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TERRITORIAL BEHAVIOUR OF THE AFRICAN LIBELLULID *ORTHETRUM JULIA* KIRBY (ANISOPTERA)

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The observations were carried out on a colony of the pale montane form of *O. j. falsum* Longf. (8 April - 4 June, 1977) at Naisi, Zomba Mountain, southern Malaŵi. 277 ♂♂ and 13 ♀♀ were given unique numbers on the wings which enabled recognition without subsequent recapture, and the positions of territorial ♂♂ were recorded accurately each time the colony was visited. The most frequently seen individuals showed the greatest consistency of localization. This indicates that the most frequently seen individuals were superior in territorial defence and hence tended to return most often to a chosen area. Whereas a territory might measure up to 10 m in diameter, the central zone, where the insect spent 75% of its territorial time, would be only about 2.5 m^2, or less. Many territories were much smaller than 5 m in diameter. The outer zone territories of neighbouring insects often overlapped. In the late afternoon, the highly structured territorial system broke down and many widely ranging ♂♂ were observed to invade the colony area. In the mornings the territories tended to be occupied as soon as they were in partial or full sunlight. The territorial ♂♂ spent 5-13% of their time in flight, depending on weather conditions. About 60% of all territorial flights were aggressive and 20% were feeding flights. ♀♀ occurred at the breeding sites at any time during the territorial period, but observed matings took place 10.13-14.45 hrs. The mean copula duration was 29.5 sec. Usually the ♀ oviposited in the ♂'s territory immediately after copulation there and was attended by him, hovering over her. The mean survival for mature ♂♂ was 9.0 days and maximum observed survival was 51 days.

INTRODUCTION

It has long been recognized that behavioural studies of Odonata are fruitful in providing valuable information about this taxon, in addition to contributing to our understanding of some of the fundamental concepts of animal behaviour. In particular, studies of territorial behaviour in the Odonata, especially the Libellulidae and Calopterygidae, are increasingly important in elucidating the complex relationship between localization (residentiality), aggression and reproductive behaviour. Such studies of specific dragonfly taxa may prove to be of value in understanding analogous behavioural patterns in other animal groups exhibiting territoriality. The work of SAKAGAMI et al. (1974) is an important attempt to begin the analysis of the inter-related and variable nature of territorial and reproductive behaviour in the Libellulidae using an evolutionary approach.

The present author considers that behavioural studies of congeneric and other related species may be especially valuable in contributing to the understanding of detailed taxonomic relationships (HEYMER, 1969; PARR, 1973; PARR & PARR, 1974). For example, the eco-behavioural work on the African libellulid, *Nesciothemis nigeriensis* Gambles (PARR & PARR, 1974) demonstrated that this species, while conforming in most respects to general libellulid behaviour, was apparently unusual in maintaining mini-territories at the roosting sites, where reproductive behaviour was observed. It is only by a series of detailed studies of the behaviour in natural surroundings that the full range of libellulid response patterns will be recognised and interpreted. However, the field worker generally has to seize any available opportunity to investigate the detailed behaviour of a given species as and when they present themselves. Circumstances very rarely allow exactly parallel studies of related species to be made in a planned sequence.

At the present time, about 25 libellulid species (representing 16 genera) have been studied in some detail with particular reference to territoriality. The best known species in this respect include *Plathemis lydia* (Drury) (JACOBS, 1955; CAMPANELLA & WOLF, 1974), *Orthetrum albistylum speciosum* Uhler (ITO, 1960; ARAI, 1972), *O. coerulescens* (Fabr.) and *O. brunneum* (Fonsc.) (HEYMER, 1969), *O. cancellatum* (L.) (KRÜNER, 1977), *Crocothemis servilia* Drury (HIGASHI, 1969), *Pachydiplax longipennis* Burm., (JOHNSON, 1962), *Nesciothemis nigeriensis* Gambles (PARR & PARR, 1974), *Leucorrhinia dubia* (Vander Lind.) (PAJUNEN, 1962a, 1962b, 1963), *L. rubicunda* (L.) (PAJUNEN, 1963, 1966), *L. caudalis* Charp. (PAJUNEN, 1964), *L. pectoralis* Charp. (KIAUTA, 1964), *Perithemis tenera* (Say) (JACOBS, 1955), *Acisoma panorpoides inflatum* Selys (HASSAN, 1978) and *Sympetrum parvulum* (UÉDA, 1979).

The population of *Orthetrum julia* on Zomba Mountain, Malaŵi, was selected for the present observations because the colony was clearly limited in distribution to a tree nursery which was surrounded either by *Pinus* plantations or seminatural forest. Furthermore, the dragonflies were numerous and the site was easily accessible by landrover from Zomba town.

As far as is known, the behaviour of *O. julia* has not been investigated previously. The main aims of this study were to gather information on localization of individual insects and the range of activities of males while in territorial sites. In addition some information was obtained on longevity and survival rates of males.

METHODS

The population of *Orthetrum julia* was studied by means of direct observations. Between 8 April and 30 May 1977, totals of 277 males and 13 females (all post-teneral) were captured and marked with a unique number using orange or yellow enamel paint on the wings. Observations were made on consecutive days for the periods 8-12 April, 18-24 April and 30 April-2 May, and continued intermittently until 4 June when the population had been observed for a total of 18 days. As far as possible, the observations commenced in the morning, as early as weather conditions would allow and continued for periods ranging from about 1¼ hours to nine hours, with a mean of 3 hours 12 minutes. From the commencement of the work on 8 April, up to and including 22 April, as many unmarked *O. julia* as possible were captured and given a unique number, and the position of each marked male was recorded accurately on a plan of the colony area. Small numbers were also marked on 24 and 30 April, primarily in areas usually occupied by already marked insects. On 24 April and 1 May individual males were observed throughout the day, in order to record detailed behaviour within their defended territories. Times of arrival at territories were noted on three occasions and reproductive behaviour was recorded whenever seen. An estimate of male longevity was obtained from the resighting data of individuals marked on the first eight sampling occasions.

THE HABITAT AND ODONATA

The habitat was a tree nursery in the area known as Naisi on the slopes of Zomba Mountain in southern Malawi. Zomba Mountain (2087 metres), more accurately described as a plateau, has its western face clearly defined by a great scarp along the fault line of the southern section of the East African rift valley system. On the other side of the mountain, including the south-eastern area of Naisi, the scarp is less impressive but is also well defined with a vertical difference in altitude between the surrounding plain and the plateau rim of approximately 1000 m. Naisi nursery (Figs. 1-2) was established at an elevation of 1220 m on one of the numerous flatter shelves between sloping spurs projecting from the mountainside. The nursery occupied an area measuring about 78 m by 72 m and was surrounded on all sides by forest. To the south-east the site drops away into a steep-sided ravine supporting semi-natural forest including *Brachystegia* spp. and *Oxytenanthera abyssinica* (bamboo) adapted to constantly moist conditions. On all other sides, the nursery site was surrounded on the steep slopes by plantations of exotic pines, dominated by mature *Pinus patula* and *P. kesiya*. A permanent, but very small stream flows through the centre of the nursery; this stream receives water from several seepages originating in the nursery area itself. In seven places the stream bed had been dug out to create small pools to facilitate collection of water for irrigation of the quarter of a million or so tree seedlings. Much of the surface of the nursery was terraced flat soil, but rank marsh vegetation was present along the stream and adjacent to the forestry road.

