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Dynamics of social interactions during group formation in males of the cichlid fish *Oreochromis mossambicus*

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After a period of social isolation all-male groups of *O. mossambicus* were observed for 5 days after which ovulated females were added. The frequency of different types of social interactions and behavioural activities along the observation period were recorded, and their patterns of temporal variation were studied. The relationships among the different variables were analysed using PCA. During the process of group formation the following regular temporal sequence of predominant activities was detected: (a) mutual assessment and hierarchy formation; (b) territorial establishment and nest digging; (c) courtship. We suggest that these results reflect the probable sequence of events during the process of lek formation in nature at the onset of each breeding period.

Key words: Social behaviour, cichlids, behavioural systems, group-formation

Introduction

Oreochromis mossambicus (Peters,1852) (Teleostei: Cichlidae) is a maternal mouthbrooding cichlid in which the males form dense nest aggregations in sandy substrates (Bruton & Boltt, 1975; De Silva & Sirisena, 1988). The territorial males dig pits that are visited by ripe females, and where spawning takes place (Baerends &

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Baerends van Roon, 1950; Neil, 1964). The social behaviour of this species has received considerable attention. Not only the basic social behaviour patterns are well described (Seitz, 1949; Baerends & Baerends van Roon, 1950; Neil, 1964; N'Gokaka, 1984), but also the causal processes underlying different aspects of social behaviour and coloration patterns have been explored (Lanzing, 1974; Lanzing & Bower, 1974; Silverman, 1978a, 1978b; Wendelaar-Bonga et al., 1984; Billy & Liley, 1985; Turner, 1986; Turner & Huntingford, 1986; Smith & Haley, 1988; Robinson & Doyle, 1990; Turner, 1994; Oliveira et al., 1996).

In other arena breeding cichlids dominance relationships have been described and were shown to affect the ability of the fish to secure a territory and even the quality, in terms of attractiveness to females, of these territories (Fishelson, 1983; Chan, 1987; Mckaye et al., 1990; McKaye, 1991; Falter & Foucart,1991; Rossiter, personnal communication).

Most studies have focused on the behaviour of groups of fishes that were together for periods of weeks or months and there is a lack of information on the short-term processes that operate immediately after group formation.

These short-term processes may play an important role in the subsequent dynamics of group formation, because early assessments by each fish of the competitive abilities [i.e. resource holding power (RHP) *sensu* Parker 1974] of other group members may constrain the subsequent patterns of social interactions that occur in later stages, and ultimately the success of the fishes in establishing territories. In a previous study it was demonstrated that in *O. mossambicus* the dominance structure that emerges in the first day after group formation is a good predictor of the dominance structure measured on the subsequent days of the experiment (Oliveira et al.,1996). In a similar vein Nelissen (1986) showed that in another cichlid (*Melanochromis auratus*) the crucial events that determine the social status of the individual occur in the first hours after group formation.

In this paper we describe the temporal dynamics of social interactions, namely agonistic, sexual, and nesting activities of males, and their inter-relationships in the first days after group formation.

Methods

Subjects and maintenance

The individuals used in the present study were obtained from a captive stock of *O. mossambicus,* founded in the early seventies at Aquário Vasco da Gama (Lisbon) from fishes captured at Incomati River, Mozambique. The size of the fishes used in the present study ranged from 7.9 cm to 10.4 cm standard length for males, and 6.0 cm to 7.0 cm standard length for females. Fishes were kept at 24±2 °C on a 12D:12L light regime. They were fed daily with commercial fish food commonly used for tropical aquarium fish.

In the present experiment we have tried to assess the sequence of behavioural events that occur at the beginning of each breeding episode, namely the establishment of dominance hierarchies among males and the subsequent displaying behaviour of males towards females after the arrival of females. Outside breeding periods male *O. mossambicus* move around in schools. At the beginning of a breeding period males establish territories in clusters (arenas) to which females are attracted when ready to spawn. Contrary to intermittent lekkers, the males of this species practice continuous lekking (*sensu* Loiselle & Barlow, 1978), not leaving their territories for foraging during an entire breeding period. Neil (1964) found that in a laboratory population of *O. mossambicus* an individual male would keep its territory for on average one week. In our captive population male territoriality is synchronised, and the duration of each territorial bout ranges from 8 to 24 days (R. F. Oliveira, unpublished data).

