

**SOME ASPECTS OF TERRITORIALITY IN *ORTHETRUM
COERULESCENS* (FABRICIUS) (ANISOPTERA: LIBELLULIDAE)**

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Received and Accepted October 18, 1982

A colony of *O. coerulescens* was observed in southern England during July, 1980. Detailed analyses of territoriality were carried out by noting the type, duration and temporal distribution of 1323 territorial flights of 7 adult males. Territorial attachment varied according to age and from individual to individual. Up to 14 territories (7-16 m in length; mean 10.5 m) were established along 154 m of small stream. Territorial males spent between 4 and 19% of their time in flight (mean 13%). Territorial flight activities were complex and often incorporated a number of different components. The dominant flight activities involved feeding (53% of flights and 12% of flight time), patrolling (40% and 61%) and aggression (17% and 18%). Aggression and patrolling were frequently associated as combined activities. Feeding, if combined, was mostly linked with patrolling. About 75% of feeding, 33% of patrolling and 25% of aggressive flights were unassociated with any other components. The mean durations of uncombined feeding, aggressive and patrolling flights were 2.7, 12.0 and 17.8 sec respectively. Other flight components (minor changes of position; stabilizing; disturbance; various types associated with reproductive behaviour) collectively comprised only 7% of the total flight time. Territoriality often commenced at about 10.30 BST, but was weather determined. Patrolling and aggressive flights were at a maximum around 12.30 hr, whereas feeding was maximised early in the morning territorial period and from 16.00-17.00 hr. Copulatory activity was observed on nine occasions (12.42-17.50 hr), when copulations ranged from 5 sec to nearly 25 min, with a mean of 7 min 11.5 sec. Mature non-territorial males ("wanderers") were seen frequently on occupied territories.

INTRODUCTION

The present paper continues a series of studies of libellid behaviour (PARR & PARR, 1974; PARR, 1980, 1983) in which the principal aim is to compare various species with particular reference to territoriality and reproductive

activities. It is hoped that these studies will further elucidate the complexities of libellulid behaviour already noted by previous authors (reviewed in PARR, 1983). In attempting to compare behaviour between species, the major problem is that circumstances rarely allow exactly parallel studies to be made in a planned sequence. This problem is, of course, very obvious when attempts are made to compare results obtained by different workers. A previous behavioural study of *O. coerulescens* (HEYMER, 1969), did not deal primarily with territorial flight components. The present paper is, therefore, largely concerned with the analysis of the manner in which male *O. coerulescens* partition their territorial time. The population selected for study was situated on Ober Heath in the New Forest, southern England. Territoriality was observed along a small stream that ran across the Heath and which ultimately joined the Oberwater River.

METHODS

The population of *O. coerulescens* was studied by direct observation, aided by the use of binoculars. Specimens were marked with unique numbers on the wings, at first (5, 6 and 11 July) with a red fibre-tipped pen, but later (16 July onwards) with yellow enamel paint. The red pen markings were unsatisfactory because they were insufficiently visible and because they weathered too rapidly. Many individuals first marked with the fibre-tipped pen had to be re-marked on subsequent dates with paint. Totals of 78 males and 13 females were marked between 5 and 25 July. Due to very wet, cool and cloudy weather, detailed observations were not started until 16 July. Thereafter, individual males were observed on 21-25, 28 and 31 July, that is to say, whenever weather conditions permitted. Detailed analyses of territoriality were made by noting the type, duration and temporal distribution of 1323 territorial flights of seven adult males. A stop-watch was used to time the observed activities. As far as possible, detailed observations of individual males spanned the whole territorial period of particular days.

HABITAT AND ODONATA FAUNA

The observations on the Ober Heath (New Forest, England) colony of *O. coerulescens* were carried out in the same general area as described in PARR & PARR (1979), and most of the detailed work was done in sectors 4 & 5 of Ober Heath stream as defined in that paper. In 1980, much of the coniferous forest around the Ober Heath stream had been cleared, so that the general habitat was more open than in 1974 and 1975 (PARR & PARR, 1979). The whole of sector 5 (90 m) and the adjacent 62 m of sector 4 were in open heathland and formed a suitable area for territorial *O. coerulescens*. The remaining 35 m of sector 4 were forested and unsuitable for the species. Most of the more open areas of the stream as well as adjacent marshy heathland were colonised by territorial *O. coerulescens*, but for convenience, the main work was restricted to the sectors stated above. Compared with 1975, the stream had become more silted up and the water volume was considerably greater.

Fifteen species of Odonata were seen in the vicinity of Ober Heath stream during July, 1980: *Lestes sponsa* (Hans.), ***Calopteryx virgo* (L.), *Coenagrion puella* (L.), *Enallagma cyathigerum* (Charp.), **Pyrrhosoma nymphula* (Sulz.), **Ceriagrion tenellum* (Vill.), ***Ischnura elegans* (Vander L.), **I. pumilio* (Charp.), *Aeshna juncea* (L.), *A. grandis* (L.), *Anax imperator* Leach, *Libellula depressa* L., **Sympetrum striolatum* (Charp.), *Orthetrum cancellatum* (L.), and **O. coerulescens*. The species marked * certainly bred in the stream in 1980; those marked ** probably did so. All of the remainder, except *O. cancellatum*, bred in ponds on Ober Heath. A single specimen of the latter

species (a pruinosed male) was seen once, flying up-stream. The most notable omission from this list is *Cordulegaster boltoni* (Don.). This species, normally common in the New Forest, was not seen at all during July, 1980. *Ceriagrion tenellum*, normally very numerous on Ober Heath stream, was very much less frequent than when studied in 1974 and 1975 (PARR & PARR, 1979).

