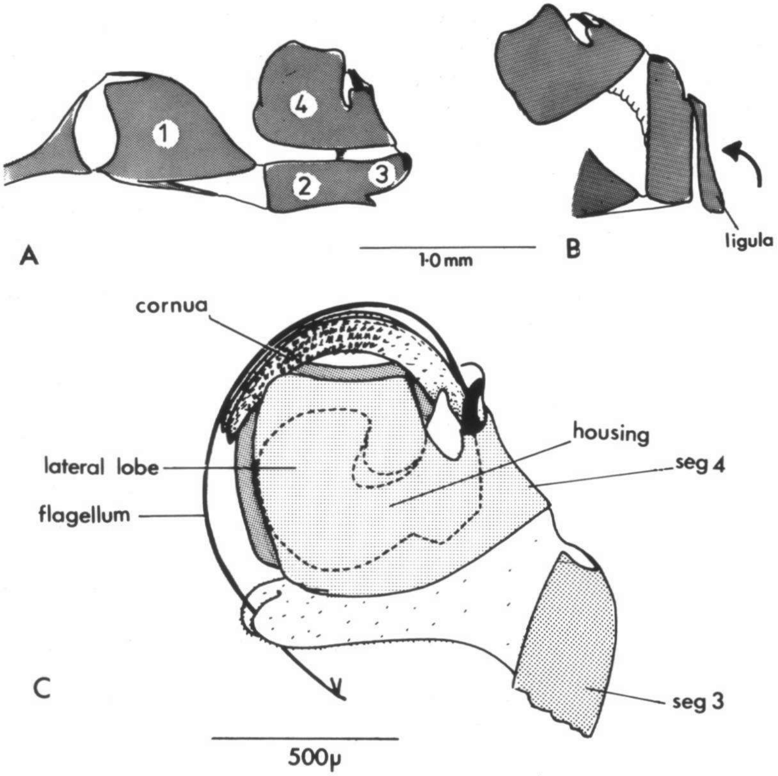

Fig. 1. ***Brachythemis lacustris.*** **Penis (vesica spermalis) viewed from the left side (anterior to the right; ventral upwards: (A) resting position: 1-4, the four segments of the penis; (B) the ligula has swung ventrally, flexing segments 2+3 and forcing the penis posteriorly, while segment 4 has been extended hydrostatically, as occurs at the start of copulation; (C) segment 4 of the penis enlarged: it has been inflated by applying pressure to segment 1, and the flagellum and paired cornua have been expelled from the housing.**

elastically on decompression, and sucks sperm in on compression.

Brachythemis lacustris. Segment 4 comprises two flattened lateral lobes which meet distally forming a wedge, which may facilitate entry into the genital opening of the female (Fig. 1). In fresh specimens it could be inflated slowly by compressing segment 1 between forceps operated with a screw clamp. Full inflation probably does not occur normally until after entry into the female tract. Gradual inflation first separated the lateral lobes so that they became parallel to each other. (In *B. leucosticta* whose penis is similar in structure, they separate by 90° to each other and may force the walls of the female tract apart.) The apical lobe, an unpaired sac with a bilobed tip, then extended ventrally from between the lateral lobes as it became inflated, an action which would push the penis dorsally in the female. Simultaneously the flagellar housing, a dark and hardened C-shaped structure lying between the lateral lobes, swung upwards on a dorsally located hinge through about 10°. This permitted the flagellum and cornua to shoot out rapidly from the upper opening of the housing (Fig. 1C). The flagellum consists of two whip-like structures, 1100 μm long, each with a large barb near its tip, but bound together by a single membrane (Fig. 2). The two crescent-shaped cornua are longitudinally inextensible structures but are capable of some lateral inflation. At rest the flagellum and cornua remain within the housing both being attached to a thick-walled rubbery cuticular tongue. The tongue which is attached to the mid-point of the C-shaped housing, was extended during experimental inflation allowing the flagellum and cornua to be expelled from the housing. The mechanism is thought to depend on hydrostatic inflation of a cuticular bag which occupies the housing. Part of the bag wall is formed by the tongue, and the suddenness of the expulsion is due to instability of the tongue as it rides over its attachment at the mid-point of the housing. Small changes in pressure applied to segment 1 were found to cause the flagellum and cornua alternately to be expelled rapidly and then retracted into the housing, the latter being due to the resilient pro-

