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PRE-TANDEM AND IN-TANDEM COURTSHIP IN LIBELLULIDAE (ANISOPTERA)

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Two types of courtship can be distinguished in odonates: pre-tandem courtship which is common in several families of Zygoptera, and in-tandem courtship which is a feature of some Zygoptera and occurs in at least a few Libellulidae. In both types the female has the option of refusing or accepting copulation, and even after copulation she has in theory a further option on the use of a particular male's sperm. Among Anisoptera, pre-tandem courtship has been described in at most five species of libellulids. Observations on pre-tandem courtship in *Palpopleura lucia lucia* and *Brachythemis lacustris*, made in Zimbabwe, are described here. In both species, courtship may enable males to distinguish receptive from non-receptive females. In *B. lacustris*, feeding and reproductive behaviour both occur late in the day at the same sites over water, and sexually active males thus encounter numerous immature and unreceptive females as well as receptive females near their territories. Courting males induce receptive females to enter their territories and then hover low over potential oviposition sites before being accepted. *B. leucosticta* has been observed to be sexually active at the same time and in some of the same places as *B. lacustris*, but it shows no courtship. This may reflect the fact that, unlike *B. lacustris*, it does not feed over water. During in-tandem courtship in Zygoptera, the male issues "copulatory invitations" by wing waving and abdominal flexing movements. In some libellulids, for example *Orthetrum coerulescens*, in-tandem courtship may also occur when a pair makes repeated dipping movements down towards the water, some females perhaps accepting copulation only after they have inspected potential oviposition sites in this way.

INTRODUCTION

Courtship is widespread in insects. Among zygopteran Odonata it is best known in the Calopterygidae (e.g. HEYMER, 1973 ; WAAGE, 1984b) and Chlorocyphidae (ROBERTSON, 1982) but it also occurs in some members of the Euphaeidae and Coenagrionidae (Corbet, 1962). In contrast it appears to be rare in Anisoptera where it has been reported in at most 5 species of Libellulidae (Jacobs, 1955 ; Corbet *et al.*, 1960 ; Williams, 1977 ; Miller, 1982a, b).

Courtship consists of close-up interactions between a male and a female, and it usually follows the encounter. The male is usually the more active partner and a female may accept or reject a male according to her own internal state or depending on her response to various external factors including the courtship of the male. In some insects (e.g. some dolichopodid or phorid flies) most courtship leads to rejection but in damselflies the acceptance rates are usually higher (Thornhill & Alcock, 1983 ; Waage, 1984b, 1988).

Many functional interpretations of courtship have been made. These include a role in species and sex recognition, preparation for copulation, inhibition of predatory behaviour, assessment of the male by the female, and nuptial feeding whereby a male may increase his acceptability or further his investment in the offspring. The selection of a particular male by the female may depend on factors such as the size, health or agility of the male as well as on the quality of his territory or nuptial gift (Thornhill & Alcock, 1983 ; West-Eberhard, 1984 ; Eberhard, 1985).

Those odonates known to court do so before tandem formation, and copulation usually follows as soon as a tandem has been formed. This can therefore be termed **pre-tandem courtship**. However in some other species not showing such courtship, there may be a variable delay between tandem formation and copulation. In some this is spent passively, but in others the pair flies about actively and I suggest that in certain species the latter may represent **in-tandem courtship** (Fig. 1).

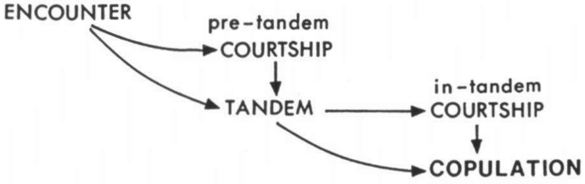


Fig. 1. Flow diagram for pre-tandem and in-tandem courtship.

A female in tandem is able to accept, postpone or refuse copulation. Copulation cannot be forced by the male in Zygoptera, nor probably in Anisoptera (Waage, 1984a). A female refusing copulation is eventually released, though quicker release may be obtained if she accepts the male. Even after copulation she may still in theory have an option on the use of the last male's sperm, for example by delaying oviposition and seeking further matings, by sequestering sperm in remote parts of her system, or by ejecting it. Such female options might be expected to have caused males to continue 'courtship' during and after copulation (cf. EBERHARD, 1985), but no evidence for this possibility exists in Odonata.