TERRITORIAL ATTACHMENT

Of the 78 males marked from 5-25 July, only 18 (23.1%) were ever seen again, and only 9 were seen three or more times. Furthermore, of the 37 males marked on the 5 July (first day of observations), only 5 were ever resighted. It is considered that one of the factors responsible for the low rate of resightings was the very unseasonal weather on 6-10, 12-15, 17-18 and 20 July. It is likely that many *O. coerulescens* either starved to death or died as a direct result of cold, wind or rain during the period 6-20 July. From 21-31 July cool, wet weather was only experienced on 26-27 and 29 of the month, with the remaining days being warm, sunny and largely cloudless. However, during 21-31 July only 9 males from a total of 23 marked were resighted. These latter figures suggest that on average, male *O. coerulescens* do not tend to return to the same territory with much consistency. Most individuals were recorded only once, and this probably implies that considerable shifting of territories from day to day occurred, although it was not possible to verify this. Some individuals were, however, highly consistent in selecting the same or adjacent areas for several days (Nos 3 and 65 were notable in this respect). Other individuals reappeared after being absent from sectors 4 and 5 for long intervals (e.g. Nos 8 and 21 were not seen for 14 and 20 days respectively). Some individuals certainly behaved as "wanderers", as defined by HIGASHI (1969) and did not defend definite, fixed territories. Nos 3 and 65 showed a tendency to become more strongly associated with a particular territory with increasing age. No. 65 was first marked on 22 July, and on that day defended a territory from 11.52 until 12.10. At 12.10 this male had a prolonged aerial dispute with an unmarked male which had recently arrived and was guarding an ovipositing female in his (No. 65's) territory. The female flew off while the males were fighting. After 3 min 15 sec No. 65 returned, but the unmarked male was still in residence and after a second fierce protracted fight No. 65 was again driven off. This was the only occasion that a defending male was seen to lose a territorial dispute. This individual, No. 65, subsequently successfully defended the same or nearly the same territorial site on a further six days, until observations ceased. No. 3, which was seen seven times from 5 th to 30 July, became more regularly present in its territory towards the end of this period.

TERRITORY SIZE

The size of individual territories was measured only once accurately, but the

number of territorial males on that occasion (25 July) was typical of other periods of fine, sunny weather. The length of Ober Heath stream surveyed on 25 July was made up of the 154 m of sectors 4 and 5 already referred to. Fourteen males defended territories along an apparently homogeneous stream habitat. However, the individual males were not spaced regularly: some territories overlapped by as much as 46 percent and in other regions gaps of between 2 and 14 m existed where no resident territorial males established themselves. The territories ranged from 7 m to 16 m (mean 10.3 m) in length (Fig. 1). Whilst the territories were linear in that the males only patrolled in one dimension over the length of the stream, they would sometimes fly several metres away from water to attack intruding males. That this did not occur very frequently was probably because vegetation limited visibility away from the stream.

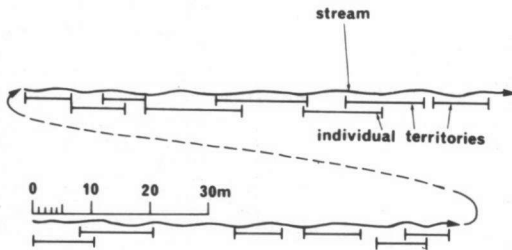


Fig. 1. Territories of *Orthetrum coerulescens*: Ober Heath Stream, New Forest, July 25, 1980. Section of stream represented = 154 metres.

which were stream-based when first caught and marked, subsequently transferred their territorial behaviour to the flooded areas of heath adjacent to the stream.

WEATHER CONDITIONS AND TIME IN FLIGHT

Seven territorial males were watched for varying periods of time for a total of 123,540.0 sec, during which time they were in flight for 16,007.7 sec (13.0%). The percentage of territorial time spent in flight each day ranged from 4.4-18.5 and this variation correlated with mean shade temperature (Fig. 2; $r = 0.8957$; $0.01 > p > 0.001$) and mean percentage of time sunny (Fig. 3; $r = 0.7909$; $0.05 > p > 0.02$) during the territorial period.

Roosting was invariably well away from water, amongst heather (*Calluna vulgaris*) and other heathland vegetation, and on sunny mornings the movement towards the territorial sites at or close to the stream commenced between 9.30 and 10.30. Many of the earliest males to arrive spent up to an hour moving from point to point along the stream before settling into a territory. The later males adopted

a territory more rapidly than the earlier arrivals.

Direct sunshine was essential for male territorial behaviour. During days when virtually unbroken sunshine occurred during the morning (5, 21-25, 28 and 31 July) the first males became territorial between 10.35 and 11.30 (mean time 10.51).

The shade temperature did not affect the time of arrival of territorial males, providing the morning was sunny (Fig. 4; $r = 0.2150$; $p > 0.2$).

If the day stayed sunny, territorial males remained until 16.30-18.10 (mean time 17.22) before flying abruptly away from water. When there was total cloud cover or when largely overcast conditions prevailed, no territorial activity occurred, even if the temperature was as high as 22.8° C. for long periods, as on 29 July. On 16 July when weather conditions were marginal for territorial activity, males arrived at the stream but spent virtually all the time perched; many withdrew by midday. After midday, when the sun shone for 52 percent of the time until 13.57 some males were territorial. However, they had all disappeared by 14.00 when there was no further sun that afternoon.

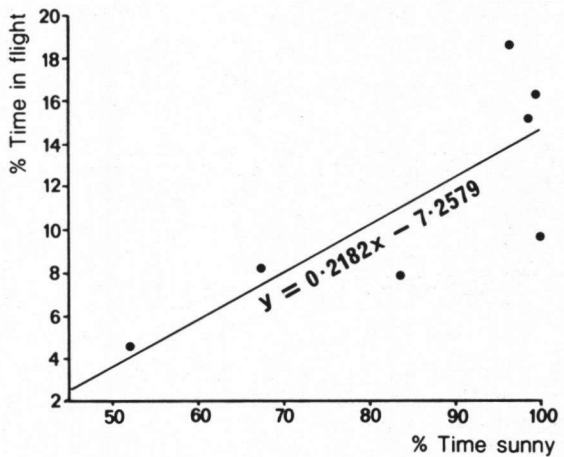


Fig. 2. Correlation between percentage time in flight and sunshine. $r = 0.7909$; $0.05 > p > 0.02$.

