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REPRODUCTIVE BEHAVIOUR OF *ACISOMA PANORPOIDES INFLATUM* SELYS (ANISOPTERA: LIBELLULIDAE)

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The observations were carried out at 2 localities in Nigeria. The ♂♂ defend territories, maintained on a temporary basis. The number of days on which individuals visited water varied from 1-14 (mean 5.33). The territory length amounted to 1.5-2.0 m (between 09.00-10.30 hrs), and 0.50-0.75 m (later in the day). The territories were defended for 8-42 min. Sperm transfer was not observed after a ♂ had secured a ♀. Copulation ranged between 3.9-6.8 sec. Both sexes mated more than once daily. After copulation the partners were resting either separately or, infrequently, in tandem (0.0-106.7 sec). Oviposition is complex and lasted for 20.9-160.3 sec (mean 74.7). The perching plants provided suitable oviposition sites.

INTRODUCTION

Reproductive behaviour of libellulid dragonflies, particularly males, had been observed and experimented on by various workers, e.g. MOORE (1952, 1957, 1960), JACOBS (1955), ITO (1060), KORMONDY (1961), PAJUNEN (1962), CAMPANELLA (1972), PARR & PARR (1974), and GREEN (1974), amongst others, revealed that libellulids hold and defend territories, and exhibit localization to varying degrees.

This investigation is an examination of the reproductive behaviour of *Acisoma panorpoides inflatum* Selys with respect to the time of arrival at water, the size and maintenance of the territory, the degree of localization, and copulation and oviposition behaviour. This species is on the wing all the year round (HASSAN, 1974) and forms one of the most abundant libellulids around ponds in the south-western region of Nigeria. The study was carried out at the peripheral areas of two ponds, viz. the Oba dam and one of the ponds of the

Faculty of Agriculture (Agric. Pond), both located at the University of Ibadan.

The Oba dam was constructed in 1962 by damming the Oba stream, impounding an area of about 2.5 ha (ITA, 1971). It was re-impounded in 1970 to cover an area of about 6 ha with a total length of 800 m and an average width of 130 m. The depth varies from 0.5 to 7 m. The dominant vegetation is *Pistia stratiotes*, with formations of *Azolla pinnata* v. *africana*, *Nymphaea* spp., *Salvinia nymphellula* and *Marsilea diffusa*. *Alternantheria sessilis*, *Cynodon* spp. and *Brachiara mutica* are abundant along the shorelines. In contrast the Agric. pond is a small (surface less than 1 ha), shallow (maximum depth 2.3 m) pond, dammed in 1965. The commonest plants are *Nymphaea* spp. *Utricularia* sp. and *A. pinnata*. The edges are dominated by *Cynodon* spp.

METHODS

Hourly counts of male and female populations at water throughout the day (08.00-18.00 hrs) were made for three sunny days to study the daily population build-up of this species. Observations were made later on marked and unmarked males and females of *A. p. inflatum* for 33 continuous days between January 6 and February 8, 1977. 50 males were captured, marked and released at Oba dam. 20 females were also marked, 10 at each body of water. The locations at which each individual was marked were noted. Using a modification of the methods of JACKSON (1953) and PARR & PARR (1974), each individual was distinguished in the field. After marking, most of the insects readily mixed back into the population. The number marked represented about 7-10% of the individuals present.

Subsequent recapture was found unnecessary, through this was carried out frequently, because the markings were readily identified, using binoculars where necessary. WAAGE (1972, 1973) and PARR & PARR (1974) were also able to identify each marked dragonfly.

Observations on the territoriality and localization, copulation and oviposition behaviour were made twice daily: 09.00-12.00 and 14.00-16.00 hrs. The identity of sighted marked males and the location where sighted were recorded daily with notes on the regularity with which they used the same or different perches. These were later matched against the individual's history. The size of the territories and behaviour associated with the defence and the duration of holding territories were recorded. The capture of females by males, pre-copulation flight, copulation and oviposition were observed and timed in 18 copulae that completed the behaviour. Plants used for oviposition were identified and the frequency of mating of marked males and females was also documented. Most of the observations on copulation and oviposition were made at the Agric. pond.

