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STUDIES ON THE BEHAVIOUR AND ECOLOGY OF *NESCIOTHEMIS NIGERIENSIS* GAMBLES (ANISOPTERA: *LIBELLULIDAE*)

M.J. PARR and MARION PARR
Department of Biology, University of Salford, Salford, M5 4WT, England

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Most of the work was carried out at two lakes near to Ahmadu Bello University, Zaria, Nigeria. By the use of painted, dead specimens of this species, other libellulids, a gomphid and models, the species-specific recognition characters have been investigated. It seems that the proportion of dark blue and red on the abdomen and overall size are the most important characters for males. The bright yellow stripe on the dorsum of the thorax of females is probably the most important character enabling males to recognize potential mates. Natural flight movements are not important in recognition of species and sex in *N. nigeriensis*. By means of mark-recapture of teneral males it has been determined that the normal period of maturation away from water is 12 - 15 days. The whole of the maturation period of males seems to be spent in the same small area. When sexually immature, male and female are practically identical in colouring and pattern; both having a brownish thorax with a vivid yellow longitudinal stripe on the dorsum and a copper coloured (brownish-orange) abdomen. At maturity, the male is dark blue with abdominal segments 5 - 9 bright red; the female is brown with a dorsal yellow stripe which is retained from the immature stage. Males live for at least 49 days. Sexually mature males are highly territorial, frequently returning to the same territory day after day, but they are more variable in their choice of roosting sites. The males arrive at their territories late and leave the water early each day, even when the weather is fine. Aggressive territorial behaviour and mating have been seen at the roosting sites. *N. nigeriensis* is a typical 'percher', only flying for about 5 - 6 percent of its time at water. Emergence commences in mid-May and the last imagines are seen in late October in Zaria, their disappearance coinciding with the onset of the harmattan and dry season. It seems likely that the species is univoltine in Zaria. It is only known to occur in the greater Zaria area and in its type locality, Awka, which is 520 km to the south of Zaria. The evidence seems to suggest that it has only recently established itself in the Zaria area.

INTRODUCTION

Nesciothemis nigeriensis was first taken in 1961 beside Agulu Lake in what is now the East Central State of Nigeria (GAMBLES, 1966). Gambles only took a single adult male and this very characteristic species was not reported again until taken by the present authors in 1971 in Zaria, North Central State (PARR & PARR, 1972). We soon discovered that the species was present in large numbers at University Farm Lake and Samaru Lake near to the campus of Ahmadu Bello University, Zaria. *N. nigeriensis* re-appeared again in the rainy seasons of 1972 and 1973 in Zaria and we have taken the opportunity of studying certain aspects of its behaviour and ecology during our three years at Ahmadu Bello University. As we pointed out in our preliminary research note (PARR & PARR, 1972) on this species, the circumstances surrounding its discovery in Zaria in 1971 are more than a little odd and a detailed study would be of interest.

THE ZARIA HABITATS

The main colonies of *N. nigeriensis* discovered in Zaria are located around two artificial lakes created by damming an intermittent stream draining a wide and shallow valley at Samaru, Zaria (11° 11′N and 7° 37′E) in northern Nigeria (Fig. 1). The topography of this catchment area is fairly representative of the surrounding low plateau which can be described as undulating, with very broad and gentle slopes lying at an altitude of 610 - 730 m above sea level. The climate is characterised by one well defined wet season with an average of 1118 mm of rain, which normally begins in April/May and ends early in October. The dry season, which lasts for about six months, is severe with low relative humidity and a very drying north-east wind, the harmattan (KOWAL & OMOLOKUN, 1969). The mean daily maximum temperature is highest in March/April (35.2°C) and there is a second peak in October (31.6°C). Shade temperatures of 40°C occur in April. The mean minimum temperature rises from its lowest value in December/January (14.0°C) to its highest value in April (21.7°C). Extreme temperature readings in the Zaria region are around 41°C and 7°C, although ground frost has been recorded occasionally during the dry season. The Zaria region may, therefore, be said to possess a tropical continental climate (HORE, 1970).

Owing to the very seasonal distribution of rain, the lake levels fluctuate greatly. The water level normally rises to the levels of the spillways in July or August and remains high until September or October. Water levels are at their lowest at the onset of the rains in April or May. Each of the years of this study, 1971, '72 and '73, have been characterized by below average rainfall which has had the effect in the current 1973 season of greatly delaying the filling of the lakes. At the time of writing (mid-July, 1973) the water level in the smaller of the two lakes (Samaru) is about two metres lower than at the same time in 1972.

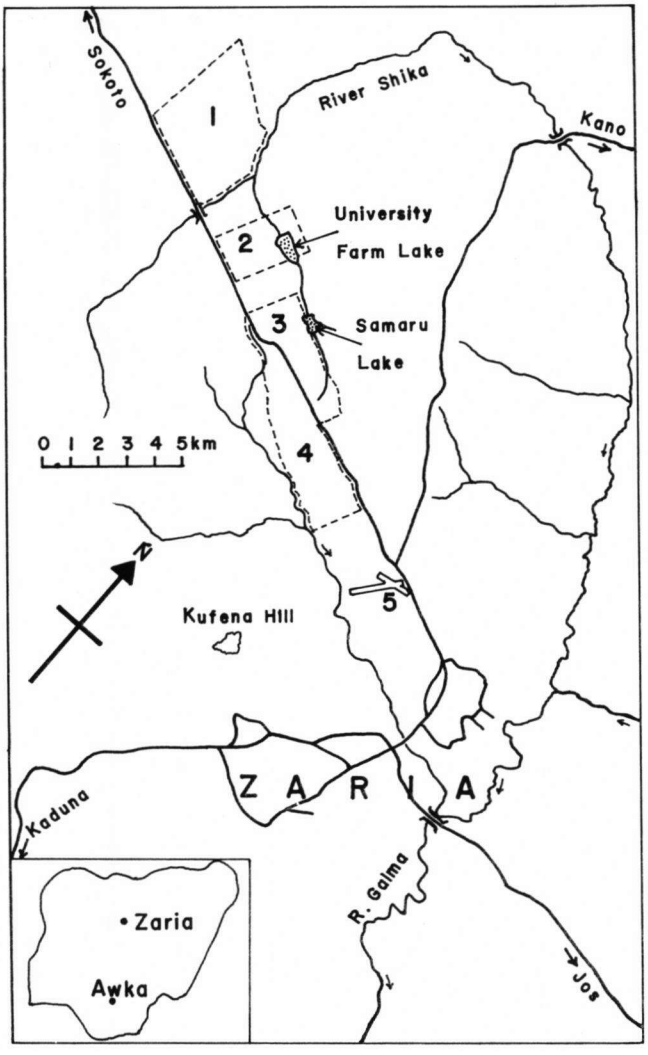

Fig. 1. Map of Zaria area showing the position of Samaru Lake and University Farm Lake in relation to Zaria city. K e y : (1) Shika Farm, Ahmadu Bello University; – (2) University Farm, A.B.U.; – (3) Institute for Agricultural Research Experimental Farm, A.B.U.; – (4) Main campus, Ahmadu Bello University; – (5) Airfield. I n s e t : Outline of Nigeria showing positions of Zaria and Awka.

This has resulted in a rapid change in the gross ecology of the lake and its margins, causing the date of the main emergence of *N. nigeriensis* to be delayed and its numbers and distribution to be altered.

Samaru Lake, also known as Bomo Lake, is surrounded by agricultural land and fadama marsh on all sides, with a small amount of rough uncultivated land near to the main sub-colony. The principal vegetation fringing the lake shore during the rainy season is made up of various grasses, *Echinochloa pyramidalis* Hitchc. & Chase and *Pennisetum purpureum* Schum. being the most important. *Echinochloa pyramidalis* seems to be a very important component of the water-side habitat at Samaru, as *N. nigeriensis* only occurs where this grass is present. It avoids the shorter vegetation on the dam side and the much taller, coarser *Pennisetum purpureum* in other areas of the lake margin. For the three seasons during which it has been studied, the *N. nigeriensis* population at Samaru Lake has been split into two sub-colonies, one on the northern side and a larger sub-colony on the southern side (Fig. 2).

