

**BEHAVIOURAL ECOLOGY OF *TYRIOBAPTA TORRIDA*
KIRBY AT THE BREEDING AND RESTING SITES
(ANISOPTERA : LIBELLULIDAE)**

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Received March 10, 1998 / Revised and Accepted August 15, 1998

T. torrida showed territoriality at the water bodies where breeding occurs and also site fidelity at the resting sites on tree trunks away from the water. At the latter, residentiality is very localised not only to a specific tree but to a narrow range of height on the tree. Activity patterns at the breeding sites commenced with the male arrival. The density and activity reached an initial peak during mid-morning which coincided with the high day temperature. Aggression peaked at this time although pursued only for brief periods. The duration for perching behaviour was low during reproductive periods which otherwise had longer bouts.

INTRODUCTION

A cursory glance at the literature reveals a wide-ranging study on odonate behaviour. The majority of these studies reported behaviour patterns mainly localised at the breeding sites MOORE (1987), MARTENS (1991), MILLER (1991) and McKINNON & MAY (1994) on the anisopterans and CONRAD & HERMAN (1987), FINCKE (1987) and CORDERO (1989) on the zygopterans. This is in contrast to the small amount of research on behaviour conducted at the resting or roosting sites, where they are found to aggregate (HASSAN, 1976; ASKEW, 1982; JOSEPH & LAHIRI, 1989 and MILLER, 1989).

In the present study, an attempt was made to compare the diurnal changes in the density and behaviour patterns in a selected species that exploit two different kinds of microhabitats, namely a breeding site (at the water bodies) and a resting site (on the main trunk of trees). *Tyriobapta torrida* is an ideal species on which to conduct behavioural studies, both at and away from the breeding sites because they typically frequent slow-flowing waters and wandered off to congregate at trees away from water. This day-time aggregative behaviour on tree bark is indicative of rest-

ing postures similar to males perching in their breeding territories. The resting posture adopted by *T. torrida* is with the body parallel, perpendicular or inclined to the perching substrate and with wings outspread. ASKEW (1982) defined resting postures in coenagrionids as when the legs are extended from the body as opposed to roosting when the legs are held close to the body. This description, however, differed greatly in certain libellulids, where head position and body posture are important indicators of roosting (HASSAN, 1976).

T. torrida is widespread in Malaysia from northern part of Peninsular Malaysia in Perak (NORMA-RASHID, 1995), on the Eastcoast of Pahang (KEMP & KEMP, 1989), throughout Kuala Lumpur, either in montane streams, forested hill-ponds or lowlands (FURTADO, 1969; BROOKS, 1981; KEMP & KEMP, 1989). It is also found in Sabah (HUISMAN & VAN TOL, 1989).

METHODS

The study was carried out in January-March 1994 on the campus of University of Malaya, Kuala Lumpur, Malaysia. Direct observation was conducted at two localities exploited by *T. torrida*. The first was a swampy area 19.0m long by 12.5m wide and with a water depth of less than 0.5m. The bottom substrate was soft mud and the swamp was connected to a sluggish stream, the first 18m of which were included in the study area. The width of the stream was 1.6-1.9m with a depth of less than 0.3m. This was a shaded area with 60-80% coverage. This habitat was the breeding site and there was vegetation bordering the banks, overhanging branches, roots, and other temporary perchers such as metal rods, sticks and debris (Fig. 1). The second locality, 15m up on the slope from the first site was the resting site. It was an open area with a row of three angasana trees, *Pterocarpus indicus* (T1, T2 & T3 = Trees Nos 1, 2 & 3; facing the trees from right to left). The circumferences of the trunks at 1.5m above ground were 1.2m, 0.7m and 1.1m for the first to the third tree, respectively. These trees were well exposed to the sun throughout the day. To aid quantitative recording of dragonfly site preference

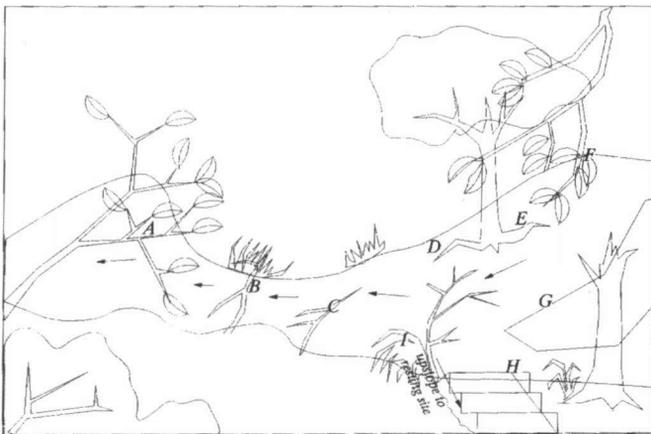


Fig. 1. Sketch map of the breeding site (not drawn to scale). Small arrows indicating water flow, males perching posts labelled A-I.

each tree was divided into 0.5m zones from the ground to 3m; no dragonflies perched above this level.

