Odonatologica 25(4): 335-345 *December 1, 1996*

TERRITORIALITY IN *NOTIOTHEMIS ROBERTSI* FRASER (ANISOPTERA: LIBELLULIDAE)*

V. CLAUSNITZER
Kirchweg 5, D-35043 Marburg, Germany

Received February 20, 1996 / Revised and Accepted May 8, 1996

The study was carried out at small ponds in the Kakamega Forest, a rain forest in West Kenya. 89 ♂♂ were marked individually and territorial ones observed for a total of 3171 min. Males behave territorially for a mean of 14 days, a maximum of 45 days. Intruders are driven out by the resident and do not show offensive behaviour. Different activities of territorial ♂♂ are distinguished. Most of the time the male spends perching in the territory (32% of total time in territory). Sun flights to the tree tops are the most frequent flight activity.

INTRODUCTION

The behaviour of tropical Libellulidae has attracted more and more attention in the recent years (e.g. MILLER, 1983, MILLER & MILLER, 1985, 1991; PARR, 1980; SORIANO, 1987). There is still a lack of information for species inhabiting tropical rain forests and only a few authors have paid attention to them (e.g. CORBET, 1962; LEGRAND, 1979; LEMPERT, 1988; MILLER, 1993, 1995; PARR, 1980). This paper deals with the so far scarcely studied rain forest Libellulidae (Tetratheminae) *Notiothemis robertsi* Fraser, 1944.

The range of territorial behaviour in male dragonflies is wide, but seems to have mainly one common purpose: the access to females (EMLEN et al., 1977). Territoriality is also described as a strategy to minimise intraspecific aggression (POETHKE & KAISER, 1987). A growing number of males at the mating places can lead to an intensification of territorial behaviour, e.g. in *Acisoma panorpoides inflatum* (HASSAN, 1978), *Nesciothemis nigeriensis* (PARR, 1983a), *Cordulia aenea*

---

* Dedicated to the memory of the late Dr Peter L. MILLER

amurensis (UBUKATA, 1975) and *Aeshna cyanea* (POETHKE & KAISER, 1987) or to a collapse of the territorial system, e.g. in *Libellula saturata* (DE BANO, 1993).

The expression of territorial behaviour is influenced by frequency, number and availability of receptive females. Further the life span of the individuals and the possible occurrence of seasonality influences territoriality. Species with a very limited temporal appearance at the mating places will spend more energy in short time actions than those with less limited mating periods. The latter we find mainly in tropical rain forests, because of the lack of a strong seasonal effect (GAMBLES, 1960). The costs and the benefits an individual male experiences will help to determine the evolution of a specific territorial behaviour (BROWN, 1964).

Much has been written about the establishment of territories in dragonflies (e.g. ALCOCK, 1987; BICK & BICK 1965; CAMPANELLA & WOLF, 1974; HARVEY & HUBARD, 1987; MILLER, 1983; PAJUNEN, 1966). Some authors, e.g. MOORE (1987), and PARR (1980, 1983b) give quantitative analyses of male territoriality. This study is focussed on territorial acts of male *Notiothemis robertsi*, giving considerations to the purpose and functional explanations of them.

The term "territory" in this paper is used according to the definition of NOBLE (1935) as "any defended area". The territories are established by the males near water bodies to gain access to females. The territorial period of the studied species differs from other dragonflies in length, a reduced intraspecific aggression and a low mating success (PARR, 1983a). The territorial male shows two major activities: perching and flying (definitions in MAY, 1976). The latter is further divided into patrolling, interspecific, intraspecific, inspection, sexual and sun flight (Tab. I). Feeding does not occur in or near the territories (MOORE, 1987).

N. robertsi breeds in small shady pools in rain forests, is unspectacular and easily overlooked. The only detailed descriptions of behaviour and ecology are given by LEMPERT (1988). The study site in the Kakamega Forest was small and observations were easy to make. At the same time two other species of the Tetratheminae - *Notiothemis jonesi* Ris, *Tetrathemis corduliformis* Longfield - occurred at the pools. All three species are similar in body shape, colour and behaviour.