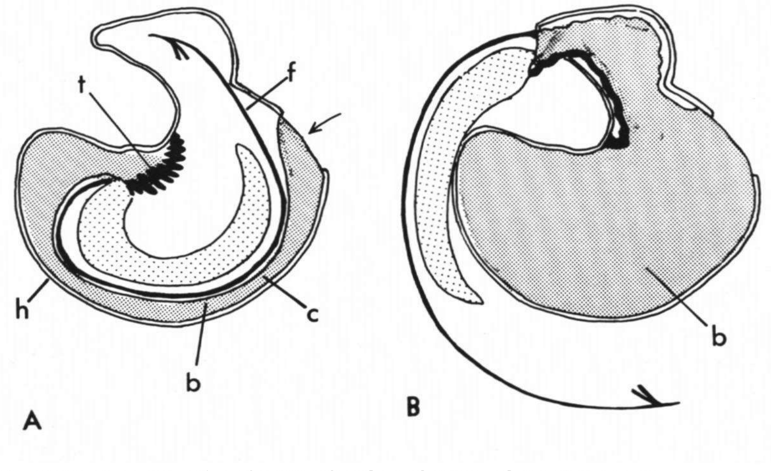

Fig. 2. Diagram representing the postulated mechanism of expulsion of the cornua and flagellum from the housing in the penis of *Brachythemis lacustris*: (A) at rest, the flagellum (f) and cornua (c) are within the housing (h) and the elastic tongue (t) is much folded; (B) expulsion of the cornua and flagellum as a result of filling up the bag (b) with liquid. Arrow in (A) indicates where liquid enters.

perties of the tongue. Examination of the tongue in ultra-violet light showed it to fluoresce at 420 nm, and it stained intensely with methylene blue, properties which suggest that it is formed partly from resilin.

The flagellum bears a pair of barbs and is otherwise smooth, but the cornua carry many flattened bristles, 10-15 μm long with from 1 to 7 spines on each (Fig. 3). The bristles are orientated mainly across the long axis of each cornu, but they point proximally in the distal part. Smaller bristles occur on the membranous cuticle surrounding the sperm opening and on the apical lobe. The inner faces of the lateral lobes also bear small bristles, thinly scattered.

Nesciothemis farinosa. Segment 1 of the penis (of this species) is relatively large. The estimated volume of 0.538 mm^3, compared to 0.125 mm^3 in *Orthetrum chrysostigma*, a libellulid of similar size,

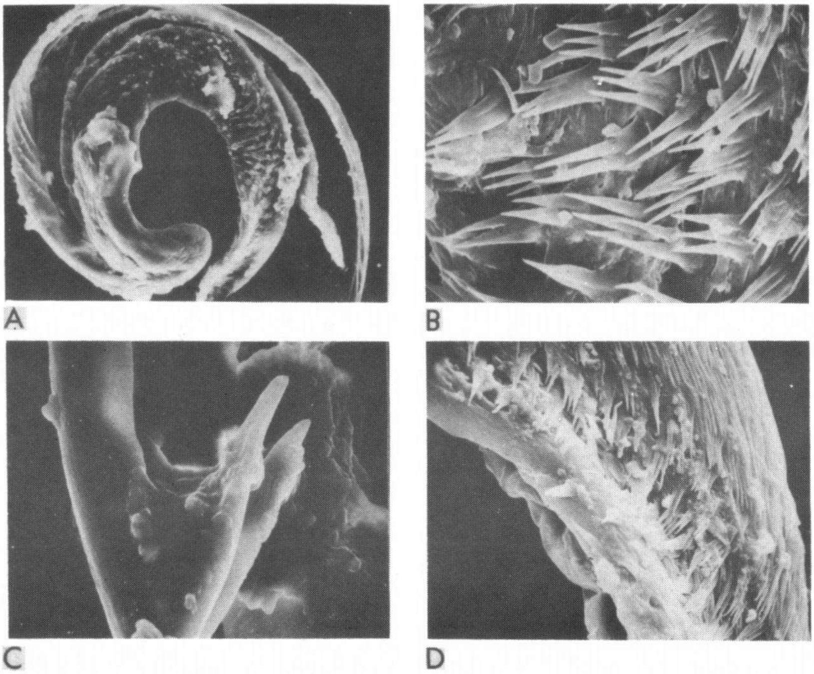

Fig. 3. Scanning electronmicrographs of the cornua and flagellum removed from their housing in the 4th segment of the penis of *Brachythemis* spp : (A) the flagellum and cornua of *B. leucosticta* attached to the tongue; (B) part of (A), enlarged to show bristles orientated at right-angles to the length of a cornu; (C) the two flagellar barbs in *B. lacustris*; (D) part of a cornu of *B. lacustris* showing the bristles. Horizontal scale, (A) 200 μm; (B) 25 μm; (C) 50 μm; (D) 50 μm.

and to 0.1175 mm^3 in *B. lacustris*. The large size of the segment in *N. farinosa* is correlated with the greater volume of inflatable structures on segment 4, and it may also allow the penis to carry a larger sperm store (see below).