Experimental procedure

Sixteen males were individually isolated in standard aquaria (46×36×40 cm) for eight days in order to minimise possible effects of prior social experience, which has been demonstrated to be a short-lived process in fishes, lasting for some hours (winner effect) to a few days (loser effect) (Chase et al., 1994).

At the end of the isolation period four groups of four individuals each were formed and placed in standard aquaria (93×36×40 cm). To avoid any residency effects, the four fishes of each group were placed simultaneously in the tanks. Care was taken to minimise the within-group variance of size (the standard length coefficients of variation for each group were as follows: CV1= 0.07; CV2= 0.04; CV3= 0.01; CV4=0.10). These all-male groups were maintained for 6 days (day zero to day five).

On the seventh day two ovulated females were introduced in each group. Ovulation was induced artificially by an intraperitoneal injection of 200μl saline containing 5μg des-Gly 10, [D-Ala &]-LHRH ethylamide (Sigma) 48 hours prior to their introduction in the all-male groups. The mixed sex groups were maintained for two days (day six and day seven).

Behavioural Observations

Daily behavioural observations were conducted between 11 am and 6 pm for each group. The fishes were individually recognised by a small clip in the dorsal fin membrane. Following Martin and Bateson (1993) two types of sampling procedures were used:

(a) Behaviour continuous sampling - During four periods of 5 min each, every social interaction that occurred in each group was recorded and its behavioural elements and the identity of the actor and the receiver of the acts were noted. The social interactions were identified based on the occurrence of the behaviour patterns described by Baerends and Baerends van Roon (1950) and Neil (1964). The following behavioural elements were considered:

Agonistic interactions - those that involved one or more of the following behavioural patterns: approach, charge, butting, biting, chasing, frontal and lateral display, circling, mouthfighting, pendelling, fleeing, submission posture. An agonistic interaction was considered terminated when one of the opponents moved away from the other and no further agonistic acts were observed in the next 3 sec or more. The agonistic interactions were classified as: Symmetrical (SIM), when a receiver of an agonistic act retaliated with another aggressive act (e.g. mouthfighting, circling, pendelling, mutual display); Asymmetrical interactions, when the actor of the aggressive act supplanted the receiver without retaliation, i.e. the receiver did not perform any aggressive act. These asymmetrical interactions were further classified according to the degree of overt aggression involved: high-intensity (AHI), involving attack-flee, chase-flee, bite-flee, display-flee; and low-intensity (ALI) involving approach-withdrawal only.

Sexual interactions - when one or more of the following acts were detected: tilting, jerking, leading, quivering, pit circling.

Colour patterns and Nests - At the beginning of each sampling period the colours of the fishes were recorded according to the patterns described by Neil (1964). We counted as black males those in the Dark 3 and Black patterns on the coloration scale proposed by Neil (1964). The number of nests present in each aquarium was also noted at the beginning of each observation.

(b) Focal instantaneous sampling - At intervals of 30 sec the behaviour of the focal individual was noted for a period of 5 min per fish. The following behavioural categories were considered: Swimming; Hovering (in the water column); Agonistic interaction (either giving or receiving an agonistic act); Sexual behaviour; Hovering in the Nest (when a territorial male hovers in its pit); Nest digging (when a territorial male actively mouth digs its pit); Others, which include other behavioural activities that occurred to seldom to be considered individually, that is, chafing, nipping at the surface, digging, feeding.

Data Analysis

In the present paper we considered the data for all the 16 fishes together. So the behavioural frequencies of a given category for all the fishes in each day were pooled. In order to uncover potential patterns of variation in the behavioural frequencies over the days, we have compared the observed data for each day against the expected frequencies that would result if the total number of observed frequencies was equally divided by the number of days. Thus our goal was to detect potential cases in which for a given day the frequencies were exceptionally higher or lower than the average. The comparison between observed and expected values was based on a χ^2 goodness-of-fit test using a simulation method. The rationale of this method was inspired by the Estabrook and Estabrook (1989) program ACTUS, developed to analyse contingency tables by simulation methods. In our case this rationale was modified to yield a goodness-of-fit test (Almada & Oliveira, 1997). One thousand simulations were run in a computer that generated n random numbers, n being equal to the total sum of the observed cases. These random numbers range from 0 to n-1, and according to their value are distributed by each of the classes of expected frequencies. The number of times out of 1000 that for a given class the observed count for that class was equal to or greater than the simulation count for that class was noted, the same being applied to the number of times in which the observation count for that class was equal to or lower than the simulation count. Using a significance level of 5%, cases in which the simulation count was lower than or equal to 50 out of 1000 were considered significantly lower than expected. The reverse was applied to find significantly higher than expected values (i.e. when 50 out of 1000 times the observed count was lower than or equal to the simulated count for that class).

