Odonatologica 12(1): 39-57

March 1, 1983

AN ANALYSIS OF TERRITORIALITY IN LIBELLULID DRAGONFLIES (ANISOPTERA: LIBELLULIDAE)

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Received and Accepted September 8, 1982

Over 30 species of libellulids (18 genera) have been studied with particular reference to territoriality. Attempts to analyse territoriality are difficult because the approach adopted by individual investigators varies and thus their results may not be directly comparable. Furthermore, the range of territorial patterns is wide and their expression is complex and variable. The pattern of territoriality in a given species or individual is created by the interaction of, (1) spatial, (2) temporal and (3) biological factors. Within these three primary determinants influencing territoriality, many other, secondary factors operate with varying degrees of importance on the overall pattern. Also, tertiary and quaternary factors are often the ultimate means of determining a territorial pattern. Spatial factors include territory type, territory size, size of insect and population density. There is a continuum of variation between discrete territories and communal territories supporting a hierarchical group of individuals. Temporal factors include waterside (daytime) and roosting-site activity. Biological factors, particularly, are numerous and complicated, and include secondary levels labelled as residentiality, territorial activities (non-sexual) and sexual activities.

INTRODUCTION

The observations of WILLIAMSON (1899) must be some of the earliest recordings of libellulid territorial behaviour. He described how males of *Celithemis elisa* were strongly localized, returning time and again to the same perch and how they attacked and drove off intruding conspecific males.

The increasing popularity in recent years of the Libellulidae as subjects for behavioural and ecological studies has resulted in a large volume of information which can be utilised in an attempt to analyse patterns of territoriality in this family. Over 30 species of libellulid and 18 genera have been studied with particular reference to territoriality. In all these examples several major aspects of territoriality have been reported on. In about another 30 species certain specific aspects of territorial behaviour have been reported, but no detailed study has been undertaken. Attempts to analyse libellulid territoriality are made difficult by two main factors. Firstly, the range of territorial patterns is very wide and their expression is complex and variable. Libellulid behaviour shows considerable plasticity (UEDA, 1979). Secondly, for several reasons, the approach adopted by individual investigators varies and thus their results may not be directly comparable. It is rarely possible to make exactly parallel studies of related species and generally, one has to seize any opportunity to investigate detailed behaviour as and when a species presents itself (PARR, 1980). Nevertheless, analysis of the often fragmentary evidence of different aspects of territoriality of over 60 species has allowed a reasonably reliable picture to emerge of the principal determinants of libellulid territorial behaviour. Five general reviews (MOORE, 1952a & 1957; KORMONDY, 1961; JOHNSON, 1964; CAMPANELLA, 1972) have been largely or wholly concerned with territoriality in the Odonata. However, none has concentrated exclusively on the libellulids, although this behaviourally complex group is probably the best studied of all major dragonfly taxa.

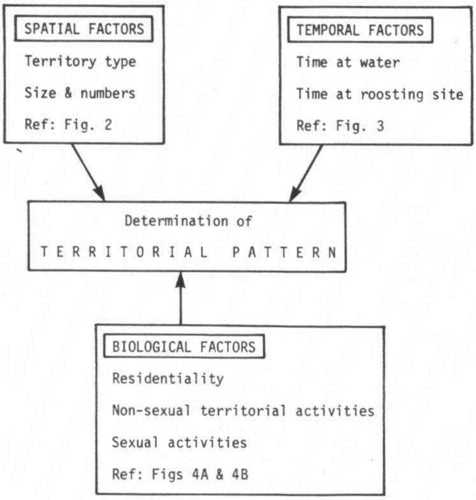

Fig. 1. Three primary determinants and major secondary factors affecting territorial pattern

In this paper, "territory" is defined as "any defended area" (NOBLE, 1939). As several workers have pointed out, this definition has the advantage that no particular function is implied for territorial behaviour. In the Odonata territoriality is highly varied and each example needs to be considered individually in the light of the precise local conditions.

Territoriality is normally recognized as being primarily a male activity, but very rarely, females exhibit aggressiveness (JACOBS, 1955) which may be true territoriality. For the purposes of this article, territoriality is understood to be a male-limited phenomenon.

DETERMINATION OF TERRITORIAL PATTERNS

The pattern of territoriality exhibited by a given individual or species is created by the interaction of (1) spatial, (2) temporal and (3) biological factors. Within these three primary determinants influencing territoriality, other, secondary factors operate with varying degrees of importance on the overall pattern (Fig. 1).

Spatial factors include such components as territory type, size of the dragonfly and density of the population. Temporal factors include the partitioning of territorial periods into time spent at the waterside (or daytime breeding/oviposition site) and away from water, including the roosting site, if territoriality occurs in the latter context. Biological factors, particularly, are numerous and complicated, and include the secondary levels labelled as residentiality, non-sexual territorial activities and sexual behaviour.

