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Mating tactics and male–male courtship in the lek-breeding cichlid *Oreochromis mossambicus*

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Data are presented on the breeding behaviour of *Oreochromis mossambicus* under captive conditions. Males tended to synchronize their occupation of territories and breeding activities. Different male mating tactics were observed, namely establishing a breeding territory, acting as a floater, or behaving as a sneaker. The majority of spawnings observed involved dominant males and were subjected to interference from other males. Males were found to court other males that frequently responded to these attempts by adopting a female-like behaviour. Results are discussed in terms of a probable time constraint in territoriality, which promotes male–male competition and a low level of sex discrimination by territorial fish.

Key words: male mating tactics; sneaking behaviour; homosexuality.

INTRODUCTION

In recent years, the intraspecific plasticity in the social systems of vertebrates, including the modes of reproduction adopted by different individuals, has become increasingly apparent (Lott, 1991; Turner, 1993). With regard to the reproductive behaviour of male teleosts, there is an increasing amount of evidence that males of each species may follow a diversity of mating tactics rather than a single pattern (Taborsky, 1994).

In cichlid fishes, several alternative male mating tactics have been described, ranging from sneaking [*Cyrtocara eucinostomus* (Regan), McKaye, 1983; *Lamprologus brichardi* Poll, Taborsky, 1984, 1985; *Pseudosimochromis curvifrons* (Poll), Kuwamura, 1987; *Pseudocrenilabrus philander* (Weber), Ribbink & Chan, 1989; Chan & Ribbink, 1990; *Lamprologus callipterus* Boulenger, Sato, 1994; *Pelvicachromis pulcher* (Boulenger), Taborsky, 1994; *Simochromis diagramma* (Günther), T. Sato, pers. comm. in Taborsky, 1994; *Pseudocrenilabrus multicolor* (Schöller), W. Mrowka, pers. comm. in Taborsky, 1994], presence of floater males [*P. philander*, Ribbink & Chan, 1989; Chan & Ribbink, 1990; *Aulonocranus dewindti* (Boulenger), A. Rossiter, pers. comm.] and piracy (*sensu* van den Berghe, 1988; *A. dewindti*, A. Rossiter, pers. comm.]. Sneaker males take advantage of the courting activities of other males, trying to fertilize eggs while the female is spawning with them. Floaters wander about a spawning area trying to occupy recently vacated territories. Pirates take over successful nests of other males in which they spawn, abandoning them subsequently to be re-occupied by the original owner.

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In tilapiine fishes, the occurrence of sneaking fertilization attempts was first described for *Oreochromis niloticus* L. (Heinrich, 1967) and was subsequently found in *Oreochromis alcalicus alcalicus* (Hilgendorf) and in *Oreochromis alcalicus grahami* (Boulenger) (Albrecht, 1968).

In *Oreochromis mossambicus* (Peters), an African maternal mouth-brooding cichlid, males form dense nest aggregations (arenas or leks) in sandy or muddy substrata during the breeding season. Within these aggregations males establish territories where they dig spawning pits, to which they attract females. Spawning takes place in the pit and the female quickly takes eggs and sperm into her mouth where fertilization occurs, before leaving the arena. In the wild, the embryos and fry are brooded in the female's mouth for 20–22 days (Fryer & Iles, 1972; Bruton & Boltt, 1975). Males that succeed in defending a territory in the substratum adopt a typical black coloration that fades away in a few seconds if the fish is disturbed or defeated (Neil, 1964). In this species, Turner (1986) has already mentioned the occurrence of interference by intruder males at the breeding pair during spawning, which he has interpreted as possible events of sneaking fertilizations or of egg cannibalism. Nevertheless, these descriptions were not very elaborate and a more detailed analysis of these episodes is still lacking in the literature.

This study presents data on the plasticity of male reproductive behaviour in *O. mossambicus* based on the observation of captive animals.

MATERIALS AND METHODS

PROCEDURES

The individuals used in this study belonged to a stock kept and bred at our laboratory (Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada). This stock was founded in 1991 with individuals kindly supplied by Aquário Vasco da Gama (Lisbon) and whose origin was the Incomati River, Mozambique. Fish were kept in standard aquaria (62 × 34 × 39 cm) with a layer of sand on the bottom, at 24 ± 2° C, and a photoperiod of 12L : 12D.

