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THE DURATION OF COPULATION CORRELATES WITH OTHER ASPECTS OF MATING BEHAVIOUR IN *ORTHETRUM CHRYSOSTIGMA* (BURMEISTER) (ANISOPTERA: LIBELLULIDAE)

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The behaviour of marked individuals of *O. chrysostigma* was observed at a small stream during 15 days in July, 1982, at Hunter's Lodge, Kenya. In a 30 m length of stream there were normally 3 resident males, 2 of which held the same territories throughout the study period. Further males visited the stream intermittently, acting as wanderers or as satellites to resident males, and showing much less spatial constancy than residents. Females appeared at the stream at a mean rate of 0.34 per half-hour throughout each 7-hour "day". One territorial male obtained 44% of all observed copulations (total 27), while 37% of the copulations were shared between about 15 satellites and wanderers. Territorial males copulated 9 times as often as non-territorial males but copulation in the latter lasted up to 17 times longer. The possible significance of long and short copulations for sperm competition is considered.

INTRODUCTION

In many libellulid dragonflies copulation lasts for short periods of a few tens of seconds (JACOBS, 1955; CAMPANELLA & WOLF, 1974; CAMPANELLA, 1975), but in some others (e.g. species of the genera *Celithemis, Sympetrum, Leucorrhinia* and *Orthetrum*) it may continue for many minutes (ROBERT, 1958; CORBET, 1962; PAJUNEN, 1962; PEZALLA, 1979). In view of the possibility of sperm removal from females during copulation in some Anisoptera (WAAGE, 1983; MILLER, 1983a), as well as in Zygoptera (WAAGE, 1979a), such variation within a family deserves more attention. Observations reported here indicate that in the African species *Orthetrum chrysostigma* resident territorial males usually copulate for about 2 min, whereas wandering or satellite males may do so for up to an hour. The possible significance of this marked difference is discussed.

STUDY AREA AND METHODS

The observations were conducted at Hunter's Lodge in Kenya, as described in MILLER (1982). The study area was a 30 m stretch of stream demarcated by overhanging bushes at each end. The stream had been artificially straightened and was 1 m wide and 20 cm at its deepest. The flow rate in the centre varied from 10 to 23 cm s^{-1}. Numbered stakes were driven into the bank at 1 m intervals, and behaviour was examined with the aid of field binoculars modified for near focus, and with a pocket tape-recorder. The stream was sunlit from 1000 to 1700 hr, and libellulids were active at the stream during this period, except when there was cloud cover. Sunrise on 20th July was at 0635 and sunset was at 1835 h. Libellulid behaviour was observed and recorded throughout the daily period of activity on 15 consecutive days in July, 1982.

Twenty-one *O. chrysostigma* were captured at the study area or nearby in the field and they were individually marked on the wings with a permanent-ink writer (Staedtler Lumocolor). Identifications were made using PINHEY (1969) and with the generous assistance of R.M. Gambles.

MALE BEHAVIOUR AT THE STREAM

In maturing male *O. chrysostigma,* blue pruinosity first appears in the last three abdominal segments and later it spreads to the remainder. In older males the thorax becomes dark blue. Twelve of the marked male *O. chrysostigma,* all with mature colouration, appeared regularly or intermittently at the study area during the 15 days of observation. Three of these (A2, K4 and WM) were identified as resident territorial males on the basis of their behaviour. A2 remained in possession of the central 12-15 m of the stream throughout the 15 days, and similarly K4 possessed the southern 7-8 m. WM took over the northern region during the last 5 days, and before that this part was intermittently occupied by J4 and H4. Territories were confined by trees and bushes to a linear strip of bank about 1 m wide on each side of the stream. Each territorial resident showed strong spatial constancy. This is illustrated in Figure 1, the data being based on

Table 1
Time spent at the stream and number of copulations by male *Orthetrum chrysostigma*

Male identity	Numbers of days on which observations were continued throughout the period of activity	Mean hours per day	Percentage of the 7-hr day	Total number of copulations	Mean daily number of copulations
• A2	12	4.53 ± 1.74	65	12	1.0
• WM	5	3.91 ± 0.63	56	3	0.6
• K4	11	3.69 ± 1.92	53	2	0.18
4P4R	8	2.28 ± 2.15	33	0	0
H4	5	1.4 ± 1.09	20	0	0
2BB	6	1.2 ± 0.66	17	0	0
G4	6	1.19 ± 1.03	17	0	0
8RS	1	1.0	14	0	0
C4	1	0.75	11	0	0
4BS	4	0.5 ± 0.2	7	1	0.25
J4	4	0.44 ± 0.43	6	2	0.5
2RB	1	0.25	3.5	0	0
Unmarked (ca. 7)	15	—	—	7	0.5