It was noticed that weather, in conjunction with the close proximity of a high over-shadowing mountain had a distinctly limiting effect on the activities of *O. julia* at the Naisi colony. Cool, cloudy, misty and wet conditions were common, so that on many days the insects would spend long periods inactively, especially in the morning. Weather patterns in Malaŵi are complex because of the influence of mountains, the very large Lake Malaŵi and the Indian Ocean. However, although the main rainfall is limited to the months of November - April, persistent low cloud, drizzle and low temperatures of chiperoni weather over rising ground and windward facing escarpments may be experienced at any time of the year. In the present study, chiperoni weather predominated during the period 9-11 April and rain or drizzle ended dragonfly activity on each of those days. The maximum temperature recorded at the colony site ranged from 18.3°C on 11 April in chiperoni conditions, to 26.1°C in clear weather on 22 April. The mean maximum for the study period was 22.6°C. *O. julia* flies throughout the year in the Zomba area, although it is less common during the cool, dry period June - August.

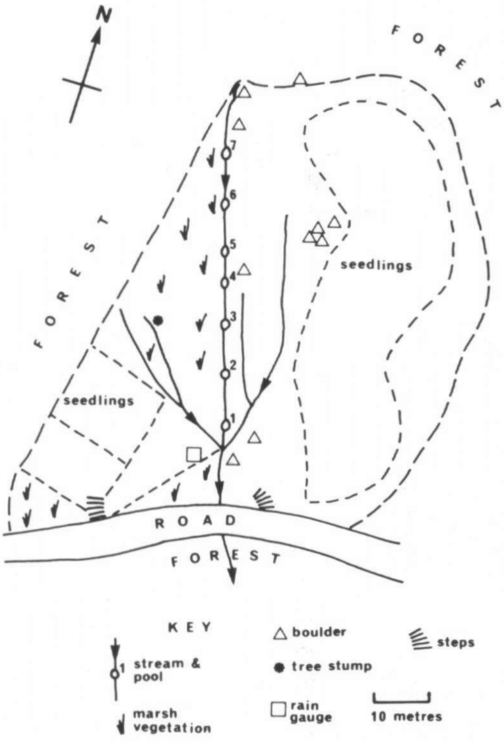

Fig. 1. Map of Naisi nursery area, Zomba Mountain Malaŵi, April-June, 1977.

Orthetrum julia (Fig. 3), which was perhaps the most frequently seen anisopteran at the Naisi nursery, has been the subject of a certain amount of taxonomic confusion. It now seems certain (LONGFIELD, 1955; PINHEY, 1970) that *Othetrum julia* Kirby, 1900, and *O. falsum* Longfield, 1955, are conspecific, and together with their main variants and *O. falsum capicola* Kimmins, 1957, form a cline of races from West to South Africa. The very dark *Orthetrum j. julia* Kirby would appear to be the dominant form in the dense forests of West Africa and the Zaire basin, but eastwards and southwards much paler *O. julia falsum* Longfield are found and *O. julia capicola* Kimmins occurs only in south-west Cape Province of the Republic of South Africa. The specimens of *O. julia* at Naisi seem to agree best with the

Fig. 2. Naisi nursery, Zomba Mountain, looking south-east.

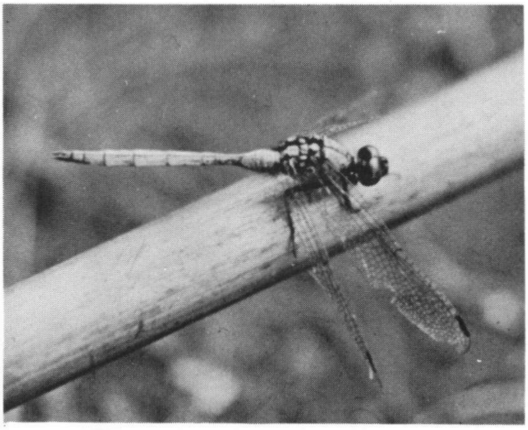

Fig. 3. Photograph of a male *Orthetrum julia*, at Naisi.

pale montane form of *O. julia falsum* described by PINHEY (1970).

In addition to *O. julia*, nine other Odonata species were seen at Naisi nursery during the observation period. Of these, *Crocothemis sanguinolenta* (Burmeister) was most common and it established territories in the same areas as *O. julia*. Small populations of *Orthetrum abbotti* Calvert and *Crocothemis divisa* Baumann existed for the duration of the study period, and large numbers of *Pseudagrion kersteni* (Gerstaecker) were associated with the stream margins. A few individuals of *Orthetrum caffrum* (Burmeister), *Palpopleura lucia portia* (Drury), *P. jucunda* (Rambur), *Diplacodes lefebvrei* (Rambur) and *Pantala flavescens* (Fabricius) were seen at the nursery but without any evidence of breeding.

LOCALIZATION

RANGE OF OBSERVED LOCALIZATION

In the colony studied, most territories were bare or relatively bare areas of soil, often, but not invariably, immediately adjacent to a stream or seepage. The territory was normally only occupied consistently in sunny weather and most favoured perches were small sticks projecting from the surface, stones or rocks. Some individuals established territories amongst waterside vegetation and then rested on tall stems, or grasses overhanging the water.

In common with many other dragonflies exhibiting territoriality, it was noticed that *O. julia* appeared to show a tendency to return repeatedly to the same small area. The detailed analysis of the positions of all marked males in the colony has allowed some conclusions to be reached regarding the predictability and constancy of localization. The information plotted on the site map each time the colony was visited (e.g. Fig. 4) allowed the position(s) of each male *O. julia* to be marked on individual site maps (selected individuals' positions are shown in Fig. 5a-l).

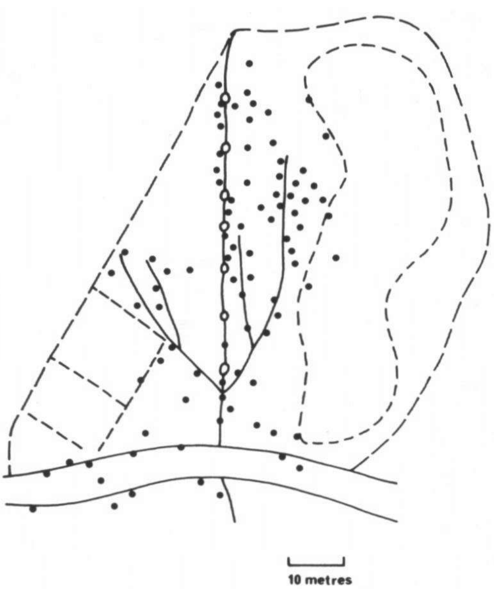

Fig. 4. Positions of territorial male *Orthetrum julia* at Naisi on 23 April, 1977. (cf. Figs. 1-2).