PRE-TANDAM COURTSHIP IN LIBELLULIDAE

Reports of pre-tandem courtship exist for only 5 species of libellulids occurring in 4 sub-families (ca. 0.5% of the family : Table I). This suggests either that the behaviour is very rare in the family or, if it occurs more widely, that it has not been recognised in most species perhaps because it is extremely brief. Why readily detectable courtship should be confined to only 5 species is unknown.

Table I

Occurrence of pre-tandem courtship in Libellulidae

Libellulinae :	*Libellula (= Belonia) croceipennis* (Sélys) (WILLIAMS, 1977)
Sympetrinae :	*Brachythemis lacustris* (Kirby) (MILLER, 1982a, b)
Palpopleurinae :	*Perithemis tenera* (Say) (JACOBS, 1955)
	Palpopleura lucia lucia (Drury) (CORBET *et al.*, 1960)
Zygonichinae :	*Olpogastra lugubris* (Karsch) (CORBET *et al.*, 1960)

I have made observations on pre-tandem courtship in *Palpopleura lucia lucia* (Drury) and *Brachythemis lacustris* (Kirby) in Kenya (MILLER, 1982a, b) and more recently during 11 days, in April 1989, in Zimbabwe on the River Zambesi above the Victoria Falls and also at the east end of Lake Kariba.

COURTSHIP IN *PALPOPLEURA LUCIA LUCIA*

Courtship in this species was mentioned briefly by MOORE (*in* CORBET *et al.*, 1960). Males have a bright blue abdomen and extensive black marking on the wings. Females are brown and have complex black and brown patterns on the wings (PINHEY, 1951). The species was abundant in small sheltered grassy inlets and streams adjoining Lake Kariba where most observations were made.

Males held territories among reeds and grasses throughout the middle hours of the day (mid-day shade temperature was 31°C). A male which had intruded into the territory of another, hovered facing away from the owner at a distance of 0.15-1.0 m while the resident hovered facing towards the intruder (Fig. 2). These positions were held sometimes for 2-3 minutes, but occasionally the intruder faced towards the owner while the latter turned way,

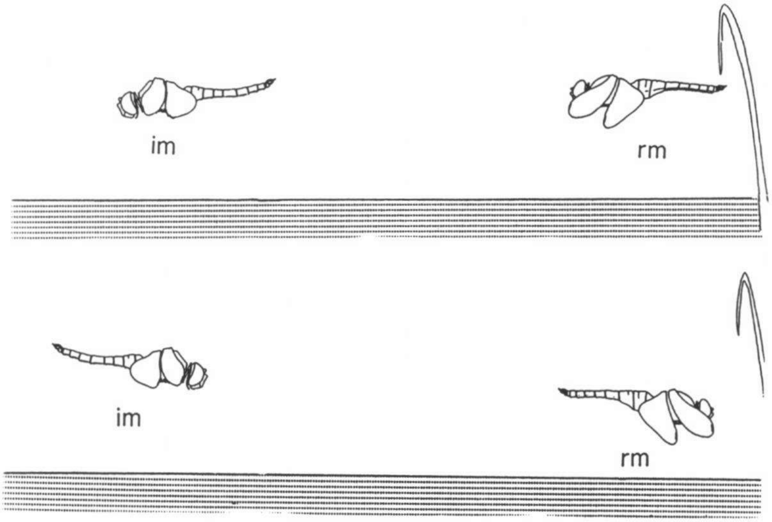
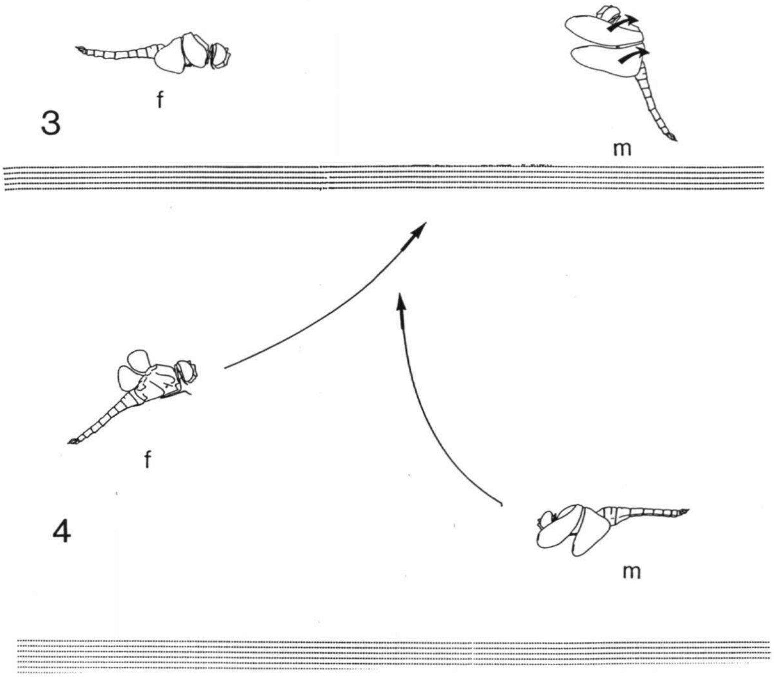