All individuals at both localities were captured, marked with numbers on the hind-wings using a permanent marker pen and released. This technique has been widely used and appears to have no adverse effects on odonate behaviour. Fewer females were marked at the breeding site compared to males as not to interrupt reproductive behaviour. However, on the tree-trunks, there were more marked females and normally only one male per tree. Records were kept of the sex, the lengths of the fore-wing, hind-wing and abdomen of the marked individuals, and of the time and place of marking.

For each visit, the population was sampled at both study sites to obtain the temporal distribution of this species during the daylight hours. Activity records of frequency and duration were gathered by focal sampling on selected marked individuals for 15min at various times during the day, and some were also videotaped. This allowed simultaneous analysis of several behavioural parameters: perching, patrol flight, interspecific aggressions, copulation, female oviposition, mate guarding, feeding flight, stabilising flight and site preference.

Environmental parameters such as air temperature and cloud cover were obtained during the periods of observation. The cloud-cover index was scaled between 0 (clear sunny day) to 10 (full cloud coverage). During the study period sunrise was on average at 07:18h and sunset at 19:28h (Malaysian Standard Time).

RESULTS

BODY MEASUREMENTS

Results for the three measurements taken for males and females at the breeding (water-bodies) and resting (tree trunk) sites are summarised in Table I. There is a general trend of females being bigger than males (Fore-wing: $p < 0.001$; Hind-wing: $p < 0.001$; Abdominal Length: $p < 0.001$). More interestingly, when the effects of female visits on male size were analysed at the breeding site, there seemed to be a preference for males with longer hind-wings (Tab. II). Fore-wings and

Table I

The range of sizes (min - max) for males and females at breeding (water-body) and resting (tree-trunk) sites. The mean values are in brackets \pm S.D. - [AL: abdomen length; - FW: fore-wing length; - HW: hind-wing length]

Sex	n	Site	Measurements (mm)		
			FW	HW	AL
♂	29	water-body	25.0 - 29.0	23.0 - 26.0	18.0 - 21.0
			(26.68 \pm 0.17)	(24.76 \pm 0.19)	(19.72 \pm 0.17)
	13	tree-trunk	25.0 - 28.0	23.0 - 26.0	19.0 - 22.0
			(26.54 \pm 0.24)	(25.0 \pm 0.30)	(20.23 \pm 0.30)
♀	6	water-body	26.0 - 30.0	25.0 - 28.0	20.0 - 22.0
			(28.17 \pm 0.70)	(27.0 \pm 0.63)	(21.0 \pm 0.37)
	30	tree-trunk	23.0 - 31.0	22.0 - 28.0	20.0 - 24.0
			(28.40 \pm 0.28)	(26.47 \pm 0.28)	(21.73 \pm 0.18)

Table II
T-test comparisons between fore-wing (FW), hind-wing (HW) and abdomen length (AB) of males in the presence or absence of female(s) in their territories

Measures of	Female	n	Mean	SD	t	P
FW	Present	15.00	26.93	1.16	0.53	0.600
	Absent	15.00	26.73	0.88		
HW	Present	15.00	25.60	1.18	3.20	0.003
	Absent	15.00	24.33	0.98		
AL	Present	15.00	20.27	1.44	1.08	0.290
	Absent	15.00	19.80	0.86		

abdominal lengths were not important. This score did not take into account the total number of female visits or her subsequent behaviour.