Compression of segment 1 caused the upper (dorsal) part of the

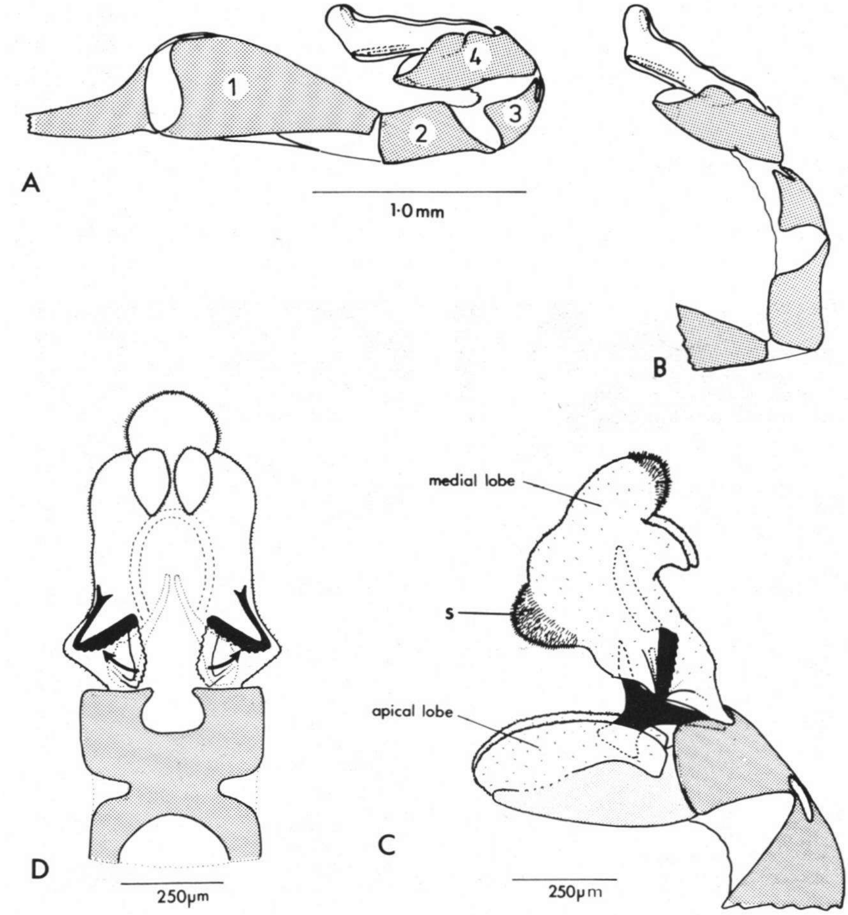

Fig. 4. *Nesciothemis farinosa*. Penis (vesica spermalis) viewed from the left side (A–C) (anterior to the right; ventral side upwards), and (D) dorsally: (A) resting position; 1-4, the four segments of the penis; (B) segments 2-4 have been swung ventrally by action of the ligula (cf. Fig. 1) and segment 4 has been extended hydrostatically; (C) segment 4 of the penis enlarged. It has been inflated by pressure applied to segment 1, causing the apical and medial lobes to expand; (S) indicates the region of the medial lobe which snaps outwards; (D) dorsal view of the 4th segment of the penis, showing the medial lobe with the serrated cuticular bars (cornua?) in black clicked out as in the fully inflated state (arrows).