SPATIAL FACTORS

TERRITORY TYPE

Figure 2

Very often it is possible to classify dragonflies according to whether they are primarily associated with lotic or lentic water conditions and this relates directly to their normal choice of territorial sites. Some species are wholly restricted to stagnant water; especially as small temporary pools (*Pantala flavescens*, SAKAGAMI et al., 1974, and *Bradinopyga strachani*), or small permanent pools and larger lakes (*Leucorrhinia dubia* and *L. rubicunda*, PAJUNEN, 1962a), or lakes only (*Nesciothemis nigeriensis*, PARR & PARR, 1974). Other species are only found in association with streams or rivers: examples of these are the North American libellulids *Belonia croceipennis* (WILLIAMS, 1977) and *Paltothemis lineatipes* (DUNKLE, 1978). Stenovalency, as exemplified by strictly stream dwelling or stagnant water species is probably much rarer than euryvalency. A large number of species, such as *Boninthemis insularis* (SAKAGAMI et al., 1974); *Orthetrum trinacria, Trithemis annulata, T. donaldsoni* (CORBET, 1962); *Orthetrum coerulescens* and *Nesciothemis farinosa*, are to varying extents euryvalent: that is to say, they can adapt to a range of lotic and lentic environments. Species which are primarily riverine apparently respond to the length of uninterrupted shore-line when selecting their habitat and the long straight shores of lakes or Man-made dams often attract the same species (CORBET, 1962).

Libellulid territories range in type from small, fully discrete areas to large, complex communal zones which are shared by two or more individuals. Some species seem habitually to occupy more or less discrete territories (*Nesciothemis nigeriensis*, PARR & PARR, 1974). Others tend to exhibit extensive overlapping of territories quite commonly and this may be associated with territories along streams (*Orthetrum coerulescens*). Such linear territories may be difficult to defend at their extremities, leading to mutual encroachment.

Overlapping territories have been reported in many pond dwellers (e.g. *Perithemis tenera,* JACOBS, 1955; *Sympetrum parvulum,* UEDA, 1979; *Crocothemis servilia,* HIGASHI, 1969; *Pantala flavescens,* SAKAGAMI et al., 1974).

A note by WARREN (1964) suggest that more than one species of libellulid may co-exist at the same habitat if they maintain patrolled territories at different heights. This author noticed that a territorial *Libellula quadrimaculata* only attacked a patrolling *Leucorrhinia dubia* if the latter flew up to the level at which the *Libellula* was perched.

The most complex expression of territoriality occurs in species having communal territories. CAMPANELLA & WOLF (1974) described the sharing of a defended area by several mature males of *Plathemis lydia;* these were not all equally effective, so that a range of dominance and submission was recognized. In this particular instance the situation was especially complex since a temporal factor was also operative, resulting in a turn-over of territorial males during any daytime period. Territorial expression also varies with time in *Leucorrhinia dubia* (PAJUNEN, 1962a, 1962b). Early season localization of mature males (especially at high densities) may be very temporary with aggressive behaviour being suppressed. Later in the season at lower densities, males were much more likely to remain in particular areas for long periods and to behave aggressively. Therefore, early season males may appear to share communal areas, which were not regarded as territories by PAJUNEN (1962a, 1962b). However, his description of the mutual approach flight of two neighbouring early-season males of *L. dubia* and their subsequent flight side by side before parting, is strongly suggestive of a display flight at the boundary between two individual territories. Later in the season, neighbouring males defend large definite areas. *L. dubia,* therefore, shows a gradual shift in behaviour with increasing aggressiveness and territoriality as population density declines and individuals age. In contrast, in *Nesciothemis nigeriensis,* males in dense mid-season populations are strongly localized and more aggressive than later in the season when population numbers have declined (PARR & PARR, 1974).

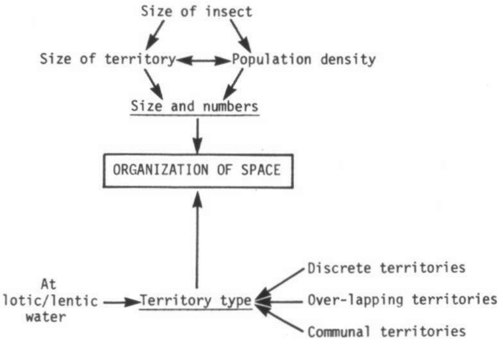

Fig. 2. Spatial factors

SIZE AND NUMBERS

Figure 2

The size of the insect, population density and size of territory interact to produce for each species a characteristic range of densities and territory sizes. Small species tend to defend small areas (*Nannophya pygmaea*, YAMAMOTO, 1968; *Perithemis tenera*, JACOBS, 1955; *Palpopleura lucia portia*, GREEN, 1974; *Sympetrum danae*, SONEHARA, 1965) and larger species are usually associated with large territories (*Pantala flavescens*, SAKAGAMI et al., 1974; *Orthetrum cancellatum*, KRÜNER, 1977; *O. coerulescens*, PARR, 1983). Exceptionally large territories of up to 50 metres long have been recorded for *Leucorrhinia pectoralis* (KIAUTA, 1964). Detailed studies have shown that increased population density may result in a larger number of males defending smaller territories (*Acisoma panorpoides inflatum*, HASSAN, 1978; *O. cancellatum*, KRÜNER, 1977; *O. coerulescens*, HEYMER, 1969; *Nesciothemis nigeriensis*, PARR & PARR, 1974; *O. microstigma*, GREEN, 1974; *Tramea virginia*, ISHIDA, 1958). However, in *Leucorrhinia rubicunda*, with increasing density, aggressive behaviour results in individual territories being ill-defined; but aggression occurs in only a minority of appropriate situations and a considerable social tolerance is developed between neighbouring males (PAJUNEN, 1966).

TEMPORAL FACTORS

AT WATER

Territoriality can be classified as full-time or part-time according to whether males spend the greater part of the daytime (usually when sunny) in their territories or only a much smaller part of the possible period each day at water.