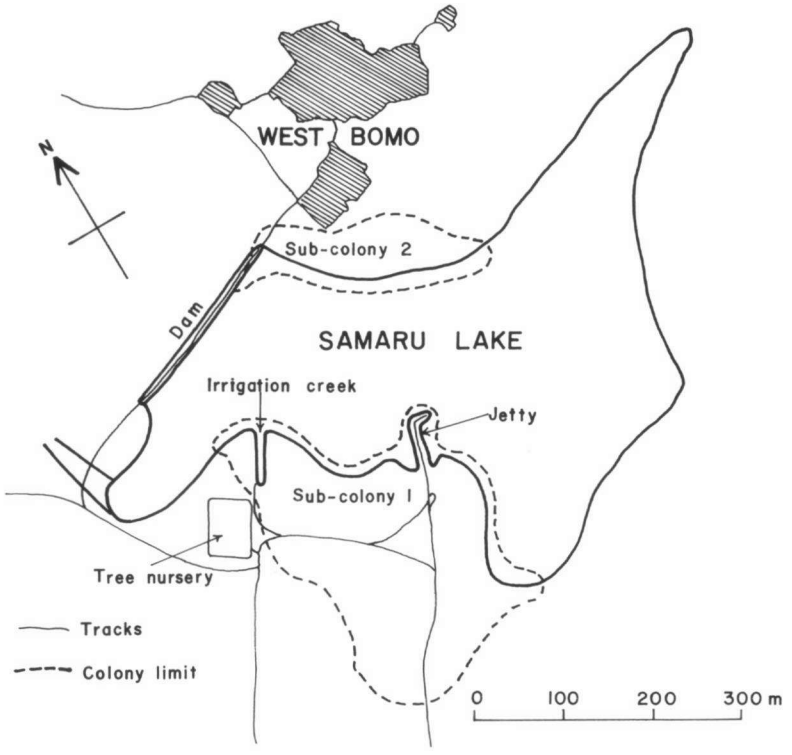

Fig. 2. Map of Samaru Lake, Zaria, showing the areas (sub-colonies 1 and 2) occupied by *Nesciothemis nigeriensis* Gambles, 1971-1973.

University Farm Lake is situated 2.1 km northwest of Samaru Lake and is a more recently constructed lake (1966/1967) than the latter (1960/1961). The growth of tall, emergent grasses around its margin is, therefore, less advanced than at Samaru Lake. There is, nevertheless, fringing emergent vegetation, especially *Echinochloa*, around the whole lake during the rainy season, and away from the lake shores there is a mixture of agricultural land, savanna woodland and fadama marsh. During the dry season, as at Samaru Lake, the water recedes far enough to expose a considerable expanse of bare mud between the water's edge and the vegetation.

METHODS

Our field experience with Zygoptera species such as *Ischnura elegans* (Vander Lind.) showed that a very great deal of information can be obtained by marking with paint and the use of the capture-recapture method. Even teneral insects can be satisfactorily marked in this way providing their wings are fully expanded and hardened sufficiently to permit flight (e.g. PARR, 1973). If the individuals are each given a unique number the amount of information gained is much larger than if only date-specific marks are utilised.

In the case of *N. nigeriensis* in Zaria we used ordinary white enamel paint and we painted actual numbers on the wings. The insects were caught with cane-handled nets and were marked and released immediately after capture. Each marked insect was released by placing its legs in contact with suitable vegetation and slowly withdrawing the hand. In this way the insects usually showed little, if any, escape reactions. Adult males, for example, would resume normal territorial behaviour immediately after being marked. As emergence of *N. nigeriensis* occurs at night, marking of teneral specimens was carried out at daybreak, before the insects had dispersed far from water. Post-teneral stages were marked later in the day when their activity made them obvious and not too difficult to capture. As *N. nigeriensis* is a relatively large libellulid it is possible to apply painted numbers to the wings of post-teneral insects which are large enough to enable specific individuals to be recognized at a distance of several metres. The use of binoculars ensured that very few marked specimens had to be recaptured in order to confirm the number borne. Teneral insects were marked using a simple date-specific coding of small paint spots on the wings. It was found that the application of one or two small paint spots could be accomplished easily, usually without obvious damage to the insect. Any of these teneral insects which were recaptured in a post-teneral state were re-marked with an actual number which was easily legible at a distance.

The investigation of the species-specific recognition characters was carried out using the 'fishing-line' technique (ST. QUENTIN, 1934; MOORE, 1952). In those cases where the 'presented' specimen was altered in colour or pattern, artists' oil paints were used. It was found that with careful mixing of colours very

good approximations to the insects' natural colours could be obtained, at least to the human eye.

In his study of the mechanism of sex recognition in *Leucorrhinia dubia* (Vander Lind.), PAJUNEN (1964) used living specimens of normal and modified males which were presented to sexually active males using the fishing-line technique. Pajunen found that it was important to use living specimens of *Leucorrhinia* as males of *L. dubia* generally showed no positive reactions to dead individuals presented to them. However, it was found in the present study that males of *Nesciothemis nigeriensis* would respond well to dead specimens and models. As many of the individuals were considerably modified in colour using oil paints, no living specimens were used in the tests on *N. nigeriensis*. Observations of territorial male *N. nigeriensis* indicated that, probably, the level of response to non-living specimens and models was somewhat lower than to normal, free-flying individuals, which seemed to suggest that flight patterns are used to some extent in species and sex recognition. The results show, however, that normal flight movements are not necessary to obtain clearly defined responses in *N. nigeriensis* to test individuals.

The test insects were secured by means of fine nylon fishing thread, which had the advantage of being unobtrusive in colour. The test individuals were swung carefully on about 1.5 metres of thread from a fishing rod in the waterside territory of a male *N. nigeriensis*: if after three such presentations no response was observed, it was scored as 'negative'. All tests were carried out in sunny, hot weather, as male *N. nigeriensis* are very sensitive to lack of sun and under such conditions they rapidly withdraw away from territorial sites and respond very little to other dragonflies.

The scoring of the responses is similar to that used by MOORE (1952) and PAJUNEN (1964), except that the term 'aggressive reaction' is used instead of 'clash'. Aggression in *N. nigeriensis* is manifested in a range of forms, from a mild swoop towards another individual, to a physical entanglement which may be prolonged and fierce. Always, however, an aggressive flight is one in which the attacked is approached from below or from the side. Aggressive flights usually last for only a few seconds, but may occasionally last longer than a minute. The term 'approach' refers to cases of investigatory approaches when the male flies towards the test individual and may face, circle or follow it, but makes no attempt to make contact before flying off. A 'sexual response' is one in which the male lands on the thorax of the test individual and attempts mating by bending his abdomen. This may result in a very brief, momentary encounter or it may be more prolonged. 'Female' test individuals were frequently severely damaged in such contacts. Care was taken not to present test individuals to the same male *N. nigeriensis* without a break of a least 20 minutes. By moving along the lake shore a considerable number of different males were available for scoring.

Although a large colony of *N. nigeriensis* existed at University Farm Lake in 1972 and 1973 (and, probably, also in 1971) it was more convenient to carry out most of the detailed observations on the southern sub-colony at Samaru Lake. All of the detailed results were, therefore, obtained at Samaru except for a final series of 'fishing-line' tests carried out at University Farm in July, 1973 when the population density was much higher than at Samaru.

The colour designations (SCS) mentioned in the text refer to Standard Colour Samples in KORNERUP & WANSCHER (1967).

The times refer to local time, which is G.M.T. + 1 hour.

