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Dominance hierarchies and social structure in captive groups of the Mozambique tilapia *Oreochromis mossambicus* (Teleostei Cichlidae)

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Groups of *O. mossambicus* were formed 10 days after the end of mouthbrooding and were observed at the onset of sexual maturity by focal sampling. The agonistic interactions were recorded and used to construct sociometric matrices. The dominant hierarchies were found to be linear ($h = 0.94 \pm 0.06$) and semi-despotic (alpha individuals participated in more than half of the group interactions). Size and sex were important factors in determining the outcome of agonistic interactions. The alpha individuals were males and the largest members of their groups. Despite the fish being raised together for a long period, agonistic interactions involving high intensity aggression were common which indicates that at this stage frequent assessment of competitive ability is performed by the group members. Agonistic interactions are especially common among males and less frequent than expected among females and between males and females. Omega individuals participated in fewer agonistic encounters than expected. According to rank distance, hierarchical neighbours were involved in less interactions than expected except for symmetrical interactions that made up a low proportion of the total number of interactions. This finding is contrary to expectations, but maybe explained by the fact that aggression is initiated by dominants presumably to maintain their status against individuals that are clearly subordinates. It was found that a single dominance index (victories/victories + defeats) was a very good predictor ($r_s = 0.963$, $n = 45$) of the rank order positions of the individuals within their groups. It is argued that in species where agonistic interactions are not controlled by processes involving complex cognitive operations this index may be a biologically realistic indicator of aggressive motivation.

KEY WORDS: dominance hierarchies, social structure, linearity, rank distance, rank order, cichlids.

INTRODUCTION

In their classical study on the behaviour of cichlid fishes BAERENDS & BAERENDS VAN ROON (1950) distinguished three basic patterns of social relationships: territoriality, dominance hierarchies and schools. These authors pointed out that more than one of these patterns of relationships can occur simultaneously in a given group, the kinds of relationships among individuals varying with their sex, reproductive state and age among other factors. These can lead to considerable complexity in the network of relationships inside a group.

Moreover, territoriality and dominance hierarchies are not mutually exclusive phenomena. OBERSKI & WILSON (1991), based on a review of the avian literature, emphasised that "territories are just one extreme of a continuum of forms of site-related dominance" (i.e. spatial variation of the outcome of agonistic interactions between individuals of different social status).

In lekking cichlids the existence of dominance among territorial individuals in a given arena strongly affects the relative reproductive success of different males, with the dominant individuals occupying more central places in the arena that are preferred by females (McKAYE et al. 1990, McKAYE 1991, ROSSITER 1992).

Despite the biological implications of the dominance relationships in groups of cichlids, there are few studies on the social structures in groups of individuals (e.g. BARLOW & BALLIN 1976), and most work has focused on the dominance hierarchies of the Mbuna complex (NELISSEN 1985, NELISSEN & ANDRIES 1988, ANDRIES & NELISSEN 1990). Indeed, although dominance relationships and factors affecting them have been intensively investigated in several cichlid species, most studies are based on pair-wise encounters between individuals (e.g. FIGLER et al. 1975, BARLOW et al. 1986, WAZLAVEK & FIGLER 1989). Despite the relevance of these type of studies there is the need to integrate the phenomena of dominance in the wider context of social relationships of groups of individuals.

Oreochromis mossambicus (Peters 1852) is an African mouthbrooding cichlid in which the males aggregate in breeding arenas where they dig nests and defend small territories centred on the nests. The females move around in schools and visit the arenas when ready to spawn, after which they leave the arenas with the eggs in their mouths (BRUTON & BOLTT 1975). Thus parental care is restricted to females in this species.

The present paper is a study of the patterns of social interactions that occur in captive heterosexual groups of *O. mossambicus* at the onset of sexual maturity. It was decided to study groups of fish at this phase of their life cycle since it is a period during which the male territories begin to be established and the sexes begin to segregate. Thus the study of the interactions that take place at this phase may shed light on the processes that shape the social structures of the adults.

METHODS

Subjects and maintenance

The fishes used in this study belong to a stock kept and bred at our laboratory. Our stock was founded in 1991, with individuals kindly supplied by Aquário Vasco da Gama (Lisbon) whose origin was the Incomati River, Mozambique, in the early seventies.

We have observed 8 groups of 6 fish each, that were formed 10 days after the fry were released from the females mouth. These groups were followed during their development until the first signs of sexual maturity (i.e. darkening of the body and digging of the first nest) were detected, when the observations reported here were made. Three fish died (two from one group and one from another) before the observation period, which took place when the fishes were 9 to 10 months of age. Males ranged in size (standard length) from 4.3 to 7.18 cm and females from 4.62 to 6.94 cm. The sex ratio (males:females) of the groups was as follows: one group 1:5, one group 1:3, one group 2:4, one group 2:3, two groups 3:3, two groups 4:2.