Table I gives the numbers of males seen two (62 insects) or more times, up to a maximum of 14 times (one insect). Column 3 of Table I gives the mean maximum number of times individuals were localised within a circle of 10 m diameter, and col. 4, obtained from the ratio col. 3/col. 1, gives the 'localization index' (I). The parameter I is a measure of individuals' mobility, within the context of territoriality, related to the number of times seen. The circle of 10 m diameter was chosen to measure localization because most individuals showing a tendency to return to a given spot were apparently responding to recognized landmarks within an area of approximately that size or less.

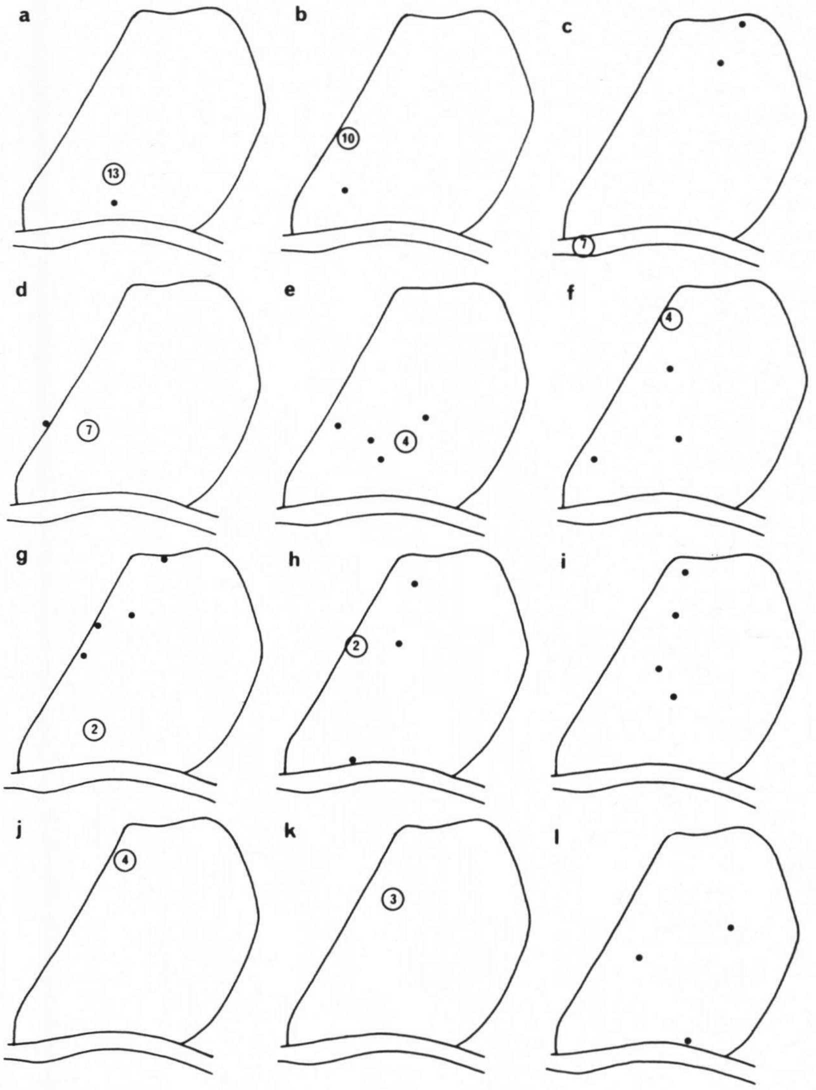

Fig. 5. Outline maps of Naisi nursery showing positions of selected males of *Orthetrum julia* on each occasion they were seen (cf. Figs. 1-2). The ringed numbers indicate the individual was seen that number of times within the 10 m diameter circle. Single dots indicate the individual was seen once in that position: (a) No. 6, seen 14 times. Localization index (I)=0,93; — (b) No. 131, seen 11 times, I=0.91; — (c) No. 34, seen 9 times, I=0.78; — (d) No. 144, seen 8 times, I=0.88; — (e) No. 100, seen 8 times, I=0.50; — (f) No. 20, seen 7 times, I=0.57; — (g) No. 32, seen 6 times, I=0,33; — (h) No. 52, seen 5 times, I=0,40; — (i) No. 103, seen 4 times, I=0,00; — No. 221, seen 4 times, I=1.00; — (k) No. 260, seen 3 times, I=1.00; — (l) No. 258, seen 3 times, I=0.00.

Table I

Calculation of localization index

1 No. times seen	*2* No. insects in sample	*3* Mean max. no. times localized within 10 m circle	*4* Localization index (I) (Col. 3/Col. 1)	*5* Standard deviation of I
14	1	13.00	0.93	—
11	2	9.50	0.86	0.045
9	4	7.00	0.78	0.078
8	7	5.57	0.70	0.188
7	7	3.71	0.53	0.144
6	9	3.00	0.50	0.158
5	22	2.09	0.42	0.255
4	32	1.75	0.44	0.354
3	51	1.18	0.39	0.384
2	62	0.23	0.12	—

It was evident from analysis of all the data that few individuals were wholly predictable in always returning to a 10 m territorial circle. However, it did seem as if the most frequently encountered individuals were generally more predictable in where they might be found. In order to remove possible bias by recording static individuals relatively more frequently than mobile ones, the colony area was searched systematically each time it was visited, so that this probable source of error was minimised. If there were no relationship between the number of times an individual was seen and the probability of its repeated appearance in the same territory, the localization indices would not be expected to rise steadily as the number of sightings increased. However, inspection of Figure 6 and Table I shows that, in fact, the parameter I is very significantly higher in frequently seen insects than in those seen few times. The correlation between the localization index and number of times seen (Fig. 6) is strongly positive, with $r = 0.955$ for 9 d.f., $p < 0.001$. Although the regression line of y on x in Figure 6 is based on a linear relationship between I and the number of times individuals were seen,

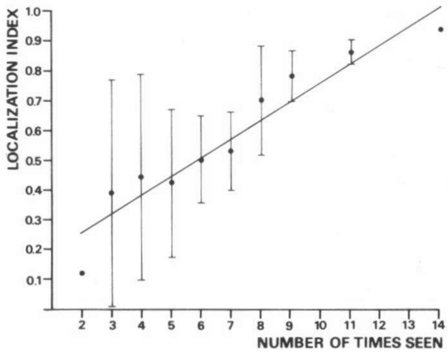

Fig. 6. *Orthetrum julia*. Correlation between Localization Index (I) and number of times seen ($r = 0.955$, $p < 0.001$; $y = 0.0637x + 0.1274$).

an exponential model is probably best used to describe the relationship between these two variables. The value of I for individuals seen only once is set at zero and this parameter's possible maximum value is 1.0, when the number of times seen is infinity. It is hoped to investigate the statistical aspects of the localization index at a later date.