SPECIES-SPECIFIC RECOGNITION CHARACTERS

Aggressive and sexual responses by adult males to conspecific dead male and female individuals

Tables I and II show that the frequency of aggressive response to males is high and to females is low. With respect to sexual responses, the reverse is true. An analysis of a 2 x 2 contingency table scoring aggressive and sexual responses to male and female test individuals shows that the differences are highly significant ($\chi^2_{(1)} = 25.36$; $p < 0.001$).

The recognition of conspecific males by adult males

Table I summarizes the results obtained by presenting adult, territorial male *N. nigeriensis* with various dead specimens or models in order to investigate the principal characters by which male *N. nigeriensis* recognize each other.

Test individual 1 was an unchanged adult male of *N. nigeriensis*, that is to say, with the thorax and abdominal segments 1 - 4 dark pruinosed blue, SCS 20F4, and abdominal segments 5 - 9 bright red, SCS 9C8. In over half of the presentations, the test individual was attacked aggressively or an aggressive approach was made, and in one third of the cases the approach was purely investigatory.

Test individuals 2 and 3 (*Orthetrum icteromelas* Ris and a wingless wooden model respectively) were painted to resemble as closely as possible in colour and pattern a normal adult male of *N. nigeriensis*. *Orthetrum icteromelas* is similar in size and shape to *N. nigeriensis* and when painted, approximated to the latter species very closely. The wooden model was a crude representation of a normal male *N. nigeriensis*, although the overall size, abdomen proportions and colouring were reasonably acceptable to the human eye. In these cases there was also a high proportion of aggressive responses with relatively few other types of reaction. If the responses to test individuals 1, 2 and 3 are compared in a 4 x 3 contingency table, $\chi^2_{(6)} = 15.11$; $0.025 > p > 0.01$. Although the overall test

Table I

Recognition of conspecific males by adult male *N. nigeriensis*

Test individuals	Response				
	Negative	Approach	Aggressive	Sexual	*Total*
1. *N. nigeriensis*, adult ♂ unchanged (abdominal segments 5 - 9 red)	1	15	27	2	*45*
2. *Orthetrum icteromelas*, adult ♂ painted as adult male *N. nigeriensis*	0	5	14	1	*20*
3. Wooden model (wingless) painted as adult ♂ *N. nigeriensis*	6	4	12	1	*23*
4. *Crocothemis erythraea*, adult ♂ painted as adult ♂ *N. nigeriensis*	8	13	1	1	*23*
5. *Chalcostephia flavifrons Hemistigma albipuncta* adult ♂♂ painted as adult ♂ *N. nigeriensis*	13	25	1	1	*40*
6. *Ictinogomphus ferox*, adult ♂ painted as adult ♂ *N. nigeriensis*	6	12	5	0	*23*
7. *N. nigeriensis*, adult ♂ with abdominal segments 1-6 painted blue; segs 7-9 red	1	8	6	5	*20*
8. *N. nigeriensis*, adult ♂ with abdominal segments 1-7 painted blue; segs 8 & 9 red	8	16	4	1	*29*
9. *N. nigeriensis*, adult ♂ painted as adult, pruinosed ♂ *Orthetrum* sp.	0	13	3	0	*16*
10. *N. nigeriensis*, immature ♀, with thorax and abdominal segments 1 - 4 painted blue of adult ♂	5	10	3	2	*20*

shows a significant difference in the proportions of the various responses, 9.50 of the total χ^2 value is accounted for by the relatively large number of negative responses to the wooden model. There is clearly a high degree of homogeneity in the proportion of aggressive and sexual responses.

Test individuals 4, 5 and 6 were chosen to test the effect of body size and abdominal shape on recognition, the colours being painted to resemble those of normal adult male *N. nigeriensis*. *Chalcostephia flavifrons* Kirby and *Hemistigma albipuncta* (Rambur) (test individuals 5) are two common libellulids of roughly similar size to each other, but are distinctly smaller than *N. nigeriensis*. They are very similar to *N. nigeriensis* in general body proportions and shape. Test individual 4 (adult male of *Crocothemis erythraea* [Brullé]) although roughly similar in size to *N. nigeriensis*, has a shorter and much broader abdomen. *Ictinogomphus ferox* (Rambur) (test individual 6) is a much larger insect than *N. nigeriensis*, although similar in overall body shape. The reactions of *N. nigeriensis* males to test individuals 4, 5 and 6 were similar in each case, with most of them being approach responses or completely negative.

Two adult male *N. nigeriensis* in which the amount of red on the abdomen was reduced to segments 7 - 9 (test individual 7) and to segments 8 and 9 (test individual 8) also produced a high proportion of negative or approach responses. There were relatively few aggressive or sexual responses. An analysis of the proportion of aggressive responses to all other responses evoked by the normal male (test individual 1) and test individual 7 showed a significant difference ($\chi^2_{(1)} = 4.98$; $0.05 > p > 0.02$). A similar analysis with test individual 1 and test individual 8 produced a $\chi^2_{(1)}$ value of 15.47, for which $p < 0.001$.

Test individual 9 was an adult male *N. nigeriensis* painted as an adult pruinosed *Orthetrum* sp; in this case only three reactions were aggressive, the rest being approach responses.

In test individual 10, which was an immature female of *N. nigeriensis*, the thorax and abdominal segments 1 - 4 were painted the dark blue of an adult male, thus obscuring the characteristic dorsal longitudinal yellow (SCS 2A6) stripe borne on the thorax of all females and also immature males. Abdominal segments 5 - 10 were the natural brownish-orange colour (SCS 7C8) of the immature insect. In this example, fifteen out of twenty responses were of the approach or negative type. The proportion of aggressive responses recorded for this test individual were highly significantly different from the proportion obtained for the normal adult male *N. nigeriensis* ($\chi^2_{(1)} = 11.28$; $p < 0.001$).

These results indicate that the proportions of the adult male blue and red, the body size and the shape of the abdomen are important characters allowing males of *N. nigeriensis* to recognize each other. Odonata painted a similar body colour to *N. nigeriensis* but differing in size or body proportions evoked few aggressive responses. *N. nigeriensis* males painted to show less red than normal also resulted in a marked lowering of the frequency of aggressive responses. Test individual 10 indicated that adult males discriminate sharply between the brownish-orange abdomen of immature examples and the bright red of mature specimens, although in this case the thorax was painted the dark blue of a mature male.

The recognition of conspecific females by adult males

Table II summarizes the results obtained by presenting adult, territorial, male *N. nigeriensis* with various dead specimens or models resembling females of this species.

Of the four specimens used in the tests, nos. 11 and 14 were immature female *N. nigeriensis*. Test individual 11 was normal, except that post-mortem changes had resulted in the abdomen being rather more brown than orange in colour: it, therefore, closely resembled an adult female in colour. Test individual 14 was similar to 11, except that the abdomen was painted pale blue, resembling a pruinosed *Orthetrum* sp. Both of these examples evoked strong sexual responses from adult male *N. nigeriensis* at the waterside. Similar results were obtained using a winged, wooden model of an adult female *N. nigeriensis*, although in this case more than half of the responses were of the approach type. The proportion

Table II

Recognition of conspecific females by adult male *N. nigeriensis*

Test individuals	Response				
	Negative	Approach	Aggressive	Sexual	*Total*
11. *N. nigeriensis*, immature ♀ with brownish abdomen due to post-mortem changes	2	8	1	9	*20*
12. Wooden model (with wings) painted as adult ♀ *N. nigeriensis*	7	28	1	12	*48*
13. *Crocothemis erythraea*, adult male painted as adult ♀ *N. nigeriensis*	15	7	0	0	*22*
14. *N. nigeriensis*, immature ♀ with abdomen painted pale blue as if pruinosed	2	4	4	10	*20*

of sexual responses evoked by the wooden model was not significantly different from the proportion of sexual responses produced by the normal test female ($\chi^2_{(1)} = 2.65$; $0.2 > p > 0.1$). On several occasions the model was attacked sexually very vigorously and it was grasped dorsally by the male in attempts to copulate.