Fig. 2. Interactions between an intruding male (im) and a territorial resident male (rm) of *Palpopleura lucia lucia*. The positions shown were maintained by hovering for many seconds.

or they hovered side by side facing in the same direction. More aggressive interactions and high-speed chases often eventually followed.

When a female entered a male's territory she commonly hovered or perched on reeds 0.5-1.0 m above the water : the male approached and then performed a slow wing-fluttering hover directly in front of her for up to 5 s with his body in a vertical position (Fig. 3). He then hovered with fast wing beats and body horizontal facing her for up to 30 s, with sometimes a brief repetition of the flutter-hover. An unreceptive female either departed or remained perched and the male quickly lost interest. A receptive female flew up towards the male and was seized in tandem, with copulation following almost immediately (Fig. 4). Copulation lasted for about 10 s and was usually completed after perching (*contra* MILLER & MILLER, 1989). A male was once observed to discover an unguarded ovipositing female and after hover-fluttering in front of her, he was accepted.

Observations of 30 courtships showed that 19 led to copulations. No male was seen to seize a female without a preliminary hover-flutter. No male hover-fluttered in front of a female more than twice in succession and males rapidly lost interest in unresponsive females. Courtship did not seem to be closely associated with potential oviposition sites, and after copulation a female searched among leaves or stems which were just under the water surface for suitable sites, not always in the male's territory. She then oviposited epiphytically while the male guarded closely but without contact.



Figs. 3-4. Courtship in *Palpopleura lucia lucia*: — (3) a male (m) hover-flutters in front of a female (f); — (4) the female accepts the male and flies up towards him.

Three females were caught and tied lightly round the base of the abdomen to a long thread. Such tethered females were allowed to fly or perch several times in front of resident males. Each time a female was presented, whether flying or perching, the male flutter-hovered in front of her, usually only once, after which the male's interest waned. No male attempted to grasp a tethered female, such females apparently not giving acceptance signals.

Males *P. l. portia* have a wing pattern which resembles that of female *P. l. lucia*. Both subspecies occur in the same grassy inlets at Kariba (cf. PINHEY, 1984) but *P. l. lucia* is much commoner. No spontaneous interaction between the two subspecies was witnessed. A tethered male of *P. l. portia* several times elicited hover-fluttering by a male *P. l. lucia*. Male *P. l. lucia* were also seen to make brief hover-flutters at brown and black wasps and lysid beetles whose colours resemble those of females. Thus black and brown colouration seems to excite courtship behaviour.

