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RATES OF OVIPOSITION AND SOME OTHER ASPECTS OF REPRODUCTIVE BEHAVIOUR IN *THOLYMIS TILLARGA* (FABRICIUS) IN KENYA (ANISOPTERA: LIBELLULIDAE)

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During April, 1984, *T. tillarga* were observed to be highly active at Hunter's Lodge, Kenya, from 0.6:20 to 07:00 (sunrise: 06:28) and from 16:30 to 18:45 h (sunset:18:32 h). At other times they were probably resting in dense vegetation. In the evening, males flew continuously within limited areas along the water margin, never perching but hovering with increasing frequency as the light intensity diminished. Hovers were made over green leaves of *Typha, Cyperus* and *Sparganium* which were floating horizontally at the water surface, and onto which females oviposited epiphytically. A female oviposited by making a series of downwards swoops onto a leaf; when guarded by a male she remained ovipositing onto the same leaf, making a swoop every 1.32 ± 0.36 s (s.d), but when unguarded she visited a succession of different leaves, making a swoop every 2.06 ± 1.03 s (s.d.). Many eggs were eaten by fish soon after being laid, but this ceased once they had become firmly stuck to a leaf. The frequent switching between leaves by unguarded females may have helped to reduce egg predation. Guarded females did not switch between leaves, possibly because of the risk of being lost by their guards particularly in dim light.

Eggs were laid in discrete batches of about 9, each egg being orientated in the batch with its anterior pole facing outwards. The eggs were covered in a thick network of spumaline which stuck them firmly to the leaf but allowed contact between the water and the chorion. The female is equipped with an egg basket, a structure on the 9th abdominal sternite in which eggs are probably stacked and orientated prior to each downward swoop. It is estimated that at 28-30° C eggs were laid at 405 min^{-1} when the female was guarded, and at 261 min^{-1} when not guarded. About 44-66 batches comprised a clutch, and thus 400-600 eggs could be laid in one bout of oviposition.

INTRODUCTION

Endophytic dragonflies lay their eggs at slow rates, usually placing them within plant material: for example *Calopteryx maculata* lays at 7-10 eggs min^{-1} (maximum 17 min^{-1}) (WAAGE, 1978), *Enallagma cyathigerum* does so at 4-8 eggs min^{-1} (DOERKSEN, 1980) and *Lestes* spp. at only 1-3 min^{-1} (BICK et. al., 1976). Compared to other modes, endophytic oviposition provides more protection for the eggs, but it may place females at greater risk from predation since it takes much longer to lay a clutch. In contrast, exophytic species, which deposit their eggs on the water surface or sometimes over land, and epiphytic species which place them on plants or sometimes on rocks or stones (SCHMIDT, 1975; P.S. Corbet, pers. comm.), release their eggs much more rapidly, perhaps with less danger to the females (cf. CORBET, 1962). Epiphytic oviposition may take place on the wing, as in *Plathemis, Perithemis* (JACOBS, 1955) and *Brachythemis* spp. (BEGUM et al., 1982; MILLER, 1982), or after settling, as in *Zygonyx* (CORBET, 1962) and *Tetrathemis* (McCRAE & CORBET, 1982).

A hand-held gravid female libellulid normally will release eggs into a tube of water, and in this way McVEY (1984) found that *Erythemis simplicicollis* laid fertile eggs at rates of up to 13 s^{-1} at 38° C, whereas *Plathemis lydia* could reach rates of 28 eggs s^{-1} (30-34° C). These may be maximal rates and it is important to know if equivalent rates occur in the field, since such knowledge might help in the assessment of various oviposition strategies. A report is presented here on oviposition behaviour and deposition rates in *Tholymis tillarga,* an epiphytic species which makes repeated dips or swoops onto submerged leaves from the air, and in which the egg batches usually remain separate and countable.