In contrast, a male *Crocothemis erythraea* painted to closely resemble an adult female *N. nigeriensis*, was ignored fifteen times out of twenty-two presentations and no sexual responses were seen. *Crocothemis erythraea* has a shorter and much broader abdomen than female *N. nigeriensis*.

These results show that two of the main recognition characters for female *N. nigeriensis* are the general body shape (especially the form of the abdomen) and the yellow dorsal stripe on the thorax. Table I shows that few sexual responses were elicited by test individuals lacking a dorsal yellow thoracic stripe. Observations have shown that both male and female immature *N. nigeriensis* are likely to be sexually attacked if they wander into adult male territories.

MATURATION AND LONGEVITY

Maturation

In June and July, 1972, an attempt was made to determine the maturation period of *N. nigeriensis*. The first specimen to be taken in 1972 was a teneral female close to the water's edge, at 15.00 hours on 23 May. On this occasion a careful search failed to reveal any other specimens of the species. On the following day, five male *N. nigeriensis* which appeared to be mature were seen at water at around 15.00 hrs, but no teneral or female specimens were noted. On 26 May, apparently adult male *N. nigeriensis* were now common at the water's edge of the southern sub-colony. Once again no tenerals or females were seen. It therefore seemed likely that emergence was occurring at night or very early in the morning and most of the teneral insects were dispersing away from the water by the afternoon. The single teneral female captured on 23 May was probably unusual in remaining relatively close to water late in the day of its emergence. On 14 June, 1972, Samaru Lake was visited at first light (about 05.30). Sunrise was at 06.05 when there was 6/8 cloud cover, the temperature 20.0°C. and there was 95 percent relative humidity. A teneral female was taken on the jetty at 06.20 and a teneral male at the irrigation creek at 07.00. During the period 19 June - 11 July, 1972, the southern sub-colony was visited on nineteen occasions for varying lengths of time between 06.15 and 09.00 in order to capture and mark as many teneral *N. nigeriensis* as possible. In all, 161 teneral individuals (82 males and 79 females) were successfully marked.

Of the 82 teneral males marked and released, 21 were recaptured at least once, and eight provided information on the length of the maturation period. One specimen (No. 1) which was recognized on 26 different occasions, was particularly informative. No. 1 was first marked close to the water's edge on 24 June between 06.35 and 08.00. This individual was next seen on 26 June at a point commonly used as a roosting site by other individuals about 70 metres from the water, between 15.00 and 16.30, and it was recognized in the same place once or twice (morning and evening) for 11 consecutive days after 26 June. It was then seen on the 9, 10, 12, 14, 19, 20, 21 and 22 July. When this individual was first recaptured on 26 June it was in teneral/immature colouring, which it retained with no change up to 2 July. (The teneral and immature stages

of both sexes are very similarly coloured and patterned, and resemble the adult female. However, the immature stage is characterized by a lighter brown thorax with the usual yellow dorsal stripe, SCS 2A6, and the abdominal segments 1 - 3 mostly reddish, SCS 7B7, with segments 4 - 10 mostly brownish-orange, SCS 7C8). On 3 July, the abdominal segments 1 - 3 were starting to darken and segments 8 and 9 were distinctly red. On 4 July, the dorsal yellow stripe on the thorax was less noticeable and the whole thorax and base of the abdomen were becoming blackish-blue. By 5 July, male No. 1 seemed to be almost in mature colours. The thorax and base of the abdomen were dark pruinosed blue (SCS 20F4) and the abdominal segments 5 - 9 were the bright red (SCS 9C8) of the mature, territorial insect. However, some traces of orange were still noticeable on the base of the abdomen and the dorsal yellow stripe although still visible was weak and fragmented. This individual was almost unchanged by 6 July, but the yellow stripe was now virtually obliterated. On 7 July it was not seen in its usual small area where it had undergone maturation, but it was recognized a little to the east of the jetty at the water's edge. On this date, however, it had not developed normal territorial behaviour as it quickly left the waterside and flew inland on being disturbed. No. 1 was next seen on 9 July in its old maturation area during the late afternoon. Thereafter, it was seen on seven occasions during the mid-afternoon, until 22 July, consistently occupying the same territorial area at water. After 9 July, this individual was not found away from water, indicating that it had selected a new and unknown roosting site. It is interesting that this individual was first seen to exhibit aggressive territorial behaviour on 5 July while still in its maturation area. During the early afternoon of this date it repeatedly flew aggressively at immature male No. 31 (which was four days younger than No. 1) also undergoing maturation in the same clump of the tall grass, *Andropogon schirensis* Hochst. The assumption of new colours and pattern coincided with a change in behaviour and it seems reasonable to assume that sexual maturity dated from about 7 July, that is to say, 13 days after emergence. The early history of male No. 1 has been presented in some detail because it was probably fairly typical of the maturation pattern for *N. nigeriensis* at Samaru Lake in 1972.

Male individual No. 31 was captured or recognized on 18 occasions. In this example the change to mature colouring was completed in 12 days, but it did not appear at water in a territorial role until it was 15 days old. Nos. 68 and 80 appeared at water twelve days after being marked as tenerals, but they were not seen during the intervening period. No. 3 was found about 200 metres from water when twelve days old and when in the process of changing to mature colouring. Numbers 30, 38 and 74 were recaptured when 15, 16 and 15 days old respectively, in mature colouring. Two of these were at water and the other one was about 55 metres from water. As the recapture history of these last three individuals was incomplete, it is likely that their maturation was completed in

less than 15 or 16 days. Unlike the libellulid *Leucorrhinia dubia* studied by PAJUNEN (1962) the maturation period of *N. nigeriensis* seems to be spent in a very localised area.

Six male specimens were dissected in order to check for the presence or absence of spermatophores in the penis. Two individuals of unknown age in typical immature colouring and pattern had no spermatophores present. A male in an intermediate condition (dorsal thoracic yellow stripe still evident, thorax partly pruinosed, base of abdomen bluish-black but not pruinosed, abdominal segments 5 - 9 almost mature red, but orange tinged) had spermatophores in the penis. Two individuals looking fairly mature (with pruinosed thorax and base to abdomen and bright red abdomen, but with still a trace of yellow on the thorax) both had sperm in the penis. A male in fully mature colouring, but taken in a roosting site in mid-afternoon with three immatures also contained spermatophores.

If technical sexual maturity is taken to be the presence of spermatophores in the penis, these results suggest that this state is attained at about the time immature colour and pattern begins to change.

Information on the maturation rates of females is practically non-existent due to the very low recapture rate. This strongly suggests that immature females, as well as adult females, have quite different behaviour patterns from males. When mature, females retain the yellow longitudinal dorsal thoracic stripe (which seems to be a generic character for females; GAMBLES, pers. comm.), but the sides of the thorax darken to chocolate brown, and the abdomen changes to light brown (GAMBLES, 1972). With advancing age the abdomen goes dark brown and considerable pale blue pruinescence becomes apparent on both thorax and abdomen.

Longevity

It was not possible to determine the maximum life span of the imagines, but a male in mature colours which was marked on 13 September, 1971, was last seen 36 days later. If one allows 13 days for maturation, this specimen must have been at least 49 days old when it disappeared. Another individual which was adult when first marked must have attained an age of at least 37 days. The longest surviving specimen marked when teneral was 30 days old when it disappeared. The last marked individuals in 1972 were seen on 25 July before we left Nigeria for England. On our return to Nigeria the Samaru Lake colony was searched carefully for marked individuals on 26 and 28 September, 1972, but none was seen. *N. nigeriensis* was numerous at the lake on these two dates.

ACTIVITY PATTERNS AND TERRITORIALITY

The diel activity pattern of adult males

Adult males of *N. nigeriensis* show a well defined diel pattern of activity, which seems to differ in a number of ways from that displayed by other libellulids in the same habitat.