• - resident male in territory

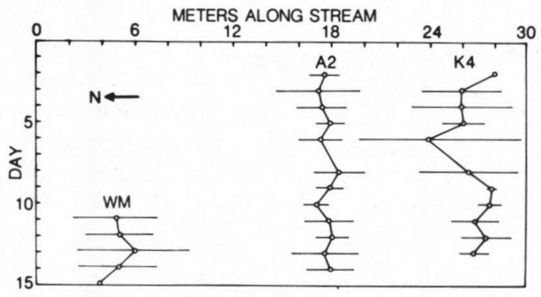

Fig. 1. Perching positions of 3 territorial resident male *O. chrysostigma* (WM, A2 and K4) along the stream in the 30 m study area (1-30 horizontal axis), on each of up to 12 days on which continuous observations were made (vertical axis). Each point is the mean of up to 37 records; horizontal bars = standard deviations. The mean perching position throughout the study period for WM was at 5.4 ± 0.77; for A2, 17.8 ± 0.42; for K4, 26.7 ± 1.15 m. (N = North).

attempts to record all the perching sites of males during each day by making surveys at approximately 10-minute intervals along the stream. The relative constancy from day to day indicates the continued use by territorial males of the same well-defined perching areas, usually on bare ground or rocks in the case of A2 and K4, but low on vegetation in WM. Figure 2 shows small changes of perching sites by A2 during the course of two days, which corresponded to increasing exposure of the east bank to the sun.

Territorial males also spent longer at the stream than other males (Tab. I), and on sunny days they remained in their territories from about 1030 to 1630 or 1700 hr. During short cloudy periods when the sun was obscured they persisted in their territories, often making feeding flights at such times (identified by seeing prey capture), but if the sun was obscured for more than 15-20 min they left their territories and perched in the field nearby. While in their territories they made frequent patrol flights and were often seen to chase out intruders.

A further 9 marked male *O. chrysostigma* (C4, G4, H4, J4, 4BS, 4P4R, 2BB, 2RB and 8RS) together with an estimated 7 unmarked males intruded intermittently at the stream (Tab. I). Their behaviour varied from wandering, in which they flew along the stream settling only briefly or not at all, to acting as satellites to

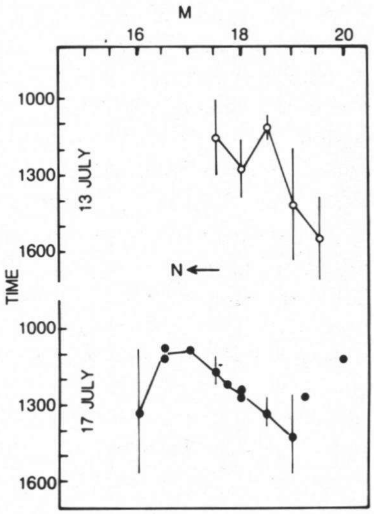

Fig. 2. Mean times at which A2 perched at successive 0.5 metre intervals within its general perching area at the territory centre. Values are given for 2 days. A slight southward drift during each day corresponds to increasing exposure of the east bank to the sun (cf. Fig. 1). (N = North; Vertical bars are standard deviations where there are more than 2 readings).

territorial males, perching sometimes for long periods in residents' territories (cf. HIGASHI, 1969; HEYMER, 1973; UEDA, 1979; CORBET, 1980; WALTZ, 1982). Figure 3 indicates the relative lack of spatial constancy shown by 2 satellites (H4 and 2BB), although they had a preference for the south end of the study area. Conflicts with resident males were common, and in every one observed the intruder was driven off to the field, often to return within a few minutes. Intruders evoked attacks from residents when in flight, but once they had settled they were commonly ignored, even when perched as close as 0.5 m. Residents were seen to fly over perched satellites many times without response, whereas if the reverse occurred the satellite was always attacked. However, on a few occasions a resident did pounce on and drive away a perched satellite. Settled satellites, which tended to select vegetation to perch on and remained immobile, were apparently seldom detected by resident males: likewise perched females normally evoked no response.