STUDY SITE AND GENERAL NOTES

Observations were carried out at Hunter's Lodge, near Simba in Kenya, as previously described (MILLER, 1982). They took place on 15 days between April 6 and 26, 1984, mainly at a small bay in a region where the dammed stream had formed a slow river ca. 30 m broad, and where *Typha domingensis, Cyperus dereilema* (identification provisional) and *Cladium mariscus jamaicense* grew abundantly along the bank, and where there were many large trees (mainly *Acacia xanthophloea*) opposite.

Tholymis tillarga (Fab.) is a medium-sized libellulid occurring throughout much of Africa, the Far East and Australia. The abdomen of the male is bright red and the hindwings have a prominent brown patch, just distal to which there is a region where upper and lower surfaces bear a waxy deposit which appears white against a dark background. It shows up prominently as a white spot when males fly, particularly as they hover towards dusk, and might possibly reflect ultraviolet light (cf. ROBEY, 1975; SILBERGLEID, 1979).

Sunrise on April 20 was at 06:28 h and sunset was at 18.32 h. Evening light intensities were measured by pointing the light meter of a Pentax camera vertically at the cloudless sky, then converting the readings to log lux using the tables in UNWIN (1980), and calibrating them from a sunrise and sunset value of 2.6 log lux (NIELSEN, 1961). Dragonflies and their eggs were collected in the field and immediately preserved in 2% formaldehyde. Observations were assisted with a close-focus field monocular and with a tape recorder. Shade temperatures during evening periods of observation varied from 26° C to 30 ° C.

REPRODUCTIVE ACTIVITY

MALE ACTIVITY

Tholymis tillarga is known to be active mainly towards dusk (PINHEY, 1961; CORBET, 1962). At Hunter's Lodge, we found many adults flying between 16:00 and 18:45 h, and also between 06:20 and 07:00 h, while at other times they were not normally seen. On two occasions males were found roosting among trees at about mid-day, and after being disturbed they quickly settled again among densely shaded bushes. From about 16:30 h, many males started to patrol along forest streams and by the more open water at our observation bay. They flew continuously and rapidly without perching until 18:40 h (8 minutes after sunset, light intensity about 2.0 log lux), when most left the water, the last being seen at 18.45 h (checked by torchlight). On arriving at the water they patrolled large areas, flying incessantly along 40-50 m of bank and frequently crossing to the other side. Between 17:00 and 17.30 h their numbers increased and the areas patrolled were correspondingly reduced to about 10-15 m of bank. Within the area patrolled a

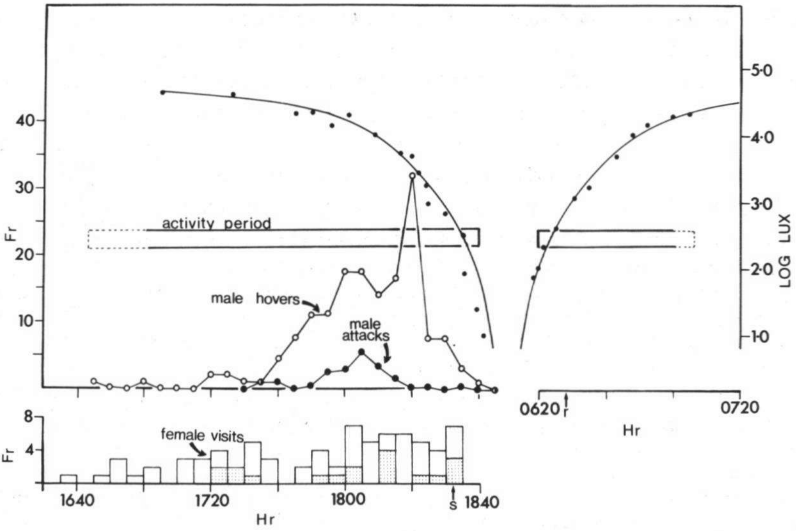

Fig. 1. The number (Fr) of hovers (O — O) and of interactions with other males (● — ●) made by a male *T. tillarga* at the observation bay on April 14th, counted during one minute every 5 minutes and plotted against time. The changing light intensity around dawn on April 12th and around dusk on April 10th is also shown. Similar plots of light intensity were obtained on 6 other evenings with small variations occurring due to slight cloud cover. Below is shown a histogram of the number of visits made by females to the observation bay accumulated over 10 days (between April 9 and 22) and shown in 5-minute periods. Hatched blocks indicate visits which included a copulation. s, sunset; r, sunrise.