The night is spent roosting in areas of tall grasses (mainly *Andropogon schirensis* and *Hyparrhenia* spp., but also cultivated *Sorghum, S. bicolor*) in the case of the Samaru Lake colony. The males always seem to desert their waterside territories to occupy different areas for roosting. Sixtyseven adult males were studied in respect of their roosting habits; in most cases (57), roosting usually occurred at distances of 20 - 200 metres from water. Some individuals, however, regularly roosted very close to the water, or actually at the water's edge, but in these cases the roosting site was almost invariably different from the daytime territory, although the insect may have only moved ten metres or so. Two individuals roosted exclusively by the water's edge and ten individuals varied from day to day in chosing between waterside and inland sites. *N. nigeriensis* males are exceptional, compared with many other libellulid species, in leaving their waterside territories and flying to their roosts as early as 15.00. Some individuals stay in their territories until 16.45, but this is unusual, and most leave the water between 15.20 and 16.15. The time *N. nigeriensis* first arrives at the roosting site is greatly dependent on the weather. If the sun is obscured for long during any time in the day they will move to the roosting sites, but will return to the water if the sun shines again, providing it is earlier than about 15.45 - 16.00. Large cumulus or cumulo-nimbus clouds at, say, 15.00 (a fairly common sight during the rainy season) will cause a rapid movement towards the roosting sites..The flight away from a waterside territory to a roosting site is always fast and direct, and is often high.

The behaviour on arrival at the roosting site varies according to whether or not the sun is shining. If it is shining between 16.30 and 18.00 the adult males frequently gather in groups of two to fifteen individuals, resting on grass stems or twigs close to the ground and occupying a compact area of about 5 or 6 metres in diameter. While associated in this manner they spend most of the time sunning themselves and feeding. During this time they frequently fly aggressively at each other and defend very small territories around a particular perch. On 29 September, 1971, at 16.45, a mature female of *N. nigeriensis* appeared in a communal roosting area. She was immediately seized and mated by one of the males. The *in copula* position was maintained for approximately 15 seconds, which is normal for the species; when the pair separated the female flew away, but the male returned to his perch close to another male. After about 18.00 the communal groups of males begin to dissolve as they take up true roosting posi-

tions in dense vegetation, usually grasses, nearby. After a few short flights they are difficult to locate deep down amongst the bases of the grasses in the fading light. Both sexes may be found roosting together but males are always dominant in number. Other species of libellulids commonly found roosting with *N. nigeriensis* in the Samaru colony include *Crocothemis erythraea, Hemistigma albipuncta* and *Diplacodes lefevbrei* (Rambur).

On 2 October, 1971, Samaru Lake was visited from daybreak (at 05.50) in order to observe the behaviour pattern of *N. nigeriensis* during all the daylight hours. The dry bulb temperature was 18.9°C at 06.25 (sunrise) and the sky was clear. A thunderstorm the previous evening had left the vegetation very wet. After a brief search, male No. 5 was found at 06.30 roosting about 15 cm from the ground in a clump of *Andropogon* where it was seen on six different occasions (Fig. 4i). Although it was dew-covered, it flew up on being disturbed and perched higher on a grass stem. It soon made other small flights, but made no attempt to leave the roosting site. On many other subsequent occasions, mainly during June and July, 1972, adult *N. nigeriensis* have been detected roosting in the same manner and behaving similarly when disturbed early in the morning.

The activity of *N. nigeriensis* in the roosting sites gradually increases from dawn onwards and resembles the evening behaviour sequence in reverse, except that communal groups have not been noticed. They do not leave the roosts until about 10.00 at the earliest, although many individuals leave much later than this, some not appearing at their waterside territories until 11.00. The mean time of arrival at water of nine adult males taken at random was 10.24, the extremes being 10.05 and 10.55. This is very much later than all the other species of Odonata except *Palpopleura deceptor* (Calvert) at Samaru and University Farm Lakes. Male *P. deceptor* may be seen arriving at water at about the same time as male *N. nigeriensis*. For example, on 6 October, 1971, the order of appearance of Odonata flying at water at Samaru Lake was: 06.30 *Brachythemis wilsoni* Pinhey, *B. leucosticta* (Burm.); – 06.45 *Pseudagrion* sp. (probably *Ps. nubicum* Selys); – 07.02 *Agriocnemis exilis* Selys; – 07.07 *Hemianax ephippiger* (Burm.); – 07.08 *Philonomon luminans* (Karsch), *Trithemis annulata* (de Beauvois); – 07.42 *Urothemis edwardsi* (Selys); – 07.53 *Diplacodes lefebvrei* (Rambur); – 08.00 *Rhyothemis semihyalina* (Desjardins); – 08.10 *Crocothemis erythraea* (Brullé); – 08.30 *Pantala flavescens* (Fabricius); – 08.40 *Orthetrum trinacria* (Selys); – 10.27 *Nesciothemis nigeriensis* Gambles; – and at 10.40 hrs *Palpopleura deceptor* (Calvert). On other occasions, *Pseudagrion glaucescens* Selys, *Ceriagrion* sp., *Acisoma panorpoides* Rambur and *Tholymis tillarga* (Fabricius) have been seen flying actively by water between 06.15 and 06.20. In their late arrival at water, *N. nigeriensis* and *P. deceptor* resemble the temperate *Libellula quadrimaculata* L. as reported by MOORE (1960).

Casual observations on the Zaria populations of *N. nigeriensis* suggested that there was a peak in flight activity in the early afternoon. Detailed observations

Table III

Summary of territorial flight activities at water of a male *N. nigeriensis* (No. 7) during 2 October 1971

Observations	Time								
	11.02-11.20	11.25-11.55	11.55-12.20	12.25-12.55	12.55-13.25	13.45-14.00	14.00-14.20	14.20-14.40	14.40-14.55
Mean duration of each flight in secs.	6.53	5.61	3.15	3.25	7.73	11.57	4.53	3.30	3.63
Max. and min. duration of flight in secs.	20/1	38/1	10/1	9/1	61/2	24/1	13/1	7/1	23/1
Mean no. of flights per minute (*Overall mean: 0.94*)	0.83	0.60	0.80	0.80	0.50	0.93	1.90	1.00	1.13
Percentage of time spent in flight (*Overall mean: 8.26*)	9.07	5.61	4.20	4.33	6.44	18.00	14.33	5.50	6.86
Number of flights in each specified period	15	18	20	24	15	14	38	20	17
Number of feeding flights	9	14	9	11	7	5	28	13	7
Number of aggressive flights	5	4	10	13	6	7	10	7	9
Number of sexual flights	0	0	0	0	1	1	0	0	0
Number of other flights (*av* - avoiding; *a/s* - aggressive/sexual; *?* - unknown)	1(*av*)	0	1(*a/s*)	0	1(*a/s*)	1(*a/s*)	0	0	1(*?*)
Shade temperature (°C) at the end of the time period	27.7		28.8		30.0		31.0		31.0

on marked individuals on two days have confirmed this. Although behaviour of adult males seems to be relatively consistent from day to day when the weather is sunny most of the time, dull conditions depress flight activity and may result in an earlier or later peak in activity. Table III summarizes the flight activities of an adult male *N. nigeriensis* (No. 7) by water at the jetty on 2 October, 1971. Throughout the period of observation the weather was fine and sunny, with a maximum shade temperature of 31.0°C being reached between 14.00 and 15.00. This individual arrived at its territory at 10.27 and perched on a low, dead stem of *Echinochloa* grass. It made two short flights of about 5 seconds each at 10.30 before disappearing at 10.40. It was seen momentarily again at 10.45, but did not settle in its territory until 11.02. Similar, restless, behaviour has been frequently noticed among male *N. nigeriensis* returning to water after roosting.