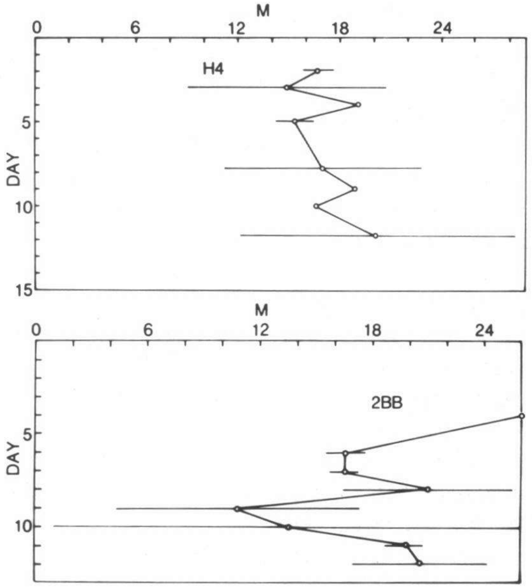

Fig. 3. The same type of plot as in Fig. 1 for 2 satellite male *O. chrysostigma*, H4 and 2BB. Each point is the mean of up to 18 records. Note the much larger standard deviations (horizontal bars) showing greater range of perch positions compared to territorial males. The mean perch position throughout the study period for H4 was 14.6 ± 6.25, and for 2BB was 16.9 ± 3.83 m. (M = metres along stream).

MATING BEHAVIOUR

Altogether only 30 female arrivals were observed throughout the study period, all occurring between 1100 and 1530 hr. The mean arrival rate per half-hour was 0.34 ± 0.17, and no peak arrival time within this period could be identified.

Most observed copulations in *O. chrysostigma* started after a female had reached the stream and was ovipositing. Once spotted by a male, a female was seized in tandem and the wheel position was adopted in flight. The pair landed but then usually made a few changes of perch before finally settling. Table I shows the total and mean daily numbers of copulations for 12 marked and about 7 unmarked males. A2 was strikingly successful in obtaining 44% of all observed copulations. The occurrence of some satellites more commonly in A2's territory than elsewhere (Fig. 3) suggests that this region may have been recognized by them as optimal (it included a gap in the bushes used as an entry point from the field), or that they had identified a highly successful territorial male (cf. WALTZ, 1982). Of the 7 copulations by unmarked males, 6 occurred at the stream in a resident's territory and were by satellites or wanderers, and the 7th was 20 m from the stream in the field by a young male (with only the 3 posterior segments of the abdomen blue). I made periodic searches of the field but found only this one copulation occurring there. I also saw that many of the marked satellite males when not at the stream were perched nearby in the field. Thus marked satellite males were not seen to obtain further copulations away from the study area.

Figure 4 shows the duration of each of 21 copulations which were observed in their entirety, and values for a further six whose start or finish was not observed are also added. The histogram suggests that a peak of short copulations occurs at 1-2 min, and that there is a long tail of extended copulations one of which lasted for over an hour. A division can be made into short copulations (< 5 min) with a mean of 106 ± 58 s (n = 14), and long copulations (> 5 min) with a mean of 1857 ± 1260 s (n = 7). The six incompletely observed copulations fall into the long-copulation category. As shown in Figure 4, 11 out of 12 of A2's copulations were short, but one was long; K4 had one short and one long but incompletely observed copulation; WM had one short copulation and there were two further incomplete ones each observed for 30 s (not included in Fig. 4). Thus among resident males, 87% of the fully timed copulations were short. Only one short copulation, that by J4, was not carried out by a resident male, and J4's status was equivocal. Most long copulations were carried out by satellites or wanderers in resident-male's territories.