METHODS

Notiothemis robertsi was studied in the Kakamega Forest (00°08' - 00°24'N, 34°20' - 34°33'E; alt. 1500-1700 m), West Kenya, at a small pond complex formed by gold-diggers along the Lugusida River. 89 males were marked individually with numbers (permanent pen EDDING 780 / silver) and released immediately after capture. Placing the animals with its legs on vegetation they showed no escape reactions and territorial males resumed normal behaviour in their territories immediately after capture (PARR & PARR, 1974). The marked dragonflies could be recognised easily with a short-focus binocular (8 x 30) without catching the animals again. Observations were made between 2 December 1994 and 10 February 1995 on 56 days between 10:00 and 16:00 h local time, when the males were active at the ponds. A stop-watch and a dictating machine were used to time and describe the observed activities. Some behavioural patterns were filmed (PANASONIC, NV-G1E) and analysed later. Forty males were observed for at least 20 minutes each (max. 265 min; total: 3,171 min). The flight types were classified into patrolling, interspecific, intraspecific, inspection, sexual and sun flight (Tab. I). Each of these behaviours is distinguishable by flight.

Table I
Classification of different flight components in territorial male *Notiothemis robertsi*

Behaviour	Initiation	Orientation	Description
Patrolling	Spontaneous	Indefinite inside the territory	Slow; hovering, short distance over the water
Interspecific	♂♂ of other territorial species, mainly *Orthetrum stemmale*	Towards other male	Rapid, direct approach from side or below, sometimes clashes
Intraspecific	♂♂ of *N. robertsi*	Towards intruder	Rapid, direct approach from side or below, rarely clashes
Inspection	Movement of objects with similar size of ♀ *N. robertsi*	Towards object being investigated	Direct, hovering before object
Sexual flight	♀ *N. robertsi, N. jonesi, Tetrathemis corduliformis*	Towards conspecific females, which do not show egg-laying behaviour	Rapid and direct, capture of female
Sun flight	? Long shady periods	Towards tree canopies	Direct and linear towards tree tops; mainly using the same route

Sun flights interrupted the observation period, hence the individuals could not be observed any longer. Sometimes I could follow a male with the binoculars and found them perching in sun spots in the tree tops.

In order to determine how new arriving males establish territories, I removed males, which had been territorial for several days before. This was easy, because size and location of the territories never changed. Experiments with the "Fishing-line" technique were carried out on territorial males. In this study I used living specimen of normal males which were presented to territorial males. Males of *N. robertsi* showed no reaction to dead individuals presented to them. The experimental insects were tied with a cotton thread, attached between the fore and hind wings and tying the hind legs. A detailed description of this application of the "Fishing-line" technique is given in MOORE (1952). Due to the small size of *N. robertsi* the "Fishing-line" technique was difficult to apply (PAJUNEN, 1964a). The experimental insects suffered from the tied cotton thread and during the experiments, e.g. the wings or wing veins broke. Hence only a limited number (n= 10) of experiments were carried out at different times of the day.

RESULTS

Seventy-one percent of the 89 marked males could be observed at least a second time and 56% of the males were seen more than twice at the ponds. Despite specific searches, none of the marked animals were recorded at other ponds. The longest period between first and last observation of a mature male was 62 days (Fig. I).

Males were territorial only for one time in their lifespan. Forty-five percent of the marked males obtained a territory during the observation period. The length of the territorial period was variable, but could extend to 43 days. After the territorial time the males were seen again for a maximum of one more day. Sometimes I found a male dead in the water of a territory it had occupied (Fig. 1).