Each group was kept in an aquarium of 50 × 30 × 25 cm^3 with a layer of sand on the bottom, at 24 ± 2 °C, and a photoperiod of 12L:12D. The fishes were fed commercial food flakes daily.

Behavioural observations

Each group was observed on 2 consecutive days between 2 and 6 p.m. On each day 6 focal observations (sensu ALTMANN 1974) of 5 min each were performed. Thus we have conducted a total of 12 focal observations per fish (summing 1 hr of observation per fish, and 6 hr per group).

The fishes were individually recognised by their relative size and by natural markings on their body.

At each observation the agonistic interactions, the identity of the participants and their outcome were recorded. The agonistic interactions were identified based on the occurrence of the behaviour patterns described by BAERENDS & BAERENDS VAN ROON (1950) and NEIL (1964).

At the end of the observation period the fishes of each group were sacrificed with a lethal dose of the anaesthetic quinaldine (Fluka Chemicals), dissected and sexed following direct inspection of the gonads. To sex immature fishes we used the aceto-carmine method proposed by GUERRERO & SHELTON (1974). This procedure was required since at this developmental stage sexual dimorphism is not fully expressed and the sexing of the individuals using only their external characteristics involves a certain degree of error (OLIVEIRA & ALMADA 1995). To assess the effects of size as a predictor of the social dominance the standard length of each fish was also taken.

Data analysis

Based on the outcome of the observed agonistic interactions sociometric matrices were constructed for each group. These matrices were reordered according to the procedure described by DE VRIES et al. (1993) that can be summarised as follows: (i) the dominant member of each pair of individuals was determined on the basis on the proportion of dyadic interactions that each individual won; (ii) for each dyad a score of 1 is attributed to the dominant fish and − 1 to the subordinate one. In the case of a tie or when no interactions occurred for a given dyad, both members were attributed a zero score; (iii) the scores for each individual were summed and the individuals were ordered according to their total scores; (iv) the relative order between two adjacent fishes in the matrix was reversed if the dominance relationship between them contradicted the order based on their total scores.

In order to characterise the social structure of each group the following variables were computed:

(a) Landau's linearity index (h), which expresses a deviation of the analysed structure from a linear hierarchy (LANDAU 1951), corrected for ties according to the procedure described by NELISSEN (1986); (b) number of circular triads (d), on which the statistical significance of the linearity found can be assessed from APPLEBY (1983); (c) g test of independence, which determines the degree of departure of the sociometric data from what could be expected if interactions were distributed randomly among individuals. Since the sociometric matrix contains structural zeros (the diagonal) the expected frequencies were computed using the procedure proposed by LEMON & CHATFIELD (1971), which is an approximation of the interactive method described by EVERITT (1992) for medium and large contingency tables; (d) *g* test of symmetry, to test if the overall pattern of dyadic interactions is asymmetrical or not (EVERITT 1992); (e) the overall success of each individual in the encounters in which it took part was assessed by computing the total number of victories over the total number of interactions (i.e. victories + defeats); (f) the proportion of interactions for each dyad that were initiated by the dominant and subordinate elements. A χ^2 goodness-of-fit test was used to test the deviation of these proportions from what could be expected if both dominant and subordinate members of a dyad had equal probabilities of initiating an agonistic interaction.

In the analysis of the social structure the agonistic interactions were classified as: (1) symmetrical, when a receiver of an agonistic act retaliated with another aggressive act (e.g. mouth fighting, circling, pendelling, mutual displays). The loser of these interactions was the first fish to disengage from the interaction, either by swimming away, fleeing or adopting a submissive posture; (2) asymmetrical interactions, when the actor of the agonistic interaction supplanted the receiver without retaliation, i.e. the receiver did not perform any aggressive act. These asymmetrical interactions were further sub-divided according to the degree of overt aggression involved: high-intensity, involving attack-flee, chase-flee, bite-flee, display-flee; and low-intensity involving approach-withdrawal only.

The effects of relative size and sex on the rank order of the individuals was assessed using a two-way ANOVA. Thus the fishes were classified in two categories according to sex (males vs females) and three relative size categories (large vs medium vs small). For each group the two larger individuals were classified as "large", the two smaller as "small", and the remaining two as "medium".

To analyse the network of interactions we investigated the effects of sex of the participants (male-male, female-female, male-female), their rank order (1, 2, ..., 6) and rank distance (sensu DE WAAL 1991; 1, 2, ..., 5) using the goodness-of-fit simulated statistical procedure as described below.

The expected frequencies for each class (*E*) , following a random model, were estimated as:

$$E_i = n\, d_i / D$$

where n = total number of observations (i.e. sum of the observed values for all the classes); d_i = number of possible dyads for the class i; D = total number of dyads of the group.