The significance of the χ^2 value was tested by this procedure without any reference to the specific properties of the χ^2 distribution. For each simulation a χ^2 was computed for simulated vs. expected values, and the number of times out of 1000 that the χ^2 for the simulations was equal or exceeded the χ^2 obtained with the observation values was noted. If in 1000 simulations the χ^2 for the observed vs. expected values was equalled or exceeded less than 50 times it was considered significant. This computer program was developed by one of us (V. C. Almada) and is available upon request to interested colleagues.

In order to uncover basic inter-relationships among the temporal patterns of variation of the different behavioural categories a Principal Components Analysis (PCA) was performed based on a correlation matrix, followed by a normalised varimax rotation. The PCA computation was performed on the software package STATISTICA for Windows version 4.0 [copyright Statsoft Inc., 1993]. To determine the number of factors extracted we used the scree test (Cattell, 1966) together with the condition that we retained only factors with eigenvalues greater than 1 (Kaiser criterion, Kaiser 1960), that is when a factor extracts at least as much as the equivalent of one original variable (Comrey & Lee, 1992).

Results

Qualitative observations

The qualitative behavioural observations suggest that the dynamics of group formation can be summarised considering five phases.

Phase 1 - Immediately after being introduced into the tanks the fishes remain motionless in the water column often in the corners of the aquaria. No social interactions were detectable during this phase that could last from a few seconds (ca 20 sec) to a few minutes, varying among individuals.

Phase 2 - Some individuals began to darken (reaching Dark 3 in the coloration scale of Neil, 1964), and engaged in symmetrical fights involving mainly circle fights, mouth fighting, and mutual displays. Possibly because not all individuals entered this phase simultaneously, in three out of four tanks, a pair of fishes engaged in symmetrical agonistic interactions while the other two fishes remained motionless near the surface or in the corners of the aquarium. In one tank, interactions involving three fishes were observed. This phase started soon after the introduction of the fishes into the tanks (from a few seconds to a few minutes) and lasted for 1 to 2 hrs.

Phase 3 - The symmetrical agonistic interactions gradually decreased while asymmetrical high intensity interactions involving attack, chase and biting emerged. This phase started a few hours (ca 2-3 hrs) after group formation and extended for the first day of observation (day zero).

Phase 4 - The asymmetrical agonistic interactions decreased but remained at relatively high levels, the few symmetrical interactions observed changed in nature. Pendelling, a behavioural pattern typical of encounters between territorial males, was now the main element of these interactions. During this phase the males began to dig nests and defend territories centred on these nests, and despite the absence of females courtship behaviour occurred (being directed by territorial males towards subordinates). At this phase, territorial males often adopt the black coloration (in the scale of Neil, 1964). This phase extended from day one to day five.

Phase 5 - After the introduction of the females in the groups (days six and seven) a marked decrease of agonistic interactions was observed with a concomitant increase in courtship behaviour, that was mainly directed towards females.

Temporal patterns of variation in the behavioural frequencies

The temporal patterns of variation of the different behavioural categories recorded are shown in Fig. 1 and Fig. 2, and the variation in the number of nests and dark males during the observation period is presented in Fig. 3.