TERRITORIAL FLIGHT COMPONENTS

A flight is defined as any aerial period between leaving a perch and re-settling.

The territorial flight activities were complex and individual flights often incorporated a number of differing components (combined flights).

The dominant flight activities in terms of both time and numbers of flights were those involving feeding, patrolling and aggression.

In order to analyse the various types of territoriality the range of different flight components was first determined by observation. The following 14 distinct components were recognized: feeding (f), patrolling (p), aggressive (a), investigatory (inv), undetermined (?), avoidance (av), stabilizing (st), pre-

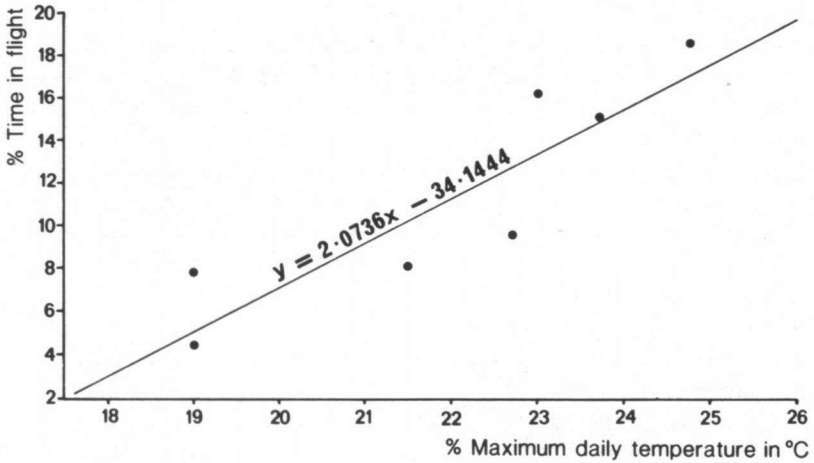


Fig. 3. Correlation between percentage time in flight and maximum daily temperature. $r = 0.8957$; $0.01 > p > 0.001$.

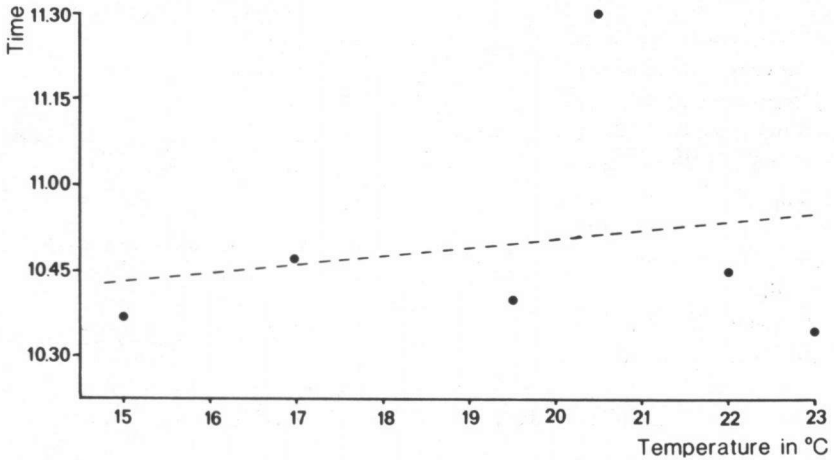


Fig. 4. Time of arrival at water of territorial males and shade temperature. $r = 0.2415$; $p > 0.2$.

copulatory (sx), copulatory (c), in tandem (t), post-copulatory (pc), attending (at), searching (se) and sexual/aggressive (sx/a) (Tab. I).

The mean duration of all uncombined flights (i.e. flights involving only one component) was calculated (Tab. II). From this information it was possible to analyse combined flights (i.e. flights including more than one component), e.g. feeding (f) and patrolling (p) designated as f/p, by dividing the total time of all

Table I
Classification of types of flight in territorial male *Orthetrum coerulescens*

| TYPE OF FLIGHT | Duration | Orientation | Description of flight | Initiated by | Comments on function |
|-------------------|--------------|---|---|---|--|
| FEEDING | Short-medium | Towards prey | Rapid and darting | Aerial prey insect | — |
| PATROLLING | Short-long | Definite or indefinite | Linear, circular or more complex; medium speed horizontal cruising | Apparently spontaneous; intrinsic behaviour pattern? | Establishes current distribution of neighbouring conspecific males. |
| AGGRESSIVE | Short-long | Towards intruder | Rapid, direct approach from side or below | Conspecific male flying within territory area | In defence of territory |
| INVESTIGATORY | Short-medium | Towards object being investigated | Leisurely and direct | Movement of nearby object, usually an insect | Uncertain function; appears to be distinct from feeding, patrolling and aggression |
| UNDETERMINED | Short | Indefinite | Usually a slight shifting of position; always uncombined with any other component | Apparently spontaneous | Uncertain function; unlikely to be confused with feeding |
| AVOIDANCE | Short-medium | Away from disturbance | Rapid | Disturbance | Protective |
| STABILIZING | Short | — | Fluttering | Loss of balance or grip on perch | To regain balance or position |
| PRE-COPULATORY | Short-long | Towards sexual partner | Rapid, direct and often sustained; short range approach from above | Appearance of conspecific female or another insect or an object mistaken for conspecific female | — |
| COPULATORY | Short-long | Towards territory | Flight with male and female in tandem and in wheel position before main copulatory period (settled) | Successful capture of female by male | Male returns to territory with female |
| IN TANDEM | Medium-long | Definite or indefinite | Occurs immediately before or immediately after copulation | Capture of female or ending of copulation | Maintains male/female contact |
| POST-COPULATORY | Short-medium | — | Following female after copulation and before oviposition | Completion of copulation or tandem flight. | Maintains the association of the recently mated pair before oviposition |
| ATTENDING | Long | Towards ovipositing female in territory | Hovering and following | Oviposition flight of female after mating | Guarding female (only seen after recent mating with same female) |
| SEARCHING | Medium | Indefinite | Rapid, irregular | Disappearance of recently mated and ovipositing female | May re-establish contact with recently mated female |
| SEXUAL/AGGRESSIVE | Medium | Towards conspecific pairs in tandem | Rapid and direct | ? Sexual or aggressive reaction | — |
| WATER DIPPING | Short | Water surface | Dipping into water | ? Drinking; thermal regulation; testing oviposition site; feeding; mirror effect | Uncertain: head or abdomen dipped into water; never seen uncombined — always part of a patrol flight |