Females of *Perithemis tenera* have a wing pattern similar to that of female *P. l. lucia*, whereas males have amber wings. Their courtship also involves a slow fluttering flight to which females may respond with a similar wing-flutter (Jacobs, 1955 ; Dunkle, 1989). Unlike *P. l. lucia*, a male *P. tenera* does appear to indicate an oviposition site during courtship. Both species are small and commonly occur at high densities at aquatic sites : their courtship may allow males to distinguish receptive females from others in the vicinity. Another palpopleurine species, *Palpopleura deceptor*, shared the habitat with *P. l. lucia* at Kariba but was less common. It has much less extensive wing markings with little sexual dimorphism and it exhibits no courtship.

Courtship in *Brachythemis lacustris*

Reproductive behaviour in *B. lacustris*, including courtship, has been described from a site in Kenya where it occurred only during the 2-2½ h before sunset (Miller, 1982a, b). At Kariba and along the Zambesi, reproductive activity was limited to a period between 16 : 00 and 18 : 00 h (sunset). The bright red males defended territories containing emergent plants along exposed regions of the lake shore or the river bank. Males responded aggressively towards intruders, the two contestants facing each other while performing a rapid bouncing flight in which the abdomen was held up and the tip curled ventrally (Fig. 5).

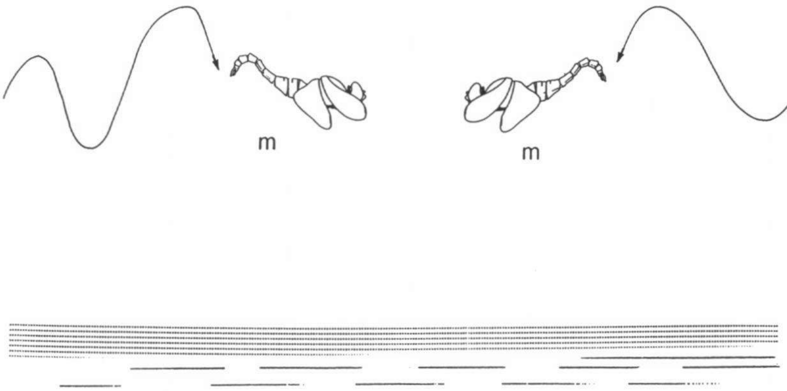
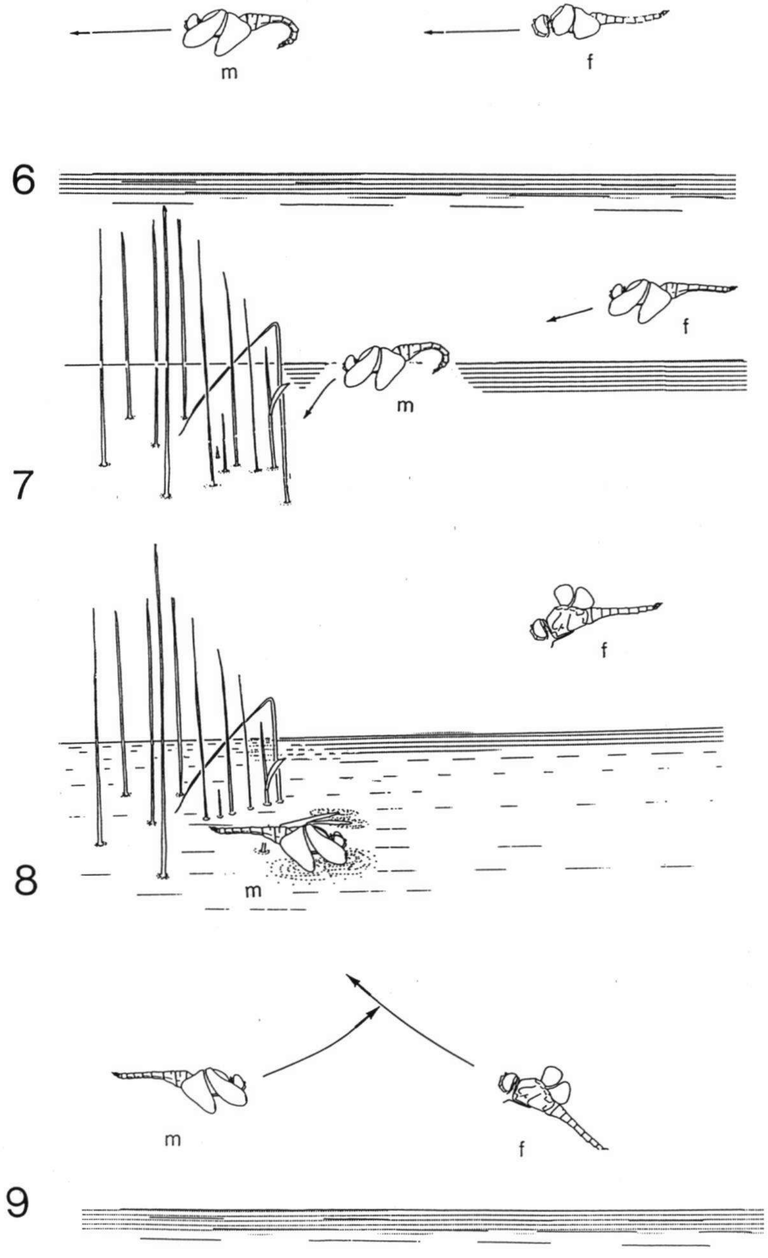