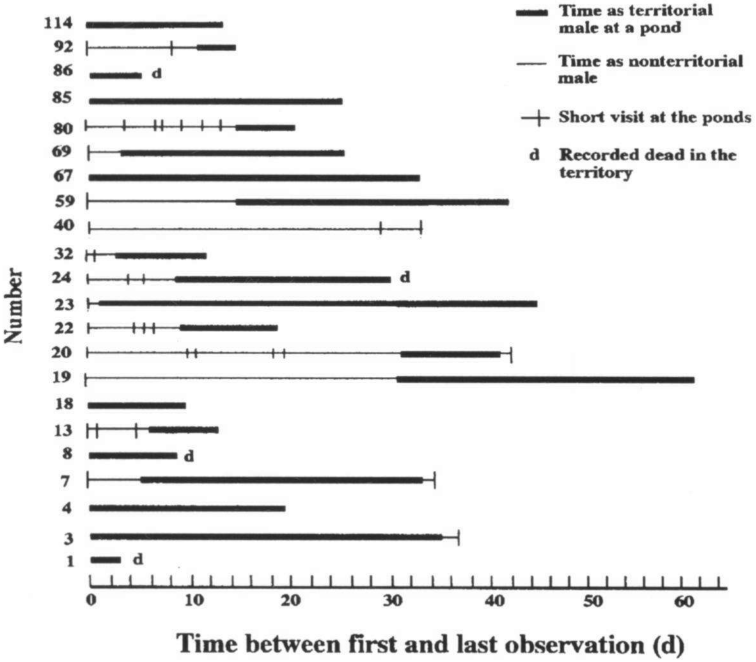

Fig. 1. Period spent as a territorial male and total observation length of some individually numbered males of *Notiothemis robertsi*.

Males arrived in a territory (single round pools; ca. 2 m in diameter) only in the morning (10:00-11:30 h). New arriving males never succeeded in winning territorial interactions. Long and aggressive fights could be observed only on very rare occasions and then it was always the resident who won. A territory, where the current owner was removed at 11:30 h or later remained empty for the rest of the day. The results from the "fishing-line" experiments showed in over 50% of the tests an attack from the resident male. The attacks were very short and could never be provoked a second time. No evidence for sexually motivated flights towards tied animals were observed.

Territorial males started activities at the ponds between 10:00 and 11:00 h. In cloudy weather they disappeared to the tree-tops. They perched on small vantage-points, which allowed a good view of their territory. From this point they started their flights. The detailed observation of the male no. 4 from 10:00-14:00 h on 5

Table II

Flight activities of one male *Notiothemis robertsi* (No. 4) in his territory on 5-XII-1994; at 13:30 h clouds appeared and at 14:00 h the male left the territory because of cloudiness

h	10:00-10:30	10:30-11:00	11:00-11:30	11:30-12:00	12:00-12:30	12:30-13:00	13:00-13:30	13:30-14:00	10:00-14:00
Total time spend in territory in min	5.67	5.07	12.52	12.67	11.48	29	24.8	20.07	121.29
No. of flights out of territory	7	14	17	16	11	0	5	5	75
Mean time in territory in s. (min/max)	48.57 (5/128)	21.79 (8/42)	44.18 (5/101)	47.5 (5/99)	62.64 (52/91)	1740 (-/-)	297.6 (273/150)	240.8 (137/401)	97.03 (5/401)
Total flight in time in s, (%)	29 (8.53)	48 (15.58)	74 (9.85)	57 (7.5)	86 (12.86)	30 (1.72)	36 (2.42)	34 (2.82)	394 (5)
No. of flights (per min)	6 (1.06)	13 (2.56)	22 (1.76)	14 (1.1)	23 (2)	15 (0.97)	18 (0.73)	17 (0.85)	128 (1.04)
Mean duration of each flight in s. (min/max)	4.83 (1/12)	3.69 (2/6)	3.36 (1/5)	4.07 (1/9)	3.74 (1/16)	2 (1/3)	2 (1/5)	2 (1/5)	3.08 (1/16)
Patrol (%)	3 (50)	6 (46.15)	18 (81.12)	11 (78.57)	11 (47.83)	-	4 (22.22)	7 (46.67)	60 (46.88)
Aggressive flights (%)	-	3 (23.08)	2 (9.09)	-	1 (4.35)	-	1 (5.56)	1 (5.88)	8 (6.25)
Inspection (%)	3 (50)	4 (30.77)	2 (9.09)	3 (21.43)	9 (39.13)	15 (100)	11 (61.11)	9 (52.94)	56 (43.75)
Other flights (sx: sexual; a: avoiding)	-	-	-	-	2(a)	-	2(sx)	-	2(sx) 2(a)
% of pool sunny	-	-	5-10	-	-	-	10	5	-