Full-time territoriality has been recorded for *Orthetrum albistylum*, *O. triangulare melania* (ARAI, 1972); and *O. julia* (PARR, 1980). However, many species do not adopt territorial positions at water until some time after the sun has appeared and may abandon their territories well before sunset (*Crocothemis servilia*, HIGASHI, 1969; *Orthetrum microstigma* & *Trithemis arteriosa*, GREEN, 1974; *Nesciothemis nigeriensis* & *Palpopleura deceptor*, PARR & PARR, 1974). These latter species are very similar to full-time territorialists, remaining by water for an unbroken period at the same site throughout much of the day.

Many libellulids do not, however, show full- or nearly fulltime territoriality, but display either regular or irregular shorter periods of territorial behaviour at water. JACOBS (1955), found that *Plathemis lydia* males could be largely categorised according to whether they arrived mostly in the morning (13 percent) or mostly in the afternoon (60 percent), with 27 percent being too irregular to classify. The same author comments that there is "continuous displacement of males throughout the day", thus pre-empting partially CAMPANELLA & WOLF's (1974) concept of the "temporal lek" as applied to *P. lydia.*

Paltothemis lineatipes (DUNKLE, 1978) is a good example of a libellulid having a simple regular pattern of part-time territoriality, being at water (mostly perching, interspersed with patrol flights) almost exclusively in the morning. Males of *Perithemis tenera* (JACOBS, 1955) only spent a relatively short period of the day in a territory, the daily arrival time differing from individual to individual, with complete displacement of territory holders each morning and afternoon. Species which are irregular in their territorial periods include *Diplacodes bipunctatus* & *Pantala flavescens* (SAKAGAMI et al., 1974), *Pachydiplax longipennis* (JOHNSON, 1962), *Leucorrhinia dubia,* (PAJUNEN, 1962a), *Acisoma panorpoides inflatum* (HASSAN, 1978), *Micrathyria atra, M. ocellata* & *M. aequalis* (MAY, 1980). Another species which is irregular and appears to conform to a temporal lek system as described by CAMPANELLA (1972) for *Plathemis lydia* and *Libellula luctuosa,* is *Crocothemis erythraea* (FALCHETTI & UTZERI, 1974).

AWAY FROM WATER

Figure 3

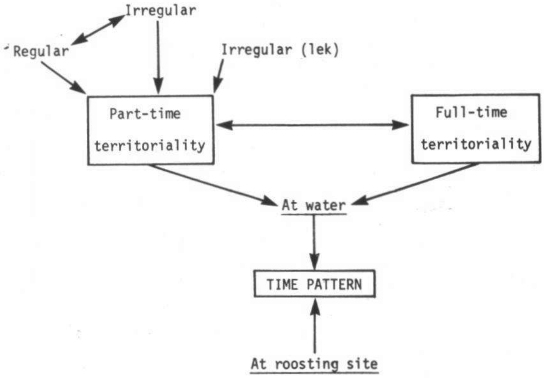

Fig. 3. Temporal factors

Territorial activities, as manifested by both defence of an area and reproductive behaviour appear to be rare away from water. However, male *Nesciothemis nigeriensis* which aggregated at 16.30 — 18.00 hrs in groups of up to 15 individuals in the general roosting area were mutually aggressive and defended very small territories around their individual perches. Copulation was also observed in this situation in *N. nigeriensis* (PARR & PARR, 1974). Copulation away from water and, hence, not in the usual water-side territory, occurs in *Brachythemis leucosticta.* It is not known whether the female flies to the water to oviposit immediately after copulation, nor whether the male escorts her to do so (ADETUNJI, 1972).

BIOLOGICAL FACTORS

RESIDENTIALITY

Figure 4A

It is assumed that generally, male libellulids develop with age from being sexually immature, non-aggressive and non-localised into mature, aggressive and localised individuals. However, information on sexually immature libellulids is scarce. Many species probably are non-localised before sexual maturation and this is definitely stated for *Leucorrhinia dubia* (PAJUNEN, 1962a). In contrast, sexually immature males of *Nesciothemis nigeriensis* are often restricted to a very small area of one or two metres in extent for the whole of their maturation period (about 13 days) away from water. In this latter species, aggressive behaviour has been seen in the maturation area two days before moving to water and becoming territorial (PARR & PARR, 1974).

The relationship between residentiality and territoriality has been studied to a much greater extent in sexually mature libellulids. Many species are known to develop a high degree of attachment to a particular site at water, in at least a proportion of adult males. Such species include *Nesciothemis nigeriensis* (PARR & PARR 1974), *Orthetrum julia* (PARR, 1980), *Acisoma panorpoides inflatum* (HASSAN, 1978), *O. coerulescens* & *O. brunneum* (HEYMER, 1969), *Sympetrum parvulum* (UEDA, 1979), *Plathemis lydia* (JACOBS, 1955) and *Pantala flavescens* (SAKAGAMI et al., 1974). Individual males displaying localisation are known to have a powerful residential advantage over intruders in territorial disputes (*Pachydiplax longipennis,* JOHNSON, 1962; *Crocothemis servilia,* HIGASHI, 1969; *C. erythraea,* FALCHETTI & UTZERI, 1974; and many other species). The study of *Orthetrum julia* (PARR, 1980) showed that the degree of localisation of individual males varied greatly and there was a strong positive relationship between the number of times an individual was observed and its degree of localisation; thus, there is a strong connexion between site attachment and the ability of males to hold territories within the main colony area.