male flew back and forth, never perching but stopping only to hover over potential oviposition sites which were formed by those green leaves of *Typha, Cyperus* and *Cladium* which floated horizontally 2-10 mm below the water surface; all patrolled areas included such leaves. When fresh floating leaves were deliberately added to a male's area, he hovered over these as well, always facing along the length of the leaf.

Figure 1 shows data from April 14, in which the number of hovers made over a leaf per min, counted for one min in every 5 min, and the number of aggressive interactions with other males, similarly counted, are plotted against time. The changing light intensity is also shown. Since males were unmarked we could not be certain that we always recorded the activity of the same male in the bay, although for much of the time we saw that this was so. Little or no hovering occurred before 17:00 h, but thereafter the number and also the duration (not measured) of hovers increased as the light intensity fell, reaching a peak at 18:20, after which they decreased. The high peak at 18:20 h in Figure 1 may have been due to the temporary entry of a second male into the bay during the counting period. Aggressive interactions were always brief but they sometimes escalated into upwards spiralling chases, after which one male quickly returned. A similar pattern of activity was observed on each of 8 evenings.

FEMALE ACTIVITY

Females were intermittently observed flying rapidly along the middle of the river. Their arrival rate in the observation bay seemed to increase slightly as the light waned (Fig. 1). On entering a male's territory a female was quickly seized, carried in tandem and then joined in copulation on the wing. Copulation, which lasted a mean of 14.4 s (s.d. ± 7.5 s; $n = 8$; maximum = 30 s), took place with the pair flying and hovering above potential oviposition sites. After copulation, oviposition sometimes commenced immediately, with the male guarding closely (without contact) on the wing. As the light intensity fell below 3.0 log lux, a male guarded his female even more closely, their wings sometimes clashing, and he turned towards her each time she rose from the water after depositing a batch of eggs.

During oviposition a female hovered about 10 cm above the water aligned along a leaf; she then swooped down, striking the water, with the end of her abdomen and at the same time deposited a small batch of eggs on the submerged leaf (Fig. 2A). She then flew upwards and forwards, executed a sharp turn and flew back to her original hovering point, turning once again to face the original direction. Less commonly, after flying up, she reversed and hovered facing in the opposite direction and then made a second swoop before returning to her original hovering point (Fig. 2B). In the latter mode, therefore, swoops were alternately from left and right. These types of movement are different from those observed in some other epiphytic libellulids, such as *Brachythemis lacustris* (Fig. 2C) (MILLER, 1982), but they resemble those reported by MATHAVAN (1975) in *B. contaminata.*

When guarded by a male, a female made repeated swoops onto the same leaf and only rarely moved to a new leaf; in the shade at a temperature of 26-28° C each swoop cycle lasted 1.32 s (s.d. ± 0.36 s; n = 168 cycles in 12 bouts). The mean number of swoops per leaf was 54 ± 31.5 (n = 17 bouts; maximum = 102), and they were delivered at 45 min^{-1}.