MICRO-LOCALIZATION AT THE TERRITORIAL SITE

The most frequently seen individuals have been shown to have very definite preferences for restricted areas within the colony boundary. However, inspection of Figure 5b-d, for example, shows that usually this is so, but the small scale of the maps obscures the fact that the territory defended on any particular day is apparently slightly different from other days. In order to investigate the territorial localization of a particular individual on a given day, male no. 144 was kept under constant observation on 1 May. This individual (Fig. 5d), was seen seven times out of eight in the same small oval area. On 1 May this male first appeared at 09.15 hrs and departed at 15.45. During this period of exactly six hours a record was kept of its exact position and the time spent on each perch. The individual perches selected by this male are marked on Figure 7 with dots and the figures denote the percentage time (out of six hours) spent at each perching site. Except in the course of some of the longer territorial defence flights, this individual spent the whole of the six hours within the territorial boundary of about 7 m x 5 m shown on Figure 7. However, 75% of its time was spent within the oval central zone of approximately 2.5 m x 1.0 m. The territory was divided by a small seepage stream and it was noticeable that most of the insect's time was spent on the right bank. It may be seen from Figure 8 that much of the territory of this insect was nearly bare soil with a very thin,

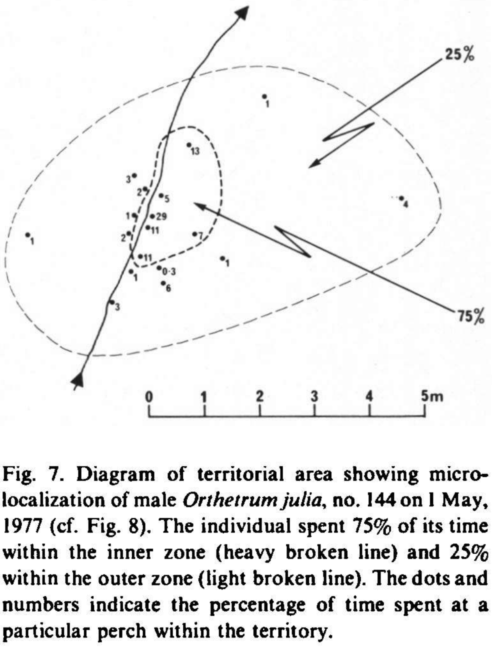

Fig. 7. Diagram of territorial area showing micro-localization of male *Orthetrum julia*, no. 144 on 1 May, 1977 (cf. Fig. 8). The individual spent 75% of its time within the inner zone (heavy broken line) and 25% within the outer zone (light broken line). The dots and numbers indicate the percentage of time spent at a particular perch within the territory.

discontinuous, grass cover. Within this area the most favoured perches were small sticks lying on or projecting from the soil surface and the white rock visible in Figure 8.

Fig. 8. Photograph of territory of male *Orthetrum julia*, no. 144 on 1 May, 1977 (cf. Fig. 7). The territorial boundary is marked with a broken line and the territorial inner zone is marked with a continuous line.

Not only did the length of time spent at each position vary greatly (Fig. 7), but also the insect spent a number of separate periods of varying lengths of time in each perching position (Tab. II). For example, during the day it defended its territory for a total of 40 min. from position 2 (11.1% of the 6 territorial hours), comprising 8 separate periods averaging five minutes each. Within each period at a particular perch the insect made a varying number of flights (mainly feeding and aggressive): if it settled on a different perch at the completion of a flight this was recorded. It may be seen that the dragonfly tended to return most frequently to those perching positions (2, 5, 6 and 8) at which most time was spent (63.6%), and that it exhibited very strong preferences for certain perching sites over other possible ones.

These observations on 1 May suggest that many male individuals are, in fact, more strictly localized when the same area is defended on successive occasions, than at first appears to be the case. For example, no. 131 (Fig. 5b) was defending the same territory on 10 out of the 11 times it was seen, although its precise perching site within that area varied. No. 6 (Fig. 5a) was recorded at almost exactly the same position (a small group of coco-yams, *Colocasia esculenta*) on 12 of the 14 occasions it was seen. This male was unusual in that it habitually rested on the leaves of these plants, and not on other vegetation or the ground.

In most cases the outer zone territories of neigbouring male *O. julia*

Table II

Micro-localization at territory site: No. 144, 1 May, 1977

1 Perching position (Fig. 7)	*2* Total time (min) spent at each position	*3* % of time (6 hrs) spent at each position	*4* No. of indiv. periods spent at each position	*5* Mean & range of length of period (min) (Col. 2/Col. 4)
1	16	4.4	1	16.0 (16)
2	40	11.1	8	5.0 (1-16)
3	9	2.5	2	4.5 (1-8)
4	6	1.7	1	6.0 (6)
5	103	28.6	8	12.9 (4-21)
6	38	10.6	3	12.7 (1-24)
7	3	0.8	2	1.5 (1-2)
8	48	13.3	5	9.6 (1-17)
9	20	5.6	5	4.0 (1-10)
10	1	0.3	1	1.0 (1)
11	4	1.1	2	2.0 (1-3)
12	17	4.7	1	17.0 (17)
13	10	2.8	2	5.0 (2-8)
14	25	6.9	2	12.5 (10-15)
15	8	2.2	2	4.0 (4)
16	4	1.1	1	4.0 (4)
17	3	0.8	2	1.5 (1-2)
18	5	1.4	1	5.0 (5)
total	*360*	*99.9*	*49*	

overlapped to a considerable extent, but it was rare to see any other male being allowed to remain within the inner zone, although this did sometimes happen. The size of territories varied in different parts of the nursery and in several areas the territories were often much smaller than five metres in diameter (Fig. 4).

A life table derived from the marking and resighting data gives a mean observed survival of 9.0 days for mature male *O. julia*. The maximum observed survival times were 51, 49 and 40 days by males no. 34 (Fig. 5c), no. 103 (Fig. 5i) and no. 166 respectively. These survival times can probably be increased by a minimum of 10 days to account for the maturation period of the young dragonfly.