TEMPORAL DISTRIBUTION

The population density at the breeding site of this species followed the usual distribution curve over the course of the day (Fig. 2). Males were the first arrivals at the pond; their earliest presence recorded was 09:00, peaking together with the air temperature to maintain a plateau within the range of 30-32°C at 10:00. The density reached a maximum at 12:00-13:00. The males started to decline in number after 13:00 and completely departed from the water at 18:00. This temporal mode was roughly maintained by the females but with lower values. There was an obvious lapse in time between male arrival and female appearance at the water-body. A

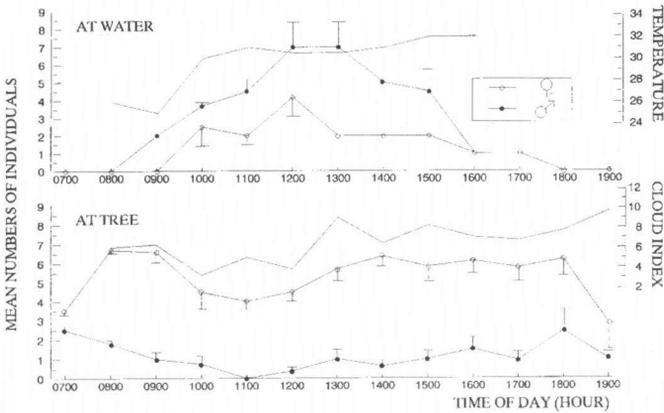


Fig. 2. Variation in the mean numbers (\pm S.D.) of males and females *Tyriobapta torrida* at the two localities during the period of study.

few marked males that were monitored for their arrival time, together with that of the first female partner to visit their territories, gave the following recorded times: male no.1 (09:45); male no.5 (09:20); male no.6 (09:55). The arrival times of unmarked female partners were 10:35; 10:31; 11:25 respectively. Males on average spent 5h 25min ($N = 11$, S.D. = 1.01, $R = 4-7h$) at the breeding site but on rainy days the males would retreat earlier from the water. Conversely, females made only short trips and attended the water-body between 10:00 and 17:00. A total of 40 female visits were recorded during the period of study; 75% (30) of these ended in mating and only one of the 30 left without ovipositing.

Comparable to the above trend, the hourly density for the resting site (tree-trunks) produced a bimodal pattern of changes (Fig. 2). Even before sunrise (07:00) individuals perched, catching the glimpse of day. However, when the sun came out and the cloud index fell below 6, males and females started to depart. Although the males left the tree sites for the breeding site, more females arrived to bask on the tree-trunks reaching a peak at 08:00-09:00 (when temperature was 25-26°C). The progressive decline of males on the trees reached zero at 11:00. Similarly, female density started to fall after 09:00 and reached its lowest level at 11:00. These results complement those obtained at the water. Many females, but only a few males, returned after midday to perch on the trees. Most females remained on the trees while the males left for the water and finally joined the tree aggregation at 18:00 until all left for their roosting sites between 19:15-19:40. This indicated a daily movement between resting and breeding sites. It is useful to give some specific examples here: on 12 Jan., male no.1 left the tree at 09:20, was found at the water at 09:26, and went back to the tree at 13:24. Contact was then lost with it, but it was found at the water again at 15:07. In contrast male no.2, which left the tree between 09:20-10:00, was spotted at the water at 10:00 and remained there until 15:28.

ACTIVITY PATTERNS

Territorial males would test a few perching posts upon arrival at the water before settling on a particular one, they always perched facing the bank or if on overhanging vegetation, backing the water flow. Figure 3 shows the diurnal fluctuations of various activities at the breeding site (water). All behaviours started to increase from 09:00 and reached an initial peak at 10:00-11:00. Perching and flight behaviours rise and fall between 10:00 to 16:00 before dropping suddenly after 16:00. Aggressive behaviour, which included chasing and fighting among interspecific males reached a maximum at 11:00 and gradually dropped to zero at 17:00. Fights were very intense during the hours of females presence, and contests between three males in circular fighting were quite common. Females began to arrive after 10:00 (Tab. III) where approaching females were immediately seized and matings were brief ($R = 20-36s$). Copulations were either accomplished while in flight or while on perching posts. Although not significant, the duration of matings seemed to

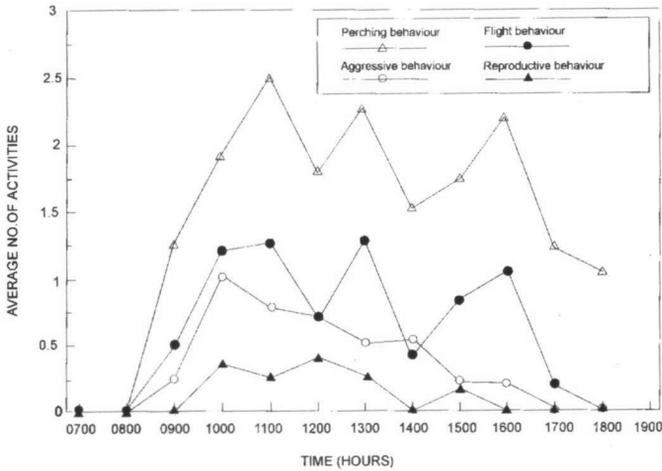


Fig. 3. Hourly fluctuations in average numbers of activities in males, based on 15 min. observation periods for each hour at the breeding site.