December gives an impression of the activities of *N. robertsi* (Tab. II).

All observations of the various flight activities of territorial males were totalled and set in relation to the respective hour. This gave a general diagram of the daily routine concerning the flight-behaviour a male of *N. robertsi* showed in his territory (Fig. 2). In the course of a day importance of different flight activities of territorial *N.*

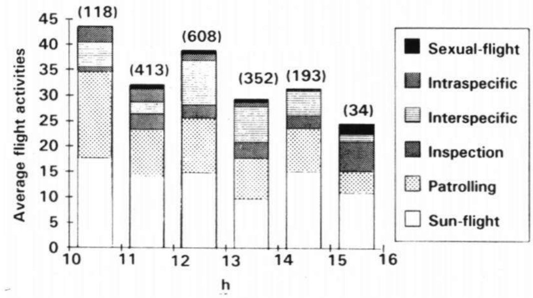

Fig. 2. Average number of the flight activities per hour of territorial male *Notiothemis robertsi* in his territory between 10:00-16:00 h (n= 1691; in brackets n per h).

robertsi shifted. Patrolling and interspecific flights decreased and the latter disappeared in the afternoon, while inspection flights and sexual flights increased.

Focussing on the possible functions of the different behavioural acts I counted the total numbers of each behaviour as a first or a second act (Tab. III). The most common behaviour was perching with 32% followed by sun flights with 28% and patrolling with 27% of the observed behaviours. Inspection, intraspecific, interspecific and sexual flights occurred less frequent.

Table III

Two-act sequences in the behaviour of territorial males of *Notiothemis robertsi*. – [The numbers show the observed action following a distinct preceding behaviour (n=2777)]

	Following action							
Preceding behaviour	Perch	Sun flight	Patrol	Inspection	Interspecific	Intraspecific	Sexual flight	*Total*
Perch	-	489	203	142	151	51	16	*1052*
Sun flight	396	-	270	-	18	17	-	*701*
Patrol	333	84	-	1	22	11	1	*452*
Inspection	90	25	7	-	7	-	-	*129*
Interspecific	240	80	14	4	-	3	-	*341*
Intraspecific	16	15	28	-	1	-	-	*60*
Sexual flight	10	7	2	-	-	-	23	*42*
Total	*1085*	*700*	*524*	*147*	*199*	*82*	*40*	*2777*

Over forty-one percent of all flights were "sun flights" to sunny spots in or near the tree tops (Fig. 2, Tab. III). The time a male spent continuous at a full sunny or a full shady perch in the territory before leaving for a sun flight was totalled and compared (Fig. 3). As this is a very subjective method I did not consider perched males in twilight or where the exposition changed during the perching time.

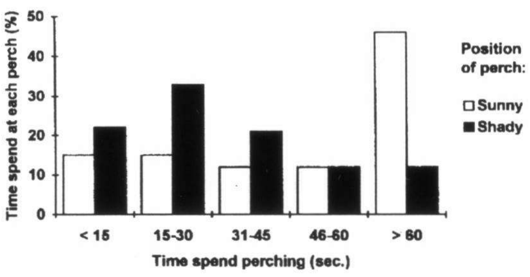

Fig. 3. Percentage of time of a male *Notiothemis robertsi* spent at full sunny (n= 247) or full shady perches (n= 86) before leaving for a sun flight. The total time spent at each position corresponds to 100%.