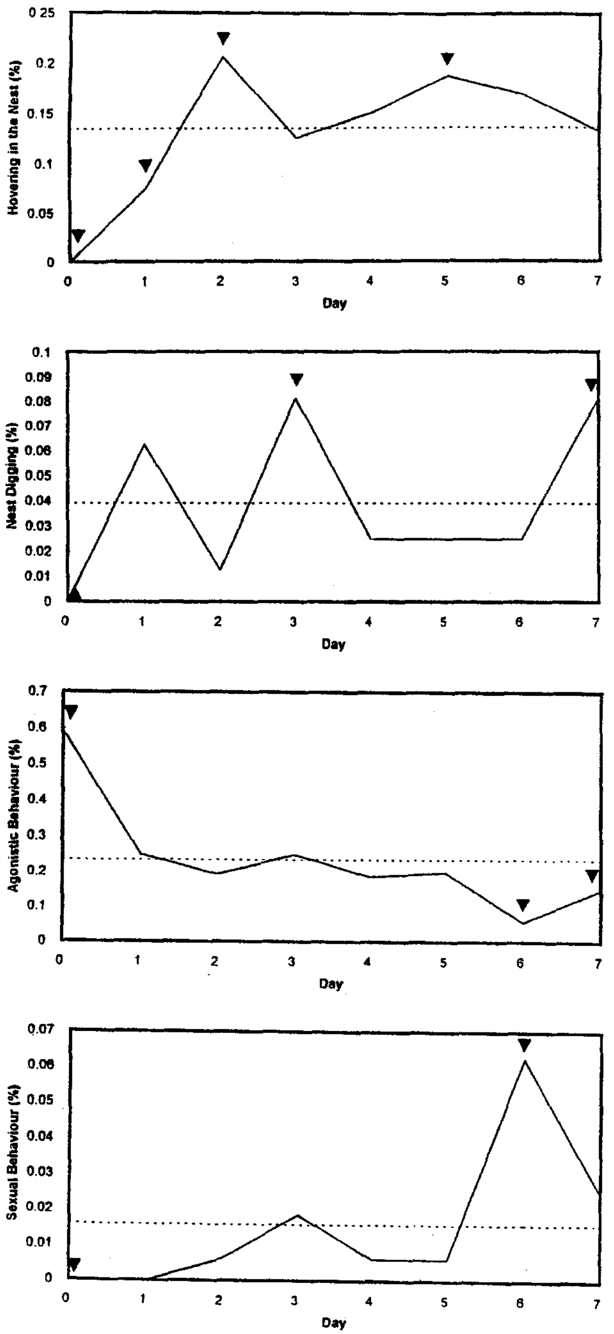

Figure 1. Temporal variation of the different behavioural activities during the eight days of the experiment: (a) Hovering in the Nest; (b) Nest Digging; (c) Agonistic Interactions; (d) Sexual Behaviour. The observed (continous line) and expected (dotted line) values are presented as percentages of time spent in the different activities. Significant lower or higher values ($p<0.05$) are marked with an arrow.