For example, for a group of six individuals with a sex-ratio of 3:3 (males:females) and with a total of 10 interactions observed, we would calculate the following expected frequencies for each class:

$$E_{\text{male-male}} = 10 \times 3 / 15 = 2$$

$$E_{\text{female-female}} = 10 \times 3 / 15 = 2$$

$$E_{\text{male-female}} = 10 \times 9 / 15 = 6$$

Based on the expected frequencies random numbers were generated assuming a uniform distribution ranging from zero to n–1 (i.e. sum of the observed values minus one). When a random number fell within the limits of each class of expected values this class was incremented by one. This procedure was repeated until n cases were ascribed to their respective classes. Thus simulating a sample of random values with probabilities proportional to each class of expected frequencies. For each simulation a goodness-of-fit chi-square was computed between simulated and expected frequencies. One thousand such simulations were run on a PC computer and the number of times out of 1000 that the simulated chi-square was equal or greater than the chi-square computed for the observed vs expected values was used to access the significance of the test.

The same program also assesses the significance of the deviation between observed and expected frequencies of each class by counting the number out of 1000 that the simulated value for that class did not exceed the observed count to test for significantly high values, and vice-versa to test for significantly low values.

The rationale for these types of simulation tests was first developed by ESTABROOK & ESTABROOK (1989) for the analysis of contingency tables. The computer program used in the present study was developed by one of us (V.C. Almada) and is in preparation for release to the interested colleagues.

RESULTS

Dominance hierarchies

In Table 1 we present a summary of the composition and sociometric data for the groups studied.

An analysis of Table 1 supports the following conclusions:

1. The pattern of interactions in heterosexual groups of *O. mossambicus* is non-random (in 7 out of 8 groups the *g* test of independence of the sociometric matrices is statistically significant). Thus, the outcome of interactions between the individuals is affected by the identity of the participants. This does not mean that the fishes are capable of recognising individually other group members, but merely that the differences among them are sufficient to affect the outcomes of the interactions.

2. The *g* test of symmetry performed on the reordered matrices is also significant for all the groups studied, indicating that the dyadic interactions follow consistent patterns in which one of the members tends to supplant the other.

3. The overall structure of the dominance hierarchies in the groups studied tended to be linear (6 out of 8 groups had a significant *d* and the average of Landau's index for the 8 groups was 0.94 ± 0.06). The dominant fish participated in the majority of the interactions of its group (0.57 ± 0.17), indicating a semi-despotic structure. The importance of the alpha fish as a factor affecting group structure was also suggested by a significant negative correlation between the number of interactions in which it participated and the number of asymmetric low intensity (ALI) interactions for each group ($r_s = -0.76$, $P = 0.044$, $n = 8$), together with a positive moderate correlation between the number of alpha interactions and the number of asymmetric high intensity (AHI) interactions for each group ($r_s = 0.667$, $P = 0.078$, $n = 8$). These findings raise the possibility that the aggressive behaviour of the alpha individual may affect its social status both by direct effects on the opponents and indirectly by its conspicuousness to other group members.

4. In the groups observed the dominance hierarchies were apparently maintained by frequent assessments of competitive ability among group members. This is supported by the high level of interactions for most groups, the finding that only one out of 106 possible dyads lacked agonistic interactions and by the fact that approximately 64% of the dyads exhibited bi-directional interactions (i.e. the subordinate member of the dyad also won some encounters). These findings are especially relevant as these groups were established for a long time before the observations were done.

5. Regarding the nature of the agonistic interactions involved, most of them were asymmetrical of high intensity (AHI), followed by asymmetrical of low-intensity (ALI) and by symmetrical (SIM) ones (Friedman ANOVA: $F = 19.24$, $P << 0.001$, $n = 8$).

6. In all the groups observed the great majority (0.88 ± 0.09) of the agonistic interactions were initiated by the more dominant individual of each dyad, and dif-

Table 1.

Sociometric characterisation and descriptive data of the groups studied.