ACTIVITY PATTERNS AND TERRITORIALITY

POST-TERRITORIAL, ROOSTING AND EARLY MORNING BEHAVIOUR

Male *O. julia* abandoned their territories on most days between 15.00 and

16.00 hrs, depending on their position in the nursery (some areas stayed sunny longer than others) and weather conditions. In very bad conditions such as chiperoni weather, the population would not appear at the territorial sites at all. Sometimes an individual would shift its position to another part of the nursery when its territory became shaded in mid or late afternoon. This resulted in some well-established territory holders adopting short-term new territories in sunny sites at the end of the afternoon, prior to leaving the area for roosting. At any time during the day one could see occasional male individuals behaving in a very nomadic fashion and clearly not associated with any definite territory (= wanderers, HIGASHI, 1969). These individuals were usually unpruinosed on the thorax and spent much of their time in active flight. It was presumed that they were young insects. It was noticeable that the numbers of such peripatetic (usually unmarked) individuals increased towards the end of the afternoon when some territory holders were changing their positions. It is assumed that many of these very mobile males were unsuccessful in establishing normal territories. This was either because they were young, or were older and unable to compete successfully with established males because of other, not necessarily age related, factors. In the late afternoon, the closely structured system of territories broke down and this presumably allowed other, less territorially successful males to remain if they flew in from surrounding areas. During this period of the day, before roosting commenced, the numbers of males was high, a great deal of flying activity took place and complex aerial combats involving groups of males (10 on one occasion) were frequent. For example, on 1 May, when male no. 144 was kept under close observation until it left its territory at 15.15 hrs, numerous flying and hovering unmarked males were present between this time and 15.45. These males were very aggressive and were patrolling areas where a few minutes previously well established territory holders such as nos. 30, 131 and 144 had been in residence. All of this late afternoon activity at Naisi nursery took place in shade and in a temperature of about 20.5°C. with a relative humidity of 81 percent. On most afternoons, by 16.00 hrs very few *O. julia* could be seen flying. Roosting appeared to occur in the *Pinus* plantation canopy, since males were seen to fly into the tree tops on leaving the open nursery area. However, because of their inaccessibility, it was impossible to confirm this observation.

The appearance of male *O. julia* in the mornings was determined mainly by the presence of sunshine. On sunny mornings males could be seen flying out of the plantations on the west side of the nursery from about 07.15 hrs. An individual's territory tended to be occupied as soon as it was in partial or full sunlight, as in the cases of *Orthetrum coerulescens* and *O. brunneum* (HEYMER, 1969). For example, on 2 May, no. 122 was in its territory at 07.30, no. 34 at 07.39, no. 131 at 07.43, no. 67 at 07.56, nos. 3 and 267 at 08.05, no. 271 at 08.11, no. 30 at 08.16 and no. 6 at 08.17 hrs. These times approximate closely with the times the territories first received sunshine that morning. When no. 131 was first noticed at 07.43 it was attending an ovipositing female when the site was just in sunlight. When individuals first arrived at their territory they exhibited only weak attachment to the area and were readily disturbed. On 2 May, nos. 131, 67 and 6 flew back to the edge of the nursery when they were disturbed soon after their arrival and perched there in sunshine for some minutes before returning to their territories. Later in the day, well established males were difficult to displace by moderate amounts of disturbance by human activities such as movements of forestry workers or myself. On cloudy mornings or in areas receiving sun relatively late in the day, males arrived very much later than the foregoing times. Females would appear and oviposit at any time during the period of normal activity of males, but the recorded matings were all between 11.40 and 14.45 hrs.

TERRITORIAL FLIGHT ACTIVITIES

On two days detailed observations were made on individuals for the whole of their territorial periods. Males no. 20 and 131 were observed from 10.51 - 11.00 and 11.27 - 15.16 hrs respectively (Tab. III) on 24 April; and no. 144 from 09.15 - 15.45 hrs on 1 May (Tab. IV). A preliminary classification of the types of flight and their characteristics in territorial male *O. julia* is given in Table V.

On 24 April, no. 20 was abandoned at 11.00 hrs because its particular territorial site made observation difficult, and no. 131 was observed for the remainder of the day. The nursery was reached at 07.20 hrs when there was total overcast and mist was drifting across the colony area; the dry bulb/wet bulb temperatures were 18.3°C/17.7°C. The first male *O. julia* to appear flew down from the forest at 07.25 hrs, crossed the nursery and disappeared. In the period 07.25-07.50 several male *Crocothemis sanguinolenta* were active by the stream and small ponds, but no more *O. julia* appeared until 07.51 when no. 32 was seen resting on tall grasses at the extreme edge of the colony area in very misty conditions. Another marked male appeared at 07.55 but flew off before it could be identified. At 08.30 (17.7°C/17.5°C) it was raining lightly and rain continued intermittently until 10.06 hrs. From this time onwards the weather conditions gradually improved and the sun appeared for six minutes at 10.41 hrs, which resulted in more male *O. julia* flying over the nursery. No. 20 arrived at its territory at 10.47 and immediately the sun was obscured by cloud. However, when the observations were transferred to no. 131 the weather became considerably brighter and dragonfly activity stayed at a high level until observations on this individual ended at 15.16 hrs.

Table III

Summary of territorial flight activities of two male *Orthetrum julia* on 24 April, 1977. The first column refers to male no.20, the others to male no. 131.

	No. 20 10.47-11.00	No. 131 11.27-12.00	12.01-12.30	12.31-13.00	13.01-13.30	13.31-14.00	14.01-14.30	14.31-15.00	15.01-15.16
Mean duration of each flight in sec (Overall mean 6.5±9.2)	3.50	11.86	8,16	5.36	5.17	7.41	3.87	6.69	5.69
Max. & Min. duration of flights in sec	8/1	51/1	45/1	19/1	47/1	86/1	12/1	38/1	30/1
Mean no. flights/min (Overall mean 1.2)	0.62	1.05	1.43	0.93	1.60	1.23	1.27	1.20	0.81
% time spent in flight (Overall mean 13.3)	3.59	20.75	19.50	8.33	13.78	15.22	8.17	13.39	15.42
No. of flights in each specified period	8	21	43	28	48	37	38	36	13
No. of feeding flights and %	5	5	4	5	5	9	6	5	4
(Overall % = 17.6)	(62.5)	(23.8)	(9.3)	(17.9)	(10.4)	(24.3)	(15.8)	(13.9)	(30.8)
No. of aggressive flts and %	1	11	27	18	31	22	25	27	5
(Overall % = 61.4)	(12.5)	(52.4)	(62.8)	(64.3)	(64.6)	(59.5)	(65.8)	(75.0)	(38.5)
No. of other flights (st = stabilizing; sx = sexual, without copn.; c = copulatory; a = avoiding; ? = undetermined)	2 (st)	1 (st), 3 (?) 1 (sx)	3 (st), 8 (?) 1 (c)	1 (a), 4 (?)	1 (a), 11 (?)	5 (?), 1 (sx)	7 (?)	4 (?)	4 (?)
Shade temp. at end of period	20.0/18.9	22.2/19.4	—	23.3/19.4	—	23.3/20.0	—	20.5/18.9	18.9/18.3
% of time sunny	0	93	100	100	100	100	83	83	100