RECOVERY OF MARKED INDIVIDUALS

Thirty-three of the marked males (66%) were sighted. The total number of days on which the individuals visited water varied from 1 to 14, (mean of 5.33 days). The longest continuous number of days on which individuals visited water was 4, whilst the longest number of days between sighting of an individual was 12. Some individuals were sighted two or three times a day. Observations on the distribution of the individuals showed that about 62% of the recovered males remained close to their area of marking. Some individuals were observed returning to the same area for upwards of 4 days while at water. A particular male (Fig. 1a) came to water twelve times throughout the study and kept territories within a length of 3.8 m. This shows a high degree of localization. ITO (1960) referred to this behaviour as "residentiality" in *Orthetrum albistylum speciosum* (Uhler) due to the high frequency of localization. However, it was observed that some individuals wandered to some extent (Fig. 1c, d). Five individuals never stayed within 3 m of their last territories and were observed to traverse between 38 and 69 m within the duration of the study.

Only 12 of the marked females (60%) were observed at water (nine at the Agric. pond and three at Oba dam). They showed no regular visiting pattern. Observed visitation to water ranged from 2 to 9 days. Five individuals visited water more than once a day.

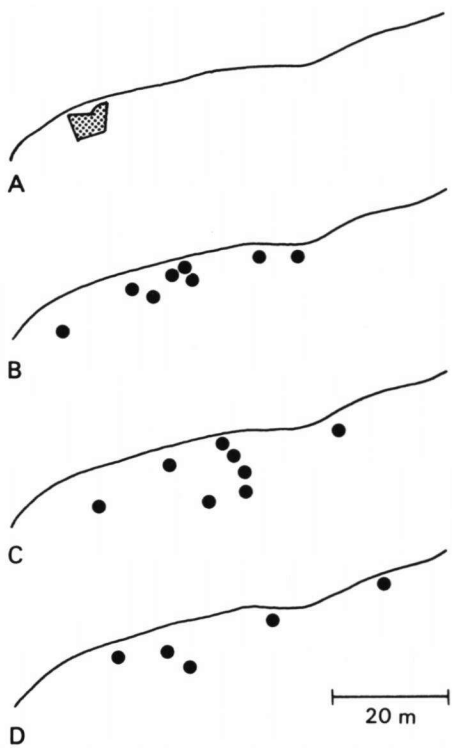

Fig. 1. Different degrees of localization in four individuals of *Acisoma panorpoides inflatum*: (A) the checked box showing the position of territories of an individual on twelve visits; – (B-D) specific territories of 3 other individuals at each visit to water.

TERRITORIALITY

Males start to arrive at water at about 09.00 hrs. From then, there is a daily

population build-up, usually reaching a peak between 12.00 and 13.00 hrs (Fig. 2). On arrival at water, males establish territories which they defend until they leave. During this period (09.00-10.30 hrs), when the numbers of individuals are low, the territory of each male is generally larger than typical (1.5 to 2.0 m); the size gradually being reduced as more males arrive at water (0.50-0.75 m). The sizes of these territories are smaller than those observed by Hassan (unpublished) for *Urothemis assignata* Selys, and by PARR & PARR (1974) for *Nesciothemis nigeriensis* Gambles, both medium sized libellulids. This difference might be due to the size of the dragonflies, since according to CORBET (1962), the smaller the dragonfly, the smaller the area occupied. However, it also appears that the pressure of the number of males at water also modifies the sizes of their territories. Indeed, a high density of males in *Palpopleura l. lucia* (Drury) can result in the breakdown of territorial behaviour (HASSAN, 1974). This has also been observed by PAJUNEN (1962) in *Leucorrhinia dubia* and by WAAGE (1973) in *Calopteryx maculatus* (P. de Beauv.). This contradicts the opinion of MOORE (1964), who attributed inter- and intra-specific aggression as one of the factors which might cause low density at water. The large territories observed by KORMONDY (1961) for *Tetragoneuria cynosura* (Say) and by MOORE (1953) for various species might be due to relatively few males at water. This has also been observed in some tropical libellulids, particularly so in *Trithemis arteriosa* (Burm.), *Crocothemis erythraea* (Brullé) and *Orthetrum* spp. (Hassan, unpublished).

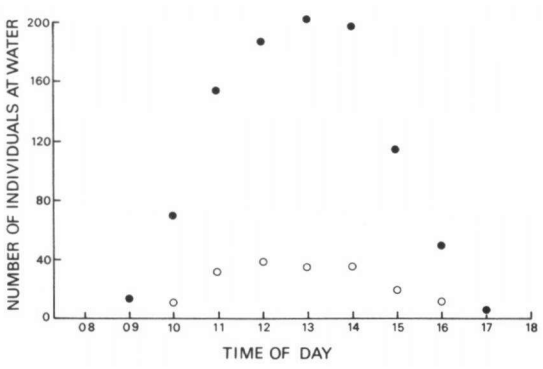

Fig. 2. Variation in the number of male • and female ○ of *Acisoma panorpoides inflatum* present at a 50 metre stretch along the bank of the Oba dam during the course of the day. (Note that the plotted data show the average of three days variations.)