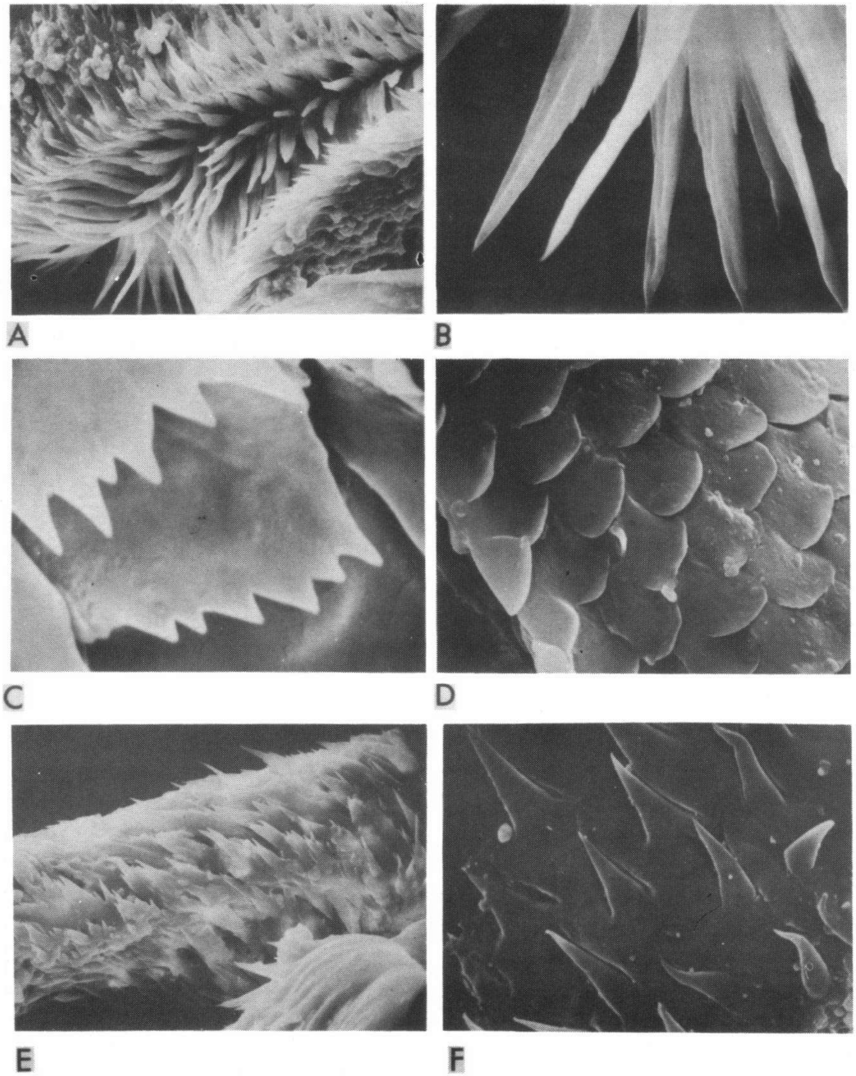

Fig. 5. Scanning electronmicrographs of the 4th segment of the penis of *Nesciothemis farinosa:* (A) the snapping zone on the lower side of the medial lobe, folded inwards; (B) serrated bristles from the snapping zone; (C) dentate scales from near the snapping zone; (D) tile-like scales from the proximal part of the medial lobe; (E) serrated bristles from the apical lobe; (F) spines from the inside of the lateral lobe. Horizontal scale: (A) 100 μm; (B) 25 μm; (C) 6 μm; (D) 25 μm; (E) 50 μm; (F) 25 μm.

segment to swing upwards through about 60° (Fig. 4), while the paired apical lobes on the ventral part were inflated, and the lateral lobes, attached to the apical lobes, were twisted laterally. The upper medial lobe then expanded into a large sac bearing two blunt inner lobes which projected anteriorly (Fig. 4C). In the uninflated state the medial lobe is highly infolded, and during inflation a region on its lower (ventral) surface snapped outwards, while on decompression it snapped inwards. This region bears longer bristles than are found elsewhere (see below). Simultaneously two serrated cuticular bars attached laterally to the medial lobe (possibly representing the cornua), clicked outwards extending the lobe sideways (Fig. 4D). In the final stage of inflation, a central region between the apical and medial lobes was expanded. With decompression the structures collapsed and folded elastically in the reverse order. Small pressure changes caused the bristly region and the bars on the medial lobe to snap in and out.

All the inflatable parts of segment 4 bear bristles. Those on the snapping region of the medial lobe are 30-40 μm long, flattened and bear many minute serrations, while others are broader and dentate. There is a gradation from simple tile-like scales to more distally located slender serrated spines (Fig. 5). A prominent crown of unserrated bristles, 20-30 μm long, occurs on the upper part of the medial lobe, while elsewhere most bristles are smaller, being 10-20 μm in length. When the lobes were inflated the bristles tended to stand perpendicular to the surface.