It may be seen from Table III that the proportion of time spent in flight by nos. 131 and 20 was relatively low, ranging from about four to 21% in different periods. The mean duration of each flight was 6.5 ± 9.2 sec. Apart from one sexual flight, all flights lasting 10 seconds or longer were aggressive in nature, the longest being 86 sec. It is particularly noticeable that apart from the first period in the day, which was sunless throughout, aggressive flights were much more numerous than flights of any other type. The overall percentage of aggressive flights was 61.4%, compared with 17.6% for feeding flights, the next most frequent. Aggressive flights were mostly directed at other male *O. julia* and could be easily recognized, being essentially similar to those described for the West African libellulid, *Nesciothemis nigeriensis* (PARR & PARR, 1974). Three of the aggressive flights made by no. 131 on 24 April were directed at male *Crocothemis sanguinolenta*, which were probably as numerous as *O. julia*. Normally, *C. sanguinolenta* were ignored by male *O. julia* even when they were perched or flew within a few centimetres of the territory defender. Feeding flights were invariably quite short (nearly always less than eight seconds duration) and were spaced relatively regularly through the day. Flights of undetermined nature were recorded throughout much of the day. In most cases these resembled feeding flights but the dragonfly did not catch any prey and no prey target could be seen by the observer. It seems likely that these were unsuccessful feeding flights and that the prey were very small insects. In verified feeding flights, the prey was either seen by the observer before being caught by the dragonfly, or masticatory movements of the insect's mouthparts were visible. Stabilizing flights occurred, for example, if the insect was momentarily unbalanced by a gust of wind. On one occasion, a sudden movement of the observer disturbed the insect, which made a one-second flight before settling. Three sexual flights were made by no. 131 on 24 April. Two were chases of females without contact being made; a third was a four-second unsuccessful copulation attempt.

During the second all-day observation of a territorial male *O. julia* (no. 144), the weather was variable with sunny and dull periods alternating (Tab. IV). In general, this individual was less active than was no. 131 on 24 April. The overall percentage of time spent in flight was 5.2 and the mean duration of each flight and mean number of flights per minute were much lower than for nos. 20 and 131 combined. There is a significant difference in the mean duration of each flight between the two dates: — nos. 20 and 131 combined, 24 April; 6.5 ±9.2 sec; no. 144, 1 May; 4.9±4.1 sec, for which $d = 2.5213$, and $0.02 > p > 0.01$. During the several overcast periods flight activity of *O. julia* males was suppressed and this factor alone is sufficient to explain the difference in overall activity levels between 24 April and 1 May. However, a very similar proportion of feeding to aggressive flights occurred on the two occasions: nos. 20 and 131, 17.6% feeding, 61.4% aggressive; no. 144, 24.4%

Table IV

Classification of types of flight in territorial male *Orthetrum julia*

	09.15-10.00	10.01-10.30	10.31-11.00	11.01-11.30	11.31-12.00	12.01-12.30	12.31-13.00	13.01-13.30	13.31-14.00	14.01-14.30	14.31-15.15
Mean duration of each flight in sec (Overall mean 4.9±4.1)	4.61	4.55	3.76	5.68	5.17	4.15	6.35	3.64	3.00	4.09	6.46
Max. & Min. duration of flight in sec	20/2	14/1	16/1	17/1	14/1	12/1	28/1	8/1	7/1	15/1	24/1
Mean no. of flights/min (Overall mean 0.6)	0.40	0.67	0.83	0.83	0.77	0.43	1.13	0.47	0.27	0.70	0.53
% of time in flight (Overall mean 5.2)	3.07	5.06	5.22	7.89	6.61	3.00	12.00	2.83	1.33	4.78	5.74
No. of flights in each specified period	18	20	25	25	23	13	34*	14	8	21	24 **
No. of feeding flights and %	4	5	7	4	3	4	8	6	4	7	3
(Overall % = 24.4)	(22.2)	(25.0)	(28.0)	(16.0)	(13.0)	(30.8)	(23.5)	(42.9)	(50.0)	(33.3)	(12.5)
No. of aggressive flts and %	9	9	12	19	16	5	24	6	1	11	21
(Overall % = 59.1)	(50.0)	(45.0)	(48.0)	(76.0)	(69.6)	(38.5)	(70.6)	(42.9)	(12.5)	(52.4)	(87.5)
No. of other flights (st = stabilizing; sx = sexual, without copulation; a = avoiding; inv = investigatory; p = patrol; ? = undetermined)	4 (?), 1 (a)	5 (?), 1 (inv)	2 (?) 3 (a) 1 (p)	1 (inv), 1 (sx)	2 (?), 1 (st) 1 (p)	3 (?), 1 (a)	2 (?), 1 (p)	2 (?)	2 (?), 1 (st)	2 (?), 1 (a)	1 (?)
Shade temp. at end of period	22.8/18.3	—	22.2/17.8	—	22.8/18.3	—	22.8/17.8	—	21.1/18.3	—	—
% of time sunny	22	67	0	100	87	17	90	13	0	33	100

** Includes 1 flight of 28 sec which commenced as *p* but ended as *a*, and is therefore scored twice.

** Includes 1 flight of 13 sec which commenced as feeding but ended as *a*, and is therefore scored twice.

feeding, 59.1% aggressive. Other less detailed observations underlined this fact that in the Naisi colony of *O. julia*, intraspecific aggression was the dominant form of flight activity during the territorial periods. One of the aggressive flights on 1 May was directed at a male *Crocothemis sanguinolenta*. Other flights performed by no. 144 included 25 of undetermined nature (probably mostly unsuccessful feeding attempts) and one sexual, which was non-copulatory. Six avoiding flights were caused by nearby disturbance, such as the movement of a large bee or wasp (Hymenoptera), a lycaenid butterfly (Lepidoptera) and once, another male *O. julia*. The latter situation is rare, since male-male interaction in *O. julia* is virtually always aggressive. On two occasions, movements of grasshoppers (Acrididae) seemed to initiate investigatory flights which were different from anyother flight pattern. These investigatory flights were of short-medium length (5 and 12 sec), more or less horizontal and relatively leisurely in pace. On 1 May no. 144 made three patrolling flights which differed from all others in being apparently spontaneous and with no definite orientation. The first two were five and six seconds long and the insect flew in a roughly circular horizontal course from its perch and then returned. On the third occasion a similar flight was transformed into an aggressive one when a neighbouring male flew up and intercepted the patrolling specimen. This resulted in a fast and extended chasing flight of 28 sec in all, which was the longest flight recorded for no. 144 that day. The function of such patrolling flights is uncertain, but they may serve to establish the current distribution of neighbouring conspecific males. However, they do not seem to have occurred very commonly in the Naisi colony and were not recorded at all on 24 April.