Fig. 5. Interactions between two reproductively active male *Brachythemis lacustris* in which they perform a rapid bouncing flight facing each other.

When a female was seen by a resident male he flew towards her, then turned and flew back to a small clump of emergent plants in his territory, keeping his abdomen curled ventrally but not raised (Fig. 6). If the female followed, he then hovered at water level beside the plants, ruffling the surface with his wings while the female hovered or perched close by (Fig. 7, 8). A receptive female flew up towards the male and was seized, copulation following



Figs. 6-9. Courtship in *Brachythemis lacustris*: the female (f) follows the male (m) back to his territory (6 & 7) where the male hovers low over the water close to reeds (8) ; a receptive female flies up towards the male (9).

immediately (Fig. 9). Unreceptive females either did not follow the male, or if they did so, they departed soon after, or sometimes remained perched. Only one attempt to seize a female without preliminary courtship was seen, and it failed. Epiphytic oviposition followed copulation, usually onto the plants at the centre of the male's territory. On windy evenings females were remarkably adept at keeping exactly at the water surface as it rose and fell with the incoming waves, spreading their egg batch along a greater length of stem than when the water was still (cf. fig. 2C in MILLER & MILLER, 1985).

In conclusion, courtship in this species does appear to indicate a potential oviposition site to the female and it incorporates a component of male-male aggressive interactions — ventral curling of the posterior segments of the abdomen.

THE ABSENCE OF COURTSHIP IN *BRACHYTHEMIS LEUCOSTICTA*

Both *B. leucosticta* and *B. lacustris* occurred together in some areas of Kariba but *B. leucosticta* generally preferred the open parts of the lakeshore and frequently settled on the ground, whereas *B. lacustris* was found mainly in well vegetated areas of the lake or river margin perching on bushes and reeds. Although they were sometimes reproductively active at the same times and in the same places, and both oviposited epiphytically onto similar plants, *B. leucosticta* showed no pre-tandem courtship behaviour. The suggestion is made below that this difference is due to their different types of feeding behaviour.

FEEDING BEHAVIOUR IN *BRACHYTHEMIS LACUSTRIS*

Mature and immature male and female *B. lacustris* tended to perch gregariously on bushes or reeds, often over the water, throughout much of the day and made only occasional feeding flights (cf. MILLER, 1982a, b). When disturbed, they usually re-formed in small groups nearby, a group being defined as a cluster of 2 or more individuals perched within 10 cm of one another. In a mid-day survey along the lakeshore 122 dragonflies were counted of which 90 were perched in groups and 32 were perched singly. Groups contained a mean of 4.95 ± 2.3 (s.d. ; n = 19 ; max. 11) dragonflies. The difficulty of estimating distances between perched dragonflies and the likelihood that many were not seen make these figures at best only rough approximations.