STRUCTURE OF THE FEMALE GENITALIA

The libellulid female genital tract comprises a vagina communicating anteriorly with paired oviducts and dorsally through a valved entrance with the bursa copulatrix. Paired spermathecae arise from the bursa, usually through a narrow duct (TILLYARD, 1917; ASAHINA, 1954). Several muscles run from a group of sclerites on the posterior dorsal region of the vagina and insert onto the body wall. In living specimens the muscles were seen to be active, and in *B. leucosticta* the activity increased greatly when a penis was inserted into the vagina, causing vigorous antero-posterior oscillatory movements of the whole tract at up to 5 Hz. This observation suggests there is active participation by the female during copulation.

In *B. lacustris* a common spermathecal duct arises at the posterior end of the bursa: it gives rise to a small dilated sac, 100 μm in diameter, before continuing anteriorly along one side of the bursa to which it is firmly bound (Fig. 6A). In 10 of 12 females examined, the common duct ran to the left of the bursa, and in 2, to the right. The common duct gives rise to right and left spermathecal ducts at a T-junction. This junction was found to be asymmetrical in both teneral and adult females. This means that when the common duct runs to the left of the bursa it curves smoothly into the right spermatheca, but communication with the left spermatheca is via a hair-pin

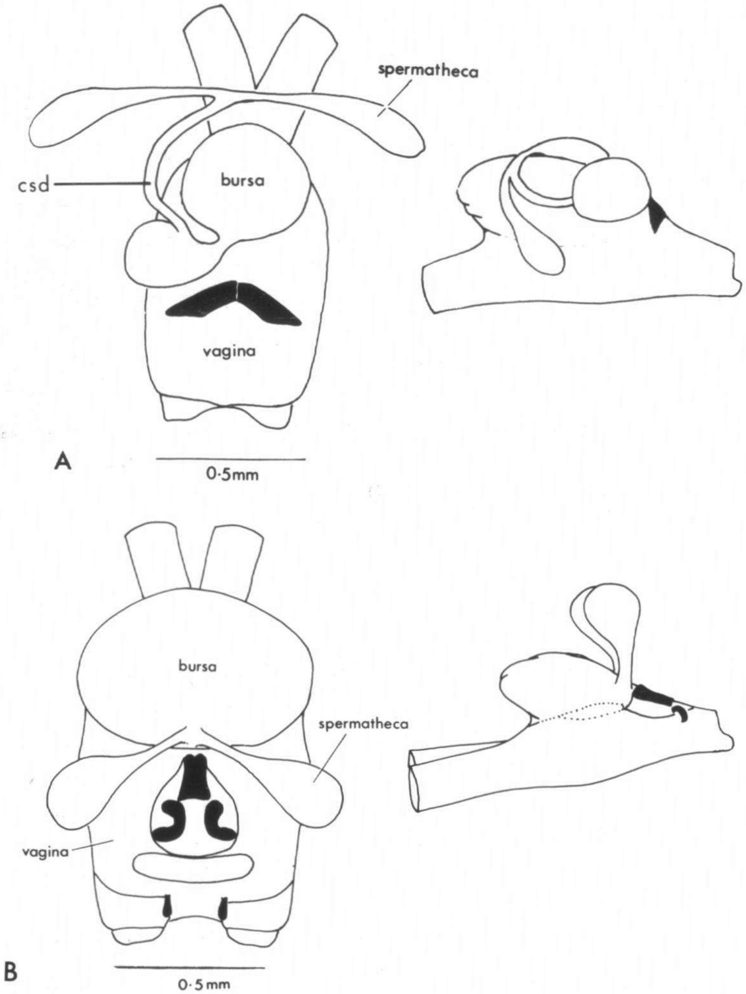

Fig. 6. Dorsal and lateral views of the genital tract of *Brachythemis lacustris* (A) and *Nesciothemis farinosa* (B). csd, common spermathecal duct.

bend. The significance of this asymmetry, which does not occur in *B. leucosticta* or in other species examined, is discussed below.

In *N. farinosa* the paired spermathecae arise separately from the posterior part of the bursa through narrow ducts (Fig. 6B).

POSSIBLE COPULATORY EVENTS AND MECHANISMS

Dragonflies caught in copula were found always to disengage their genitalia, and copulatory behaviour could not be induced in captive individuals. The following account is therefore speculative and based on genital structure and on attempts to simulate copulation by inserting a penis into a living intact or dissected female, and then inflating it. Only segment 4 is anatomically capable of entering the female tract.