reflect the oviposition bouts. The males guarded their partner closely as soon as she commenced oviposition. Hovering flight above her was interspersed with perching nearby or in pursuing disturbances (especially rival males) to return later, never abandoning the ovipositing female. Occasionally, two females were simultaneously guarded by the same partner, in which they oviposited side by side. Females always oviposited facing the banks, rotating about a point while flicking their abdomens in the water. Reproductive behaviour reached a plateau from 10:00 to 13:00, with little evidence of it after this time.

From the standpoint of duration for various behaviour patterns at hourly intervals (Fig. 4), perching times at the breeding site were low during peak copulation time and there were progressively longer bouts after 11:00. Flights were brief throughout, while aggressive behaviour was not pursued for long periods.

It is clearly of interest to see what behaviours occurred at the aggregation zone (tree-trunk) where space was limited. Evidently, there was a greater incidence (48%) of perching behaviour (Fig. 5) and comparable amount of flight behaviours (a total of 44%). The various flight strategies available can be categorised into:

- hopping = swift jump (loop shaped) either to a level above or below the original position (21%);
- stabilizing = short flights close to the surface of the trunk (11%); and
- long flight = distance flight which may take the individual to another locality (12%).

Hopping and long flights might contain feeding components. Other behaviours (8%) included low incidences of interaction, where a female was seen attempting to land on a perched male. Individuals were also seen to twitch their abdomens or

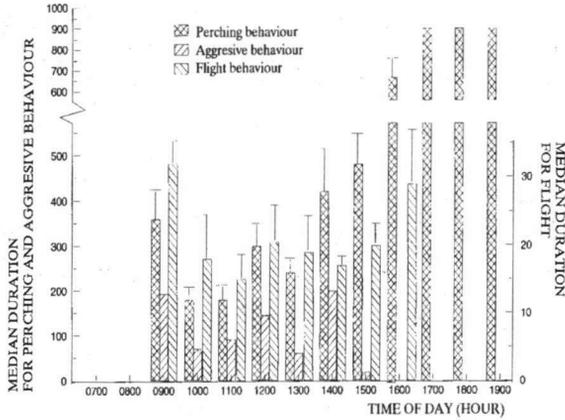


Fig. 4. Median duration (seconds) spent by males on each activity, based on 15 min. observation period for each hour at the breeding site.

beat their wings in order to fan off disturbances, e.g. crawling ants (which were not preyed upon).

Teneral males sometimes appeared on the trees and could be mistaken for females if not examined closely, because they are devoid of the patterned hind-wings. During bad weather (drizzle or heavy rain) individuals persistently perched when it was not time to depart for roosting.

SPATIAL DISTRIBUTION

Males at the breeding site were typically territorial (size of territories ranged between 3-5m), and disputes were commonly seen within overlapping territorial boundaries. Males were classified as territorial when they occupied a particular spot for at least two consecutive days. Sixty seven percent (i.e. 18) of the territorial males studied for site fidelity between 15 January and 28 February, showed marked attachment to a particular site, one holding the territory for 26 days. A further

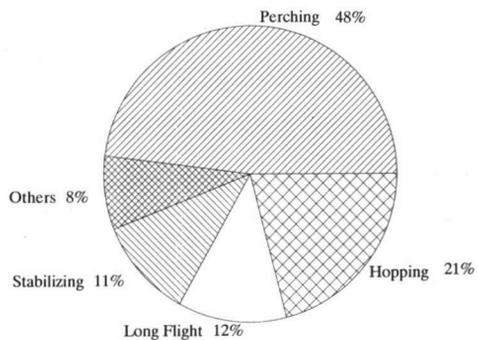


Fig. 5. Mean percentage of activities of *Tyriobapta torrida* at the tree trunk (resting site) between 0800-1900 h.