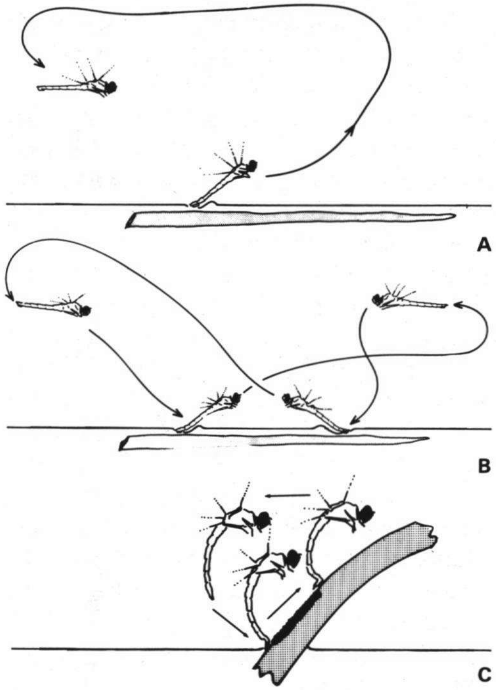

Fig. 2. Types of epiphytic ovipositing movements of *T. tillarga* (A, B) and of *Brachythemis lacustris* (C): (A) a female makes swoops onto a leaf in one direction from a hovering station; — (B) a female makes swoops from alternate directions and there are two hovering stations; — (C) a female deposits a batch of eggs onto a stem by spreading the eggs along the surface with her abdomen, just above the water level.

During unguarded oviposition, a female frequently changed to a new leaf, making a mean of only 5.4 swoops (s.d. ± 9.3; n = 35; maximum 43) per leaf, i.e. significantly less than when guarded ($P < 0.001$). Including the time for moving between leaves, the mean swoop cycle lasted for 2.06 ± 1.03 s (n = 514), i.e. significantly longer than when guarded ($P < 0.001$). The mean duration of a bout of oviposition, i.e. the time between the start of oviposition and departure of the female, was 90 s (s.d. ± 40 s; n = 12; maximum 178 s), the end of oviposition being indicated by the female flying rapidly upwards.

Many small fish (*Lebistes* and *Tilapia* spp. 10-15 mm long) were seen to gather at the leaves being used for oviposition by *T. tillarga* and to snap up eggs continually as they were laid. The swooping female appeared to attract fish which quickly congregated around an oviposition site. Frequent changes of leaf therefore probably reduce egg predation but they may also lower the rate of laying (cf. below). A few seconds after being laid eggs appeared to be firmly glued to the leaves and they were ignored by fish.

DAWN ACTIVITY

At dawn, males first appeared at the water at 06:20 h, 8 minutes before sunrise at a light intensity of about 2.0 log lux, which was similar to that at which many left the water in the evening. The air temperature was 18-20° C and surface water temperature was 25° C, indicating that light intensity rather than temperature determined the onset and cessation of activity, as in some other species (CORBET, 1962). Many males were intensely active at the water from 06:30 until 06:50 h but by 07:00 h all had departed. Unguarded ovipositing females were seen on several occasions at this time but no morning copulation was witnessed. Oviposition continued until 07:10 h on one morning.

EGG COUNTS

Eggs were examined and counted on leaves on which oviposition had been observed. They were also found on many similar leaves at other sites. With each swoop cycle, eggs were deposited either in a double row, or in a flattened ring to form a batch (Fig. 3). Each batch was covered in spumaline, a glue-like secretion which quickly hardened in water and presumably came from the accessory (colleterial) glands (HINTON, 1981). Figure 4 shows a summary of the number of eggs per batch. The mean value was