In *B. lacustris* segment 4 of the penis can readily be inserted into the vagina but it is probably too large to enter the bursa. The anterior end of the bursa and vagina lie about 900 µm from the genital opening while segment 4 of the penis is about 800 µm long. Inflation of segment 4 presses it dorsally in the vagina and I suggest that further inflation causes the cornua to shoot out into the bursa whose entrance lies just above the mid-region of segment 4 (Fig. 7). Similarly the flagellum may enter the spermathecal duct. Repeated exten-

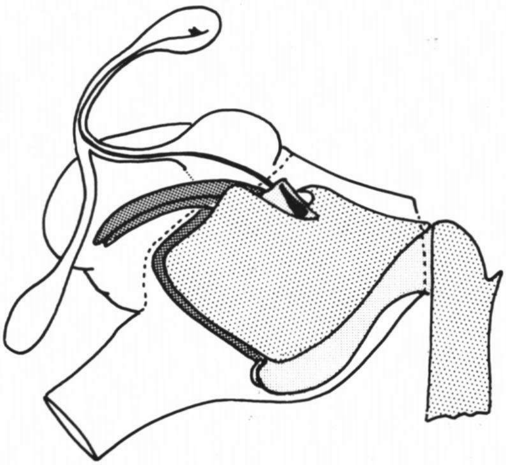

Fig. 7. The suggested positioning of the 4th segment of the penis of *Brachythemis lacustris* in the female tract during copulation. The cornua are shown entering the bursa, and the flagellum is extended into the common spermathecal duct, which passes to the left of the bursa, and then into the right spermatheca.

sion and retraction of the bristly cornua might sweep up sperms from the bursa whose diameter is about 250 μm, while a straightened cornu is 500 μm long. In a female with its common spermathecal duct passing to the left of the bursa (as in 83% of those examined), the flagellum could pass smoothly into the right spermatheca from where its barbs might withdraw sperm. However, it could probably not negotiate the hair-pin bend and enter the left spermatheca. The asymmetry of the female system may therefore prevent both spermathecae from being emptied of sperm by the flagellum, and could thus permit the female to retain some sperm from previous copulations.

Attempts to simulate sperm removal in *B. leucostica* were not successful. A penis was first emptied of its own sperm and then introduced into the female. It was inflated and deflated several times and then withdrawn. No sperm was found on the penis although sperm was present in both the spermathecae and bursa. Possibly the co-operation of the female is required before the flagellum or cornua can enter a spermatheca or the bursa.

In *N. farinosa* the anterior end of the vagina and bursa are about 1100 μm from the genital opening, while segment 4 of the penis is about 950 μm long. The slender point of the uninflated medial lobe probably allows the distal part of segment 4 to enter the bursa which is about 600 μm long and up to 1200 μm wide when filled with sperm. However no part of the penis can enter the narrow spermatthecal ducts and reach the spermathecae whose distal ends lie about 1100 μm from the mid line. The bristly lobes of the penis seem well adapted to packing down sperm already present in the female, but they might also remove some sperm as they were being folded and withdrawn. In 5 males caught at the end of copulation or immediately after it, 4 were found to have a thin crust of sperm adhering to the penis lobes, and sperm were also seen to be trapped in the mouth-like snapping fold on the lower surface of the medial lobe. Possibly the serrated spines of that region successfully entangle sperm, but the origin of the observed sperm is unknown. Thus while the structures on the penis of *B. lacustris* suggest a sperm-removing function, those on *N. farinosa* can be interpreted to act both for removing and for packing down sperm.

Libellulid sperm are considerably smaller than those of Zygoptera. In *Libellula quadrimaculata* and in *Orthetrum coerulescens*, live sperm are 17-19 μm long, whereas in some Zygoptera they are 50-80 μm long: the serrated bristles of *N. farinosa* seem well adapted for trapping such small sperm. The inflated penis of *L. quadrimaculata*, which is similar in structure to that of *N. farinosa*, has been examined in scanning electromicrographs by plunging a fresh and fully inflated penis into liquid nitrogen and then freeze-drying it. The penis was found to bear a variety of types of toothed and serrated bristles, and in some males these were also found to be encrusted with sperm.