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

such flights into parts proportional in length to the uncombined values of the relevant components. For example, 94 aggressive/patrolling flights (a/p or p/a) lasted a total time of 2,700.8 sec. The mean times for uncombined a and p flights were 12.0 and 17.8 sec respectively. Thus the a/p or p/a flights contributed approximately 1,087.6 sec of aggression and 1,613.2 sec of patrolling to the total times involving those components. Using this technique, all the time in flight could be allocated to the 14 components already listed. Territorial flights ranged from very short, single-component flights (e.g. f) to long, complex flights including several components, some being repeated before settling (e.g. sx/a/p/inv/p). The full range of combinations of observed flight components is given in Table III. For convenience, the various flight combinations may be divided arbitrarily into two groups (Tab. III). The major territorial flight combinations are defined as those comprising more than 1 percent of the total flight time; those accounting for less than 1 percent are classified as "minor". The main components of major flight combinations are patrolling, feeding and aggression, with investigatory and attending flights also being included. The 30 various minor/combinations include all the 14 distinct flight components. While these do not contribute much in terms of total time in flight (11.1%), many are of vital importance in the overall behaviour patterns of the species.

Table IV shows the results of an analysis of total time spent in flight under the headings of all the various flight components. Patrolling occupies by far the largest fraction of total flying time (61.4%) and only aggression (17.8%) and feeding (11.7%) among the other components contribute significantly towards the total.

The various flight components of 1323 separate flights are analysed in Table V.

Table II
Duration (sec) of uncombined territorial flights

| Type of flight | No. of flights | Total time | Arithmetic mean | Range |
|--------------------------|----------------|------------|-----------------|-------------|
| Feeding (f) | 520 | 1422.9 | 2.7 | 1.0-11.0 |
| Patrolling (p) | 184 | 3269.4 | 17.8 | 2.2-110.0 |
| Aggressive (a) | 61 | 753.3 | 12.0 | 2.5-43.0 |
| Investigatory (inv) | 68 | 237.5 | 3.5 | 1.0-16.2 |
| Undetermined (?) | 72 | 140.0 | 1.9 | 1.0-6.0 |
| Avoidance (av) | 12 | 33.4 | 2.8 | 1.0-10.5 |
| Stabilizing (st) | 16 | 27.8 | 1.7 | 1.0-4.0 |
| Pre-copulatory (sx) | 5 | 90.8 | 18.2 | 5.0-58.6 |
| Copulatory (c) | 7 | 31.8 | 4.5 | 1.1-20.0 |
| In tandem (t) | 4 | 114.6 | 28.7 | 12.0-43.6 |
| Post-copulatory (pc) | 7 | 23.9 | 3.4 | 1.5-10.0 |
| Attending (at) | 2 | 226.3 | 113.2 | 106.3-120.0 |
| Searching (se) | 2 | 24.2 | 12.1 | 11.2-13.0 |
| Sexual aggressive (sx a) | 1 | 14.5 | 14.5 | |

Table III

The range of combinations of territorial flight components (cf. Tab. II for key to abbreviations). — [For example: the most frequent MINOR type (inv/p/a/p) were flights involving a sequence of investigation-patrolling-aggression-patrolling which accounted for 0.95% of the total time in flight (151.2 sec/16007.7 sec)].

| MAJOR COMBINATIONS | | | MINOR COMBINATIONS | | |
|--------------------|----------------------|--------------|--------------------|----------------------|--------------|
| Type of flight | Total duration (sec) | % | Type of flight | Total duration (sec) | % |
| p | 3269.4 | 20.42 | inv/p/a/p | 151.2 | 0.95 |
| f/p | 2839.7 | 17.74 | a/sx/a | 144.0 | 0.90 |
| a/p | 2700.8 | 16.87 | ? | 142.6 | 0.89 |
| f | 1410.4 | 8.81 | av/p | 129.2 | 0.81 |
| a | 753.3 | 4.71 | sx/a/p/inv/p | 120.0 | 0.76 |
| f/p/a/p | 723.9 | 4.52 | t | 114.6 | 0.72 |
| p/a/p | 718.8 | 4.49 | sx/p | 111.2 | 0.69 |
| inv/p | 404.3 | 2.53 | inv/a/p | 109.1 | 0.68 |
| a/p/a/p | 402.2 | 2.51 | sx | 90.8 | 0.57 |
| f/p/a | 323.1 | 2.03 | p/a/p/a/p | 67.5 | 0.42 |
| inv | 237.5 | 1.48 | at/t | 65.0 | 0.40 |
| at | 226.3 | 1.41 | f/p/f | 56.0 | 0.35 |
| a/p/a | 213.9 | 1.34 | sx/p/a/p | 51.6 | 0.32 |
| <i>Totals</i> | <i>14223.6</i> | <i>88.86</i> | at/p | 48.2 | 0.30 |
| | | | st/p | 44.0 | 0.27 |
| | | | sx/t | 40.0 | 0.25 |
| | | | f/p/a/p/a | 34.8 | 0.21 |
| | | | av | 33.4 | 0.21 |
| | | | c | 31.8 | 0.20 |
| | | | sx/a | 28.0 | 0.18 |
| | | | st | 27.8 | 0.17 |
| | | | pc | 26.2 | 0.16 |
| | | | sx/a/p | 25.1 | 0.16 |
| | | | se | 24.2 | 0.15 |
| | | | sx/c | 17.6 | 0.11 |
| | | | p/sx/t | 16.0 | 0.10 |
| | | | "sx/a" | 14.5 | 0.09 |
| | | | f/a | 13.2 | 0.08 |
| | | | f/st | 3.5 | 0.02 |
| | | | inv/f | 3.0 | 0.02 |
| | | | <i>Totals</i> | <i>1784.1</i> | <i>11.14</i> |

[Total time in flight: 16007.7 sec]

Feeding, patrolling and aggression are again seen to be dominant activities when territoriality is presented in this way. For example, out of a total of 1323 flights, 699 had feeding components (52.8%). Many flights were constituted of more than one different component, e.g. f/p/a, so that the total of the various components does not equal the total number of flights.