DISCUSSION

Notiothemis robertsi does not show seasonality and larval development lasts two months (LEGRAND, 1977). This fits the observations for many tropical species, where the adult life exceeds the larval life (GAMBLES, 1960). The long life-span and the lack of seasonality is associated with a long territorial period (average: 14

d; max: 43 d; n= 31). For many libellulids much shorter territorial times are described (e.g. JACOBS, 1955; PAJUNEN, 1966; CAMPANELLA, 1975). In *N. robertsi* the competition for territories is low and a resident is recognized and accepted by intruders. Other libellulids show often a great deal of physical aggression to establish and to keep territories (e.g. PAJUNEN, 1966; PARR & PARR, 1974). The slow establishment of new territorial males in *N. robertsi* is possible because of the long life-span and non-seasonal breeding behaviour. DAVIES (1978) describes similar results from the Speckled Wood Butterfly *Pararge aegeria*. They can perform such a defensive behaviour, because there is a high probability of finding another territory and the non-territorial males have a 90% chance to establish an own territory later without fights. Territorial fights in dragonflies between the intruder and the resident cost energy which reduces their territorial time (MARDEN, 1989; MARDEN & WAAGE, 1990). As female *N. robertsi* appear very rarely at the ponds (CLAUSNITZER, 1995) the length of the territorial period is very important for males to obtain successful copulations.

Territorial males spend most of the time perching. Only 5% of the total time in the territory are spent in flight activities. This classifies *N. robertsi* as a "percher", like many species of the Libellulidae, e.g. *Trithemis*, *Nesciothemis*, *Sympetrum*, *Diplacodes* and *Urothemis* (PARR, 1983a). Perching is one way of dragonflies inhabiting shady rain-forest pools to save energy (SHELLY, 1982). The importance of the latter will be shown in the reasons and functions of the different flight activities practised by territorial male *N. robertsi* (Tab. I).

The total number of flights decreases with the time of the day (Fig. 2). An average of 43.6 different flight activities between the hours of 10:00 and 11:00 halves to only 24.6 flight activities between the hours of 15:00 and 16:00. This is based mainly on a reduction of patrolling and intraspecific flights and corresponds with the establishment of territories only in the morning hours.

REASONS FOR, AND FUNCTIONS OF THE DIFFERENT BEHAVIOURS

An important factor is the shady environment of the mating places. Over forty-one percent of all flights were sun flights. The total number of sun flights per hour does decrease only very little (Fig. 2) over the day. Seventy percent of all sun flights follow perching (Tab. III). Over fifty percent of the males perching in a shady position have left for a sun flight after 30 seconds. Only twelve percent stay longer than 60 seconds in comparison to over 45% of the males perching in sunny positions (Fig. 3). These supports the idea that sun flights are probably important for thermoregulation. By sun basking in sun spots and the tree tops the males obtain a sufficient body temperature for activities inside their shady territories (MAY, 1976, 1977, 1991; McGEOCH & SAMWAYS, 1991). As I could not observe the animals in the tree tops, I can not exclude activities like mating or feeding when they leave the territories for sun flights. But feeding is unlikely an important stimulation for the frequent sun flights, as there is a lot of possible prey at the pools. I have never seen *N. robertsi* hunting or feeding at the pools, but other species and I suppose *N. robertsi* hunts in the morning and afternoon hours. There seems to be no reason to feed exclusively in the tree tops during the territorial time, which also supports thermoregulation as the main function of the sun flights.

Perching has been regarded as an energy conserving act and to prepare metabolically for flying (MAY, 1976; HEINRICH & CASEY, 1978). This probably applies to *N. robertsi* as its habitat are shady rain forest pools (SHELLY, 1982). Perching may announce to other males that the pond is already occupied (MOORE, 1987). To some extend this interpretation may be a function for the perching behaviour performed by male *N. robertsi* as the territorial males perch visible in the centre of their territories. Further the permanent presence in the territory except the sun flights enables the territorial males to get a high percentage of the rarely appearing females. Females and non-territorial males only appear irregularly for short times at the ponds. Especially the females spend most of their adult lives in the tree tops. As territorial males spend most of the day at the ponds, they have to conserve energy for maintaining their territorial possessions.