COPULATORY BEHAVIOUR

Brachythemis lacustris. At the observation site reproductive behaviour in this species occurred only between 16:00 and 18:15 hr. It took place along ca. 40 m of lake margin where there were short emergent reeds. *B. lacustris* was also seen to feed gregariously over the water in the same region at 06:20-07:00 and at 18:00-18:50 hr each day. At other times of the day it avoided the water and was found perching inland. Males started to adopt waterside territories from 16:00 hr or sometimes a little earlier, and these were defended against intruding males. When a female was sighted she was approached, and the male then flew back to his territory with the end of his abdomen flexed ventrally. A receptive female followed the male and after a brief courtship in which the male hovered facing the female rippling the water with his wings, copulation ensued. Most of the females approached, however, ignored the invitation. Copulation which took place on the wing lasted a mean and s.e. of 39 ± 8.26 s (n = 6) and was followed by oviposition close to where copulation had occurred. The male guarded the female throughout oviposition by hovering about 5 cm away but always facing her, and chasing away intruding males. The female hovered throughout oviposition remaining very close to the water and to an emergent reed stem on which she pasted her eggs at and just below water level. This was done by lowering her abdomen periodically and tapping the stalk. Examination of such stalks revealed several hundred eggs firmly glued to them over a distance of up to 2 cm.

In this species copulations were relatively uncommon events and on several evenings a territorial male was watched for 2 hr without a copulation being seen. Twelve females were collected at the waterside at 07:00 hr and their genital tracts were examined. In four the bursa and spermathecae were swollen with sperm, in two there were small amounts of sperm present, and in six no sperm could be found. Three of the last group also lacked mature eggs and were teneral, while the other three had mature eggs. Thus 50% of the females examined contained sperm. Some copulations may therefore start with sperm already present in the bursa and spermathecae, and this is in agreement with the hypothesis that sperm removal occurs during copulation.

Nesciothemis farinosa. In contrast to the previous species, copulations in *N. farinosa* were frequent events and over 100 have been observed at the stream. To make it possible to follow the behavior of identified individuals, 62 mature males were marked with a code of gold and white paint on the abdominal tergites and wing bases. Marking was carried out at 06:45 hr at the roosting site without the need to handle the insects. Prior to copulation no preliminary courtship was detected, and males displayed territorial behaviour only for part of the time they spent at the stream. Although intermale aggression was common, with chases and clashes occurring frequently, no indication of a hierarchical organization among males was seen (cf. CAMPANELLA & WOLF, 1974). When a female appeared at the stream she was sometimes chased by up to 5 or 6 males and she was seized by one or more of them. Copulation was initiated on the wing, but was always completed with the pair settled either on the ground or on bushes. It had a mean duration of 27.2 s ± 17.2 (n = 33; max. 95 s; min. 9 s), and fast rhythmical movements could be seen during the early stages, as has been reported in other species (MILLER, 1981). Oviposition followed immediately, or sometimes after a short rest, with the female scooping drops of water, presumably containing small batches of eggs, 5-15 cm to land accurately on the bank at water level. The male guarded at a distance of 0.5-1.5 m often facing away from the female. Guarding frequently lasted for no more than 5-10 s and much oviposition was unguarded with females returning to oviposit at times and in places where males were less abundant. Guarding males frequently did not return after chasing another male, or would abandon the ovipositing female, if another appeared. Females were sometimes grasped by a new male as soon as they commenced oviposition, and the end of one copulation might be separated from the start of the next by less than 10 s.

Thus while *B. lacustris* was seen to copulate infrequently, and females were closely guarded throughout oviposition, *N. farinosa* copulated frequently but guarding was weak and short-lived perhaps due to the high density at which this species occurred. The frequency of copulation suggested that males deposited only a portion of their sperm-vesicle contents in a female. This was verified by catching males immediately after copulation. In five such males abundant sperm was found in segment 1 of the penis. Likewise another 5 males which were sexually active at the stream were found to have well-filled sperm vesicles, as were a further 7 mature males caught when they were sexually inactive and resting in long grass 10-20 m from the stream. Most mature males therefore seem to carry sperm ready for use, and presumed sperm translocation was observed only twice, at 10:00 and at 16:00 hr, on the wing by the stream. As mentioned earlier, segment 1 of the penis is relatively large and this may in part reflect the need for a large sperm store in a species which copulates rapidly and often, and liberates only a portion of its store on each occasion. It stands in contrast to some Zygoptera which transfer sperm while in tandem with a female and deposit most or all of the contents of the sperm vesicle in one copulation (cf. CORBET, 1962; WAAGE, 1982).

No survey of the sperm contents of females was made, but three which were caught near the stream and had not been seen to copulate, all carried extensive sperm stores in their spermathecae and bursa.