The data presented in this paper were gathered during three different behavioural studies published elsewhere (Oliveira, 1995; Oliveira & Almada, 1996*a*,*b*; Oliveira *et al.*, 1996). A total of 20 groups of six fish were observed. In study 1 (Oliveira, 1995; Oliveira & Almada, 1996*a*), eight groups that were formed when individuals were 10 days old (time after release from the female's mouth) were observed. These groups were kept during the development of the fish until the first signs of sexual maturity were detected (at 9–10 months old), when the observations were made. Twelve focal observations (Martin & Bateson, 1993) of 5 min each were performed for each fish on 2 consecutive days. The sex ratios (males : females) of these groups were as follows: one group 1 : 5, one group 2 : 4, two groups 3 : 3, two groups 4 : 2, one group 2 : 3, one group 1 : 3 (in two of the groups mortality occurred during the study period and the individuals were not replaced to avoid any effects on the established social structures). Male mean (± S.D.) standard length was L_s 61·7 ± 7·5 mm.

In study 2 (Oliveira, 1995; Oliveira & Almada, 1996*b*), at the age of sexual maturity (9 months) eight groups were established in standard aquaria and were observed weekly for 8 consecutive weeks. Behavioural observations were conducted following a behavioural sample procedure (six periods of 5 min each group^{-1} week^{-1}) (Martin & Bateson, 1993) for the social interactions. During each observation period, the identity of the individuals actively defending an area on the substratum was also noted, from which the proportion of time holding a territory was computed for each individual. Three of these groups had a sex ratio (males : females) of 3 : 3 and the remaining five of 4 : 2. Male mean (± S.D.) L_s was 59·9 ± 11·4 mm.

In study 3 (Oliveira, 1995; Oliveira *et al.*, 1996), four groups of four adult males were formed and placed in standard aquaria. Five days after group formation, two ovulated females were introduced to each group. Twenty minutes of behavioural sampling observations (Martin & Bateson, 1993) were conducted each day for each group for the 7 days of the experiment. Male mean (± standard variation, s.v.) L_s was 90·0 ± 6·0 mm. More details on the experimental and maintenance conditions of these studies can be found in the above mentioned papers.

All social interactions were identified based on the occurrence of the behaviour and colour patterns described by Baerends & Baerends van Roon (1950) and Neil (1964) (Table I). Any behavioural interaction involving courtship behaviours was counted as a courtship episode.

To investigate the occurrence of a temporal pattern in the breeding episodes, a community tank (200 × 50 × 40 cm) with 38 individuals (23 males and 15 females) was observed for 123 consecutive days between January and May 1993. On each day the number of dark males (darkness ≥ dark 1 pattern: Table I), which is the territorial colour pattern adopted by males of this species, and the number of nests present in the tank were recorded. To avoid any variation due to a circadian fluctuation in territoriality (Falter, 1986) daily inspections were conducted between 0900 and 1100 hours.

DATA ANALYSIS

To assess whether the temporal pattern of the distribution of the number of nests and the number of dark males was random, the sequence of days with a number of nests/dark males larger or smaller than the median was tested using a Runs test.

Due to the small size of some of the samples, simulation statistical procedures were used, namely an analysis of contingency tables using simulations (Actus test; Estabrook & Estabrook, 1989) and a goodness-of-fit simulation test (Adersim test; Almada & Oliveira, 1997), based on the same rationale. Actus analyses contingency tables by simulating 1000 tables with the same number of cases of the table of the observed values. Each case is assigned randomly to one of the rows with a probability that is proportional to the frequency of each row total. A similar procedure is used to assign each case to one of the columns. Thus, the program generates tables with the same row and column totals of the entered table in which rows and totals are independent. These tables are then compared with the original table, allowing detection of cells with significantly high or small values. For the simulated tables, χ^2 values were computed and compared with the value obtained for the entered table. If the χ^2 values obtained from random tables exceeded those from the data table less than 50 times out of 1000, it can be assumed that the original χ^2 is significant at $P<0·05$. This procedure has the advantage of being applicable to tables with low expected values, in which a conventional χ^2 test would not be adequate. The Adersim test follows a similar rationale for an array of expected frequencies instead of a contingency table.