Interspecific and intraspecific flights are a response to the presence of other dragonflies. The assumption, that these flights are sexually motivated (e.g. PAJUNEN, 1964b; MOORE, 1952) does not apply to *N. robertsi*. The share of intraspecific flights in all flight activities is only 10% and decreases during the day (Fig. 2). This fits the observations that territories have to be defended mainly in the morning. ALCOCK (1987) describes for *Paltothemis lineatipes* also a reduction of intraspecific clashes in the routine of a day.

Sexual flights are caused by females of *N. robertsi*, *N. jonesi* and *Tetrathemis corduliformis* (all females look and behave very similarly). Only a small number of these flights leads to a successful mating, either because the female belongs to another species or is unwilling. The number of sexual-flights increases over the day, but is not correlated to an increasing number of matings. I think that the appetence for mating increases over the day and also the number of females of *T. corduliformis* appearing at water. Sexual flights depend on an external stimulus in the form of a female.

The proximate reason for the inspection flights is the movement of a possible mate. It includes other dragonflies, insects and even a small water rivulet. The ultimate reason for these flights is not easy to explain – it might be of aggressive or sexual nature. As I have never observed the animals hunting or feeding in the territories, this cannot be regarded as a possible stimulus. The number of inspection flights increases over the day (Fig. 2). At the same time the number of inter- and intraspecific flights decreases, while the number of sexual flights increases. Therefore I interpret the inspection flights as sexually stimulated.

All flight activities discussed so far show a more or less distinct trigger mechanism, e.g. presence of males, females, movement of other objects, shadiness of the perch. More difficult is the explanation of patrolling. These flights seem to be spontaneous and indefinite (Tab. I) and I regard them as unspecified in comparison to inspection flights, but endogenous stimulated by sexual and territory-defence motivation.

Patrolling is a common behaviour of territorial male dragonflies (e.g. DeBANO, 1993; HASSAN, 1978; PARR & PARR, 1974; WATANABE et al., 1987), but seldom explained. WATANABE et al. (1987) describe this flight as an analogue behaviour to the territorial songs of birds. In the case of *N. robertsi* I regard patrolling together with perching as the behaviours to demonstrate that this territory is already occupied.

Most of the behaviour the territorial males of *N. robertsi* show corresponds to their long territorial period, nonseasonality and scarcity of females. It is an adeption to their habitat – small and shady rain forest ponds. Other species, which belong to the Tetratheminae and live in similar habitats, show comparable territorial behaviour and mating systems, e.g. *Micromacromia camerunica, Notiothemis jonesi, Tetrathemis corduliformis* and *T. camerunensis* (e.g. LEMPERT, 1988; MILLER, 1993).

ACKNOWLEDGEMENTS

I am most grateful to Mr WILBERFORCE OKEKA for his help and hospitality in the Kakamega Forest and to Dr ANDREAS MARTENS for various supporting ideas and comments and for a considerable amount of time. I also wish to thank the late Dr PETER MILLER for inspiring ideas, Mr GRAHAM VICK for the determination of some species, Professor MIKE PARR for valuable criticism on the manuscript, my parents for financial support and help in the field and Professor REINHARD REMANE and Professor GEORG RÜPPELL, who made this work possible.

REFERENCES

ALCOCK, J., 1987. Male reproductive tactics in the libellulid dragonfly Paltothemis lineatipes: Temporal partitioning of territories. *Behaviour* 103: 157-173.

BICK, G. H. & J. C. BICK, 1965. Demography and behaviour of the damselfly, Argia apicalis (Say), (Odonata: Coenagriidae). *Ecology* 46: 461-472.