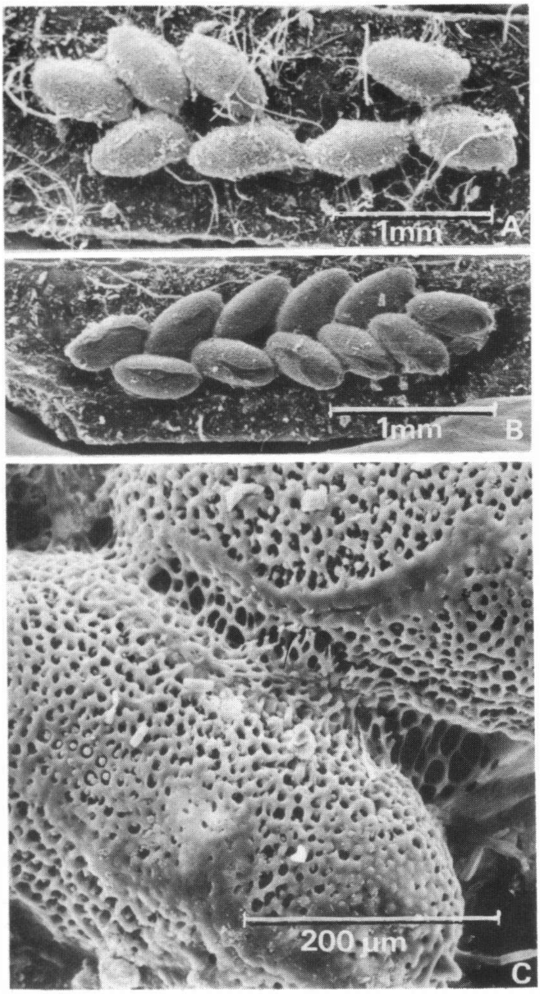

Fig. 3. Scanning electronmicrographs of egg batches of *T. tillarga* on leaves of *Typha:* (A) an incomplete batch, one egg having been removed, probably by a predatory fish (the strands are of algae) ; — (B) a large batch of 11 eggs; — (C) parts of 2 eggs showing the continuous spumaline coat covering them.

7.2 (s.e. ± 0.161; n = 386 batches) and the modal value 9.0. Much larger clusters of eggs which were not counted clearly consisted of several superimposed batches which were sometimes distinguishable by their differing orientations. The batches on one leaf were often of different ages, as seen from the development of embryonic eyes and the darkening of the chorion, as well as from the presence of empty egg shells, showing that more than one female had oviposited there. Batches which contained fewer than 9 eggs sometimes had the spumaline imprints of missing eggs, but in other cases there was no imprint, suggesting that females sometimes laid smaller batches. The 33 batches containing only 1 egg each (Fig. 4) probably represent eggs that had been separated from their original batch and then stuck to the leaf. In general, eggs remained firmly stuck in formaldehyde, and losses after collection were negligible.

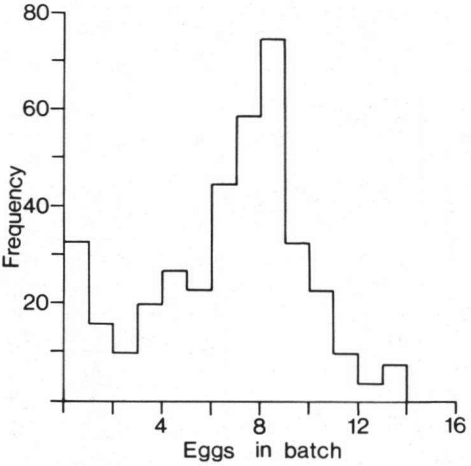

Fig. 4. Histogram of the numbers of eggs per egg batch.

Within a batch, eggs are arranged with the anterior pole containing the micropyle facing outwards, and the hatching larvae, which emerge from this end, would probably interfere with each other minimally. The orientation of a batch on a leaf reflects the direction of flight of the female, as shown in Figure 5.

The spumaline covering each egg forms an open mesh, which provides some protection while allowing free access of water to the chorion for respiration (Fig. 6). The spumaline of neighbouring batches was sometimes fused, indicating that it remained sticky for some time after oviposition (Fig. 3C). The egg chorion is highly sculptured (Fig. 6) and may be capable of supporting an air layer, and can perhaps act as a plastron (HINTON, 1981).

An interesting question is whether the egg-flow rate can be adjusted by the female according to the length of the interval between swoops. We found no indication that the number of eggs in a batch increased when unguarded females made frequent changes of leaf, and therefore suggest that the female can control the egg-flow rate during a bout of oviposition. This is in contrast to what has been suggested in some other libellulids (McVEY, 1984).