The mean copulation duration by known resident males was 190.6 ± 330 s (n =

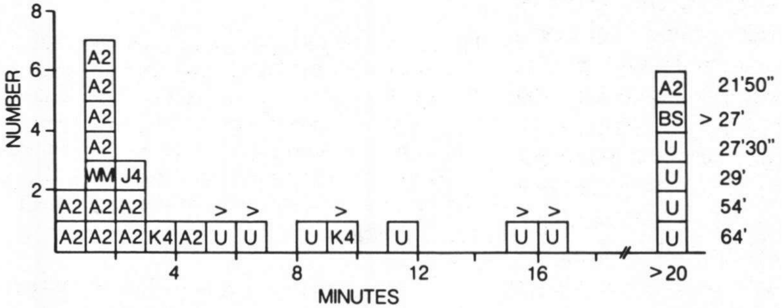

Fig. 4. Distribution of the durations of copulations. Each square is labelled with the identity of the male for that copulation (cf. text). U, unmarked males acting as satellites or wanderers. >, indicates a minimal value since either the start or finish of copulation was not seen. A2, WM and K4 were territorial resident males. The last column contains copulations lasting more than 20 min, with the duration of each given alongside.

14), or, omitting the one long copulation by A2, it was 101 ± 60 s. That by males identified as satellites or wanderers was 1699 ± 1398 s or nearly 17 times longer than short copulations, the difference being significant at the 1% level.

Resident males usually copulated in a horizontal position on the ground close to the centre of their territory. Non-territorial males copulated in a vertical position usually hanging from vegetation and often in the shade. The 54- and 64-min copulations both took place in A2's territory 1-2 m above the water and were by unmarked satellite males. Both these long copulations were watched closely: characteristic rhythmic movements of the male's anterior abdominal segments were detected which took place in short bouts at up 5 s^{-1} and then decelerated and became more powerful before stopping (Fig. 5a, b). Alternatively there were several series of much shorter bouts (Fig. 5c). Such activity persisted for most of the copulatory period except for the final 5-10 min. In shorter copulations this activity was not seen, but instead both partners made rapid synchronised ventilatory movements throughout. The observations show that long copulations represent periods of prolonged activity, and that they differ from short copulations in the type of activity shown.

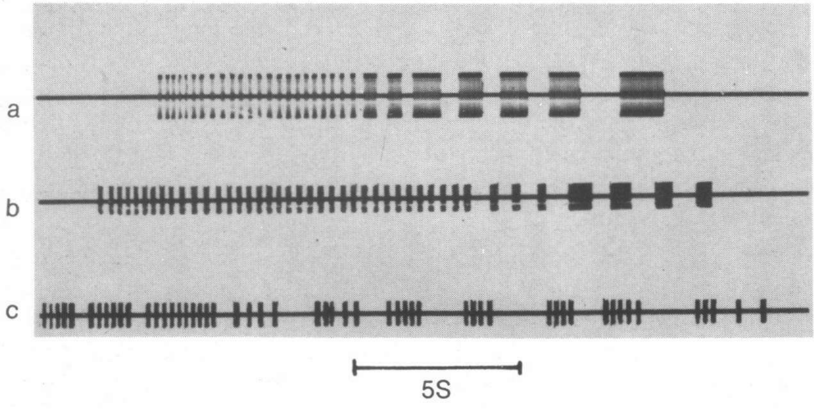

Fig. 5. Oscillograms based on tape recordings of verbal descriptions of activity seen in an unmarked male *O. chrysostigma* during a 64-min. copulation: (a - b), two bouts of rhythmical movements made by the 2nd and 3rd segments of the male abdomen, which decelerate and become more powerful before terminating; — (c) a period of short bouts of rhythmical movements. (Each bar represents one cycle of the repetitive movement; increase in width of the bar indicates increase in intensity.)

POST-COPULATORY BEHAVIOUR

Immediately after copulation ended, the male normally perched beside the female for a mean period of 86 ± 38 s (n = 10) before oviposition commenced.

One unusual female perched for 505 s after copulation and then oviposited alone since the male had previously flown off. Twice A2 was seen to terminate copulation abruptly in order to chase an intruder and he then returned to perch beside the female without resuming copulation. On 4 occasions (twice by A2, once by WM and once by an unmarked male), the male was seen to take off immediately copulation had finished and to fly at the female, butting or striking her vigorously. On the four occasions, this was done 3, 4, 4 and 9 times respectively in quick succession. The female did not normally respond but in the last case, after nine strikes the male landed on the female and appeared to bite her abdomen whereupon she flew off. This remarkable behaviour may be interpreted as an attempt by the male to initiate oviposition in the female.