REPRODUCTIVE BEHAVIOUR

Mating always seemed to occur without any prior courtship, the female frequently being chased and seized immediately she appeared over the territorial areas of the nursery. However, females were also seen, on occasions, ovipositing unattended, and apparently in view of territorial males. Although females could be seen throughout the day flying over the breeding sites, all matings took place between 10.13 and 14.45 hrs, but the restrictiveness of these sightings is probably misleading. For example, on 2 May at 07.43 hrs, male no. 131 was seen hovering above an ovipositing female, whose oviposition site was just in sunshine at that time. Since attending flights always appear to be associated with the very recent mating of the female concerned, this may be taken as evidence for an early morning copulation. The female is seized in flight and commonly, the pair fly in tandem for a few seconds before assuming the wheel position. When copulation has commenced, the pair may continue flying for some seconds

Table V

Classification of types of flight in territorial male *Orthetrum julia*

Type of flight	*Duration*	*Orientation*	*Type of flight*	*Initiated by*	*Comments on function*
Aggressive	Short-Long	Towards intruder	Rapid & direct approach from side or below	Conspecific ♂ flying within territory area	In defence of territory
Feeding	Short	Towards prey, often vertical or nearly so	Rapid and darting	Aerial prey insect	—
Stabilizing	Short	—	Fluttering	Loss of balance or grip on perch	To regain balance or position
Avoiding	Short	Away from disturbance	Rapid	Disturbance	Protective
Sexual, incl. copulatory	Short-Long	Towards ♀	Rapid & direct approach from above	Appearance of conspecific ♀	—
Investigatory	Short-Medium	Towards object being investigated	Leisurely and direct	Movement of nearby insect	—
Undetermined	Short	Usually upwards	Rapid and darting	?	May be unsuccessful feeding flights
Patrolling	Short-Long	Indefinite	Circular (or more complex) medium speed horizontal cruising	Apparently spontaneous: intrinsic behaviour pattern?	Establishes current distribution of neighbouring conspecific ♂♂?
Attending	Medium-Long	Towards ♀ ovipositing in territory	Hovering over ♀	Release of ♀ after copulation	Guarding ♀ (only seen after recent mating of same ♀)

Note: Short = 1-5 sec; — Medium = 6-15 sec; — Long = 16+ sec.

before settling or may settle immediately.

Completed copulations of *O. julia* were observed on six occasions. These lasted 11, 21, 28, 29, 39 and 49 sec: mean time 29.5±13.3 sec. Thus *O. julia* falls within the upper range of short-type copulations (CORBET, 1962, p. 178). In all but one of these cases, the female began oviposition attended by the male immediately the pair separated. The female in the copulation lasting 28 sec rested for 6 sec before ovipositing attended by the male. In the same habitat *Orthetrum abbotti* was observed to mate for 6 min 55 sec and 9 min 36 sec while settled. In both of these instances the female did not oviposit on separation, but flew away and out of sight, in one case after resting for some minutes. The males of *O. abbotti* made no attempt to stay with their mates after separation had occurred. A complete mating of *Crocothemis sanguinolenta* on 24 April lasted 7 sec.

DISCUSSION

In recent years, it has become clear that the form localization or residentiality may take in libellulid dragonflies varies considerably. In part, some of these variations seem to depend on whether males respond differently to the two sexes or whether all approaches initially are sexual (JOHNSON, 1964). In mature male libellulids, localization within a small area of a few square metres always appears to be linked with territoriality. However, in male *Nesciothemis nigeriensis* which show strong localization during maturation, territorial behaviour is not in evidence until sexual maturity is attained (PARR & PARR, 1974). The variable degree to which localization may be said to apply to male dragonflies was recognized by MOORE (1957) who pointed out that localization of territory is not complete and that there is a gradation between unlocalized fighting, and fighting and displaying in a clearly defined area. FALCHETTI & UTZERI (1974) make the observation that in *Crocothemis erythraea*, only flying periods are defence periods; resting spells occur outside the territory, so that there is discontinuous defence of territory. The present study demonstrated that in *Orthetrum julia*, some individuals are strongly localized at the breeding area whereas others are not. PAJUNEN (1964), KRÜNER (1977) and HASSAN (1978) have commented on the same fact in their respective studies of *Leucorrhinia caudalis*, *Orthetrum cancellatum* and *Acisoma panorpoides inflatum*. This seems to involve at least two major factors. Newly matured males of *O. julia* may have difficulty in establishing a definite residential area and will then function as opportunistic 'wanderers'. Secondly, more experienced males may or may not establish long-term localization depending on other factors which may collectively be termed 'reproductive fitness'. Those insects with relatively low 'reproductive fitness' may join the inexperienced 'wanderers' and tend to appear anywhere in the breeding area. The study of *Crocothemis servilia* by HIGASHI (1969) introduced the concept of 'wanderers', i.e. in this context, mature males without territories, and suggested an important relationship between the total number of males present and the number of territory holders at a pool. HIGASHI (1969) and HEYMER (1969) also collected evidence that the residentiality of male libellulids increased when a territory is established. This principle has been seen to apply to the Naisi population of *O. julia* and a strong correlation between the localization index and the number of times seen (Fig. 6) was demonstrated. This phenomenon is clearly linked with the variable localization noted by several workers. It appears that the most frequently seen individuals of *O. julia* were superior in their defence of a territory and, therefore, tended to return most often to a particular chosen area. Unsuccessful males, because they were unable to compete effectively with the dominant individuals, tended to return to the general colony area less frequently, in addition to failing to defend a particular territory for many successive occasions. These relatively unsuccessful 'wanderers', therefore, spent a considerable proportion of their time away from the breeding sites.

In *Leucorrhinia rubicunda*, PAJUNEN (1969) reported that some males persistently occupied certain sites, moved less than others and tended to be strongly aggressive, which lead to a regular spacing of males. Some individuals of *Plathemis lydia* also showed almost total localization (JACOBS, 1955). The fact that in dense populations there was a contraction of territory size compared with sparse populations was emphasized by KORMONDY (1961), HEYMER (1969) and KRÜNER (1977), and this does seem to be a general occurrence in other Odonata. There may be a direct relationship between size of the insect and size of territory defended, with the smallest species, such as *Nannophya pygmaea* (YAMAMOTO, 1968) utilizing the smallest territories. The density of male *O. julia* at the Naisi nursery was high and most of the territories had boundaries that overlapped to varying extents: for example, no. 144 on 1 May shared some of his outer zone territory with numbers 8, 30, 131, 170 and 271. Although considerable overlapping of territorial boundaries occurred in *O. julia*, any particular male's dominance and aggression was clearly evident in the central zone he was defending.

The territoriality demonstrated by *O. julia* seems in some ways to be intermediate between that shown by *O. coerulescens* and *O. brunneum* (HEYMER, 1969). *O. julia* perched on a variety of surfaces and the territory may be very open and flat soil or tall waterside vegetation such as grasses, whereas the other two species observed by Heymer were much more distinctly polarised towards vegetation or open rock surfaces.

In considering the length of time a particular male dragonfly occupies a given territorial area some cognizance must be taken of how this is measured. Some species may have individuals which repeatedly return to the same territorial area for several days but may not remain in the territory for the whole day, as in *Leucorrhinia dubia* (PAJUNEN, 1962a). In *L. dubia*, several males may utilize the same territorial area, but at different times in the day. Male *Plathemis lydia* were shown to be largely classifiable into those arriving at water in the morning (13%) and those arriving in the afternoon (60%) and *Perithemis tenera* apparently behaved similarly (JACOBS, 1955). JOHNSON (1962) recorded males of *Pachydiplax longipennis* as remaining in their territory for periods of between 10 minutes and three hours. Males of *Nesciothemis nigeriensis* remained in waterside territories for about five hours each day (PARR & PARR, 1974) and *Orthetrum julia*, in the present study were territorial for up to eight hours per day (usually about six), depending on the hours of sunshine. HEYMER (1969) established that male *O. coerulescens* and *O. brunneum* also tend to remain in their territories throughout the day.