BROWN, J. L., 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160-169.

CAMPANELLA, P. J. & L. L. WOLF, 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera) 1: Plathemis lydia (Drury). *Behaviour* 51: 49-87.

CAMPANELLA, P. J., 1975. The evolution of mating systems in temperate zone dragonflies (Odonata: Anisoptera) 2: Libellula luctuosa (Burmeister). *Behaviour* 54: 278-309.

CLAUSNITZER, V., 1995. *Verhaltensökologie von Notiothemis robertsi Fraser, 1944 (Odonata: Libellulidae).* DiplArb. Philipps-Univ. Marburg.

CORBET, P. S., 1962. *A biology of dragonflies.* Witherby, London.

DAVIES, N. B., 1978. Territorial defence in the Speckled Wood Butterfly (Pararge aegeria): the resident always wins. *Anim. Behav.* 26: 138-147.

DeBANO, S. J., 1993. Territoriality in the dragonfly Libellula saturata Uhler: Mutual avoidance or resource defense? (Anisoptera: Libellulidae). *Odonatologica* 22: 431-441.

EMLEN, S. T. & L. W. ORING, 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.

FRASER, F. C., 1944. A note on the genus Notiothemis Ris, with the description of a new species (order Odonata). *Proc. R. Ent. Soc. Lond.* (B) 13: 40-43.

GAMBLES, R. M., 1960. Seasonal distribution and longevity in Nigerian dragonflies. *Jl W. Afr. Sci. Ass.* 6: 18-26.

HARVEY, I. F. & S. F. HUBARD, 1987. Observations on the reproductive behaviour of Orthemis ferruginea (Fabricius) (Anisoptera: Libellulidae). *Odonatologica* 16: 1-8.

HASSAN, A. T., 1978. Reproductive behaviour of Acisoma panorpoides inflatum Selys (Anisoptera: Libellulidae). *Odonatologica* 7: 237-245.

HEINRICH, B. & T. M. CASEY, 1978. Heat transfer in dragonflies: "fliers" and "perchers". *J. exp Biol.* 74: 17-36.

JACOBS, M. E., 1955. Studies on territorialism and sexual selection in dragonflies. *Ecology* 36: 566--586.

LEGRAND, J., 1977. Deux Tetrathemis Brauer nouveaux du Gabon et la larve de l'un d'eux (Anisoptera: Libellulidae). *Odonatologica* 6: 245-251.

LEGRAND, J., 1979. Morphologie, biologie et écologie de Malgassophlebia aequatoris, n. sp., nouveau Tetratheminae du Gabon (Odonata; Libellulidae). *Revue fr. Ent.* (N. S.) 1: 3-12.

LEMPERT, J., 1988. *Untersuchungen zur Fauna, Ökologie und zum Fortpflanzungsverhalten von Libellen (Odonata) an Gewässern des tropischen Regenwaldes in Liberia, Westafrika.* DiplArb. der Friedrich-Wilhelms Univ. Bonn.

MARDEN, J. H., 1989. Bodybuilding dragonflies: costs and benefits of maximising flight muscle. *Physiol. Zool.* 62: 505-521.

MARDEN, J. H. & J. K. WAAGE, 1990. Escalated damselfly territorial contests are energetic wars of attrition. *Anim. Behav.* 39: 954-959.

MAY, M. L., 1976. Thermoregulation and adaption to temperature in dragonflies (Odonata: Anisoptera). *Ecol. Monogr.* 46: 1-32.

MAY, M. L., 1977. Thermoregulation and reproductive activity in tropical dragonflies of the genus Micrathyria. *Ecology* 58: 787-798.

MAY, M. L., 1991. Thermal adaptations of dragonflies, revisited. *Adv. Odonatol.* 5: 71-88.

McGEOCH, M. A. & M. J. SAMWAYS, 1991. Dragonflies and the thermal landscape: implications for their conservation (Anisoptera). *Odonatologica* 20: 303-320.