	Group								
	1	2	3	4	5	6	7	8	X ± σ
n	6	6	4	6	6	5	6	6	—
Sex ratio (mm:ff)	2:4	4:2	1:3	4:2	3:3	2:3	1:5	3:3	20:25
CV_{SL}	0.139	0.084	0.113	0.087	0.146	0.133	0.149	0.092	0.12±0.03
h	0.914	1.0	1.0	1.0	0.843	0.950	0.914	0.886	0.94±0.06
d	0.75*	0*	0*	1.75	2.5	0.25*	1*	1*	6/8
g	67.9***	77.8***	18.4*	53.8***	8.7	70.5***	419.1***	91.7***	7/8
Symmetry (g)	914***	811***	1089***	1161***	31.5**	465***	450***	720***	8/8
Total of interactions	526	580	599	743	48	356	651	493	3996
Alfa interactions (%)	0.690	0.633	0.461	0.661	0.458	0.618	0.255	0.799	0.57±0.17
One-way dyads (%)	0.40	0.33	0.33	0.46	0.46	0.20	0.20	0.46	0.36±0.11
Blank dyads (%)	0	0	0	0	0.13	0	0	0	0.02±0.05
SIM (%)	0.032	0.057	0.045	0.092	0.166	0.084	0.072	0.085	0.08±0.04
AHI (%)	0.797	0.814	0.688	0.766	0.271	0.680	0.737	0.789	0.69±0.18
ALI (%)	0.171	0.129	0.267	0.143	0.563	0.236	0.191	0.126	0.23±0.14
IIDD (%)	0.958***	0.916***	0.955***	0.913***	0.708*	0.882***	0.780***	0.897***	0.88±0.09

n = number of individuals in the group; CV_{SL} = coefficient of variation of the standard length; h = Landau's index of linearity; d = number of circular triads; g = value of the *g* test of independence for the sociometric matrices of each group; symmetry g = value of the *g* test of symmetry for the sociometric matrices of each group; one-way dyads = percentage of dyads for each group on which only unidirectional interactions were observed; blank dyads = percentage of dyads for each group on which no interactions were observed; SIM = percentage of symmetrical interactions for each group; AHI = percentage of asymmetrical interactions of high intensity for each group; ALI = percentage of asymmetrical interactions of low intensity for each group; IIDD = percentage of interactions initiated by the dominant element of each dyad, with an * marking for significant χ^2 goodness-of-fit tests. The significance level of all statistical tests is indicated by asterisks: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. In the last column of the table the mean and the standard deviation are presented for all variables except for the sex-ratio and the total number of interactions, for which the sum for the eight groups is given, and in the case of statistical tests the proportion of groups on which the null hypothesis is rejected is given.

fered significantly from the frequencies expected if dominance did not affect the likelihood of the initiation of an encounter by each dyad member. Furthermore the proportion of interactions initiated by each fish (over the number of interactions in which it participated) was positively correlated with its social status as measured by the dominance index (V/V+D) ($r_s = 0.934$, $P < 0.001$, n = 45).

To assess the importance of sex and relative size as predictors of social dominance (i.e. rank order), we performed a two-way ANOVA whose results are presented in Table 2. Both sex and relative body size are good predictors of rank order, and in this respect, it is worth noting that all the alpha individuals were males and belonged to the "large" relative size class.

Lastly we investigated the relationship between the rank of each fish in its group and a commonly used index of social dominance (V/V+D; e.g. BARLOW & BALLIN 1976, WINBERG et al. 1991, GOMEZ-LAPLAZA & MORGAN 1993) (Fig. 1). There was a positive correlation between these two variables ($r_s = 0.963$, $P < 0.001$, $n = 45$). This finding is interesting because it suggests that the individual's overall success in agonistic interactions is a very reliable predictor of their position on the rank order of the group. Additionally inspection of Fig. 1 suggests that the dominance index of the fishes tend to fall in three levels: the alpha fish is well demarcated from intermediate ones (ranks 2 to 3.5), that in turn are separated from the lowest rank fishes (ranks 4 to 6).

Table 2.

Two-way ANOVA for the effects of sex and size in the rank order of the individuals.

Effects	SS	df	MS	F	*P*
Main effects	66.53	3	22.18	18.16	< 0.0001
Sex	12.32	1	12.32	10.09	0.0029
Size	28.30	2	14.15	11.59	0.0001
Interaction	5.15	2	2.58	2.11	0.1349
Residuals	47.63	39	1.22		

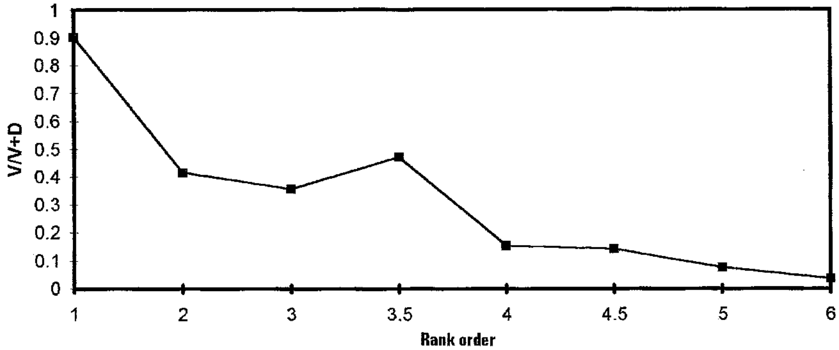

Fig. 1. — Average dominance index (V/V+D) for each position in the rank order. Individuals within a group that attained the same rank score by the procedure described by DE VRIES et al. (1993) (see Methods) were given an average rank position (e.g. 3.5). The *n* for each rank order position is: $n_1 = 8$, $n_2 = 7$, $n_3 = 8$, $n_{3.5} = 2$, $n_4 = 7$, $n_{4.5} = 2$, $n_5 = 5$ and $n_6 = 6$.