For about half-an-hour after sunrise, and from about one hour before sunset until half-an-hour after sunset, many immatures of both sexes and mature females (but fewer bright red mature males until sunset) of *B. lacustris* were seen up to 10 m from the shore flying slowly about 5 cm above the water, apparently feeding on swarming insects such as Chironomidae and

Chaoboridae. After sunset, the slow flight took place mainly towards the west, parallel to the shore (Fig. 10) and this may have enabled the dragonflies to detect airborne prey against the pale western sky. The apparently unidirectional flight was not related to wind direction and it gave the impression of a westward migration, However the dragonflies were very localised with individuals periodically and quickly flying back to the east end of the feeding area. It is not known if the dragonflies chose particular areas because of a local high density of prey or for other reasons such as the proximity of day perches but they were seen in the same localised regions on each of 7 successive evenings.

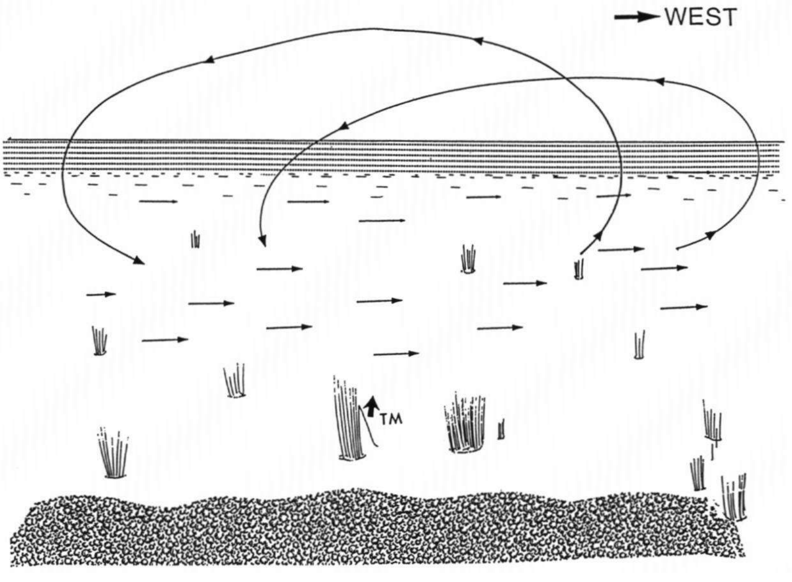


Fig. 10. Feeding behaviour in *Brachythemis lacustris* at sunset. Each small arrow indicates an individual flying slowly low over the water towards the west and then periodically looping back. One male (TM) continues to defend a territory.

FEEDING BEHAVIOUR IN *BRACHYTHEMIS LEUCOSTICTA*

In contrast *B. leucosticta* showed no temporally or spatially localised feeding behaviour. It appeared to feed mainly over land at any time during the day including the evening and often exhibited the well-known 'accompanying' behaviour whereby it catches insects disturbed by the passage of large mammals (CORBET & MILLER, 1991).

Thus *B. lacustris* commonly feeds and shows reproductive behaviour in the same place, whereas *B. leucosticta* does not usually do so. Courtship may therefore enable *B. lacustris* males to distinguish the minority of receptive females from others.

IN-TANDEM COURTSHIP IN ZYGOPTERA

In many zygopteran species, males in tandem issue 'copulatory invitations' by making slow wing movements while flexing the abdomen (see e.g. UTZERI *et al.*, 1983 ; CORDERO, 1989). A receptive female responds by curling her abdomen towards the male's secondary genitalia whereupon the male translocates sperm and copulation ensues (ROBERTSON & TENNESSEN, 1984). If the female does not respond the male may persist with such invitations although he eventually releases the female. I suggest that such male behaviour may represent in-tandem courtship.

IN-TANDEM COURTSHIP BEHAVIOUR IN LIBELLULIDS

In some libellulids a variable interval between tandem formation and copulation has also been observed. For example in a high-density population of *Sympetrum depressiusculum* in Southern France, tandem formation was seen at dawn but subsequent copulations were delayed for 2-3 hours, probably until the temperature had risen sufficiently for oviposition. In the interval the pairs perched without movement and the behaviour probably represents pre-copulatory guarding (MILLER *et al.*, 1984).