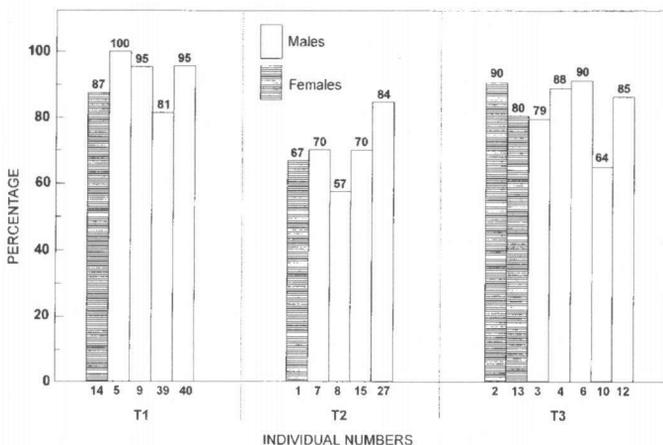


Fig. 6. The maximum percentage of individual choice of perch for the three trees, T1, T2 and T3.

16.6% alternated between two territories, while the remaining 16.6% had three territories at the water.

The next question that arises is that whether site fidelity exists at the trees where they perch to rest during the day. To examine this spatial distribution on tree trunks, four males and thirteen females were traced for a total of thirty-eight sampling periods from 10 January until 18 February. Figure 6 shows a clear individual choice for preferred trees where a single male on T1 and T2 clustered with four females, and two males congregated with five females on T3. However, on few occasions individuals flew to neighbouring trees. These displacements were shown (Fig. 7) to be significantly confined to also specific levels ($t = 3.18$, $n = 15$, $p = 0.006$). The analysis was made by comparing preferred levels (based on maximum values) and non-preferred levels (summation of other smaller values).

Perching site preference was investigated further. Selected individuals were monitored for localised movements at a favourite post, both at the water and tree perches. Generally, at the water the results showed a clear overlap with the activity periods, i.e. low rates of shifting when activity was low and vice versa. Tree perches revealed slight shifts from the chosen spots during the morning basking, but bouts of restlessness (indicated by the frequent localised shifts) were evident during the afternoon period, and especially before the onset of roosting departure. An example of this localised movements at the tree is shown in Figure 8.

DISCUSSION

Size is an important fitness component because of its correlation with mating success. Many odonate studies have attributed characteristics of body size to mating efficiency. Thus CORDERO (1992) related body size to female fecundity in

Ischnura graellsii, and males of the same species showed positive correlation between ejaculation and body size (CORDERO & MILLER, 1992). Also, *Nannophya pygmaea*, larger males held better ranking territories (TSUBAKI & TOMOHIRO, 1987). In contrast, BANKS & THOMPSON (1989) reported a high mating rate in smaller sized males. Parallel to this, numerous studies have reported on the female strategy for mate selection based on morphological criteria, e.g. ROBERTSON (1986), JOHNSON (1988) and SIMMONS (1988). Although preliminary, there is some evidence here of female choice for a partner with longer hind-wings, indicative of larger patterned areas at the base of hind-wings (typical wing feature for *T. torrida* males), one speculative explanation is that it could serve the purpose of being an extrinsic stimulus for attracting females. This is further enforced by observations of some female *T. torrida* which oviposited directly in front of an engrossed, perched territorial male who then became aware of, caught and mated the female. PAULSON (1981) suggested the importance of wing features for courtship displays in the chlorocyphids.

The movement patterns back and forth between the breeding (water) and resting sites (trees) are distinctly temporal throughout the day because movements are influenced predominantly by an endogenous rhythm and exogenous air temperature and cloud index. To obtain an overall picture of the daily movement patterns of *T. torrida*, the various interacting factors involved need to be understood. These appear mainly to be density, activity and sex differences. The densities at the trees and water were closely linked with the activity rhythms, especially the repro-

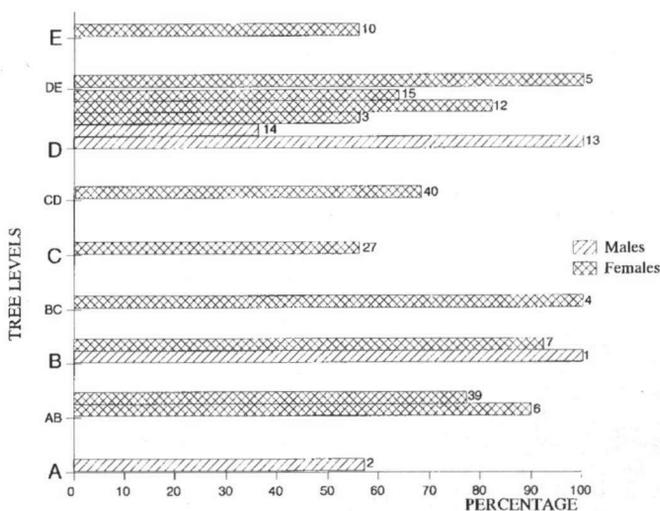


Fig. 7. The maximum percentage of individual choice of perch for levels A, B, C, D, E and inter-boundaries (AB, BC, CD, DE) regardless of whether on trees T1, T2 or T3. Numbers on bars indicate marked individuals.