Agonistic interactions and social structure

In order to assess the extent to which the sex of the participants, rank order and rank distance affect the distribution of agonistic interactions inside the groups, we tested the observed frequencies of SIM, AHI and ALI against a random model. The results are presented in Tables 3, 4 and 5 respectively.

Based on data presented in these tables each cell for a given group was scored 1 if there were significantly more interactions observed than would be expected by chance and – 1 for the reverse situation. All non-significant differences between observed and expected values were allocated a score of zero. The scores for each class were summed over all the groups in which that class occurred, and subsequently divided by the number of groups yielding an index that can vary between – 1 (if all the groups showed significantly lower observed values than expected by chance for that class) and 1 (if all the groups showed higher observed values than expected by chance for that class). In Figs 2, 3 and 4 we present the data for the variables considered. In the analysis that follows only cases in which the index were equal to or larger than |0.5| (i.e. half or more than half of the groups showed a given trend) are considered.

It could be argued that the same data set was tested several times in the present analysis increasing the likelihood that some significant results were due to chance. We think however that this type of error was adequately controlled in the present analysis. Indeed, although the significance level used was 0.05, all, but five values, of χ^2 that were classified as significant had an associated probability of less than 0.01. Additionally the restriction of the interpretation to cases that were consistently significant in more than half of the groups further decreases this type of error, since the likelihood of chance effects being repeated in several groups is much smaller.

Sex of the participants

Inspection of Table 3 shows that in 7 out of 8 groups the interactions according to the sex of the participants were non-random. From Fig. 2 it can be seen that male-male interactions are clearly in excess of what could be expected by chance for the three types of interactions considered. For the sum of all types of interactions both inter-female and male-female encounters were less common than would be expected. Thus agonistic behaviours tended to be concentrated in male-male dyads.

Concerning female-female aggression the results indicate that both AHI and ALI interactions were less common than expected, a conclusion that does not apply to symmetrical interactions.

The more interesting feature of male-female interactions was the low number of symmetrical interactions in this class.

Rank order

From Table 4 we can conclude that the interactions according to the rank order of the individuals were non-random (6/8 of the groups for SIM, 7/8 of the groups for AHI and ALI, and all groups for the sum of the three types of interactions). Inspection of Fig. 3 shows that the alpha individuals participated in more

Table 3.

Goodness-of-fit simulation statistics for the effect of the sex of the participants on the network of social interactions. Significant results are marked with an *.

		Total				SIM				AHI				ALI			
Group	Rank dist.	O	E	*P*(O=E)	χ^2	O	E	*P*(O=E)	χ^2	O	E	*P*(O=E)	χ^2	O	E	*P*(O=E)	χ^2
1	MM	105	35.1	<0.001*	264.1*	6	1.1	0.012*	23.8*	87	27.9	<0.001*	155.5*	12	6	0.013*	15.2*
	FF	298	210.4	<0.001*		6	6.8	0.616		97	167.6	<0.001*		20	36	<0.001*	
	MF	123	280.5	<0.001*		5	9.1	0.048*		235	223.5	0.125		58	48	0.021*	
2	MM	428	232	<0.001*	279.4*	29	13.2	<0.001*	31.6*	348	188.8	<0.001*	226.5*	51	30	<0.001*	25.1*
	FF	6	38.7	<0.001*		0	2.2	0.119		5	31.5	<0.001*		1	5	0.038*	
	MF	146	309.3	<0.001*		4	17.6	<0.001*		119	251.7	<0.001*		23	40	<0.001*	
3	MM	—	—	—	467.2*	—	—	—	23.2*	—	—	—	361.6*	—	—	—	87*
	FF	564	299.5	<0.001*		1	13.5	<0.001*		13	206	<0.001*		21	80	<0.001*	
	MF	35	299.5	<0.001*		26	13.5	<0.001*		399	206	<0.001*		139	80	<0.001*	
4	MM	488	297.2	<0.001*	219.9*	45	27.2	<0.001*	21*	377	227.6	<0.001*	175.7*	66	42.4	<0.001*	23.8*
	FF	2	49.5	<0.001*		0	4.5	0.011*		1	37.9	<0.001*		1	7.1	0.004*	
	MF	253	396.3	<0.001*		23	36.3	0.001*		191	303.5	<0.001*		39	56.5	0.001*	
5	MM	15	9.6	0.061	3.8	4	1.6	0.109	5.3	6	2.6	0.057	5.6	5	5.4	0.415	0.59
	FF	8	9.6	0.3		2	1.6	0.634		2	2.6	0.394		4	5.4	0.455	
	MF	25	28.8	0.229		2	4.8	0.128		5	7.8	0.199		18	16.2	0.287	
6	MM	85	35.6	<0.001*	99*	14	3	<0.001*	47.1*	46	24.2	<0.001*	44.8*	25	8.4	<0.001*	43.2*
	FF	50	106.8	<0.001*		9	9	0.57		32	72.6	<0.001*		9	25.2	<0.001*	
	MF	221	213.6	0.2		7	18	<0.001*		164	145.2	0.005*		50	50.4	0.526	
7	MM	—	—	—	17.9*	—	—	—	20.6*	—	—	—	26.3*	—	—	—	22.2*
	FF	485	434	<0.001*		46	31.3	<0.001*		373	320	<0.001*		66	41.3	<0.001*	
	MF	166	217	<0.001*		1	15.7	<0.001*		107	160	<0.001*		58	82.7	<0.001*	
8	MM	197	98.6	<0.001*	137.5*	25	8.4	<0.001*	48.2*	144	77.8	<0.001*	96.8*	28	12.4	<0.001*	24.6*
	FF	41	98.6	<0.001*		11	8.4	0.167		22	77.8	<0.001*		8	12.4	0.122	
	MF	255	295.8	<0.001*		6	25.2	<0.001*		223	233.4	0.164		26	37.2	0.004*	