The work of CAMPANELLA & WOLF (1974) has suggested that in *Plathemis lydia* the system of localization and territoriality which has evolved is different from any which has previously been described for the Odonata. In the *P. lydia* habitat studied by Campanella & Wolf, males defended certain traditional areas for the primary purpose of mating. At any one time within a particular territorial area two, three, or more males would interact aggressively with each other to establish a dominance hierarchy and each individual on the area appeared to recognize and maintain the territorial boundaries. Thus, territories of *P. lydia* were not used exclusively by a dominant individual. This involved the recognition of dominance and submission by the insects using a particular area, so that the dominant male was most successful in mating attempts. Campanella & Wolf describe the territoriality and mating of *P. lydia* as a temporal lek system where males return to a traditional communal site for the primary purpose of mating. Within the temporal lek system the most dominant individuals command the optimum time for reproductive activities. The temporal lek system described for *P. lydia* seems to be a complex evolutionary solution to the problem of high density of male reproductive individuals competing for the limited resources of space, time and females.

In contrast to the complexities of territoriality and localization in *P. lydia*, the systems in *Orthetrum albistylum speciosum* (ITO, 1960; ARAI, 1972), *O. coerulescens* and *O. brunneum* (HEYMER, 1969), *O. triangulare melania* (ARAI, 1972), *O. cancellatum* (KRÜNER, 1977) and *O. julia* are relatively simple in that mature males defend definite territories of their own. In *O. julia*, each territory has a virtually inviolate central zone, although the outer zone does overlap with the outer zone of other neighbouring territories.

Hence, in *O. julia*, and presumably in other *Orthetrum* species too, there is no hierarchy of dominance, and no multiplicity of males occupying the same small area. Since females show no preference for visiting the breeding site at any particular time of the day, there is no optimal period for males to exhibit territoriality in *O. julia*. It is, therefore, not surprising that males, once established in a territory tend to remain there all day. The West African libellulid *Nesciothemis nigeriensis* conforms quite closely with the general pattern of localization and territoriality set by *O. julia*. However, in *N. nigeriensis* the situation at water is perhaps simpler than for *O. julia* in that the territories were usually larger and appreciable overlapping was certainly absent in the northern Nigerian colonies studied by PARR & PARR (1974). *P. lydia* would appear to be a 'percher' that spends more of its time in flight than *O. julia* or *N. nigeriensis*. Other libellulids such as *Pantala flavescens* and *Tramea basilaris* are typical 'flyers'. With such a wide range in flight activity levels amongst the libellulids it is to be expected that localization and territoriality patterns vary greatly.

Detailed analyses of territorial activity patterns have been made on relatively few Odonata. In the present study of *Orthetrum julia*, and in the work on *Nesciothemis nigeriensis* (PARR & PARR, 1974) individual males were kept under observation for as long as they remained at their territories in order to obtain a clear picture of exactly how the territorial period is spent. From these two studies it is seen that territorial activities are much influenced by weather and that the two species do behave similarly. It should, perhaps, be pointed out that the genus *Nesciothemis* is assumed to be very closely allied to *Orthetrum* and that one might expect close similarities in behaviour. However, the amount of time in the territory that is actually spent in flight differed in the two species (*O. julia* about 13% in fine sunny weather, 5% in mixed weather with some sun and overcast periods; *N. nigeriensis* 8% in fine weather, 3% in mixed weather). These seem to be genuine specific differences since the more active *O. julia* lived under relatively cool and effectively temperate conditions in Malaŵi compared with the much hotter and sunnier climate experienced by *N. nigeriensis* in the north of Nigeria. The proportion of feeding flights was quite different in the two species. In *O. julia* about 20% of all flights within a territorial context were feeding flights and 60% were aggressive flights directed mainly at conspecific males. In *N. nigeriensis*, over 60% were feeding and about 30% were aggressive flights. The difference in the rates of aggressive encounters is probably associated with the observation that in *O. julia* neighbouring territories overlapped and hence the males were often closer together than in *N. nigeriensis* where territories were more individually defined. It is uncertain whether territory size and aggressiveness is a simple reflection of population density in *O. julia* and *N. nigeriensis*: it is possible that each species has its own intrinsic upper and lower limits of territory size. Quite often, the territories of *N. nigeriensis* were larger than in *O. julia.*

It is interesting to note that some libellulids have been reported as feeding in their territories. Amongst these species are included *Libellula quadrimaculata* (CORBET, LONGFIELD & MOORE, 1960), *Leucorrhinia caudalis* (PAJUNEN, 1964), *L. rubicunda* (PAJUNEN, 1966), *Nesciothemis nigeriensis* (PARR & PARR, 1974), *Orthetrum coerulescens* and *O. brunneum* (HEYMER, 1969), *O. cancellatum* (KRÜNER, 1977) and *O. julia* (present study). However, in contrast, other studies have provided evidence that feeding occurs only before and after territorial periods and never or rarely at the waterside reproductive site. Species falling into the latter category include *Plathemis lydia* (JACOBS, 1955; CAMPANELLA & WOLF, 1974), *Perithemis tenera* (JACOBS, 1955), *Crocothemis servilia* (HIGASHI, 1969), *Orthetrum microstigma, Palpopleura l. lucia, P. l. portia, Trithemis arteriosa* and *Crocothemis* sp. (GREEN, 1974).

HIGASHI (1969) makes the specific comment that males of *Crocothemis servilia* tend to feed in the evening in fields away from water, and CORBET (1962) is of the opinion that male dragonflies do not, as a rule, feed at the water, but come to water to meet females. It seems highly likely that there is a relationship between the length of a particular period of time a libellulid remains at a waterside territory and whether or not it feeds in that area. Certainly, of those species regularly feeding in their territories, *Libellula quadrimaculata, Leucorrhinia rubicunda, Nesciothemis nigeriensis, Orthetrum cancellatum, O. coerulescens. O. brunneum* and *O. julia* do tend to remain there for long periods of time. Conversely, non-feeders such as *Plathemis lydia, Perithemis tenera* and *Palpopleura lucia* seem to be species where each individual stay at water is of relatively short duration.

On the whole, the few detailed studies of *Orthetrum* and the closely related *Nesciothemis* demonstrate fundamental behaviour patterns common to most of the species. However, each species also shows characteristic and specific behavioural features. When more information is available, the statement of HEYMER (1969) "The two species [*O. coerulescens* and *O. brunneum*] have developed behaviour patterns from which they can better and more clearly be identified than from their morphological systematic characters" will surely be seen to have general applicability.

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