After copulation, territorial males guarded ovipositing females closely. A guarding male flew immediately above the female frequently clashing his wings with hers. He initially led or nudged the female to an oviposition site in the centre of his territory and then prevented her from moving elsewhere during egg-laying by physically blocking her path. In this way A2 was seen to compel five females to lay successively at the same site. While guarding he drove away intruders, and then swiftly returned to the female. Only when the female had finished oviposition, which she signalled by elevating her abdomen and flying rapidly upwards, did the male return to normal territorial activity. Guarding, which lasted for a mean of 85 ± 33 s ($n = 5$) seems to be more intense than in other *Orthetrum* spp., judging from published illustrations (HEYMER, 1969; ARAI, 1972; EDA; 1981), but this is likely to be density-dependent. Satellite males were not seen to guard, and were quickly driven off when spotted by territorial males.

On one occasion while A2 guarded an ovipositing female, a satellite male flew down to the stream with a female after copulation. A2 drove off the male and alternately guarded the new female and the original one on opposite sides of the stream. After 30 s he shepherded the new female across the stream to join the first and then maintained a simultaneous guard over both as they oviposited within a few cm of each other. The guarding of more than one female by a single male has been described in *Calopteryx maculata* (ALCOCK, 1979; WAAGE, 1979b) and in a few libellulid species (e.g. JACOBS, 1955; ARAI, 1972; UEDA, 1979; McVEY, 1981). A male may be unable to distinguish a female he has mated with from others, and does not attempt to mate with a second female because of the risk of losing the first (cf. WAAGE, 1979b; ALCOCK, 1982).

Female *O. chrysostigma* oviposited by scooping small drops of water containing eggs towards the bank using the slightly expanded flanges of the 8th abdominal tergite to do so. The activity was similar to that in *Nesciothemis farinosa* (MILLER, 1982b) but it was weaker and the females hovered only 3.5 cm above the water surface. The water drops commonly fell back into the water, but sometimes they landed on the bank at or just above water level. Unguarded females flew along the tream scooping at about 1 s^{-1}, but guarded females scooped more rapidly at 2-3 s^{-1} and in one place.

During oviposition females were exposed to predation by fisher spiders (*Dolomedes:* Pisauridae) which lurked in marginal vegetation and leapt upon hovering females (cf. JACOBS, 1955; BRISTOWE, 1958; Fig. 21). Other libellulids and some zygopterans were also caught in this way. The numerous remains of females of several species at the water's edge suggested that this form of predation was common.

DISCUSSION

Two territorial males were present in the study area throughout the study period and a third was present for 5 days: these three males obtained 63% of all observed matings. A further 9 marked and about 7 unmarked males visited the area intermittently and they shared the remaining 37% of observed matings. It is not known if some of the latter group obtained additional matings elsewhere, but those which acted as satellites divided their time between the stream and the field nearby and only one mating was observed in the field. No territorial male was seen to be ousted from the stream and no satellite obtained a territory; thus marked males maintained particular roles for at least two weeks. The mean survival time for this species is not known, but for mature *Orthetrum julia* it is 9.9 days, with a maximum of 51 days (PARR, 1980). Role changes are therefore at most rare events, unlike the situation in *Plathemis lydia* where changes may occur each day (CAMPANELLA & WOLF, 1974).

Mating frequency is known to be unevenly distributed among males in species as different as red deer and fruit flies (KREBS & DAVIES, 1981), and this is also true for some damselflies (WAAGE, 1979a; FINCKE, 1982) and dragonflies (McVEY, 1981). UEDA (1979) reported that territorial male *Sympetrum parvulum* have a mean mating frequency of 1.4 per day, whereas wandering males scored only 0.5 per day. My results for *O. chrysostigma* suggest that territorial males had a 9 times better chance of mating than non-territorial males. The mean daily rate for A2 was 1.0 but this figure conceals much daily fluctuation, since on two days A2 mated 4 and 6 times respectively, but only twice on the remaining 13 days.

Preliminary measurements of the size suggest that territorial males are larger than satellites or wanderers. Five territorial males were found to have a mean size index (forewing length × body length in mm) of 1512 ± 77, whereas six non-territorial males had a mean of 1327 ± 52. Measurements of 27 males of unknown status from collections gave a value of 1398 ± 116. In *Enallagma hageni,* however, FINCKE (1982) has found no evidence to suggest that male size is correlated with mating success.