Table 4.

Goodness-of-fit simulation statistics for the effect of the rank order of the individuals on the network of social interactions. Significant results are marked with an *.

Group	Rank dist.	Total				SIM				AHI				ALI			
		O	E	P(O=E)	χ^2	O	E	P(O=E)	χ^2	O	E	P(O=E)	χ^2	O	E	P(O=E)	χ^2
1	1	363	175.3	<0.001*	291.8*	8	5.7	0.244	5.4	305	139.7	<0.001*	275.1*	50	30	0.001*	24.9*
	2	211	175.3	0.003*		7	55.7	0.402		168	139.7	0.006*		36	30	0.125	
	3	145	175.3	0.007*		9	5.7	0.15		104	139.7	<0.001*		32	30	0.378	
	4	100	175.3	<0.001*		2	5.7	0.049*		81	139.7	<0.001*		17	30	0.002*	
	5	92	175.3	<0.001*		4	5.7	0.466		69	139.7	<0.001*		19	30	0.011*	
	6	141	175.3	0.002*		4	5.7	0.398		111	139.7	0.004*		26	30	0.249	
2	1	367	193.3	<0.001*	306*	11	11	0.57	33.5*	308	157.3	<0.001*	265.8*	48	25	<0.001*	37.3*
	2	178	193.3	0.129		10	11	0.46		136	157.3	0.03*		32	25	0.069	
	3	226	193.3	0.006*		17	11	0.52		190	157.3	0.006*		19	25	0.118	
	4	231	193.3	<0.001*		24	11	<0.001*		181	157.3	0.022*		26	25	0.457	
	5	70	193.3	<0.001*		2	11	0.002*		57	157.3	<0.001*		11	25	0.001*	
	6	88	193.3	<0.001*		2	11	0.001*		72	157.3	<0.001*		14	25	0.007*	
3	1	564	299.5	<0.001*	340.6*	26	13.5	<0.001*	20.2*	399	206	<0.001*	261.5*	139	80	<0.001*	64.2*
	2	214	299.5	<0.001*		11	13.5	0.339		148	206	<0.001*		55	80	<0.001*	
	3	276	299.5	0.071		14	13.5	0.555		184	206	0.041*		78	80	0.401	
	4	144	299.5	<0.001*		3	13.5	0.002*		93	206	<0.001*		48	80	<0.001*	
4	1	500	247.7	<0.001*	374.3*	48	22.7	<0.001*	43.1*	378	189.7	<0.001*	286.8*	74	35.3	<0.001*	61.4*
	2	239	247.7	0.289		25	22.7	0.369		173	189.7	0.095		41	35.3	0.194	
	3	247	247.7	0.458		26	22.7	0.288		189	189.7	0.496		32	35.3	0.319	
	4	243	247.7	0.378		14	22.7	0.022*		205	189.7	0.133		24	35.3	0.026*	
	5	145	247.7	<0.001*		16	22.7	0.086		114	189.7	<0.001*		15	35.3	<0.001*	
	6	112	247.7	<0.001*		7	22.7	<0.001*		79	189.7	<0.001*		26	35.3	0.046*	
5	1	22	16	0.071	17.4*	5	2.7	0.161	7.3	7	4.3	0.22	8.7	10	9	0.403	6.7
	2	15	16	0.45		4	2.7	0.36		4	4.3	0.42		7	9	0.287	
	3	14	16	0.348		2	2.7	0.375		4	4.3	0.6		8	9	0.441	
	4	27	16	0.004*		5	2.7	0.173		8	4.3	0.035*		14	9	0.052	
	5	12	16	0.173		0	2.7	0.115		1	4.3	0.062		11	9	0.283	
	6	6	16	0.001*		0	2.7	0.127		2	4.3	0.205		4	9	0.038*	
6	1	227	142.4	<0.001*	98.5*	16	12	0.128	15.7*	153	96.8	<0.001*	66.9*	58	33.6	<0.001*	35.4*
	2	164	142.4	0.018*		19	12	0.029*		103	96.8	0.268		42	33.6	0.072	
	3	65	142.4	<0.001*		11	12	0.435		41	96.8	<0.001*		13	33.6	<0.001*	
	4	129	142.4	0.125		13	12	0.418		85	96.8	0.095		31	33.6	0.312	
	5	127	142.4	0.09		1	12	<0.001*		102	96.8	0.273		24	33.6	0.045*	
7	1	166	217	<0.001*	115.4*	1	15.7	<0.001*	71.8*	107	160	<0.001*	147.2*	58	41.3	0.008*	16.2*
	2	252	217	0.006*		4	15.7	<0.001*		214	160	<0.001*		34	41.3	0.089	
	3	243	217	0.025*		30	15.7	0.001*		170	160	0.211		43	41.3	0.359	
	4	228	217	0.215		37	15.7	<0.001*		153	160	0.297		38	41.3	0.344	
	5	307	217	<0.001*		5	15.7	<0.001*		252	160	<0.001*		50	41.3	0.075	
	6	106	217	<0.001*		17	15.7	0.44		64	160	<0.001*		25	41.3	0.003*	
8	1	394	164.3	<0.001*	401.9*	24	14	0.005*	19.6*	326	129.7	<0.001*	392.3*	44	20.7	<0.001*	35.4*
	2	98	164.3	<0.001*		19	14	0.11		63	129.7	<0.001*		16	20.7	0.148	
	3	102	164.3	<0.001*		14	14	0.546		77	129.7	<0.001*		11	20.7	0.006*	
	4	94	164.3	<0.001*		12	14	0.329		62	129.7	<0.001*		20	20.7	0.449	
	5	157	164.3	0.296		13	14	0.468		122	129.7	0.235		22	20.7	0.344	
	6	141	164.3	0.03*		2	14	<0.001*		128	129.7	0.455		11	20.7	0.013*	