HIGASHI (1969) used the term "wanderers" to describe males of *Crocothemis servilia* which did not establish territories, possibly because of the residential advantage of the territory holders. Many mature males of *Sympetrum parvulum* (UEDA, 1979), *Diplacodes bipunctatus* (SAKAGAMI et al., 1974), *Orthetrum julia* (PARR, 1980), and *O. coerulescens* (PARR, 1983) apparently do not hold territories and thus may be classified as wanderers. In *O. julia,* wanderers were most numerous and active towards the end of the afternoon, as the territorial colony became shaded and territory holders shifted positions or dispersed (PARR, 1980). In contrast, wanderers in *O. coerulescens* (PARR, 1983) were likely to be present in low numbers throughout the day, with no peak of activity or numbers at a particular time.

NON-SEXUAL TERRITORIAL ACTIVITY
Figure 4A

Within territorial activity are numerous subsidiary factors determining the overall pattern for a given species or situation. The main tertiary factors include the perching/flying time ratio and flight components involving feeding, patrolling and aggression.

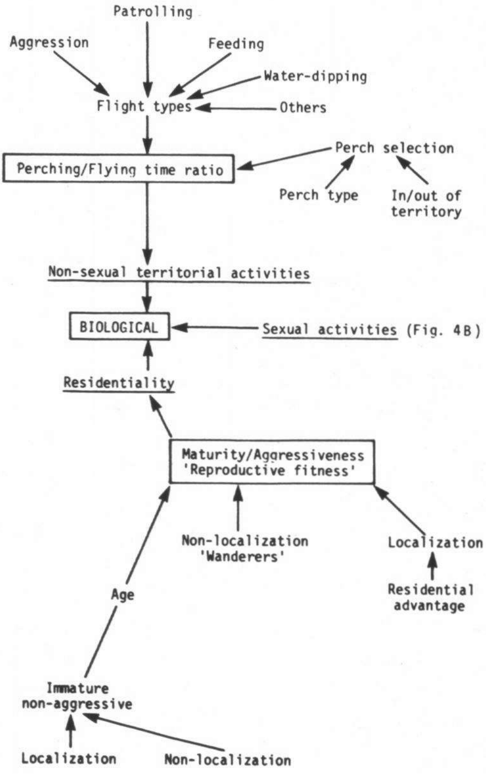

Fig. 4A. Biological factors — residentiality and non-sexual territoriality

Many libellulids may be clearly classified as either perchers, spending less than 20 percent of their time in the air (e.g. many *Nesciothemis, Orthetrum, Trithemis, Sympetrum, Diplacodes* and *Urothemis* spp.) or flyers, whose resting periods are relatively short (e.g. *Pantala, Tramea, Rhyothemis, Tholymis* and *Zygonyx* spp.). However, others are more difficult to categorise either because they vary from time to time, or because they spend roughly equal lengths of time perched and flying. Variable species include *Micrathyria atra* and *M. ocellata* which thermoregulate by remaining continuously in flight until temperatures exceed 23°C. and then fly less (MAY, 1980). Close observation will probably reveal other species which behave similarly. Individual males in the population of *Crocothemis erythraea* studied by FALCHETTI & UTZERI (1974) spent roughly equal amounts of time in flight and perched, with each flying and perching period lasting between one and five minutes. During territorial periods, most species perch within the area actively patrolled. But FALCHETTI & UTZERI (1974) reported that *C. erythraea* did not do so, and thus effectively, territoriality consisted of a series of brief spells limited to when the insect was in flight; a perched *C. erythraea* could not view its territory and thus did not defend it from such a situation. *Libellula quadrimaculata, L. depressa* and *Plathemis lydia* are species where long flight periods may alternate with long spells of inactivity in the breeding area.

The type of perch selected may be very restricted in form or may be variable. *Nesciothemis nigeriensis* is very dependent on emergent *Echinochloa* grass for territorial perches (PARR & PARR, 1974) and *Acisoma panorpoides inflatum* usually rests on flat floating leaves (HASSAN, 1978). Some species are especially dependent on waterside rocks for territorial perches (e.g. *Paltothemis*, DUNKLE, 1978 and *Bradinopyga strachani)*. More usually, perching sites are variable, although they may be consistently of the same pattern in some habitats and populations. In the New Forest, Southern England, territorial *Orthetrum coerulescens* use twigs, emergent vegetation, grasses, logs, stones and flat soil on which to perch (PARR, 1983), whereas the population studied by HEYMER (1969) perched selectively on stems of plants. *O. julia* will also utilise a great variety of perching sites (PARR, 1980). KRÜNER (1977) noted that *O. cancellatum* mostly perched on branches at temperatures above 26°C., but at lower temperatures tended to use stones. *Leucorrhinia rubicunda* perch on a variety of emergent vegetation or other objects projecting above the water level (PAJUNEN, 1966).

Whilst it is possible to recognize several different territorial flight components in all species (e.g. feeding, patrolling, aggression, investigatory, etc.) there is variability in their expression. In some species most individual flights have a single function (*Orthetrum julia*, PARR, 1980), whereas in others many flights have more than one type of flight component (*O. coerulescens*, PARR, 1983).