Taking batch size to be 9, then eggs could be laid by a guarded female at 6.75 s^{-1} (405 min^{-1}), and by an unguarded female at 4.35 eggs s^{-1} (261 min^{-1}). During a bout of guarded oviposition lasting 90 s, a total of 608 eggs could therefore be laid, whereas without guarding 392 eggs could be laid in the same period.

When comparisons were made between the number of swoop cycles observed on a leaf and the number of egg batches subsequently counted on the same leaf, only about half as many batches were found as swoops observed (55% in 7 observed bouts; range 14 to 81%). This suggests either that not every swoop released an egg batch, or that some egg batches failed to become attached to the leaf and sank, or that fish consumed many whole batches before they were attached. The abundance of fish at the leaves inclines us to believe that the last of these possibilities accounts for much of the discrepancy: predation at egg-laying may therefore dispose of nearly half of all eggs laid. However once firmly attached to the leaf surface when the spumaline had hardened, eggs appeared to be immune from further fish predation.

THE EGG BASKET OF THE FEMALE

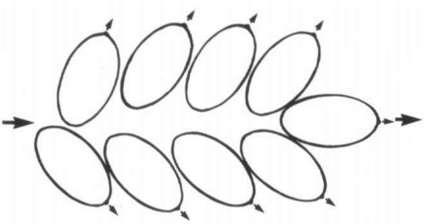

Fig. 5. Diagram of an egg batch of *T. tillarga* showing the orientation of each egg (small arrow indicates anterior pole) and the direction of flight of the ovipositing female (large arrows).

In Zygoptera and Aeshnidae, the ovipositor is formed from a pair of anterior gonapophyses on the 8th sternite, and two pairs (medial and lateral) on the 9th sternite (TILLYARD, 1917; ASAHINA, 1954). In Libellulidae, the ovipositor is usually absent and the anterior gonapophyses form the subgenital plate (vulvar scale or valvulae vulvae) which the hamules probably grip firmly during copulation (WALKER, 1953; WATSON, 1966; MILLER, 1981). The medial and lateral gonapophyses are much reduced but in some species the 9th sternite is secondarily modified to assist with oviposition. Thus in *Brachythemis lacustris* and *B. leucosticta* it forms a flat plate which may help to glue eggs to vegetation (MILLER, 1982), while in *Tholymis tillarga*, and in the American species, *T. citrina* (NEEDHAM & WESTFALL, 1954), it forms a hollowed structure with a central longitudinal rib and lateral fringes of long hairs (Fig. 7). This basket is adapted to receive 8 or 10 eggs from the genital opening: they are probably stacked side by side in it, with a 9th (or 11th) egg remaining near the subgenital plate. The batch can then be pressed firmly onto a leaf surface during an oviposition swoop without altering the eggs' relative positions. Captive females were commonly seen to make a strong ventral flexure with the 9th segment, which caused the sharp points on the extended subgenital plate (Fig. 7) to ride into the grooves in the basket. This movement could either dislodge an egg batch from the basket or it could help to arrange the eggs in the basket.

DISCUSSION

MALE HOVERING

Male *T. tillarga* increased the number and duration of hovers they made over potential oviposition sites (horizontal leaves) as the light intensity fell, reaching a maximum at 18:20 h, but thereafter declining. We suggest that hovering rather than flying forwards improves the chance of a male perceiving a female, particularly in dim light: by remaining stationary a male's eyes may capture more of the photons reflected from a distant target in the visual field, thus improving discrimination. Males commonly hovered 30-40 cm above the water surface and would therefore be likely to detect ovipositing females in front and below them with the ventral part of the compound eyes, a region known to have less good acuity (HORRIDGE, 1977). Hovering also occurs in