DISCUSSION

WAAGE (1982) has considered a number of possible functions for the complex structures on the penes of dragonflies. They include the facilitation of sperm transfer, the anchorage together of the genitalia, and the prevention of hybridisation by lock-and-key devices. Some of these functions are served by other structures and none seems adequate to explain the hooks, bristles and inflatable sacs which decorate segment 4 in many species; on the other hand as Waage points out, these are readily interpreted to be mechanisms which assist in sperm competition. The significance of sexual selection has been re-emphasized in recent years (PARKER, 1970, 1979), and post-copulatory mechanisms have received particular attention in insects (BLUM & BLUM, 1979). Most examples concern the displacement of sperm and genetic markers have been used to show that the last male to mate may fertilize most of the eggs (BOORMAN & PARKER, 1976). Only in damselflies has direct evidence for sperm removal been obtained (WAAGE, 1979a), but there is suggestive evidence for its occurrence in a dragonfly *Celithemis elisa* (WAAGE, 1982), although in a related species, *C. eponina*, MILLER (1981) thought that sperm might be packed down rather than removed during copulation.

The observations on the genital structure and the reproductive behaviour of *B. lacustris* and *N. farinosa* reported here can do no more than indicate possible copulatory events and mechanisms. In the first species the barbed flagellum and the cornua with proximally pointing bristles suggest a sperm-removing function, whereas the bristly lobes of *N. farinosa* seem to be adapted more for compressing sperm already present in the female, acting perhaps as a filter and concentrating sperm at the distal end of the bursa. However some sperm removal may also occur, and in females already packed with sperm this may be essential to make room for fresh sperm. Similarly WAAGE (1982) believes that the internal lobes of the penis of *Sympetrum rubicundulum* served mainly to pack down sperm which were already present.

Copulation was observed much less frequently in *B. lacustris* than in *N. farinosa*, although both were abundant at the observation sites. In the former species copulation was preceded by an invitation from the male and then by a courtship flight, and feeding flocks of tenerals and adults flew close to territorial males with little interaction. In *N. farinosa*, however, all females seen at the stream were chased and seized by one or more males, and males spent more energy in chasing fresh females than in guarding those with which they had just copulated. WAAGE (1982) has argued that sperm competition should be strongest in species which are territorial, copulate rapidly, mate frequently, and guard closely during oviposition. On these grounds both species described here might be expected to exhibit sperm competition, but it should be greater in *B. lacustris*, a species apparently equipped to remove sperm from females during copulation, than in *N. farinosa*, which may push other sperm away and place its own in the most favoured region of the female tract where they can have immediate access to ripe eggs.

Females may benefit from sperm removal if they are subsequently guarded during oviposition (WAAGE, 1979b). However a female will be at a marked disadvantage if a copulation is broken off after all her previously deposited sperm has been removed and before fresh has been deposited. The asymmetry of the spermathecal ducts of *B. lacustris* can be interpreted as a mechanism which might prevent the removal of all sperm by a copulating male, since the flagellum probably cannot pass round the hair-pin bend and enter the spermatheca on that side (normally the left). No female has been found with only one spermatheca filled, as might be expected after copulation, but such a state might not persist for long if sperm were quickly redistributed, and my examinations were made only several hours after mating. Packing down, rather than removing sperm, as is suggested for *N. farinosa*, will be less disadvantageous to a female if copulation is broken off since she will retain previously introduced sperm.

Both species described here would be classified as short-duration copulators (CORBET, 1962, 1980) but it may be useful to distinguish them from some very fast copulating species which were observed in the same habitat (cf. JACOBS, 1955). For example *Ictinogomphus ferox* copulated on the wing and the mean duration was 6.6 ± 1.33 s (n = 9), while *Trithemis arteriosa* also copulated on the wing and the mean duration was 8.49 ± 3.05 s (n = 15). Both species possess inflatable structures on the penis which seem designed to pack or press down sperm rather than to remove it. In contrast *Orthetrun chrysostigma*, which occurred at the stream, copulated when settled and the mean duration was 821 s (n = 5; max 1650 s; min. 300 s). This species possesses a penis with a long nonretractile whip-like process armed with many barbs which could act as a sperm remover. Although it seems unlikely that effective sperm removal could occur in a very rapid copulation, it does not follow that long copulations necessarily involve sperm removal. Interpretations based on structure and behaviour need to be backed up by direct evidence from experiments using identifiable sperm, and the data discussed here can inindicate only what may occur.

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