It may be seen from Table III that a relatively small proportion of the territorial period was spent actually flying, the maximum being 18 percent during the period 13.45 - 14.00. The longest flight recorded (61 seconds) was sexual and involved the preliminary chase of the female, a very brief mating flight and a long flight hovering over the ovipositing female. This individual male made one other attempt at mating, which was unsuccessful, and this flight lasted 22 seconds. The other long flights recorded are largely classified as 'aggressive' when the male chased and attacked other dragonflies, mostly libellulids, especially *N. nigeriensis*. The numerous short flights were mostly feeding flights. On three occasions the male flew at and clashed with mating pairs of libellulids (one pair of *N. nigeriensis*; two pairs of *Urothemis edwardsi*) and as it was not clear if these were aggressive or sexual acts, they have been scored accordingly. On one occasion the male was disturbed by a male *Urothemis edwardsi* nearby: this flight has been classified as an 'avoiding flight' and was not aggressive in nature. Unfortunately, at 14.55 the stopwatch which was being used to time the flight periods ceased working and so no more detailed observations could be recorded. At 15.45 No. 7 caught a male *Pseudagrion ? nubicum* and consumed it head first, finishing at 15.51. At 16.43, male No. 7 flew off away from water, but could not be located again that day.

On 25 July, 1972, another attempt was made to observe a single male *N. nigeriensis* during the whole of its territorial waterside period (Table IV). There was rain on the night of 24/25 July and cloud was slow in clearing, the sky remaining totally overcast until 10.30. Although the low cloud was well broken by 11.00, a strong south-west breeze was blowing and there was still a general cover of high cirrus cloud, which remained until about 13.30. The sun shone brightly from 14.00 until 14.30, but thereafter, it became largely overcast again with intermittent sun for the remainder of the day. Male No. 29 arrived at water soon after 10.30 and appeared to settle in a territory near to where it had been seen on earlier occasions (Fig. 4d). However, after making a number of feeding flights and sunning itself, it flew off along the lake shore at 10.51 and was

Table IV

Summary of territorial activities at water of two male *N. nigeriensis* during 25 July, 1972. The first column refers to male No. 29, the others to male No. 73

Observations	Time								
	10.30-10.51	11.10-11.30	11.39-12.00	12.10-12.30	12.40-13.30	13.30 14.00	14.10-14.30	14.40-15.00	15.10-15.30
Mean duration of each flight in secs.	1.63	1.55	2.63	2.35	3.09	5.44	6.05	2.48	1.42
Max. and min. duration of flight in secs.	2/1	5/1	6/1	4/1	6/1	9/3	24/1	6/1	2/1
Mean no. of flights per minute (*Overall mean: 0.57*)	0.48	0.65	0.67	0.55	0.45	0.23	1.00	0.55	0.55
Percentage of time spent in flight (*Overall mean: 2.98*)	1.29	1.68	2.92	2.15	2.32	2.12	10.75	2.28	1.30
Number of flights in each specified period	10	13	14	11	9	7	20	11	11
Number of feeding flights	10	13	13	9	7	2	2	10	8
Number of aggressive flights	0	0	1	0	0	5	12	1	1
Number of sexual flights	0	0	0	0	0	0	0	0	0
Number of other flights (*av* - avoiding; *a/s* - aggressive/ sexual; *st* - stabilising; *inv* - investigatory)	0	0	0	2(*st*)	2(*st*)	0	6(*st*, *inv*, *av*, *a/s*)	0	2(*st*, *inv*)
Shade temperature (°C) at the end of the time period	27.0	28.0	29.0	29.0	30.0	30.5	31.5	30.0	29.5

not seen again that day. It was realised later that this individual's territory was actually located a short distance to the west along the lake shore. As male No. 73 had established itself in a territory adjacent to the one occupied temporarily by No. 29, it was decided to watch this individual for the remainder of the day (Table IV and Fig. 4h). Probably owing to the sub-optimal weather conditions, both No. 29 and No. 73 showed a lower level of activity in all the criteria used to assess it than No. 7 had the previous October. It is noticeable that for most of the time the majority of the flights were short feeding flights with practically no aggressive activity until 13.30 - 14.30 when the sun was shining brightly. During this time feeding flights were mostly replaced by aggressive flights, some of fairly long duration. No purely sexual flights were recorded, but No. 73 did fly at, but did not clash with, a mating pair of *N. nigeriensis* which flew across his territory. On three occasions the male made short flights towards a male *Chalcostephia flavifrons* Kirby, but as no clash occurred and no close approach was made, these have been termed 'approach' flights. On a number of occasions short stabilizing flights were made when the strong wind upset the male's balance. On one occasion a large grasshopper (*Acrididae*) jumped and disturbed the male *N. nigeriensis* under observation; this caused the libellulid to make a short 'avoiding' flight before returning to the same perch. At 15.35 No. 73 became restless and made several flights of about 4 - 5 metres around the territory periphery. These flights were different from the normal flights made in the territory area because the insect flew directly and repeatedly to different widely spaced perches. It then flew to the water's edge and disappeared from view. At 15.37 it re-appeared and perched near to the territory centre, and at 15.39 it flew to the edge of the tall grass of the roosting site adjacent to its territory (Fig. 4h). After several short stabilizing and feeding flights it finally secreted itself in the centre of the *Echinochloa* clump at 15.45. The weather was totally overcast at this time and it remained so until nightfall at about 19.00.

This normal 24 hour pattern of activity of adult male *N. nigeriensis* may be summarized diagrammatically (Fig. 3) in a similar manner to that of the circumboreal *Libellula quadrimaculata* discussed by MOORE (1960). It is interesting to note the several points of similarity between the activity patterns of the two species, despite considerable differences in temperature of the habitats and day-length. Most other dragonflies in the same habitat as *N. nigeriensis* are active at the waterside much earlier than 10.00 and may remain later than 16.00. The total daily period of activity of the two species is similar, about 12 hours in each case. *L. quadrimaculata* spends about four hours in the early morning in a largely immobile state, presumably warming up slowly, whereas *N. nigeriensis*, probably because of the much higher ambient temperature becomes active shortly after daybreak. A major difference seems to be that a peak in territorial behaviour (aggression and sexual) in *L. quadrimaculata* occurs soon after the males have

arrived at water, whereas in *N. nigeriensis* territorial behaviour reaches a peak at around 14.00, that is in the latter third of the period normally spent at the water.

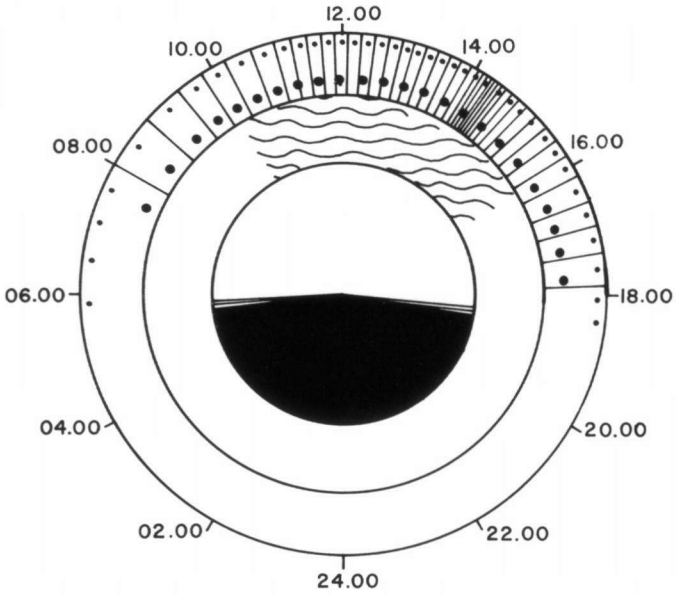

Fig. 3. Diagram showing the typical pattern of activity of adult male *Nesciothemis nigeriensis* Gambles on a sunny day. Inner ring: day – white, night – black; – Middle ring: time spent at roosting site – white, time spent at waterside territory – wavy lines; – Outer ring: time spent perched and motionless – white, slight activity while perched (cleaning eyes, head movements etc.) – small dots; hunting for prey – large dots; reproductive behaviour (territorial fighting, mating etc.) – black lines. (With acknowledgements to N.W. MOORE, 1960).