These territories are kept but for a short time, ranging between 8 and 42 min (mean 16.8 min in 138 timed individuals). The individuals either shift to another area or move completely away from water. Such males rarely come back to water. This behavioural pattern of keeping a territory for a short period of the day and returning to it daily is similar to what CAMPANELLA & WOLF (1974) observed in *Plathemis lydia* (Drury). They referred to this type of organization as "temporal lek".

A. p. inflatum males maintain territories on a temporal basis. This species usually perches on flat surfaces of floating leaves and rarely on emergent plants. Territoriality becomes marked around 11.30-15.00 hrs, when the density of males at water is high (Fig. 2) and consequently, intraspecific aggression becomes pronounced. Violent interspecific aggression also occurs between our species and *Diplacodes lefebvrei* (Ramb.). The reason for this interspecific aggression, which is rare in tropical libellulids and which is involving wings and body clashes, is obscure. It might be because the females of *D. lefebvrei* have a similar body colour to the males of *A. p. inflatum*, the two species are of approximately the same size (although of different shape), and they occupy the same ecological habitats.

A male defending a territory constantly parades his territory and perches regularly. The frequency of the parade is dependent on the intensity of the sun. At 5,500-7,100 lux and an average ambient temperature of 32.0°C, between 10 and 23 parades/pursuits were made in 200 sec. During dull periods of the day, with light intensities between 2,080 and 3,900 lux and an average ambient temperature of 28.7°C, only up to 5 parades/pursuits were made during the same duration. These observations were each based on 50 individuals.

Aggression to conspecific males entering territories followed a pattern of pursuit and wing clashes which generally result in no injuries. The intruder dodges and flies out of the territory while being pursued. This pursuit behaviour lasts between 3 and 39 sec (in 2 timed observations, mean 15.8 sec). However, occasionally such clashes might be prolonged into a spiritual flight attack, usually resulting in one of them leaving water. HEYMER (1972) also observed such body clashes in *Calopteryx* species resulting in no body injury. However, MOORE (1952) reported some individuals of dragonflies dropping into water as a result of such body clashes. KORMONDY (1961) and PAJUNEN (1962) also reported violent body clashes in *T. cynosura* and *L. dubia* respectively.

REPRODUCTION

Observations and timing of the reproductive activities of *A. p. inflatum* made on marked and unmarked males and females show that the process involved seizure of the females, copulation, resting after copulation and oviposition. 18 copulations that completed the total sequence of events took between 80.0 and 205.6 sec (Tab. I).

SEIZURE AND COPULATION

The males generally seize females in flight when the latter are in their territories. After the female had been secured, tandem flight results. Neither intra male sperm translocation as observed by BICK, BICK & HORNUFF (1976)

in *Chromagrion conditum* (Hag.), nor sperm translocation observed by MOORE (1960) in *Libellula quadrimaculata* L., BICK & BICK (1965a, 1965b) in *Argia apicalis* (Say), BICK & SULZBACH (1966) in *Hetaerina americana* (Fab.) and by CORBET (1962) in many species, was observed in *A. p. inflatum*. According to CORBET (1962), the period of sperm transfer varies between and within species, and may occur in unpaired males, after a male has secured a female or during pre-copula tandem. It is most likely that *Acisoma* performs sperm translocation prior to coming to water and that such translocation suffices for the copulation taking place in a day, since they may mate more than once.

Table I

Duration (in sec) of the reproductive activities of *Acisoma panorpoides inflatum*

	Pre-copula tandem flight	Mating	Resting	Oviposition ♂ with ♀	Total duration
	0.0	6.8	47.2	56.0	110.0
	0.0	6,7	63.3	43.0	113.0
	0.0	5.8	91.2	62.7	159.7
	1.0	5.0	59.4	113.6	179.0
	1.4	5.4	80.6	20.9	108.3
	0.8	4.6	72.5	71.5	149.4
	1.3	4.8	75.7	51.7	133.5
	0.0	6.1	90.0	43.5	144.3
	0.0	5.8	57.6	115.5	178.9
	0.7	4.7	43.1	45.3	93.8
	1.1	3.9	0.0	75.8	80.0
	1.8	6.5	106.7	70.3	185.3
	0.8	4.6	58.5	70.9	134.8
	0.9	4.8	65.6	84.9	156.2
	1.0	5.8	52.6	79.4	137.8
	0.0	5.4	54.9	97.5	157.3
	1.2	5.6	38.5	160.3	205.6
	1.0	4.7	33.2	81.9	120.8
Range	0.0-1.8	3.9-6.8	0.0-106.7	20.9-160.3	80.8-205.6
Mean	*0.7*	*5.4*	*60.6*	*74.7*	*141.4*