To classify the individuals into social dominance classes the following procedure was used. For each group a contingency table of $n \times 2$, where the individuals (n), both males and females, are represented in columns and the number of victories and defeats of each individual appear in rows, was constructed and the Actus simulation procedure was applied. For that purpose a defeat was scored every time a fish engaged in an agonistic interaction withdrew, fled or adopted a submissive posture. In these cases a victory was scored for the opponent. If the χ^2 for this table was significant it was considered that the distribution of victories and defeats was not random among the group members. In such cases, individuals were classified into three social dominance classes according to the following criteria: dominants, if their number of victories was greater than would be expected by chance with a probability less than 0·05; subordinates, if their number of defeats was greater than expected by chance with a probability less than 0·05; intermediate rank, if their number of victories and defeats lay between the above mentioned limits (Almada & Oliveira, 1997). This procedure was made possible by the ability of the Actus test to assess the significance of the individual cells of the table. According to this procedure, 24 males were classified as dominants, 13 as of intermediate rank and 27 as subordinates (Table II).

TABLE I. Brief description of social behavioural patterns and colour patterns according to Baerends & Baerends van Roon (1950) and Neil (1964)

Behavioural pattern	Description
Agonistic interactions	
Butting	The fish swims rapidly towards the opponent and rams it in the head or in the flanks usually with open mouth.
Lateral display	With the opponents in a parallel or antiparallel position they erect fully the dorsal and anal fins and spread fully the caudal and pelvics; at its maximum intensity it can be combined with erecting the branchiostegal membrane.
Tail beating	While displaying laterally the fish beats the tail sideways.
Carouseling	The opponents circle each other in lateral display.
Frontal display	When the opponents approach each other frontally they erect the gill covers and the branchiostegal membrane. Usually the mouth is open.
Mouth fighting	Both opponents try to grip the jaws of the other one, and having seized each other firmly by the mouth, they push and pull with tail beats.
Submission posture	The fish hangs in the water column at an angle of 20° relative to the horizontal with the head upwards.
Pendeling	Two nestholder males in a head to head position rush at each other with the dorsal and anal fins closed against the body. Just before contact with the opponent the fish brakes to keep it from colliding with the other fish.
Courting	
Tilting	Body is held at an angle of about 30° with the horizontal with the unpaired fins against the body.
Leading	In a tilting posture the male swims in front of the female towards the nest.
Circling	When the female is close to the nest the male circles around the nest; when the female joins the male they start to circle the nest with the male behind.
Tailwagging	Inside the nest the male wags his caudal fin in front of the female.
Quivering	The male vibrates the body and presumably ejects sperm.
Coloration patterns	
Neutral	Body and fins silver dull.
Dark 1	Body begins to darken in the region above the pelvics.
Dark 2	Darkening of the body progresses with scattered darker areas on the belly and on the caudal fin; the sub-opercular region lightens.
Dark 3	Dark dotted body with black dorsal and caudal fins and white sub-opercular region.
Black	Body presents a velvet texture with lower jaw and opercle white; the tips of the dorsal, anal and caudal fins and the pelvics are bright red.

TABLE II. Classification of males from studies 1, 2 and 3 into social status classes according to the procedure described in the text

Study	Rank			Total
	Dominant	Intermediate	Subordinate	
1	8*	6	6	20
2	9	7	12	28
3	7	0	9	16
Total	24	13	27	64

*Two males classified here as dominants were the only males in their groups.

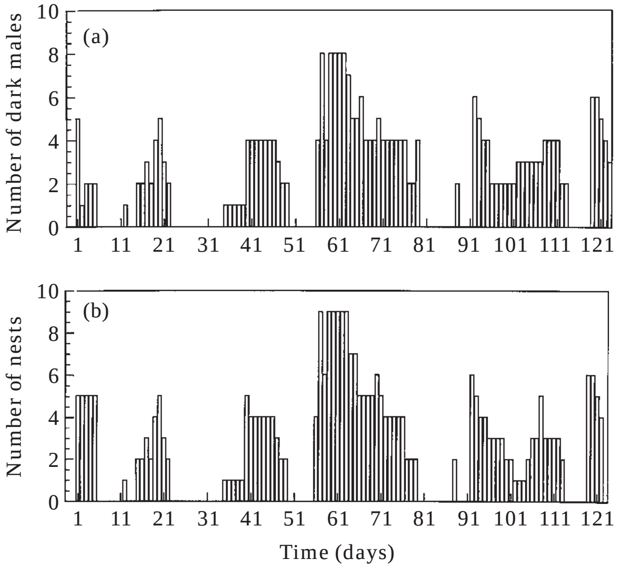

FIG. 1. Daily variation in the number of dark males (a) and nests (b) present in a community tank during 123 consecutive days.