Table IV
Analysis of total time spent in flight: the different flight components expressed as time in seconds and percentages of the total time

| | Totals | f | p | a | inv | ? | av | st | ss | c | t | pc | at | ac | "a/a" |
|--------|---------|--------|--------|--------|-------|-------|------|------|-------|------|-------|------|-------|------|-------|
| Σ time | 16007.7 | 1870.4 | 9834.0 | 2848.3 | 333.6 | 142.6 | 51.0 | 33.0 | 315.4 | 35.3 | 159.3 | 26.2 | 319.9 | 24.2 | 14.5 |
| % | 100.0 | 11.7 | 61.4 | 17.8 | 2.1 | 0.9 | 0.3 | 0.2 | 2.0 | 0.2 | 1.0 | 0.2 | 2.0 | 0.2 | 0.1 |

Dipping flights into water not timed, but were all momentary diversions from other (patrolling) flights.

Table V
Analysis of total numbers of flights: the different flight components expressed as numbers and percentages

| | Totals | f | p | a | inv | ? | av | st | ss | c | t | pc | at | ac | "a/a" |
|-----------|--------|------|------|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|
| Σ numbers | 1323 | 699 | 531 | 223 | 96 | 75 | 21 | 20 | 17 | 10 | 8 | 8 | 3 | 2 | 1 |
| % | 100 | 52.8 | 40.1 | 16.9 | 7.3 | 5.7 | 1.6 | 1.5 | 1.3 | 0.8 | 0.6 | 0.6 | 0.2 | 0.2 | 0.1 |

The individual component totals do not total 1323 and the individual percentages do not total 100 because many flights had more than one different component, e.g. f/p/a. — [The table indicates, for example, that of a total of 1323 flights, 699 had feeding components (52.8%).]

THE MAJOR TERRITORIAL FLIGHT COMPONENTS

Feeding

The frequency distribution of feeding-flight durations (Fig. 5) demonstrates a mode within the range 1-2 sec, but with an arithmetic mean of 2.7 sec. The absolute range was 1.0-11.0 sec. Feeding flights were rapid and darting, and were initiated by aerial prey insects. Feeding was the most frequent component of flight activity recorded for territorial males. Many feeding flights (520/699; 74.4%) were uncombined with other flight types. Feeding, like all other activities, can occur at any time during territorial periods; its temporal distribution, however, was distinctly bimodal with peaks of activity at 10.30 and from 16.00 to 17.00 hr (Fig. 6). The success rate for feeding flights was not accurately determined, but it certainly did not approach 100 percent.

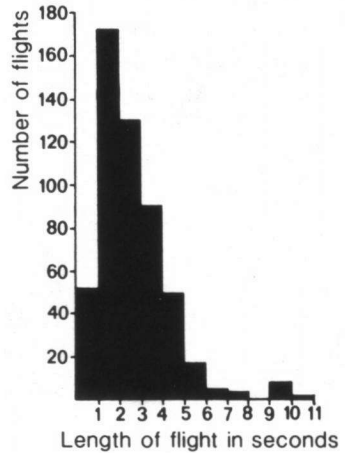


Fig. 5. Duration of feeding flights (N = 520 flights): total time spent feeding (feeding-only flights) = 1422.9 sec; arithmetic mean = 2.7 sec, range 1.0-11.0 sec.

Patrolling

The frequency distribution of patrolling-flight durations (Fig. 7) has a strongly skew pattern, ranging from 2.2-110.0 secs and with a mode of 10-15 sec. The

arithmetic mean is 17.8 sec. Patrolling was most frequent during the period 12.30-14.00 hr and was not common early in the morning or after 16.00 hr, so that there was an inverse relationship between the occurrence of feeding and patrolling (Fig. 6). Stream-based males made linear patrolling flights cruising at medium speed and at about 18-25 cm above the water surface. On any particular flight, they might, or might not, patrol the full extent of their territory. Patrolling was the second most frequent form of territorial activity after feeding (Tab. V), being represented in about 40% of all flights. It was the dominant activity when measured in terms of time (Tab. IV). There was little indication that any extrinsic stimuli initiated patrolling and these flights appeared to be spontaneous, intrinsically controlled behaviour patterns. It would appear that patrolling serves to establish the current distribution of neighbouring conspecific males and may also serve to help locate conspecific females.

Exclusively associated with patrolling was the rare phenomenon of water-dipping, during which the insect would touch the water surface. Seven instances of water-dipping were observed and in all cases the tip of the abdomen was placed momentarily in the water. In all cases this activity merely punctuated a normal patrolling flight.

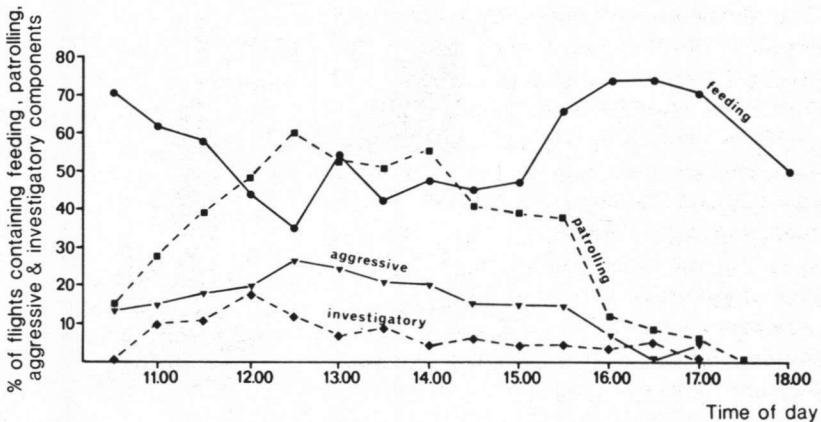


Fig. 6. Percentages of flights by territorial males containing feeding, patrolling, aggressive and investigatory components (analysis of 1323 territorial flights).