In contrast a shorter but variable period intervenes between tandem formation and copulation in *Orthetrum coerulescens* and it is occupied by intense activity. Observations were made on *O. coerulescens* at a stream in the South of England during June and early July, 1989. They showed that in 36 tandem pairs (69%) of a total of 52 observed, the interval was less than 10 s whereas in 6 pairs (12%) it was more then 20 s (Fig. 11). During the longer intervals the pair dipped down repeatedly to the water as they flew rapidly along the stream. Prolonged tandem flights occurred mainly in non-territorial males which formed tandems away from the water and flew through the territories of several other males. They also sometimes climbed to ca. 10 m and then descended to other streams or pools which in turn were inspected. PARR (1983) has described wanderers as being common in this species. In contrast territorial males usually started copulation within a few seconds of tandem formation, flying rapidly back and forth within the same region of the stream during the brief tandem flight.

Tandem flights are probably steered by the male, and the behaviour, both in territorial and non-territorial males, can be interpreted as one in which the male shows potential oviposition sites to the female. Copulation may depend on the acceptance of a site by the female, and the behaviour may

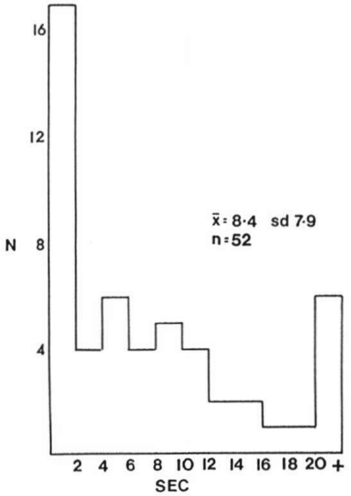


Fig. 11. The duration of the interval in seconds between tandem formation and copulation in *Orthetrum coerulescens*. The last column, 20 +, includes pairs which flew out of sight while still in tandem.

thus represent in-tandem courtship. It will be of interest to see if comparable behaviour is widespread in libellulids.

CONCLUSIONS

The events immediately following tandem formation in odonates have received little attention in the past: in Anisoptera they take place at high speed on the wing and are difficult to observe, but in Zygoptera they may occur after settling and are sometimes prolonged. I suggest that in some species which show no pre-tandem courtship such activity may represent in-tandem courtship. Males probably cannot force copulation and females are thus provided with an opportunity for rejecting or accepting their partners.

Male *O. coerulescens* when in tandem sometimes make dipping movements down towards the water, apparently demonstrating potential oviposition sites to the female. MOORE (1952) and UTZERI (1989) have both noted that a male *Sympetrum* sp. in tandem with a dead female may make dipping movements resembling oviposition and they suggested that this indicates control of oviposition by the male. However such behaviour may alternatively represent in-tandem courtship, a possibility which does not invalidate the proposal that males also control oviposition when in tandem.

Pre-tandem courtship is common in Zygoptera but rare in Anisoptera. In the libellulid *B. lacustris* my observations suggest that it is connected with an unusual feeding pattern. Feeding takes place principally during eocrepuscular periods (dawn and dusk) over water where the prey encountered is likely to be swarming insects. The species therefore feeds at times when and in places where it is also reproductively active. Territory-holding males make frequent sallies out towards feeding females attempting to entice them back to their territories, but they are usually unsuccessful. Only an estimated 1-5% of such overtures induced a female to follow. Copulations were infrequent and territory-holding males sometimes gained none during an evening: of 10 copulations seen at Kariba, all took place within 46 min of sunset at a time when numerous other *B. lacustris* flew over the water in the near vicinity. Courtship may therefore allow males to distinguish the minority of receptive females from the majority of unreceptive feeding individuals. Were they to seize females first and attempt copulation subsequently, as is the practice in many other libellulids, time and energy costs might be higher since most females seized would probably be unwilling to mate.

Pre-tandem courtship is known in only 4 other libellulids [1]. Feeding behaviour does not apparently explain its occurrence in these species. However if for other reasons many unreceptive females occur near water, males may benefit similarly by being able to distinguish the minority of receptive females from others in the vicinity.

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