MILLER, P. L., 1983. The duration of copulation correlates with other aspects of mating behaviour in Orthetrum chrysostigma (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 12: 227--238.

MILLER, P. L., 1993. Some dragonflies of the Budongo Forest, Western Uganda (Odonata). *Opusc. zool. flumin.* 102: 1-12.

MILLER, P. L., 1995. Some dragonflies of forests near Kampala, Uganda, with notes on their ecology and behaviour (Odonata). *Opusc. zool. flumin.* 136: 1-19.

MILLER, P. L. & A. K. MILLER, 1985. Rates of oviposition and some other aspects of reproductive behaviour in Tholymis tillarga (Fabricius) in Kenya (Anisoptera: Libellulidae). *Odonatologica* 14: 287-299.

MILLER, P. L. & A. K. MILLER, 1991. The dragonflies of Hunter's Lodge, Kenya, 1981-1991. *Notul. odonatol.*, 3(8): 123-129.

MOORE, N. W., 1952. Notes on the oviposition behaviour of the dragonfly Sympetrum striolatum Charpentier. *Behaviour* 4: 101-103.

MOORE, A. J., 1987. Behavioral ecology of Libellula luctuosa (Burmeister) (Anisoptera: Libellulidae). 2. Proposed functions for territorial behaviors. *Odonatologica* 16: 385-391.

NOBLE, G. K., 1935. The role of dominance in the social life of birds. *Auk* 56: 263-273.

PAJUNEN, V. I., 1964a. Aggressive behaviour in Leucorrhinia caudalis Charp. (Odonata: Libellulidae). *Annls zool. fenn.* 1: 357-369.

PAJUNEN, V. I., 1964b. Mechanism of sex recognition in Leucorrhinia dubia v. d. Lind. with notes on the reproductive isolation between L. dubia and L. rubicunda (Odon., Libellulidae). *Annls zool. fenn.* 1: 357-369.

PAJUNEN, V. I., 1966. The influence of population density on the territorial behaviour of Leucorrhinia rubicunda L. (Odonata: Libellulidae). *Annls zool. fenn.* 3: 40-52.

PARR, M. J., 1980. Territorial behaviour of the African libellulid Orthetrum julia (Kirby) (Anisoptera). *Odonatologica* 9: 75-99.

PARR, M. J., 1983a. An analysis of territoriality in libellulid dragonflies (Anisoptera: Libellulidae). *Odonatologica* 12: 39-57.

PARR, M. J., 1983b. Some aspects of territoriality in Orthetrum coerulescens (Fabricius) (Anisoptera: Libellulidae). *Odonatologica* 12: 239-257.

PARR, M. J. & M. PARR, 1974. Studies on the behaviour and ecology of Nesciothemis nigeriensis Gambles (Anisoptera: Libellulidae). *Odonatologica* 3: 21-47.

POETHKE, J. & H. KAISER, 1987. The territoriality threshold: a model for mutual avoidance in dragonfly mating systems. *Behav. Ecol. Sociobiol.* 20: 11-19.

SHELLY, T. E., 1982. Comparative foraging behaviour of light- versus shade-seeking damselflies in a lowland neotropical forest (Odonata: Zygoptera). *Physiol. Zool.* 55: 335-343.

SORIANO, E. G., 1987. Dythemis cannacrioides Calvert, a libellulid with unusual ovipositing behaviour (Anisoptera). *Odonatologica* 16: 175-182.

UBUKATA, H., 1975. Life history and behaviour of a corduliid dragonfly, *Cordulia aenea amurensis* Selys. 2. Reproductive period with special reference to territoriality. *J. Fac. Sci. Hokkaido Univ.* (VI) 19: 812-833.

WATANABE, M., N. OHSAWA & M. TAGUCHI, 1987. Territorial behaviour in Platycnemis echigoana Asahina at sunflecks in climax deciduous forests (Zygoptera: Platycnemididae). *Odonatologica* 16: 273-280.