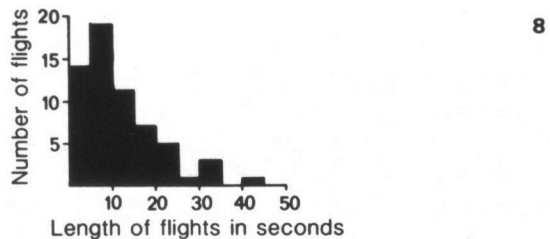
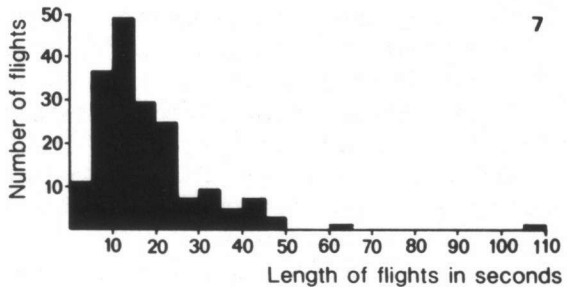
Aggressive flights

The analysis of 63 non-combined aggressive flights (Fig. 8) indicates a skew distribution when frequency is plotted against duration of flight. The mode is 5-10 sec, but the arithmetic mean is 12.0 sec, within a range of 2.5-43.0 sec. The temporal distribution of aggressive flights follows closely the pattern for

patrolling, with a plateau at around 12.30 hr when about 27% of flights included an aggressive component. Thereafter, a gradual decline in the number of flights containing aggressive components occurred throughout the afternoon (Fig. 6). Overall, 16.9% of territorial flights contained an aggressive component (Tab. V) and this flight form accounted for 17.8% of the total time spent in the air (Tab. IV). Aggressive flights, which ranged from short to long in duration (Tab. I) were usually easily recognized. They were usually clearly directed towards a conspecific male flying within the territory area.

The attack involved a rapid and direct approach from the side or below, usually only developing into a physical clash if the intruder also showed an aggressive response. Most intruding males would flee immediately the territory-holder attacked, so that aggressive flights are the actual means of defending a territory and of maintaining its integrity. Approximately 10% of aggressive flights were directed towards insects other than male *O. coeruleus*. For example, males of *Libellula depressa*, *Orthetrum cancellatum*, *Pyrrhosoma nymphula*, *Ischnura elegans* and workers of *Bombus* spp.

(Hymenoptera) were subject to aggressive attacks by *O. coeruleus*.



Figs 7-8. Duration of patrolling and aggressive flights: (7) Patrolling flights (N = 184 flights): total time spent patrolling (patrolling-only flights) = 3269.4 sec; arithmetic mean = 17.8 sec, range 2.2-110.0 sec; — (8) Aggressive flights: (N = 61 flights): total time spent in aggression (aggressive-only flights) = 753.3 sec; arithmetic mean = 12.0 sec, range 2.5-43.0 sec.

Investigatory flights

Investigatory flights are almost wholly within the short-medium range, with a mean duration of 3.5 sec (Tabs I, II). This type of flight was recorded throughout the period 10.30 to 17.00 hr, with a peak at 12.00 noon (Fig. 6). The term "investigatory" describes the apparent function of these flights but there are problems in accepting this explanation. The flights are orientated towards

definite moving objects and are direct and relatively leisurely, contrasting with feeding, patrolling and aggressive flights. The principal objects investigated were: Odonata (*Libellula depressa*, *Ceriagrion tenellum*, *Pyrrhosoma nymphula*, *Ischnura elegans*, in-tandem *O. coerulescens* and teneral *O. coerulescens*); Lepidoptera (*Maniola jurtina*, pierids, hesperids and small moths); Hymenoptera (*Apis mellifera*, *Bombus* spp. and *Vespula* spp.) and Human beings.

Non-combined investigatory flights involved a close approach to the object being "investigated" and an immediate return to the dragonfly's perch: these flights never became feeding, aggressive or sexual flights with reference to the object initiating the "investigatory" response. When investigatory flights were combined with aggression and feeding (Tab. III), the insect releasing these responses was always different from the one initiating "investigation". In terms of total numbers of flights (7.3%; Tab. V) and total time spent in flight (2.1%; Tab. IV), investigatory flights were the fourth in importance of the various flight components.

MINOR TERRITORIAL FLIGHT COMPONENTS

Undetermined

"Undetermined" flights were generally short in duration (range 1.0-6.0 sec; mean 1.9 sec; Tab. II) and uncombined with other components. These flights were indefinitely orientated, were apparently spontaneous and usually involved a slight shifting of perch position. The function of undetermined flights is uncertain, but confusion with feeding activities is unlikely. It is possible that these flights represent displacement fidgeting, but if so, it is surprising that none ever continued into other flight types, such as patrolling. Another possibility is that undetermined flights are a form of stabilization activity, but where the loss of balance or grip on a perch is not obvious.

Stabilizing

Stabilizing flights occur if there is a loss of balance and are short, fluttering bursts lasting about two seconds (Tabs I-V). A gust of wind is the most frequent obvious cause of such flights, which may be combined or uncombined.

Avoidance

Any close, moving object will elicit a short to medium-range flight away from the disturbance. The most frequent causes of avoidance flights were *Apis mellifera*, *Bombus* spp. (Hymenoptera) and human disturbance.

Sexual (Reproductive)

Six clearly distinguishable types of sexual flights were recognized: pre-copulatory, copulatory, in tandem, postcopulatory, attending and searching. Collectively, sexual flights account for 5.6% of the total time in flight and 3.7% of the total flight components (Tabs IV, V), Reproductive flights were noted between 10.50 and 17.50 hr. Successful sexual activity late in the afternoon would prolong the male's stay within his territory much beyond the time when most other males had withdrawn from the stream area. The latest any non-copulating individual remained was 17.42, however, on 28 July, No. 3 copulated at 17.40 and at 17.50 hr and did not leave its territory until 18.10 hr.