Aggressive flights appear to be the most nearly universal major flight component in territorial libellulids. These flights are generally directed at conspecific males, but inter-specific aggression is not rare and may represent redirected activities (HINDE, 1970). Inter-specific aggression had, for example, been noted in *Acisoma panorpoides inflatum* (HASSAN, 1978), *Orthetrum albistylum* (LOHMANN, 1979), *O. coerulescens* (PARR, 1983) and *Micrathyria ocellata* (MAY, 1980). Territorial male libellulids normally only respond to intruding conspecific males if the latter are in flight. An exception to this is *Pachydiplax longipennis*, the male of which maintains a threat display with its abdomen raised when perching, as well as when flying in the breeding area (JOHNSON, 1962). He showed that posture and colour were important recognition factors in male to male interaction in *P. longipennis*. A number of other species give clear threat displays while in flight (e.g. *Plathemis lydia* & *Perithemis tenera*, JACOBS, 1955; *Leucorrhinia dubia*, PAJUNEN, 1962a, 1963b; *L. rubicunda*, PAJUNEN, 1966; *Crocothemis erythraea*, FALCHETTI & UTZERI, 1974). Males of *Nesciothemis nigeriensis* respond to models of conspecific males if the body shape, size, colour and pattern are accurate, but natural flight movements are not important (PARR & PARR, 1974). In

Plathemis lydia (JACOBS, 1955) and *Leucorrhinia dubia* (PAJUNEN, 1962a) natural movements of potential rivals are necessary to elicit an aggressive response from territory holders. In typical intraspecific aggressive flights approach towards the intruder is from the side or from below and may result in a physical clash or merely a rapid chase before the intruder is driven off. In the few species where territorial activity budgets have been calculated, the percentage of flights incorporating an aggressive component varied greatly. In *Orthetrum julia*, 60 percent of all territorial flights were aggressive (PARR, 1980), whereas the equivalent values for *Nesciothemis nigeriensis* (PARR & PARR, 1974) and *O. coerulescens* (PARR, 1983) were 30 percent and 17 percent respectively.

Patrolling flights are linear, circular or more complex medium-speed horizontal cruising flights within the male's territory. They appear to have the function of establishing the current distribution of neighbouring conspecific males and may represent an intrinsic spontaneous behaviour pattern. Patrolling has been reported in a large number of species (e.g. *Sympetrum parvulum*, UEDA, 1979; *Diplacodes bipunctatus* & *Pantala flavescens*, SAKAGAMI et al., 1974; *Leucorrhinia rubicunda*, PAJUNEN, 1966; *Belonia croceipennis*, WILLIAMS, 1977). However, closely related and congeneric species may differ markedly in their use of patrolling. In *Orthetrum coerulescens* 40 percent of all flights had a patrolling component (PARR, 1983) and *O. microstigma* was described as a "percher and patroller" by GREEN (1974). In contrast, in *O. julia* (PARR, 1980) only 0.6 percent of territorial flights were patrolling and the closely related *Nesciothemis nigeriensis* was never seen to patrol (PARR & PARR, 1974).

Feeding may or may not occur during territorial periods. Amongst the species reported as feeding are *Libellula quadrimaculata* (CORBET et al., 1960), *Leucorrhinia caudalis* (PAJUNEN, 1964b), *Nesciothemis nigeriensis* (PARR & PARR, 1974), *Orthetrum coerulescens* & *O. brunneum* (HEYMER, 1969), *O. cancellatum* (KRÜNER, 1977), *O. julia* (PARR, 1980), *Boninthemis insularis* (SAKAGAMI, et al., 1974) and *Sympetrum frequens* (HIGASHI, 1973). Other species apparently never, or only very rarely, feed at the waterside territorial site. These 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* (GREEN, 1974), *Micrathyria atra* & *M. ocellata* (MAY, 1980). Many of the feeders are species which tend to remain in their territories for long periods of time, whereas the non-feeders are often species where each individual stay at water is relatively short. Individual feeding flights of perchers are generally of short duration, usually less than five seconds.

Flights classified as "investigatory" have been recognized in *Orthetrum julia* (PARR, 1980), *O. coerulescens* (PARR, 1983) and *Nesciothemis nigeriensis* (PARR & PARR, 1974). Investigatory flights are leisurely and direct, and orientated towards the object being investigated, which is usually an insect whose movement initiates the flight. The precise function of investigatory flights is unclear since they are distinct from feeding, patrolling and aggressive movements.

The phenomenon known as water-dipping has been observed by several workers. In most cases the tip of the abdomen is placed momentarily in the water as the insect flies over the surface e.g. *Plathemis lydia* & *Perithemis tenera* (JACOBS, 1955), *Libellula quadrimaculata* (MOORE, 1957), *Belonia croceipennis* (WILLIAMS, 1977) and *Orthetrum coerulescens* (PARR, 1983). In contrast, water-dipping in *Nesciothemis nigeriensis* occurred only by head-dipping on the water surface, which was interpreted as drinking (PARR & PARR, 1972).

SEXUAL ACTIVITIES

Figure 4B

Numerous subsidiary factors contribute to the full pattern of sexual activities and it is in this category of territorial determinants that the variability and plasticity of libellulid behaviour is most evident. For the purposes of this analysis, territorial sexual activities have been classified into four main tertiary-level factors, each being divisible into various quaternary components of behaviour.