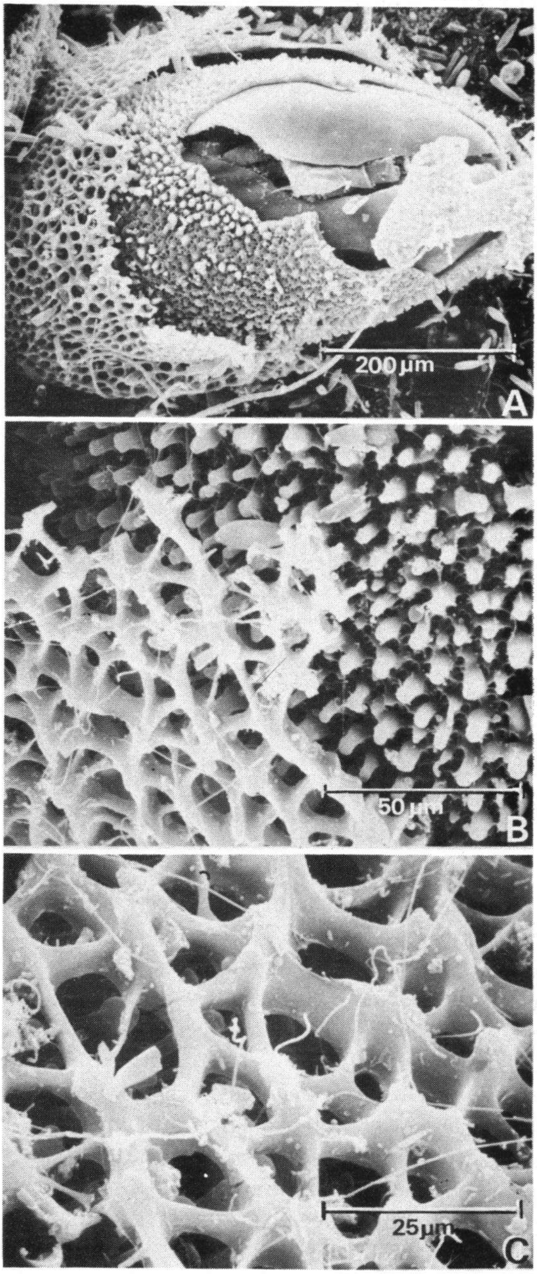

Fig. 6. Scanning electronmicrographs of parts of eggs of *T. tillarga*: (A) the spumaline covering has been partly removed and the chorion is broken showing part of the larva within; — (B) spumaline is shown to the left and the sculptured chorion to the right; — (C) part of the spumaline overlying the chorion which is just visible between the interstices.

some species when non-territorial males appear to search for females, or when females may inspect oviposition sites, both activities requiring high acuity. The apparent decline in the number of hovers by one male *T. tillarga* after 18:20 h may have been partly due to our occasional failure to see him in the poor light.

RATES OF EGG RELEASE

McVEY (1984) has shown that the rate of release of eggs from hand-held libellulids is strongly influenced by temperature (Q_{10} = up to 2.2 for the range 28-38° C). The rate also covaries with the size of the species, larger species tending to lay at faster rates than small ones. The highest rate was found in *Plathemis lydia* which oviposits at up to 28 eggs s^{-1} (32° C), and the lowest was in *Sympetrum rubicundulum* which lays eggs three times as large as those of most other libellulids at only 1.3 eggs s^{-1}. The release rate in free *T. tillarga* was estimated to be about 7 eggs s^{-1} at an air temperature of 28° C which is close to the rates for *Erythemis simplicicollis* at the same temperature: these were, in Florida, 6 s^{-1}, and, in New York, 8 s^{-1}. However, the temperature of the abdomen of a freely ovipositing female is unknown: it may be slightly raised by the much warmer thorax (cf. MAY, 1978; VOGT & HEINRICH, 1983), or it may be slightly lowered by evaporative cooling if water clings to the cuticle surface after swooping.