Pre-copulatory flights varied between short and long in duration, were rapid and direct, and were orientated towards a prospective sexual partner. Usually these flights were initiated by the appearance of a conspecific female which might be recognized at close range in the male's territory or at a considerable distance and height. Occasional errors were made when males would pursue other insect species, or even other objects in a typical sustained sexual flight. Male No. 65 once made a determined effort to approach a bird (swift, *Apus apus*) flying high overhead and this same individual even made a spirited attempt to make contact with an over-head aeroplane.

In tandem flights occur immediately before or immediately after copulation and are always classifiable as medium-long (12.0-43.6 sec; mean 28.7 sec).

Copulatory flights were directed towards the male's territory and followed immediately after successful precopulatory and in tandem flights. After the female was seized the pair would fly in tandem for a variable time until the wheel position was adopted (the commencement of the copulatory flight) shortly before they settled. Most copulatory flights lasted about 4 seconds; the greater part of the copulatory period was spent settled within the male's territory.

Post-copulatory flights are defined as short-medium flights which occur either immediately after the separation of a copulating pair or after an in tandem flight which sometimes follows copulation. Post-copulatory flights are essentially movements allowing the male to keep close to the recently mated female before she commences oviposition.

Attending flights occur as soon as the recently mated female flies towards the male's territorial water. The female seems to initiate the move to water and the male follows closely. In this flight the male guards the ovipositing female by following her and hovering over her when oviposition is actually occurring. Males have never been seen to attend females with whom they have not recently mated. Attending flights are the longest (mean 113.2 sec) of all the territorial flight components and often extend outside the male's normal territorial limits.

Searching flights are frenetic efforts by the male to relocate the recently mated female after the latter has disappeared. The only occasion that searching flights have

been recognized occurred when male No. 65 lost sight of his female after a short postcopulatory flight and made two rapid and irregular attempts of 13.0 and 11.2 sec to relocate her. The second of these searching flights was followed by a long aggressive bout with a neighbouring male, during which the female left her mate's territory and was not seen again.

In addition, sexual/aggressive flights are defined as those in which the territorial male makes a rapid and direct approach towards a conspecific pair in tandem or during copulation. This type of response was only seen once and it was uncertain whether the in tandem pair had elicited a sexual, an aggressive, or a dual reaction.

COPULATION

Copulation, as indicated by the assumption of the wheel position, commenced in the air and after a few seconds continued after the pair had settled near the centre of the male's territory. Nine complete copulations were recorded (Tab. VI). The great range of undisturbed copulation durations in essentially similar conditions is remarkable. It is known that the first two matings for 23 July were certainly with the same female. It is also suspected that the last two matings for 24 July and the pair recorded on 28 July were with the same females: this may indicate that second matings after a very short period, with the same female, are

Table VI
Copulation times under sunny conditions

| Date (July 1980) | Number borne by male | Time at start of copulation | Duration of copulation | Shade temperature | |
|---------------------|-------------------------|--------------------------------|---------------------------|------------------------------|------|
| 22 | 66 | 12:42 | 6 min: 46 sec | 22.0°C | |
| 23 | 65 | 13:55 | 3:55 | } same female | 26.0 |
| | | 14:00 | 0:05 | | 26.0 |
| | | 16:45 | 14:29 | 24.0 | |
| 24 | 65 | 13:45 | 8:06 | 23.5 | |
| | | 14:50 | 3:58 | } possibly same female | 26.5 |
| | | 15:07 | 0:45 | | 26.5 |
| 28 | 3 | 17:15 | 24:50 | } possibly same female | 24.0 |
| | | 17:50 | 1:50 | | 24.0 |

either incomplete or exceptionally rapid. With such a wide range of copulation durations, the mean of 7 min 11.5 sec may not have a great deal of significance.

WANDERERS

Mature males, apparently without any attachment to a fixed territory, were often seen flying along the stream, passing through several males' territories quite rapidly. The defending males often attacked and were able to drive away the intruders. However, quite often the resident male either would not see the wanderer or would ignore it. This sometimes resulted in a wandering male remaining in one area for some minutes. It was evident that constantly wandering males were common and their chances of a successful mating were by no means negligible, although detailed observations on them were not made because of their mobility. Some matings by non-territorial males were seen and since copulating pairs settle rapidly they do not easily attract the attention of resident males. Perched, stationary individuals of either sex are always ignored by flying males.

DISCUSSION

This study of *O. coerulescens* has illustrated the variability of behaviour within a single libellulid species. For example, the territoriality and site attachment displayed by some males is by no means common to the whole population. In good weather conditions only 39% of newly marked males were resighted even once and in periods of poor weather this value was reduced to 23%. Therefore, we can say that a high degree of localization of most male *O. coerulescens* is probably not the norm. But some individuals consistently occupy the same territory and there is some evidence that they tend to become increasingly associated with specific areas as they age. Other individuals after being localized territorially for some days, disappear for up to 20 days before reappearing at the same or nearby territorial area. MAY (1980) found that the Central American libellulids *Micrathyria atra*, *M. ocellata* and other species were often extremely variable in their behaviour. *M. atra* showed peak activity and largest numbers in the early morning in 1975, but two years later the peak activity period was early in the afternoon. Before the ambient temperature reached 23° C most males of *M. atra* flew continuously, but at higher temperatures they were much less active. Observations such as these on *Orthetrum* and *Micrathyria* indicate the need to observe individuals and populations for prolonged periods and under different conditions to ensure that the full range of behaviour is being recorded. The present observations on *O. coerulescens* may, therefore, not be typical of the species as a whole.