Waterside territories and roosting sites

Under normal or optimum conditions it seems as though adult male *N. nigeriensis* always establishes a well defined territory at the water's edge. When the population density is high, the territory may be only three or four metres in diameter, whereas when it is low, the area defended may be as long as 20 metres. In the areas where established colonies of this species have been seen, it always occurs along the shores of large open bodies of water having plenty of emergent vegetation and medium sized and tall grasses inland from the lake. In the present 1973 season the water levels in the Zaria lakes fell very low in May and June, exposing large expanses of bare mud for many metres from the waterline. When the first adult males of *N. nigeriensis* were seen in June, 1973 at Samaru Lake, the habitat was clearly unsuitable for the species. None was seen along the open

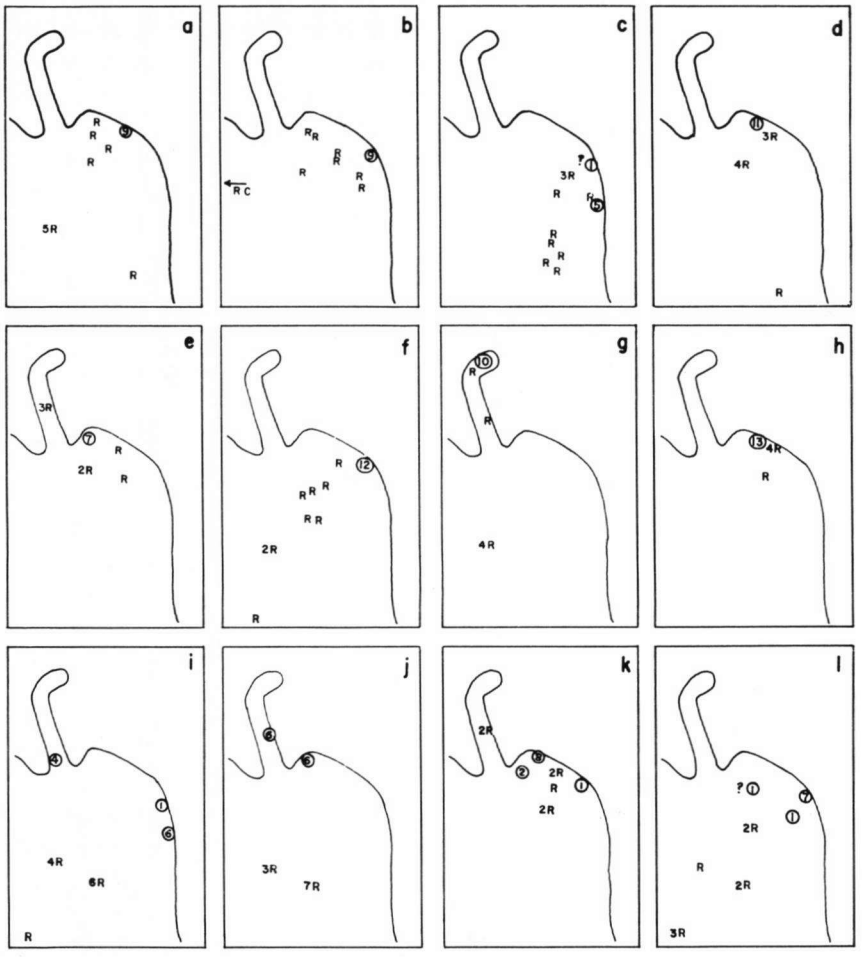

Fig. 4. The locations of waterside territories and roosting sites of twelve adult males of *Nesciothemis nigeriensis* Gambles at Samaru Lake near the jetty (cf. Fig. 2). (a) No. 12, seen 19 times between 28 June - 22 July, 1972: 9 – seen in same waterside territory nine times, R – seen roosting once in the position indicated, 5R – seen roosting five times in the position indicated; – (b) No. 15, seen 17 times between 28 June - 18 July, 1972: RC – seen roosting once at irrigation creek (cf. Fig. 2); – (c) No. 23, seen 16 times between 29 June - 14 July, 1972: ? 1 – uncertain if it was really defending a territory or in transit; – (d) No. 29, seen 19 times between 30 June - 14 July, 1972; – (e) No. 32, seen 14 times between 30 June - 11 July, 1972; – (f) No. 46, seen 21 times between 2 July - 24 July, 1972; – (g) No. 56, seen 16 times between 3 July - 22 July, 1972, – (h) No. 73, seen 18 times between 6 July - 25 July, 1972; – (i) No. 5, seen 22 times between 13 September - 19 October, 1971; – (j) No. 4, seen 22 times between 13 September - 15 October, 1971; – (k) No. 17, seen 18 times between 28 June - 15 July, 1972; – (l) No. 11, seen 17 times between 13 September – 11 October, 1971: ? 1 – uncertain if defending territory; probably in transit to usual territory, as the time was 10.30.

lake margin which was devoid of perches, but a few individuals could be found near to water along a narrow marshy creek at University Farm Lake in the first half of June. In this latter site there were small isolated pools of water with fairly tall fringing grasses and shrubs, and the individuals flew in an unsettled manner within a wide area. No territorial behaviour was apparent although the insects were in mature colouring and it was well past the time of the year when large numbers of territorial individuals were seen in the previous season. In the current 1973 season numerous individuals showing territoriality were seen only after 10 July, when the lake levels rose high enough for there to be some emergent grasses.

A detailed study of waterside territories and roosting sites of *N. nigeriensis* was made at Samaru Lake in September-October, 1971 and June-July, 1972. In the analysis of the results a fairly consistent pattern soon became apparent. Most individuals were extremely localized in their waterside territories, returning to exactly the same spot day after day. However, with respect to roosting, all individuals showed a greater variability in their choice of sites than in their daytime territories.

Twelve individual adult male *N. nigeriensis* which were recaptured or recognized 13 - 22 times have been selected to illustrate this pattern of daytime territories and roosting sites (Fig. 4a - 1). The twelve examples fall into two groups – those individuals (a - h) which virtually invariably used the same small territory, and those (i - l) where more than one distinct territory was established on different days. In both (i) and (j) the first waterside territories were established on the jetty, but the insects later moved to new sites, (j) only a short distance, but (i) a considerable distance along the lake shore. In the case of (j) the change of site coincided with a change in roosting site, but in most other cases the choice of roosting site did not seem to be very strongly correlated with the choice of territory. The waterside position marked by a question mark in (c) may not represent a territory as this was recorded late one afternoon and the individual may have been moving to one of the nearby roosting positions. Similarly, the position marked by a question mark in (l) probably represents the individual moving to its usual territory, since this was recorded at 10.30. The other distant or isolated positions recorded for (i), (k) and (l) were true, but temporary territories. Roosting positions were quite often confirmed by evening and early morning observations.

SEASONAL AND GEOGRAPHICAL DISTRIBUTION

Seasonal distribution

In Zaria, *N. nigeriensis* has only been seen flying during the rainy season. The earliest recorded date for imagines at the Zaria lakes is 23 May (1972) when a

teneral female was taken at Samaru. However, on 24 May, 1972, five adult males were seen at water, and if one allows 13 days for maturation, these specimens must have emerged not later than 11 May. In 1973, when the lake levels were much lower than in 1971 and 1972, the first individual seen was a mature male at University Farm on 27 May (probable emergence date about 14 May). On 14 June, 6 or 7 individuals were counted at University Farm Lake. The first individuals seen at Samaru Lake in 1973 were two adult males on 10 June. By 10 July, the species was numerous at University Farm, with smaller numbers at Samaru Lake, presumably because the water level was still very low at the latter lake. In 1971, at a time when the species was not known to occur in the Zaria region, the first specimen seen was an immature male (not a female, as reported by PARR & PARR, 1972) taken at University Farm by J.C. Deeming. The latest dates recorded for *N. nigeriensis* in Zaria are 21 October, 1971, at Samaru, and 28 October, 1972, at University Farm.