RESULTS

SYNCHRONIZATION OF REPRODUCTIVE EPISODES IN MALES

The number of dark males was positively correlated with the number of nests present in the tank ($r=0{\cdot}94$, $n=123$, $P<0{\cdot}01$, Fig. 1). On some days there were more nests than black males, a fact that can be due either to the presence of males that defended temporarily more than one nest, or by unsuccessful attempts to establish territories by additional males. Figure 1 shows a trend for an alternation between periods when males dug nests and held territories [duration of 13·2 ± 8·5 days, $n=6$ (mean ± S.D.) with periods where no breeding activities were observed (8·8 ± 3·3 days, $n=6$) (median Runs test, nests: $R=16$, $n=8$, $m=8$, $P<0{\cdot}05$; dark males: $R=15$, $n=8$, $m=8$, $P<0{\cdot}05$). Since there was no change in the ambient conditions during the observation period, these results suggest strongly that the fishes synchronized their breeding activity.

MALE MATING TACTICS

Three different sets of sexual behaviour patterns were found in the males:

(a) territoriality, the males dug nests, assumed a dark coloration, defended a territory centred in the nest and courted females actively;

(b) semi-territoriality, the males lived in the water column, displayed a light dark coloration and occupied territories temporarily for a short period (seconds to minutes) when the owners were absent, to court females;

(c) sneaking, the males intruded into nests during a spawning episode and tried to remain near the female exhibiting quivering behaviour, a behaviour pattern usually related to sperm release. That these males were indeed trying to achieve fertilizations and were not eating eggs is indicated by the fact that, for 16 intruders, in only one case did the male try to steal eggs. Moreover, only males were observed to intrude during spawning, which would be unlikely if egg cannibalism was the purpose of such intrusions (Table III).

Only fishes that were dominant in the hierarchy established and defended territories. Indeed the proportion of time an individual was observed holding a territory varied with social status (data from study 2, dominant *v.* intermediate *v.* subordinate: Kruskal–Wallis, $H_{2,n=28}=9{\cdot}92$, $P<0{\cdot}01$). Dominant individuals defended territories for a significantly higher proportion of time than did subordinates (multiple comparisons Dunn test: $Q=2{\cdot}94$, $P<0{\cdot}01$), and intermediate rank individuals did not differ from dominants or subordinates (multiple comparisons Dunn test, intermediates *v.* subordinates: $Q=1{\cdot}26$, NS; intermediates *v.* dominants: $Q=1{\cdot}38$, NS; Fig. 2).

Semi-territoriality was especially common in males of intermediate rank that had often attempted to establish their own territories without success. Sneaking was performed predominantly by males of low rank (i.e. subordinates or non-territorial males, Table III). However, even territorial males were observed to leave their territories, intrude into the territories of their neighbours when spawning was occurring, and engage in sneaking attempts.

Although quantitative data on the success of the different tactics are lacking, a preliminary estimate can be made based on the following findings. During the study period 12 successful spawnings were observed. On nine (75%) of these occasions, sneaking attempts by one or more males at the same time were observed, comprising a total number of 16 intruders. Of these, one intruder was observed stealing eggs from the substratum and therefore its intrusion is not considered as a sneaking attempt. In eight of the successful spawnings, the rank of the territorial mating male was known. In seven cases it was a dominant male with an established territory. In only one case was the resident mating male of intermediate rank. These findings emphasize the importance of social status for the mating success of the males (data from studies 1, 2 and 3—Adersim test: $\chi^2=8{\cdot}95$, d.f.$=2$, $P<0{\cdot}05$; $n_1=24$ dominant males; $n_2=13$ intermediate rank males; $n_3=27$ subordinate males).