Copulation occurs after a pre-copula tandem flight or without it. This flight is momentary (0.0-1.8 sec, mean 0,7 sec) and copulae later settle on a perch at water. Copulation lasts 3.9 to 6.8 sec, (mean 5.4 sec) – a short copulation duration according to CORBET's (1962) classification. Unlike in *Palpopleura lucia* (HASSAN, 1974), the influence of other males has no significant effect on the duration of copulation. Undisturbed copulations lasted 3.9 to 6.1 sec

(147 observations), whilst disturbed ones lasted 4.3 to 6.8 sec (118 observations.

Copulation frequency in both males and females was studied with marked individuals. Results obtained indicated that both sexes may copulate more than once a day. The maximum number of matings recorded were: five for a male and three for a female in one day. This multiple mating has also been observed in other species. JACOBS (1955) recorded 20 matings a day for *Plathemis lydia* males and 127 matings in six successive days in *Perithemis tenera* males in an experimental removal of many males from their habitats, while BICK & BICK (1972) recorded more than one mating a day in *Argia moesta* (Hag.) females but no more than one in *A. plana* (Hag.) females.

RESTING AFTER COPULATION

After copulation, resting follows. The male and female usually rest separately on different perches, although occasionally the copula does not separate. In all cases, the female remains on the perch where copulation occurred. If any other male disturbs the resting female, the male puts up a protective behaviour and chases away the intruding male. The distance between the pair, when they separate, varies between 5 and 34 cm. The duration of this rest also varies from 0.0 to 106.7 sec (mean 60.6 sec) (cf. Tab. I).

OVIPOSITION

Exploratory activities do not occur in *A. p. inflatum*, probably because they are always perched on their ovipositing sites. The female breaks the resting period by taking wing and starts ovipositing. Immediately, the male takes to the wing to offer protection to the ovipositing female against other males. The female oviposits in areas where *Azolla, Utricularia* and *Nymphaea* occur, though areas with *Pistia* and *Cynodon* are visited frequently. Figure 3 shows a characteristic oviposition site of *A. p. inflatum.*

Fig. 3. A characteristic oviposition site of *Acisoma panorpoides inflatum.*

Oviposition is complex in this species. Generally the eggs are "oozed" out onto the submerged vegetation

by the female dipping the posterior end of its abdomen in water. A total of 3 to 9 such dips might be made before oviposition is completed. However, oviposition is usually alternated with resting periods which vary from two to five in number. This is responsible for the long duration of oviposition: 20.0-16.3 sec (mean 74.7 sec). When no resting was occasionally observed, oviposition duration was shorter (20.0-51.8 sec; mean 31.9 sec; 10 observations) than when it did occur. During these resting periods of the female, the male also rests and only takes to the wing when the female restarts oviposition.

Oviposition is not usually completed in our species when the density of males at water is high. At these times, there is persistent interference with the ovipositing female by males. When more than one male interferes, one usually succeeds in seizing the female. Occasionally, the ovipositing female leaves the water. This act probably explains the incidences of females seen ovipositing unguarded by males in the evenings (16.00-18.30 hrs), when most males had left the water for their roosting sites (HASSAN, 1976). This behaviour also occurs extensively in *Palpopleura lucia* (HASSAN, 1974), and has also been observed in *Plathemis lydia* (JACOBS, 1955).

After oviposition is completed, both male and female *Acisoma* engage in an upright spiral flight resulting in the female leaving the water. In doing so, the posterior end of the abdomen of the female (abdominal segments 6-10) is curved ventrally downwards. BICK (1966) observed this ventral abdominal curving in females of *Ischnura verticalis* (Say). This coupled with wing warning, he stated, constitutes threat display in unaccompanied females of *I. verticalis*. The function of this ventral curvature of the abdomen in our species is obscure. The height reached during such flights ranges from 1.5 to 2.0 metres. Occasionally, the males may not accompany the females.

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