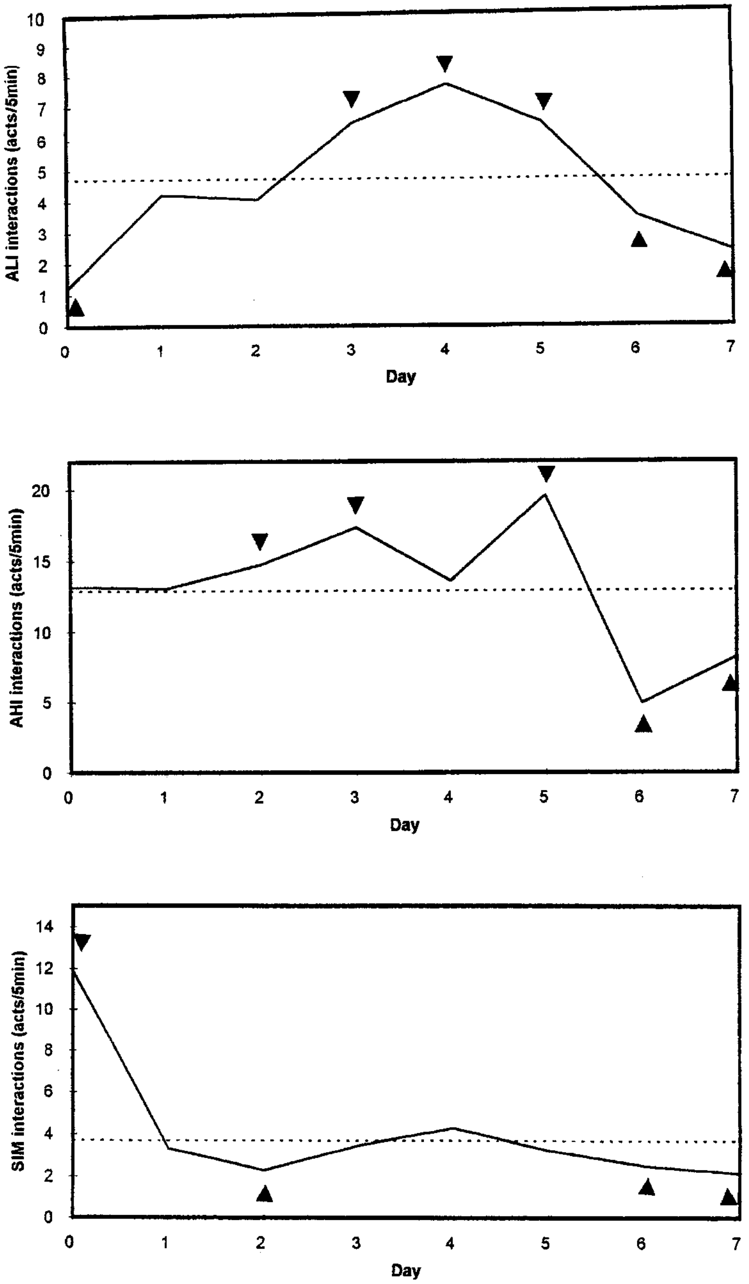

Figure 2. Temporal variation of the different types of agonistic interactions considered during the eight days of the experiment: (a) Asymmetric low intensity interactions; (b) Asymmetric high intensity interactions; (c) Symmetrical interactions. The observed (continue line) and expected (dotted line) values are presented as the mean number of acts per observation period (5/min). Significant lower or higher values ($p<0.05$) are marked with an arrow.

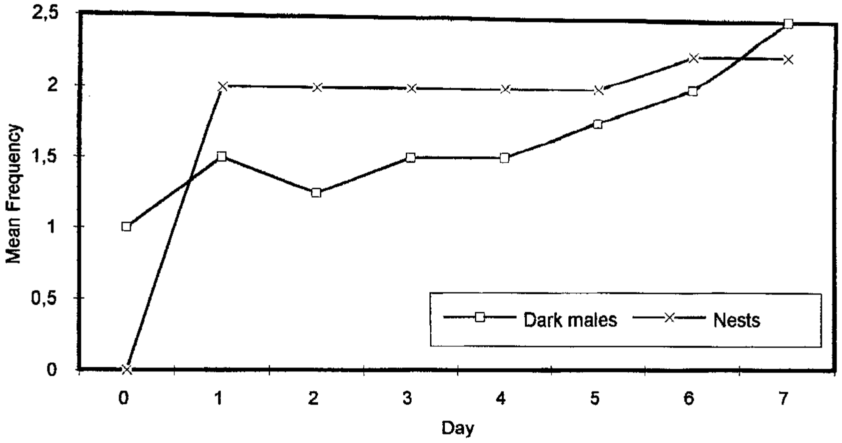

Figure 3. Mean number of dark males and nests per aquarium along the eight days of the experiment.

Inspection of Figures (1, 2 and 3) leads to the following conclusions:

(a) The proportion of time spent in agonistic interactions and the frequency of symmetrical interactions peaked at day zero, quickly decreasing to a baseline afterwards.

(b) Asymmetrical agonistic interactions reached significantly higher values at day two for high-intensity interactions (AHI) and at day three for low-intensity ones (ALI). It is interesting to note that ALI were significantly lower than expected at day zero.

(c) All three types of agonistic interactions and the proportion of time spent in agonistic behaviour by males, decreased significantly after the introduction of the females in the groups.

(d) Hovering in the nest and Nest digging appeared at day one (when both had significantly low values) and peaked respectively at days two and three.

(e) Sexual behaviour was already present before the introduction of the females in the groups, raising to a significant high value at day six, when the females were introduced.

(f) Males assumed the dark coloration from day zero onwards, while the nests appeared at day one and were consistently present during the observation period.

Relationships among social behaviours

In order to access the inter-relationships of the temporal patterns of variation of the behavioural activities studied, a PCA was performed on the correlation matrix among them (see Fig. 4 and Tables 1 and 2).

Table 1. PCA results: factors extracted with Eigenvalues and the percentage of variance explained.

Factor	Eigenvalues	% total Cumulative	Cumulative Eigenvalue	% Cumulative variance
1	2.49	27.66	2.49	27.66
2	2.16	23.99	4.65	51.65
3	1.70	18.93	6.35	70.57

Table 2. Factor loadings of the behavioural variables after a varimax normalized rotation.