To evaluate the effectiveness of the sneaking attempts ($n=15$) they were classified into four categories, according to the level of proximity to the females achieved by the sneakers, as follows:

(a) the sneaker only entered the nest and approached the mating pair; this happened in three cases;

TABLE III. Interferences by other individuals during successful spawnings, with data on the social status of the intruders

Study (group)	Sex ratio (male : female)	Group characteristics			Spawning interferences (Yes/no)
		Number of dominant males	Number of intermediate rank males	Number of subordinate males	
1(D)	4 :2	1	1	2	Yes: subordinate male
2(C)	4 :2	2	1	1	Yes: subordinate male
2(H)	4 :2	1	1	2	No
2(H)	4 :2	1	1	2	Yes: subordinate male
3(B)	4 :2	1	0	3	Yes: two subordinate males*
3(B)	4 :2	1	0	3	No
3(B)	4 :2	1	0	3	Yes: two subordinate males
3(D)	4 :2	1	0	3	No
Stock aquarium I	9 : 5	—	—	—	Yes: one NT and one T male
Stock aquarium I	9 : 5	—	—	—	Yes: three NT and one T male
Stock aquarium I	9 : 5	—	—	—	Yes: NT male
Stock aquarium II	4 : 5	—	—	—	Yes: one T and one NT male

In groups for which the social status of the intruders was unknown, they were classified as territorials (T) if they presented a dark coloration and were defending a spawning pit in the substratum at that time, or as non-territorials (NT) if they presenterd a neutral coloration and were not defending a spawning pit at the bottom.

*One of the intruders tried to steal some eggs from the substratum.

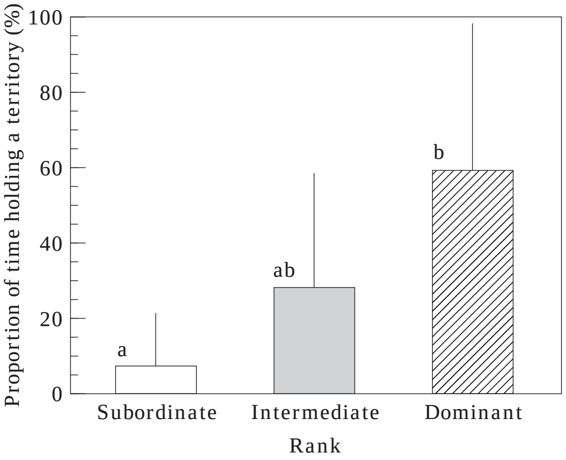

FIG. 2. Proportion of time spent holding a territory on the substratum by males of different social status (data from study 2). Different letters (a, b) note groups that present significant differences between them (error bars = S.D.; significance level = 5%).

(b) the sneaker managed to approach the female and remain parallel to her during a few seconds (four cases);
(c) the sneaker, standing by the female, exhibited quivering behaviour (seven cases);
(d) the sneaker exhibited quivering after which the female approached her mouth to the genital papillae of the sneaking male (one case).

If for sneaking to be successful the fourth level is required, then sneaking would have been effective in one case out of 15 (6·67%). On the other hand, if quivering and concomitantly releasing sperm into the water are sufficient to ensure fertilization of some eggs, then eight out of 15 attempts (53·3%) could have been successful. These data are not intended to serve as an estimate of the fertilization success of sneaking and only indicate the proportion of sneaking episodes in which the sneakers may have fertilized at least part of the clutch.

MALE–MALE COURTSHIP

Territorial males were observed to court other males, presenting the full courtship repertoire found in this species: tilting, signalling the nest, circling and quivering. The courted males never had the dark coloration, being usually in the neutral light coloration in which they school. These courted males performed the typical female sexual behaviour, including immobility when courted, following the courting male to the nest and assuming a pivot position in the nest while the other male circled them. In three cases out of 204 observed, the courted males were observed to put their mouth close to the genital papillae of the courting male and when it was quivering they performed chewing movements which are typical of females inhaling sperm to ensure the fertilization of the eggs inside the mouth.