Table 5.

Goodness-of-fit simulation statistics for the effect of the rank distance between the participants on the network of social interactions. Significant results are marked with an *.

		Total				SIM				AHI				ALI			
Group	Rank dist.	O	E	P(O=E)	χ^2	O	E	P(O=E)	χ^2	O	E	P(O=E)	χ^2	O	E	P(O=E)	χ^2
1	1	128	175.3	<0.001*	63.1*	4	5.7	0.215	6.8	93	139.7	<0.001*	66.8*	31	30	0.455	9.8*
	2	143	140.3	0.384		9	4.5	0.033*		116	111.7	0.333		18	24	0.091	
	3	87	105.2	0.022*		3	3.4	0.617		67	83.8	0.013*		17	18	0.474	
	4	97	70.1	<0.001*		1	2.3	0.401		85	55.9	<0.001*		11	12	0.447	
	5	71	35.1	<0.001*		0	1.1	0.383		58	27.9	<0.001*		13	6	0.003*	
2	1	173	193.3	0.023*	54.1*	22	11	<0.001*	19.3*	127	157.3	0.002*	59.8*	24	25	0.482	5.9
	2	199	154.7	<0.001*		5	8.8	0.076		176	125.9	<0.001*		18	20	0.379	
	3	150	116	<0.001*		6	6.6	0.446		123	94.4	0.001*		21	15	0.073	
	4	36	77.3	<0.001*		0	4.4	0.015*		31	62.9	<0.001*		5	10	0.055	
	5	22	38.7	0.002*		0	2.2	0.149		15	31.5	<0.001*		7	5	0.26	
3	1	214	299.5	<0.001*	49.9*	10	13.5	0.099	6.3*	147	206	<0.001*	34.2*	57	80	<0.001*	13.2*
	2	265	199.7	<0.001*		15	9	0.014*		181	137.3	<0.001*		69	53.3	0.007*	
	3	120	99.8	0.011*		2	4.5	0.202		84	68.7	0.015*		34	26.7	0.053	
4	1	216	247.7	0.006*	7.5	25	22.7	0.328	9.1*	160	189.7	0.011*	7.4	31	35.3	0.17	9.6
	2	211	198.1	0.14		20	18.1	0.336		165	151.7	0.111		26	28.3	0.367	
	3	149	148.6	0.491		9	13.6	0.099		119	113.8	0.292		21	21.2	0.535	
	4	108	99.1	0.18		14	9.1	0.053		81	75.9	0.28		13	14.1	0.472	
	5	59	49.5	0.065		0	4.5	0.015*		44	37.9	0.185		15	7.1	0.005*	