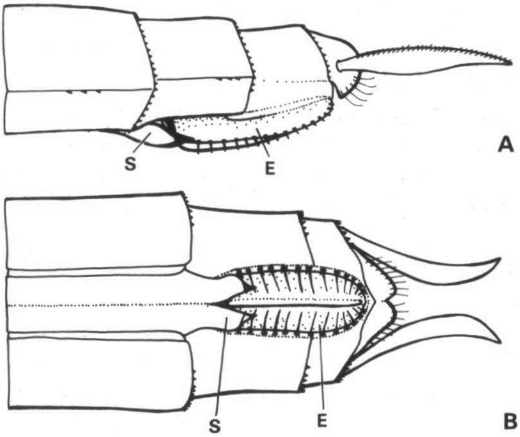

Fig. 7. Diagrams of the terminal abdominal segments of a female *T. tillarga* to show the egg basket: (A) lateral view; — (B) ventral view. — S: subgenital plate; — E: egg basket.

Little is known of the natural rates of egg release in other libellulids but a corduliid, *Cordulia aenea*, may lay at 7 s^{-1} (UBUKATA, 1981). We measured the rates of dipping in a few species at Hunter's Lodge, but rates of egg release cannot be calculated from these unless the size of egg batches is also known. We attempted to measure egg-batch size in *Nesciothemis farinosa* by spreading sheets of black cloth along the water margin, and then examining the eggs stuck to the sheets after having been scooped up by ovipositing females (cf. MILLER, 1982). Although some successful collections were made, the eggs did not remain in discrete batches, and batch size could not therefore be determined. The dip cycle in unguarded *N. farinosa*, ovipositing in the shade at 30° C, lasted for a mean of 0.89 s (s.d. ± 0.17 s; $n = 357$ dips in 8 bouts) which was significantly shorter ($P < 0.001$) than that of guarded *T. tillarga*. In *Crocothemis sanguinolenta* rapidly ovipositing in the sun, dip cycles had a mean of 0.33 s (s.d. ± 0.026 s; $n = 54$ dips in 7 bouts), during which the female remained very close to the surface, dipping only her abdomen.

Experiments with hand-held insects suggest that egg-flow rates are independent of dip-cycle duration (McVEY, 1984; pers. comm.; M. Siva-Jothy, pers. comm.), and those species with long cycles may therefore deposit more eggs with each dip. However, as already described, we believe that *T. tillarga* can control the egg-flow rate and that lower frequencies of swooping do coincide with lower rates of oviposition. It is planned also to look at this question in *Brachythemis lacustris*, a species in which the number and frequency of dip cycles can be determined and the total egg batches can then be collected (MILLER, 1982). It may be noted that a few species which oviposit epiphytically while settled, such as *Zygonyx natalensis* and *Z. torrida*, both observed at Hunter's Lodge, deposit large piles of eggs without marked abdominal movements.

GUARDED AND UNGUARDED OVIPOSITION

Many of the eggs laid by *T. tillarga* were promptly eaten by fish. Egg predation may be reduced by coating eggs with spumaline which hardens quickly in water and stops them from being sucked up by fish, and by the ovipositing female making frequent changes of leaf which prevents the fish from congregating at a particular oviposition site. Unguarded females moved from leaf of leaf frequently, making a mean of only 5.4 swoops per leaf. This may also prevent eggs from piling up on each other, which otherwise might impede hatching (cf. JACOBS, 1955). However, guarded females placed all the batches of a clutch on one or at the most two leaves, with a mean of 54 swoops per leaf; they oviposited 1.55 times faster that unguarded females, but with an increased risk of egg predation and egg piling. We suggest that a guarded female which changed leaves frequently would have risked the loss of her guard, particularly at low light intensities, and she might have been confused with a new arrival and been seized for a further copulation. Females which oviposited alone were seen to attract males quickly and were either seized or driven off (cf. SHERMAN, 1983). Thus, we conclude that unguarded females used a sequence of leaves in quick succession, thereby increasing egg survival, whereas guarded females remained at one site, which ensured the retention of their guards and enabled them to oviposit more rapidly, but which placed their eggs in greater jeopardy.

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