Variable	Factor 1	Factor 2	Factor 3
Swimming	-0.654*	0.445	0.323
Hovering	-0.364	0.071	-0.814*
Nest digging	0.636*	0.205	0.081
Sexual behaviour	0.052	0.657*	0.381
Agonistic Interactions	0.144	-0.896*	0.291
Hovering in the Nest	0.791*	0.284	0.239
ALI interactions	0.140	0.090	-0.767*
AHI interactions	0.859*	-0.218	-0.050
SIM interactions	-0.292	-0.708*	0.355

Three factors were extracted that explain ca 70 % of the total variance. In Fig. 4 and Table 2 the factor loadings of each behavioural variable, after a varimax normalised rotation, are presented. We suggest that these 3 factors may be interpreted as representing 3 vectors in the temporal organisation of male social behaviour in this species. Using a cut-off value of 0.63, considered by Aspey and Blankenship (1977) as very good (variable and factor sharing approximately 40% of the variance in common), one can interpret these factors as follows.

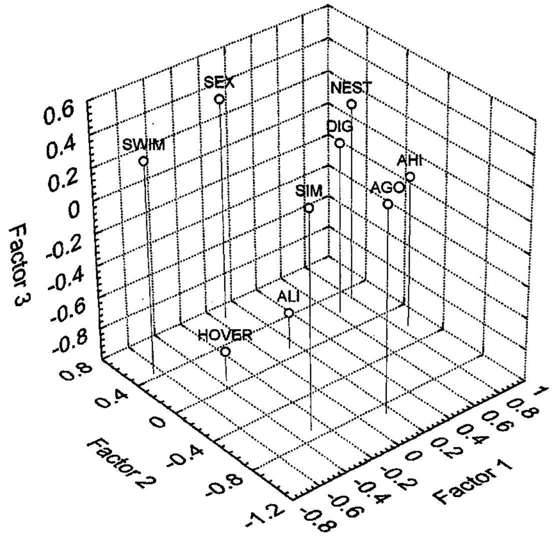

Figure 4. Associations among the different behavioural variables considered as expressed by their PCA factor loadings on the 3 factors extracted.

Four behavioural variables were associated with Factor 1: Hovering in the nest, Nest digging, and Attack, with positive loadings and Swimming with a negative value. We suggest that this factor expresses a territorial vector with activities related to territorial defence (Hovering in the nest and Attack) and nest building and maintenance (Nest digging). The finding that swimming is negatively related with these activities may simply reflect the fact that when a fish is territorial it is strongly site-attached and its locomotory activity is very restricted.

In Factor 2 we find the proportion of time spent in Agonistic interactions (AGO) and frequency of symmetrical agonistic interactions (SIM) with positive signs, and sexual behaviour with a negative sign. The association between AGO and SIM is not surprising, since symmetrical interactions are the only forms of agonistic behaviour that last for a detectable amount of time, thus comprising the bulk of time spent in agonistic interactions (AGO). Indeed, other aggressive activities such as attack or bite are so brief as to be better viewed as acts, that only rarely lasted sufficiently to be recorded. The negative association of Sexual behaviour (SEX) and symmetrical fights (SIM) is the more interesting feature of this factor and suggests that it expresses an incompatibility between courtship and competitive assessments of the males.

In association with Factor 3 we find Hovering and Approaching, both with negative signs. Since these fishes are gregarious except when defending territories or in the case of females, when defending broods, and non-breeding individuals tend to school, we suggest that this factor may express affiliative activities involved in social behaviour other than breeding, dominance and territoriality.

Discussion

From the present results a clear temporal pattern emerges concerning the order in which the different activities begin to appear and reach their peaks. At day zero symmetrical fights reached their peak and the first fish in black "breeding" coloration was detected. At day one the first signs of territoriality were observed: the first nest beginnings were present in the substrate and nest digging and hovering in the nest were observed for the first time. From day two to day five, the level of asymmetrical agonistic interactions (mainly attacks and chases) reached their peaks. These interactions were directed by territory holders towards intruders and thus appear to have a function in the active defence of the nest site.

This sequence of events during group formation makes sense if one considers the probable course of events in lek formation under natural conditions. It is known that in this species nest arenas are formed in habitats that differ from those where fishes usually feed (Bowen, 1984). Thus, the males must move to the breeding grounds at the onset of each breeding period. In such circumstances it is likely that agonistic activities that enable each male to assess the RHP of other males should be one of the first activities to be expressed, since it affects the quality and location of the territories to be established, and even which fish are able to get territories if breeding space is in short supply. Symmetrical agonistic interactions are likely to serve this assessment function.

The fact that black fishes are already present at day zero suggests that the possession of a nest is not a necessary causal factor of this colour pattern. In fact, our data showed that the number of dark fishes tend to be higher then the number of nests present.