In 3880 min of observation (i.e. studies 1, 2 and 3 combined), a total of 618 courtship episodes was observed of which 204 (33%) were directed to other males, and the remaining 414 (77%) towards females (Table IV). Male–male

TABLE IV. Courtship episodes for each group from studies 1, 2 and 3

Observation time (min)	Group	Sex ratio (male : female)	Courtship episodes: Towards males	Courtship episodes: Towards females	Courtship episodes: Total	Courtship episodes: % towards males	*P* value
Study 1							
360	A	2 : 4	0	0	0	—	—
360	B	4 : 2	12	68	80	15	<0·001
240	C	1 : 3	0	19	19	0	—
360	D	4 : 2	1	33	34	2·9	<0·001
360	E	3 : 3	1	11	12	8·3	0·037
300	F	2 : 3	38	46	84	45·3	<0·001
360	G	1 : 5	0	1	1	0	—
360	H	3 : 3	12	22	34	35·3	0·611
Study 2							
40	A	4 : 2	9	5	14	64·3	0·829
40	B	3 : 3	0	0	0	0	—
40	C	4 : 2	2	12	14	14·3	<0·001
40	D	3 : 3	8	35	43	18·6	0·008
40	E	4 : 2	31	3	34	91·8	<0·001
40	F	3 : 3	6	4	10	60	0·351
40	G	4 : 2	1	23	24	4·2	<0·001
40	H	4 : 2	0	18	18	0	<0·001
Study 3							
125	A1	4 : 0	19	—	19	100	—
125	B1	4 : 0	4	—	4	100	—
120	C1	4 : 0	54	—	54	100	—
120	D1	4 : 0	4	—	4	100	—
50	A2	4 : 2	1	27	28	3·6	<0·001
50	B2	4 : 2	1	36	37	2·8	<0·001
40	C2	4 : 2	0	27	27	0	<0·001
40	D2	4 : 2	0	24	24	0	<0·001

The difference between the number of courtships directed towards males and females in each group was assessed by computing a *P* value using the Adersim test, for each group. Groups with only one male or for which courtship episodes were not observed were not analysed.

courtship occurred in all but one of the groups in which the males could court both sexes and for which courtship episodes were observed. Thus, it is unlikely that male–male courtship was a peculiarity of a particular individual or group. Nevertheless, a large variation in the percentage of courted episodes directed to males was observed (range 2·8–91·8%, Table IV). In contrast to heterosexual spawning, the intermale pseudo-spawning acts ($n=3$) did not suffer intrusions from other males.

In order to assess the causes of courtship interruption, the courtship episodes for which these data were available, i.e. courtship episodes that had been recorded in focal observations (study 1), and for which detailed sequences of behavoiurs were known ($n=264$, 64 towards males, 200 towards females), were classified as:

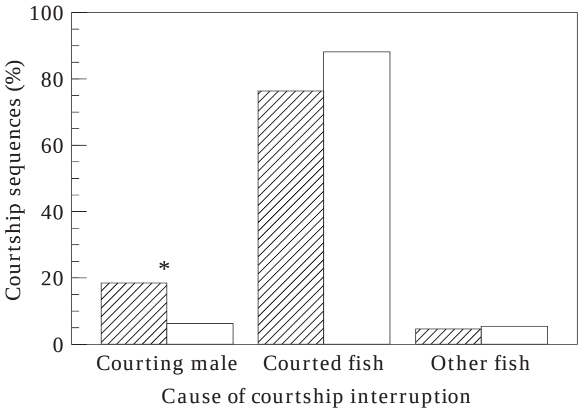

FIG. 3. Comparison of the number of courtships ended by the courting male, the courted individual or by the interference of a third individual. Classes which show a significant difference between observed and expected values are marked with an * (Adersim test, $P<0{\cdot}05$). ▨, Male–male courtships; □, male–female courtships.

(a) ended by the courting male, when he attacked the courted individual causing it to escape;
(b) ended by the courted male, by ignoring the courtship behaviour of the courting individual or by moving away from it;
(c) ended due to interference by a third individual.

In both courtship types (male-directed and female-directed) the majority of courtship episodes ended due to the lack of response from the courted individual (Fig. 3). However, there was a significantly higher number of cases in which courtship was interrupted by the courting male when the courted individual was male than when the courted individual was female, and the proportion of courtship episodes ended by the courted individual was significantly smaller in male–male courtships (Fig. 3).