Despite several attempts to secure larvae of *N. nigeriensis* none has been found, and so it is not possible to elucidate the life history by examination of larval samples. However, it seems probable that the species is largely univoltine in the Zaria region. When extensive sampling was carried out in September, 1971, emergences had probably ceased as no teneral specimens were seen. The population at Samaru Lake in 1972 was not large until the beginning of June and it seems unlikely that there would be more than one generation in the period June-September.

Geographical distribution

Gambles' original specimen, an adult male, was taken on 17 December, 1961 at Agulu Lake, near Awka, East Central State. According to UDO (1970), Agulu Lake, which is 12 metres deep and covers 121.5 ha, was formed naturally by damming of the upper Idemili River by sand deposits eroded from gullies. Awka, which is about 520 km south of Zaria, has a rainy season which extends from March to November inclusive (PAPADAKIS, 1965), that is, considerably longer than for the northern city. According to Papadakis, Awka lies almost exactly on the dividing line between the southern Guinea Savanna and the Rain Forest zones. It is probable that Gambles visited Agulu Lake at the end of the flying season in that area, which may account for the fact that he only took a single specimen. When the authors visited Agulu Lake on 28 June, 1973, *N. nigeriensis* was common there, both males and females being seen along the northern lake shore. A teneral male was also taken near the path running past the eastern end of the lake. At Agulu Lake *N. nigeriensis* occurred most commonly along the edge of the lake having much mixed emergent vegetation, including grasses, sedges, a great variety of herbaceous plants and *Raphia* palms. The area away from the northern shore of the lake was very reminiscent of the characteristic

roosting areas at Samaru, having tall *Andropogon* and *Hyparrhenia* grasses.

Attempts were made during June and July, 1973, to locate *N. nigeriensis* in other areas of southern Nigeria which seemed ecologically suitable. Lakes and pools in the following areas were investigated: Wuya, near the Kaduna River (North Western State); Ife and Ibadan (Western State); Benin (Mid Western State); Onitsha (East Central State); and near Ugep (South Western State), but *N. nigeriensis* was not found. Mr A.T. Hassan, an odonatologist at the University of Ibadan, says that he has never seen the species, although he has made large collections in the Ibadan area. Other lakes and ponds, in northern Nigeria searched unsuccessfully in 1972 for *N. nigeriensis* include: Maigana Fish Farm and Yakawada Lake, near Zaria; Maska Fish Farm and Mairuwa Lake, near Funtua (North Central State); and Lake Natu, about 96 km north west of Gusau (North Western State).

However, on 6 August, 1973, thirteen adult male *N. nigeriensis* were seen at Maska Fish Farm, which is 45 km north west of University Farm Lake, on the Zaria-Funtua road. In the past three years Maska Fish Farm has become progressively neglected, so that many of the ponds now appear to be suitable ecologically for the species, having a great deal of emergent grasses, especially *Echinochloa*. Also on the 6 August, 1973, a single adult male was seen at Mairuwa Lake which is 65 km north west of University Farm Lake, on the Funtua - Gusau (Sokoto) road.

In our preliminary report (PARR & PARR, 1972) we mention a colony of *N. nigeriensis* near Giwa, about 35 km north west of Zaria. This colony was found in July, 1972, but during the 1972 - 1973 dry season the fadama pool around which the colony was centred dried out completely. The colony at this pool cannot, therefore, be a permanent one, but may be repopulated from time to time from one of the Zaria colonies or another colony, as yet undiscovered. This fadama pool at Giwa, was, in fact, not repopulated by *N. nigeriensis* up to early August in 1973.

In summary, we may state that, despite careful searches, the known range of *N. nigeriensis* is still only the greater Zaria area and its type locality, Awka.

DISCUSSION

Nesciothemis nigeriensis is of interest from a number of standpoints. The fact that it was first seen in 1961 and not seen again until ten years later when it was numerous in a different geographical area may not, *per se*, seem to be very notable. However, *N. nigeriensis* is a highly conspicuous insect and one would have expected it to have been recorded earlier and in a greater number of areas than in fact it has. General entomological and specific odonatological collecting in the Zaria area by several entomologists and students from Ahmadu Bello University and England over a number of years did not result in any reports of

this species until 1971. The fact that Gambles collected Odonata extensively in Nigeria, particularly in the north, and yet did not see *N. nigeriensis*, except at Awka, seems to add to the problem. P.H. Ward (British Museum, Nat. Hist.) collected over 1000 Odonata from Zaria, including many from University Farm and Samaru Lakes in the rainy season of 1970 and yet did not see a single specimen of this species. We, therefore, conclude that it could not have been very common at that time. On the other hand, it seems unlikely that the population of *N. nigeriensis* could have increased from nearly zero in 1970 to the large numbers observed at the Zaria lakes in 1971 in a single generation, unless the habitats were exceptionally suitable and larval survival rates high. Another possibility is that a relatively large scale migration of imagines from elsewhere colonised the Zaria lakes late in the 1970 rainy season, resulting in the two very well established populations at the present time. The discovery of 13 adult males at Maska Fish Farm in August, 1973, when despite careful searches it could not be found there in 1972 seems to point to recent colonization of the area, which now appears very suitable for it. Similarly, the single adult male seen recently at Mairuwa Lake is suggestive that colonization is imminent, since that lake is maturing into a body of water which is very similar to University Farm Lake. It may be that, until recently, very few suitable lakes and pools existed for it within its preferred climatic and vegetational limits. At the present time many artificial lakes are being created for town water supply and irrigation schemes in Nigeria, especially in the north. It is probable that as these lakes mature they may provide further habitats for *N. nigeriensis* colonies.

Observations of adult behaviour at water left no doubt that the numerous clashes and chases between mature males of *N. nigeriensis* in the neighbourhood of water were primarily aggressive in nature. This aggression has the effect of spacing the males regularly along the waterside. Mating usually occurs within a waterside territory. The female normally starts oviposition immediately after the pair have separated and while she is still in her most recent mate's territory. The male remains in very close attendance, hovering a few centimetres above the female while she is ovipositing, as in the case of the libellulids studied by JACOBS (1955). It is clear that this behaviour results in the female being able to oviposit relatively unmolested by other males. As might be expected in a species displaying such marked sexual dimorphism, males rarely appear to attack females aggressively, or to approach other males sexually. The specific and sexual sign stimuli presented by the sexes are clearly recognized by both *N. nigeriensis* and human observers. It is not clear to what extent territoriality in this species causes dispersal to new habitats, but that it does so to some extent is probably unquestionable. It is probably the reason why so many immature males of *N. nigeriensis* after having been observed for several days away from water do not eventually establish waterside territories nearby. We gathered some evidence that newly matured males took some time, sometimes several days, to settle down in

a definite territory on their arrival at water. Rather similar behaviour occurs in the late maturation period of *Anax imperator* Leach (CORBET, 1957). This is probably a critical time during which many disperse to new areas, whereas a few compete successfully *in situ* with already established males. MOORE (1964) makes a similar point in discussing his observations on populations of Odonata in England.

Experiments with dead Odonata and models to test the species-specific recognition characters yielded results which indicated that colours, pattern, shape and size were important features. The fact that male *N. nigeriensis* would respond strongly to dead examples and crude models suggested that wing movements and normal behaviour were not important recognition characters, providing the test insect was suspended as if in flight, and not 'perched'. *N. nigeriensis* males virtually always ignore perched individuals of any dragonfly of either sex. The experiments of PAJUNEN (1964) with *Leucorrhinia dubia* and *L. rubicunda* show that in these libellulids it was primarily the flight patterns of the sexes which were very important specific and sexual recognition characters, not colours or colour patterns. In *Perithemis tenera*, studied by JACOBS (1955), the wing coloration is an important aid to sex recognition, although the flight pattern is also used. There is certainly a wide range of characters which are utilized by different libellulids as specific and sexual sign stimuli. It would be interesting to have detailed information on a large number of libellulids in order to assess the relative importance of size, shape, colour, pattern and movement as releasers in the family as a whole.

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