Sexual Interaction of Males with other Odonates. — Males respond sexually to other individuals when various stimuli are perceived. In many examples the specific stimuli have not been identified, but JACOBS, (1955) says of *Plathemis* that "... if a female stops suddenly ... a pursuing male may assume the coupling position on the female's shadow or wing spot". Jacobs assumes males of *Plathemis* recognize females primarily by their flight pattern. Flight patterns have been mentioned by PAJUNEN (1962a) and by ITO (1960) as being the most important releasers allowing males to recognize females of *Leucorrhinia* spp. and *Orthetrum albistylum speciosum*, respectively. Some form of movement, not necessarily natural, is usually necessary if a male is to respond sexually towards another insect or model. Male *Nesciothemis nigeriensis* recognize females through a combination of colour, colour pattern, size and shape, but normal flight movements are not necessary (PARR & PARR, 1974).

The ability of males to distinguish sex is variable. In many species, mistakes are rarely made (e.g. *Leucorrhinia dubia*, PAJUNEN, 1964a; *Orthetrum julia*, PARR, 1980; *Nesciothemis nigeriensis*, PARR & PARR, 1974; *Plathemis lydia* & *Perithemis tenera*, JACOBS, 1955). Others, however, do not seem to discriminate well between the sexes or even species (*Libellula quadrimaculata*, *Sympetrum striolatum*, *S. sanguineum* and *Orthetrum cancellatum*, MOORE, 1952a), so that homosexual behaviour may be common in some populations. A male *Orthetrum coerulescens*, on the same day, made typical high, fast and direct

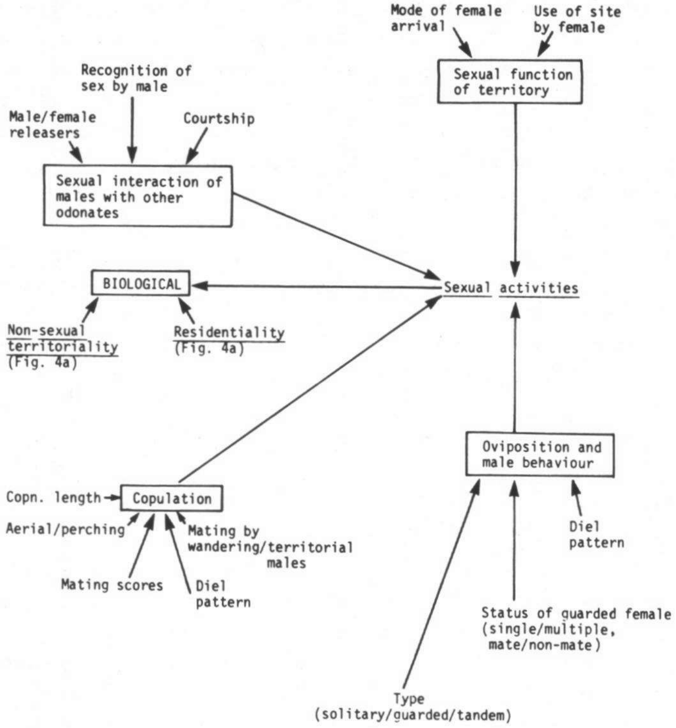

Fig. 4B. Biological factors — sexual activities

sexual flights, firstly towards a bird (the swift, *Apus apus)* and later towards an airplane flying high overhead (PARR, 1983). When the density of *Libellula quadrimaculata* was very high, males of *Leucorrhinia pectoralis* were seen to attack this species sexually (KIAUTA, 1964). In most species of libellulids no courtship can be recognized, females do not appear to be attracted towards males and territorial males attempt to seize conspecific females as soon as they appear. In some species, however, a courtship flight occurs and females apparently respond directly to the males (e.g. *Perithemis tenera,* JACOBS, 1955; *Olpogastra lugubris,* CORBET et al., 1960; *Belonia croceipennis,* WILLIAMS, 1979; *Palpopleura lucia portia).*

Sexual Function of Territory. — Mature females most often arrive at a territory solitarily and thus, the territory is a meeting ground for the sexes; however, occasionally they have been seen to arrive in tandem (*Tramea transmarina euryale,* SAKAGAMI et al., 1974) or in copula (*Sympetrum parvulum,* UEDA, 1979). An *Orthetrum coerulescens* female may arrive unaccompanied or she may appear in a territory in tandem or in copula if the territory holder has flown outside his territorial limits to intercept her (PARR, 1983). In many cases, the territory functions as a dual mating and oviposition site, but in *Hadrothemis camarensis* (NEVILLE, 1960) and *Orthetrum abbotti* (PARR, 1980), after mating in the territory, the female oviposits elsewhere. In *Sympetrum* (sp. not named) mating occurs away from water (MOORE, 1964) and in *Leucorrhinia dubia*, although the pair first couple at the water, copulation is completed away from it (PAJUNEN, 1962a). Exactly similar behaviour occurs in *L. pectoralis* (KIAUTA, 1964). *L. intermedia* has been recorded as mating at water, but on one occasion a pair in copula were in a forest one kilometre from water (ISHIDA, 1959).