The frequently observed "wanderers" of *O. coerulescens*, appearing at water

any time during the territorial period, represent sexually active individuals about which very little is known. In *O. coerulescens*, as in *O. julia* (PARR, 1980), wanderers appear to be a class of males apart from the better known territorial group, but it is not known if they are always non-territorial. The fact that no wandering individuals of *O. julia* (PARR, 1980) and *O. coerulescens* (the present study) were caught bearing marks, indicating they had not been caught on an earlier occasion, suggests that they may, indeed, be a different behavioural class from territorial insects. Further studies could indicate a continuum of behavioural patterns from wanderers through to fully territorial individuals displaying very predictable localization. There is clearly a need for detailed studies on wandering males in an attempt to elucidate their role in the reproductive biology of selected libellulid species.

The plasticity of behaviour typical of euryvalent dragonflies is illustrated by the two different types of territory which may be used. Stream-dwelling individuals defend linear territories and patrolling is essentially unidimensional. In contrast, those individuals patrolling over marshy heathland maintain surveillance over a wide area and, hence, their flight patterns are more complex and two-dimensional. Individuals may switch several times between different types of territories during their reproductive spans. *O. coerulescens* therefore, responds periodically to different stimuli in territory recognition.

The time of arrival of territorial males was independent of temperature (within the range 15-23° C) providing the morning was cloudless. *Micrathyria atra* in Central America was reported to behave similarly to *O. coerulescens*, whereas *M. ocellata* was probably affected by temperature and arrived later when the morning was cool, but still sunny (MAY, 1980).

The various territorial flight components are complex and numerous, often with the incorporation of several different components into a single flight. This complexity contrasts with the simple flight types seen in *Orthetrum julia* (PARR, 1980) and *Nesciothemis nigeriensis* PARR & PARR, 1974) where different territorial flight components were not generally combined into a single flight period. There is a need for further studies to determine whether the proportions of patrolling, aggressive and feeding flights are similar in other populations and with varying population densities. The observations reported here and those on *O. julia* (PARR, 1980) suggest that aggression would be expected to be less in low population densities, but this might not necessarily be the case if territories were much larger and the individuals were very active and mobile. PAJUNEN (1962a, 1962b) found that *Leucorrhinia dubia* in Finland was more aggressive in low densities late in the season, than when crowded in early season populations.

Feeding accounts for an appreciable (11.7%) fraction of the total time spent in territorial flights. Different species of libellulids appear to be classifiable according to whether or not they feed during territorial periods (PARR, 1980, 1983). The available evidence suggests that those feeding in their territories tend

to be species staying for long uninterrupted periods at water, whereas the species not recorded as feeding there spend only short spells at water before withdrawing to feed. However, further detailed observations of a range of species are needed to confirm this suggestion as being a general rule for libellulid behaviour.

Patrolling flights which are such a prominent feature of territoriality in *O. coerulescens*, have hardly been recorded in the closely related species *O. julia* (PARR, 1980) and *Nesciothemis nigeriensis* (PARR & PARR, 1974). Patrolling, which appears to be a spontaneous, intrinsically controlled behaviour pattern, may be related to the extent to which a territory holder can survey his area from a selected perch. Such flights would serve to determine the current distribution of neighbouring conspecific individuals of both sexes. Hence the long, linear territories of *O. coerulescens* and the large two-dimensional territories of *Libellula quadrimaculata* are regularly patrolled, but the small easily surveyed territorial areas of *O. julia* and *N. nigeriensis* are not.

The length of time *O. coerulescens* spends in copula is notable for its variability. Some of the variation may possibly reflect differences in temperature or some other weather factors, but the present data do not support this. In the three cases when males mated twice within a short period of time, the second mating was much the briefer of the two. In one of these cases, the two matings definitely involved the same pair and in the other two instances it is suspected that this was so. Very short repeated matings may indicate relative sexual incompetence after only a short rest period. If performed with the same female, repeated matings may involve initial sperm removal or displacement, which would probably need to be most complete in the first copulation to ensure any evolutionary advantage, and brief second matings which might only involve sperm transfer in *O. coerulescens*.

REFERENCES

- HEYMER, A., 1969. Fortpflanzungsverhalten und Territorialität bei *Orthetrum coerulescens* (Fabr., 1798) und *O. brunneum* (Fonsc., 1837) (Odonata: Anisoptera). *Rev. Comp. animal* 3(2): 1-24.
- HIGASHI, K., 1969. Territoriality and dispersal in the population of dragonfly, *Crocothemis servilia* Drury (Odonata: Anisoptera). *Mem. Fac. Sci. Kyushu Univ.*, (E) 5(2): 95-113.
- MAY, M.L., 1980 Temporal activity patterns of Micrathyrina in Central America (Anisoptera: Libellulidae). *Odonatologica* 9(1): 57-74.
- PAJUNEN, V.I., 1962a. Studies on the population ecology of *Leucorrhinia dubia* V.d. Lind. (Odon., Libellulidae). *Ann. zool. Soc. "Vanamo"* 24(4): 1-79.
- PAJUNEN, V.I., 1962b. A description of aggressive behaviour between males of *Leucorrhinia dubia* V.d. Lind. (Odon., Libellulidae). *Ann. ent. fenn.* 28: 108-118.
- PARR, M.J., 1980. Territorial behaviour of the African libellulid *Orthetrum julia* Kirby (Anisoptera). *Odonatologica* 9(1): 75-99
- PARR, M.J., 1983. An analysis of territoriality in libellulid dragonflies (Anisoptera: Libellulidae). *Odonatologica* 12(1): 39-57.

- PARR, M.J. & M. PARR, 1974. Studies on the behaviour and ecology of *Nesciothemis nigeriensis* Gambles (Anisoptera: Libellulidae). *Odonatologica* 3(1): 21-47.
- PARR, M.J. & M. PARR, 1979. Some observations on *Ceriagrion tenellum* (de Villers) in Southern England (Zygoptera: Coenagrionidae). *Odonatologica* 8(3): 171-194.

Note added at proof stage:

A useful general review of territoriality (including references to Odonata) which appeared recently is: J.H. KAUFMANN (1983). On the definitions and functions of dominance and territoriality. *Biol. Rev.* 58:1-20.