Table II lists the duration of copulation reported in different species of *Orthetrum:* the value for *O. chrysostigma* may be more than twice that

Table II
Duration of copulation in *Orthetrum* species

Species	Duration	Author
cancellatum	10-15 min	ROBERT, 1958
	1-15 min	KRÜNER, 1977
coerulescens	10-15 min	ROBERT, 1958
	5s to 25 min	M.J. Parr, pers. comm.
	50s-2 min	HEYMER, 1969
brunneum	3.5 min	ROBERT, 1958
	50s-2 min	HEYMER, 1969
albistylum	5 min 13 s	ARAI, 1972
triangulare	4 min 9 s	ARAI, 1972
abbotti	6 min 55 s	PARR, 1980
	9 min 36 s	PARR, 1980
j. julia	29.5 ± 13.3 s (n = 6)	PARR, 1980
chrysostigma	34 s - 64 min	this paper

reported for any other *Orthetrum* spp. In *Leucorrhinia dubia*, however, copulation may last for 40 min (PAJUNEN, 1962). The correlation of short copulations (< 5 min) in *O. chrysostigma* with territoriality and of others, up to 17 times as long, with satellite or wandering behaviour is significant. Similarly UEDA (1979) has shown that wandering male *Sympetrum parvulum* copulated for 5 times as long as territorial males. Several possible explanations to account for the differences may be considered:

— It is not a real effect, but is due to aberrant behaviour by A2 which contributed most of the short copulations. This is improbable since two other territorial males also each copulated briefly at least once (WM additionally made two further copulations which were observed for 30 s). Moreover A2 performed one long copulation whose characteristics were like those of other long copulations and which occurred at a time when few other males were present at the stream.

— It is a real effect:

(a) It arises because first copulations are always long, but subsequent copulations by a male with the same female are short, unless there has been an intervening copulation by another male (Parr, pers. comm.). This implies either that males recognize individual females or that they can detect the presence of their own sperm within a female. Since few females were marked, this cannot be discounted, but it would demand a capacity for identification not known elsewhere.

(b) Long copulations benefit satellites or wanderers by allowing them to hold a female out of circulation for long periods until an opportunity for undisturbed oviposition arises. However the intense abdominal activity which persists for most of a long copulation does not suggest a passive function. Moreover, females released from long copulations were seen on two occasions to be immediately remated by territorial males. The second copulations were brief, which is also in disagreement with the proposal in (a) above.

(c) Long copulations permit males to introduce more sperm and possibly to fertilize the eggs laid in several subsequent bouts of oviposition (cf. LEW & BALL. 1980). A larger sperm volume might also pack down previously deposited sperm more effectively and guarantee last-in-first-out priority. This suggestion is not in agreement with the fast sperm ejection mechanism of libellulids (PFAU, 1971), and there is no evidence of further sperm transfer from the primary genitalia during copulation. Moreover the morphology of the penis suggests a "hooking out" rather than a "packing down" function; cf. (d) below.

(d) Long copulations might allow a male to remove a greater fraction of the sperm previously deposited by other males. Some libellulid species may pack down sperm already in females during copulation, but others may hook it out before depositing their own (WAAGE, 1983; MILLER; 1982a). The penis of *O. chrysostigma* is equipped with a barbed flagellum which may be swung dorsally within the female during copulation. It is possibly capable of entering the narrow spermathecal ducts of the female where most sperm is stored, the bursa being very small in this species (Miller, in prep.). The structure of the penis therefore suggests that sperm removal may be an important feature of copulation in *O. chrysostigma*. PARKER (1970) has shown that in dungflies, males which perform long copulations displace more sperm and fertilise more eggs.

(e) Short copulations may benefit territorial males by allowing them access to a greater number of females. Observations confirm that they mate more frequently than satellites.

(f) Short copulations allow males to defend territories more effectively. A2 was seen to break off copulation twice to give chase to an intruder. This behaviour does not however account for the normal brevity of a territorial males' copulations since no other copulation was seen to end in this way.

In conclusion, therefore, it may be suggested that satellites and wanderers have access to fewer females but spend more energy on each copulation than territorial males. They may derive a greater benefit from this by a more complete removal of other males' sperm from the female. In contrast, territorial males mate briefly but more frequently and are therefore able to spend more time in defence of a territory. Territorial males may copulate at greater length at times when intruders are uncommon and male density is low. From the dissection of females caught during long and short copulations, it is hoped to determine if sperm removal occurs in this species, and if its magnitude correlates with the type of reproductive behaviour observed (cf. WAAGE, 1983).

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