Copulation. — PAJUNEN (1963a) has stressed the importance of the male's flight manoeuvres in attaining the copulation position, the movements of the partner's body being of minor significance. Copulation may occur wholly whilst in flight, (*Pantala flavescens, Diplacodes bipunctatus* & *Tramea transmarina euryale*, SAKAGAMI et al., 1974; *Paltothemis lineatipes*, DUNKLE, 1978; *Brachythemis leucosticta*, ADETUNJI, 1972 and *B. contaminata*, MATHAVAN, manuscript), or may be usually completed whilst at rest (*Sympetrum parvulum*, UEDA, 1979; *S. danae*, SONEHARA, 1965; *Acisoma panorpoides inflatum*, HASSAN, 1978; probably all *Orthetrum* spp.). The length of time a copulation lasts is not necessarily correlated with whether the process is entirely aerial or partly accomplished while perched. Some species habitually having very short mating times (e.g. *Acisoma panorpoides inflatum*, HASSAN, 1978 — about 5 sec; *Crocothemis sanguinolenta*, PARR, 1980 — about 7 sec) perch for most of the copulation period. Copulation in *Tramea transmarina euryale* is aerial and lasts about two minutes (SAKAGAMI et al., 1974). However, very long copulations are always accomplished while the pair is settled. The length of time the wheel position is maintained may vary greatly within a species and even for an individual; for example, the time range for *Orthetrum coerulescens* was 5 seconds — 24 mins 50 secs., (PARR, 1983) and for *O. sabina* was 2—28 minutes (MATHAVAN, manuscript). The variation in length of copulation time recorded for *Crocothemis erythraea* (7-26 sec) was related to wind strength and the need to settle in order to complete mating in a strong wind (AGUESSE, 1959). However, despite such variations, the classification into species having short, medium and long copulations proposed by CORBET (1962) is useful if one is aware of the possible range of time and the usual mean for a species.

Studies on *Perithemis tenera* and *Plathemis lydia* (JACOBS, 1955) showed that under natural conditions these species achieved maximum mating scores of 6 and 4 respectively per day. However, when most of the males were removed the scores were 21 and 80 per day respectively. HASSAN (1978) recorded a natural maximum of 5 copulations in a day for male *Acisoma panorpoides*. The normal number of copulations per day for other species may be much lower than those given by Jacobs and Hassan. For example, *Orthetrum julia* (PARR, 1980), *O. coerulescens* (PARR, 1983) and *Nesciothemis nigeriensis* (PARR & PARR, 1974) averaged only 0.5, 1.3 and 0.5 copulations per day respectively. MATHAVAN (manuscript) reports that 81 percent of female *Brachythemis contaminata* arriving at male territorial areas mate with the first male which catches them, but only 44 percent accept a second male if they are disturbed during oviposition immediately after an initial copulation. Little detailed information is available on the periodicity of copulation in relation to territorial spells. Most libellulids are apparently variable in that copulation is not restricted to any particular territorial period in the day, but detailed study would probably reveal more definite patterns in at least some species.

In some libellulids wanderers (mature males without a territory) may have a considerable impact on the reproductive structure of a colony. Whilst ITO (1960) states that females of *Orthetrum albistylum speciosum* will not mate with males not defending a territory, wandering males of *Orthetrum julia* (PARR, 1980), *O. coerulescens* (PARR, 1983) and *Sympetrum parvulum*, (UEDA, 1979) may have varying degrees of success in mating. In *O. julia* this is primarily dependent on the time of the day: wanderers in late afternoon may be highly successful in achieving copulation, but not at other times in the day. In *Sympetrum parvulum* and probably *O. coerulescens*, the mating success of wanderers is much more related to low densities of territorial males.

Ovipositon and Male Behaviour. — A female may oviposit either attended or unattended by the male with whom she has recently mated. When a female is attended during oviposition, in most species the male hovers over her, or nearby, and guards her against interferance from other males. This is probably the commonest form of behaviour when the female oviposits in the male's territory immediately after copulation is complete. Some species, most notably *Sympetrum* (*S. madidum*, CANNINGS, 1980; *S. striolatum*, MOORE, 1952b; *S. danae*, SONEHARA, 1965; *S. sanguineum*, JURZITZA, 1965; and *S. parvulum*, UEDA, 1979) frequently oviposit in tandem, but not exclusively. In *S. parvulum*, typical guarding behaviour of the female by the male is often seen if the latter has an established territory. If the male is a "wanderer", he may release the female and guard her if the population density is low, but if the probability of interferance during oviposition is high, then the female is likely to oviposit in tandem (UEDA, 1979). In some of the Trameini (*Tramea onusta*, NEEDHAM & HEYWOOD, 1929; *T. virginia*, OKAMOTO, 1954 & ISHIDA, 1958; *T. transmarina euryale*, SAKAGAMI et al., 1974; and sometimes in *Pantala flavescens*, SVIHLA, 1961) there is a repeated flight cycle of copulation; in tandem; separation; oviposition while male guards; in tandem; copulation. This cycle may be repeated many times in the male's territory. Very few species appear to oviposit exclusively without male attendance, although this had been reported for *Trithemis festiva* (KUMAR, 1972), *Orthetrum sabina* (MATHAVAN, manuscript) and *Paltothemis lineatipes* (DUNKLE, 1978); in addition, *Nannophya pygmaea* (YAMAMOTO, 1968) may do so.

Normally, guarding behaviour by a territorial male is reserved for a female with whom he has just mated. However, a male *Sympetrum parvulum* may guard many females at once (UEDA, 1979), and under such conditions it seems likely that some of the females may not always be his recent mates. Male *Orthetrum albistylum speciosum* (ARAI, 1972) and *Plathemis lydia* (JACOBS, 1955) may also guard multiple females.