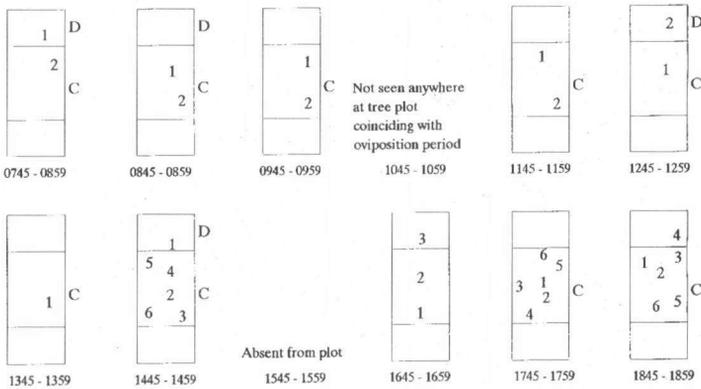


Fig. 8. Time series of localised movements of female No. 11 during 15 min periods each hour at the tree trunk. C & D indicate tree levels. Numbers show the sequence of perching shifts.

ductive phases. During mid-morning, males left for the water before females, after basking on the trees to resume, establish or take-over territorial sites. Before the onset of female arrivals at the water, male density and activity peaked. Females, however, spent a longer time basking in the morning; later they made intermittent visits to copulate and oviposit with an obvious synchrony at certain periods within a day. Some males exploited this situation by being fully active during peak female arrival, and left the water when female numbers declined to perch on resting site (tree-trunk), while other males which were unable to compete effectively for females (during the maximum reproductive period) prolonged occupancy at the water to grab mating chances. Clearly this is a different tactic from the unsuccessful or inferior males who abandon the water sites to copulate elsewhere (e.g. *Orthetrum caledonicum*; ALCOCK, 1988) or defended basking sites instead to obtain potential mates (e.g. *Argia vivida*; CONRAD & PRITCHARD, 1988). After a short or prolonged resting bout at the trees, the males of *T. torrida* returned to the water for more mating opportunities but with lesser intensity. The movement from water to the trees in other anisopterans has been ascribed as reducing heat stress (McGEOCH & SAMWAYS, 1991). This is doubtful in the case of *T. torrida*, where the breeding site is shadier in contrast to the open area of the trees. It is probable that the males of this population were escaping from a different stress, i.e. competition for resources (space and females). Prolonged stay at the water keeps the males under constant pressure to guard their territory and mate. Although this work has established the fact that localization on the tree-trunk exists aggression was almost non-existent between sympatric individuals; this could be due to no mating episodes happening at the resting site.

Localisation of residency existed at the tree site. Individuals constantly perched on preferred trees (as had been reported in *Potamarcha congener*; MILLER, 1989).

Furthermore, they also used specific zones within a tree and if/when shifting occurred they confined their activities to consistent horizontal height levels. The term micro-localization to describe a highly preferred perching site was used by PARR (1980) at the breeding territories where aggression levels between rivals were strong. It is apparent here that individuals do not invest in high energy expenditure by being aggressive but instead maintain a spatial partitioning by avoidance behaviour to achieve a harmonious, stable situation in their community.

ACKNOWLEDGEMENTS

My sincere appreciation to many who have helped in various ways; WAN ABDUL RASHID, HAJI MOKHTAR, SASEKUMAR and an anonymous reviewer.

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Table III

Arrivals of females that were timed for durations of mating and oviposition at breeding sites. Values in brackets are frequency of abdominal dips. (a) and (b) were females that were simultaneously guarded by the same male

Time of arrival	Duration (seconds)	
	Mating	Oviposition (dips)
10:17	29	552 (937)
10:31	26	no oviposition
10:34	25	425
10:45	26	625 (1256)
10:56	29	511 (786)
10:56	27	343 (684)
11:25	20	503 (781)
11:25	27	342 (697)
11:34	24	370 (873)
11:51	24	321 (647)
12:08	(a) 31	351 (687)
12:09	(b) 21	300
15:13	36	336

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