The nest group of activities that became predominant during group formation represents behaviours involving territory maintenance (AHI and hovering in the nest) and pit digging. Only after this phase courtship (among males) was observed. This finding is again consistent with what was to be expected in lek formation in nature, since in this species courtship is centred on a nest (Baerends & Baerends van Roon, 1950). The occurrence of male-male courtship by fishes that are strongly motivated to breed is not an artefact of our experimental setting since it was documented in the literature (Baerends & Baerends van Roon, 1950; Neil, 1964; Pinheiro, 1980).

The introduction of females, at day six, was immediately followed by a sharp drop in agonistic interactions among the males and a concomitant increase in courtship behaviour. This finding must be interpreted with caution, since we had no adequate control for the possibility of a similar temporal pattern emerging in all-male groups. This point deserves further study since in other lek-breeding species the presence of females promotes an increase of agonistic interactions among lekking males, which is supposed to be important in the females choice of mates (see Wiley, 1991). If our results can be confirmed it indicates that such a mechanism of mate choice does not operate in *O. mossambicus.*

The results of PCA seem to confirm the interpretation of the sequence of predominant activities that was outlined above. Indeed, the first Factor grouped behaviours that correspond to territorial defence and nest digging, the same behaviours that peaked together in the second phase of the observation period.

The analysis also separated the asymmetrical interactions associated with territorial defence from the symmetrical fights involved in mutual assessments and hierarchy formation that was represented in Factor 2. Thus, the temporal difference in the peaks of these two types of agonistic interactions was reflected in the PCA results. The position of courtship in Factor 2, with an opposite sign relative to symmetrical fights, suggests an incompatibility between the two types of activities. The association between the decrease of agonistic interactions and the increase of courtship after day five points in the same direction.

The third Factor contains Approach and Hovering. We suggest that this factor may represent a natural distinct group of "gregarious behaviour" probably linked to the schooling activities of this species when not breeding.

PCA and Factor Analysis have often been used in ethological investigations as a means to uncover underlying mechanisms involved in the causation of behaviour (Wiepkema, 1961; Balthazart, 1973; Heiligenberg, 1973; Huntingford, 1976; Baerends, 1984). In such studies the raw data on which the analysis is based are typically transitions between behavioural patterns (e.g. Baerends, 1984). In the present study however, the basic data were frequencies of different types of interactions in a given group and not behavioural transitions at the level of the individual. Thus, our results are not directly comparable to the above mentioned studies. Despite this difference it is likely that many properties that emerge in the study of groups are the result of the mechanisms underlying the behaviour of the individuals that constitute that group, as pointed out by Hinde (1976) in a broader context.

Baerends (1984) in a study on the organisation of the pre-spawning behaviour in a substrate-brooding cichlid (*Aequidens portalegrensis*) found 3 causally distinct groups of behaviour: agonistic, transitory, and courtship which includes digging movements associated with nest building. In our study, digging was expressed in the territorial factor together with attack and hovering in the nest. Barlow (1974) also viewed pit building as an expression of territorial behaviour among cichlids including *O. mossambicus.*

Heiligenberg (1965) had already noted that digging could be interpreted as a form of re-directed aggression, a view that was also expressed by Baerends (1984) for A. portalegrensis. We suggest that the strong association of nest digging with territorial defence in *O. mossambicus* and its stronger association with courtship in *A. portalegrensis* may reflect evolutionary differences associated with the change from biparental substrate brooding to uniparental mouthbrooding. In substrate-brooders courtship is a complex and prolonged process involving the formation of a strong pair-bond and a gradual shift from agonistic to sexual behaviour (Baerends & Baerends van Roon, 1950; Barlow, 1970; Barlow & Green, 1970; Polder, 1971; Lamprecht, 1973; Baylis, 1974, 1976; Reyer, 1975; Baerends, 1984; Neil, 1984; Schwanck, 1987; Barlow, 1991). Several behavioural patterns involving the nest such as digging and substrate cleaning seem to play an important part during this process of pair formation (Baerends, 1984). In maternal-mouthbrooding cichlids courtship is much simpler and brief, without any pair bond formation, and the possession of a nest by the male is a pre-requisite for courtship and spawning in most cases (Baerends & Baerends van Roon, 1950; Fryer & Iles, 1972; Fishelson, 1983; Trewavas, 1983; Barlow, 1991). Thus, a strong association of digging with territorial defence and its decoupling from courtship is to be expected in cichlids with this type of breeding system.

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