To investigate to what extent males tended to direct courtship attempts preferentially to individuals of a given sex, expected values were computed according to the sex ratio of each group ($m-1$ males: n females). In most groups (12 of 16 analysed, Table IV) males courted females significantly more times than they did males, while only in one group were males courted preferentially (group E from study 2, Table IV). Moreover, when females were added to a group that previously contained only males (study 3), the number of courtship episodes directed towards other males decreased (Adersim test: $\chi^2=24{\cdot}7$, d.f.$=1$, $P<0{\cdot}001$, Fig. 4) despite an increase in the total number of courtship events (Adersim test: $\chi^2=107$, d.f.$=1$, $P<0{\cdot}001$, Fig. 4).

The social status (i.e. dominant *v.* intermediate *v.* subordinate rank) of the males seemed to be a very important factor determining the courtship directed towards other individuals and that received (Table V). Dominant males performed courtship behaviours towards both males and females and were not courted by other males, the reverse being true for subordinate individuals (Table V). Males of intermediate rank received courtship acts from other males and courted both females and males (Table V). The proportion of dominant males (100%) that courted other males and the proportion of subordinate males (50%)

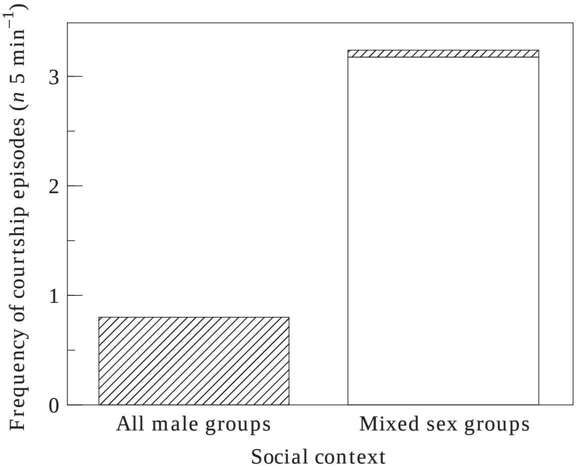

FIG. 4. Variation of the total number of courtships and courtships directed towards other males between the two phases of study 3. ▨, Male–male courtships; □, male–female courtships.

TABLE V. Proportion of males of different social status from study 1 that performed courtship towards males, females and that received courtship bouts from other males

Courtship episodes	Male social status			P value
	Dominant (n=6 males)	Intermediate rank (n=6 males)	Subordinate (n=6 males)	
Directed towards males	1·0*	0·333	0	<0·05
Directed towards females	1·0	0·833	0†	0·06
Received from other males	0	0·333	0·5*	0·21

Groups C and G were not included in this analysis as there was only one male in each of these groups. An Adersim test was computed for each courtship type and the P value is given.

*Significantly high values; †significantly low values (P<0·05).

that received courtship bouts from other males were both significantly high (Table V). On the other hand, the proportion of subordinate males that courted females (0%) was significantly low (Table V).

DISCUSSION

There are several lines of evidence which show that male territoriality in *O. mossambicus* is associated with an energetic cost that forces the males to leave the territories after some time (i.e. weeks) (Bowen, 1984; Turner, 1986; Oliveira, unpubl. obs.). This time constraint in territoriality may be relevant to the interpretation of several of the findings presented above. If a male has a limited amount of time to stay in a territory and if the females tend to synchronize their spawnings as is apparently the case (Burton & Boltt, 1975) the stage would be set for the evolution of any mechanism that would allow the males to adjust the timing of territory establishment to the periods of maximum availability of ripe females.

Thus, the synchronization of breeding males could have been a response to the presence of ovulated females in the tanks, which could release sex pheromones into the water. Ovulation in teleosts involves a peak of progestin levels and the mere by-products of steroid metabolism in the urine could be used by the males as a chemical signal, as described for several species (Dulka *et al.*, 1987; Stacey & Sorensen, 1991; Sorensen & Scott, 1994). Silverman (1978) showed that males of *O. mossambicus* with unlimited access to ripe females had higher levels of courtship activity than males with only visual access to females. Furthermore, Falter & Dolisy (1989) demonstrated in binary choice tests that the water of ovulated females not only was more attractive to the males but also stimulated courtship behaviour in the males to such a level that they engaged in courting their own image in a mirror.

Regardless of the causes of male breeding synchronization, it must have the net effect of increasing the competition among males, which must be already high due to the existence of male breeding aggregations. High levels of competition coupled with a limited amount of time available to stay in a territory would result in two consequences: (a) the existence of a substantial proportion of males that are unable to keep territories in the arena; (b) a high sexual motivation in territorial males that would imply a loss of sex discrimination. In this situation it may be advantageous for males without territories to stay in the nest aggregations behaving both as sneakers or, if their fighting ability is strong enough, as floaters ready to occupy vacant territories.