DISCUSSION

Although a considerable body of information is available on libellulid territoriality and other aspects of the behaviour of this taxon, it is clear that very many gaps remain. It is hoped that this article will help to identify the particular areas and species groups where further detailed work is desirable. If the full spectrum of territoriality of any given species is to be well understood, many varied components of this aspect of behaviour need to be identified and studied. In this way, the acquisition and analysis of data of selected species and genera will clarify the complex patterns of libellulid territorial behaviour, which will then in turn be capable of being compared adequately with similar behaviour in other groups of animals. However, to be able to achieve this long term aim, there is a need to observe individuals, populations and species for long periods, under different conditions of habitat and season.

The detailed studies of *Leucorrhinia* spp., especially *L. dubia* (PAJUNEN, 1962a), show how the behaviour within a population may alter greatly during a flying season. The various differences in behaviour recorded for *Plathemis lydia* by JACOBS (1955) and CAMPANELLA & WOLF (1974) may illustrate, for example, variability between populations or merely differences in interpretation. The lack of patrolling flights in *Nesciothemis nigeriensis* (PARR & PARR, 1974) may be characteristic of only certain population densities, colonies or habitats, since patrolling is a very widespread behaviour pattern in other closely related libellulids. MAY (1980), in his study of *Micrathyria* spp., considered that some of the differences of behaviour he noted could have been ascribed to age and hormone variations. Other possible sources of variation leading to apparently contradictory results are taxonomic differences. For example, PINHEY(1979) has named *Crocothemis erythraea* Brullé as a synonym of *C. servilia* (i.e. *C. servilia erythraea*). YADAV (1979) concludes that the karyotypic variability of *C. servilia & ervthraea* is not much help in the clarification of their taxonomic status. However, B. KIAUTA (personal communication) considers that, on cytogenetic evidence, the African *C. erythraea* is certainly specifically distinct from the Oriental *C. servilia*. On the basis of a study of prophallus structure, LOHMANN (1981) also considers that *servilia* and *erythraea* are distinct species. In this connexion, it is interesting to note that HIGASHI (1969) states that *C. servilia* is effectively a full-time territorial species, whereas FALCHETTI & UTZERI (1974) indicate that *C. erythraea* is periodically territorial and the temporal lek system described by CAMPANELLA & WOLF (1974) probably operates in this species.

FALCHETTI & UTZERI (1974) state that *C. erythraea* behaves territorially only when flying; its perching periods are spent outside the territory, where it would not have the view necessary to defend that area. *Orthetrum coerulescens* (PARR, 1983) may use a great variety of perching sites when behaving territorially. Usually a good view of much of its territory is commanded when at rest, but quite often, the chosen perch does not allow this. Nevertheless, *O. coerulescens* will usually behave very aggressively towards conspecific males, even if it does not have a view of much of its nearby territory.

Territorial and reproductive behaviour have usually been associated with water. However in *Nesciothemis nigeriensis* PARR & PARR, 1974) and *Brachythemis leucosticta* (ADETUNJI, 1972; ADETUNJI & PARR, 1974), copulation, and in the former, aggressive behaviour also, have been seen away from the aquatic, oviposition areas. J. LEMPERT (personal communication) has observed aggressive, territorial-type, behaviour in *Sympetrum danae, S. flaveolum* and *S. vulgatum* during pauses in migratory flights. *Diplacodes bipunctatus* in New Zealand holds territories away from water, with the interaction between males resulting in the individuals being well spaced out. The function of such territories in *D. bipunctatus* is apparently primarily concerned with feeding (W.J. WINSTANLEY, personal communication). It is possible that such apparently deviant behaviour is more common than is at present recognized, since it is rarely looked for, or expected, away from water.

The phenomenon of "wandering" males would repay closer attention than it has hitherto received. HIGASHI (1969) considered that wanderers in *C. servilia* were the result of territorial competition, but UEDA (1979) concluded that in *Sympetrum parvulum* this was not necessarily so. In *Orthetrum julia,* wanderers were of a wide age range, and since they were most active (fast flying and aerial for long periods) during late afternoon when normal territoriality was less ordered, were then apparently reproductively successful (PARR, 1980). The presence of both territorial males and wanderers may represent a genetic dimorphism and not merely normal "successful" and "unsuccessful" individuals.

Most species of libellulids are classifiable as either flyers or perchers. However, species which spend more nearly equal periods in the air and perched, or are variable in this respect, may be more common than is apparent. They might be less conspicuous than the species clearly spending most of their time airborne or perched and, thus, would have been less studied. Some *Crocothemis* and *Micrathyria* spp. appear to apportion their territorial time roughly equally between flying and perching.

Another problem is that some species are territorial from sunrise to sunset, whereas others arrive relatively late in the morning and/or leave relatively early in the afternoon, but otherwise behave similarly to the full-time territorial species. The significance of these differences is quite obscure. Similarly, the good ability of some species to distinguish sex, whereas others frequently fail to do so, is another problem which would repay a detailed study.

It seems probable that some species of libellulids practice sperm displacement, as originally described for *Calopteryx maculata* (WAAGE, 1979). The variable length of copulation in certain species (e.g. *Orthetrum coerulescens*) and the difference between closely related species (e.g. *Nesciothemis nigeriensis* and some *Orthetrum* spp.) needs to be investigated in relation to possible sperm displacement or other reproductive phenomena.

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