This scenario is likely to involve frequent disruption of spawning acts favouring females that divide their spawn into several clutches instead of risking it in a single attempt. In fact, during the present observations females were observed to spawn in quick succession in the nests of two different males (Oliveira, 1995), a phenomenon frequently suggested for lek breeding cichlids but never previously documented in this species. Moreover, the occurrence of multiple paternity in clutches of lek-breeding cichlids has been described for a number of species (Hulata *et al.*, 1981; Kellogg *et al.*, 1995).

It should be pointed out that the present results, although showing that the males of this species may engage in different breeding tactics, do not provide estimates of their relative success. Indeed, the dynamics of sperm competition inside the female's mouth is unknown. Moreover, the process is probably complicated by the fact that the sperm of mouth-brooding tilapiines is released in a colloidal matrix (Grier & Fishelson, 1995) that may render irrelevant considerations based on simple dilution and distance between the males and the eggs.

It can be argued that the present results are an effect of crowding under captive conditions and that the alternative mating tactics described may not be present in free living individuals. There are no studies on the behaviour of *O. mossambicus* in its natural environment. However, other lek-breeding cichlids for which there are available data on their breeding behaviour in the wild have been shown to exhibit multiple male mating tactics (*P. philander* Ribbink & Chan, 1989; Chan & Ribbink, 1990; *A. dewindti*, A. Rossiter, pers. comm.). Moreover, in artificial ponds in Puuhonua O Honaunau (Big Island, Hawaii) male breeding aggregations have been observed in which the number of dark males exceeded the number of nests present (R. Oliveira, pers. obs.). Thus, it seems quite likely that the male mating tactics described for captive groups are indeed present in natural populations.

The occurrence of inter-male courtship has been described for other teleosts (*Pungitius pungitius* L. 1758, Morris, 1952), and even for *O. mossambicus* (Baerends & Baerends von Roon, 1950; Neil, 1964; Pinheiro, 1980), although no attempts were made to discuss its possible functional significance. Such an attempt should consider two perspectives: that of the dominant courting male and that of the courted fish.

Relative to the courting male, it is suggested that courtship attempts directed towards other males may be a by-product of a very high level of sexual motivation which would make them non-discriminative. In the scenario of high level of male–male competition described above, it may pay for males in dense aggregations to attract any individuals that look like potential mates (i.e. in a neutral light colour pattern) postponing discrimination to a later stage of courtship when the courted individuals are already attracted to their nests. The fact that courtship attempts were never observed towards black individuals is in favour of this view and may indicate that this coloration pattern acts as an inhibitor of courtship.

The situation is more interesting when the perspective of the courted male is considered. Why do they co-operate in these courtship attempts? The first obvious possibility of female mimicry is to function as a tactic to approach spawning pairs, as described for other teleost species (Centrarchids: Dominey, 1981; Gross, 1982; Cyprinodontids: Kodric-Brown, 1986; Labrids: Taborsky *et al.*, 1987; Blenniids: Gonçalves *et al.*, 1996). This hypothesis is unlikely since in this species this behaviour was never observed when a pair (i.e. male and female) was spawning. In contrast, it could serve as a means of prolonging the presence of the courted males in the arenas, incurring a reduced level of attacks by resident males. In a dense aggregation, a floater or a sneaker that is expelled from one nest has a high probability of being driven through a succession of neighbouring nests. In such a situation, saving some time by acting like a female could stop or control chasing.

A less parsimonious possibility would involve indirect sperm competition in which the courted males would force the territorial males to spend sperm and energy with them, thus depleting their sperm reserves and shortening their permanence in the territories. Such an indirect sperm competition tactic would be possible only if the costs for the courted fish were smaller than those for the courting individual, which is likely to be true due to the more active role of the courting male in the courtship sequence. It would also be made easier if the number of wandering courted males is high. Another alternative explanation would be a benefit to the courted male that, by eating sperm from the courting male, would receive from the sperm exactly the nutrients required for its own sperm production. Further experimental work is needed to investigate which of these possible mechanisms are acting.

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