5	1	17	16	0.419	5.1	3	2.7	0.611	5.8	4	4.3	0.595	3.3	10	9	0.389	0.77
	2	10	12.8	0.209		1	2.1	0.351		3	3.5	0.609		6	7.2	0.271	
	3	15	9.6	0.071		4	1.6	0.134		5	2.6	0.169		6	5.4	0.38	
	4	4	6.4	0.28		0	1.1	0.351		0	1.7	0.119		4	3.6	0.605	
	5	2	3.2	0.396		0	0.5	1		1	0.9	0.65		1	1.8	0.634	
6	1	138	142.4	0.332	79.3*	25	12	<0.001*	23.6*	77	96.8	0.003*	85.4*	36	33.6	0.377	11.9*
	2	47	106.8	<0.001*		3	9	0.01*		32	72.6	<0.001*		12	25.2	0.002*	
	3	101	71.2	<0.001*		1	6	0.014*		77	48.4	<0.001*		23	16.8	0.082	
	4	70	35.6	<0.001*		1	3	0.187		56	24.2	<0.001*		13	8.4	0.059	
7	1	232	217	0.121	108.7*	24	15.7	0.017*	12.4*	173	160	0.122	119.9*	35	41.3	0.102	8.9
	2	107	173.6	<0.001*		14	12.5	0.425		62	128	<0.001*		31	33.1	0.377	
	3	217	130.2	<0.001*		8	9.4	0.465		176	96	<0.001*		33	24.8	0.045*	
	4	84	86.8	0.368		1	6.3	0.016*		61	64	0.36		22	16.5	0.085	
	5	11	43.4	<0.001*		0	3.1	0.041*		8	32	<0.001*		3	8.3	0.052	
8	1	104	164.3	<0.001*	304.6*	26	14	<0.001*	16.9*	56	129.7	<0.001*	353.5*	21	20.7	0.537	27.6*
	2	74	131.5	<0.001*		5	11.2	0.02*		64	103.7	<0.001*		5	16.5	<0.001*	
	3	72	98.6	0.001*		4	8.4	0.061		59	77.8	0.006*		9	12.4	0.209	
	4	132	65.7	<0.001*		6	5.6	0.583		106	51.9	<0.001*		20	8.3	<0.001*	
	5	111	32.9	<0.001*		1	2.8	0.213		104	25.9	<0.001*		7	4.1	0.098	

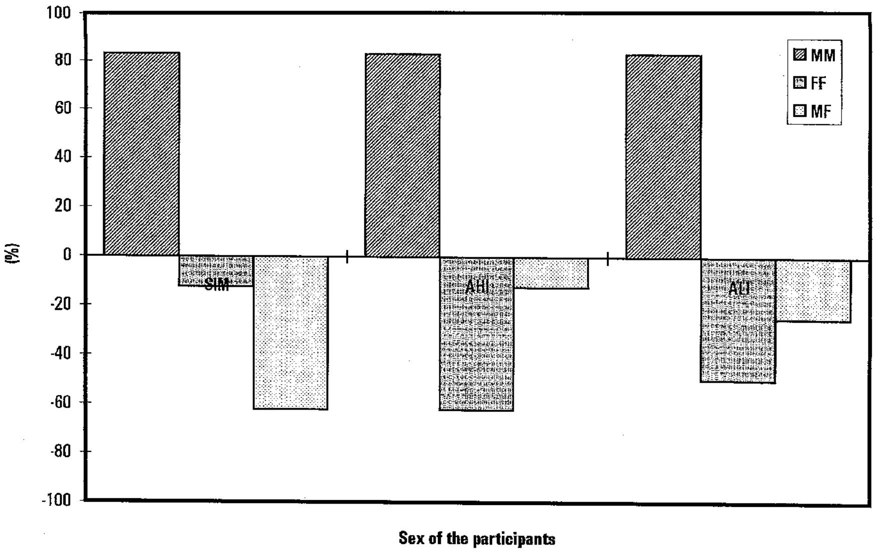

Fig. 2. — Proportion of groups in which the observed values for each class of interactions (MM = male-male; FF = female-female; MF = male-female) were significantly different, larger (+) or lower (–), from the expected ones.

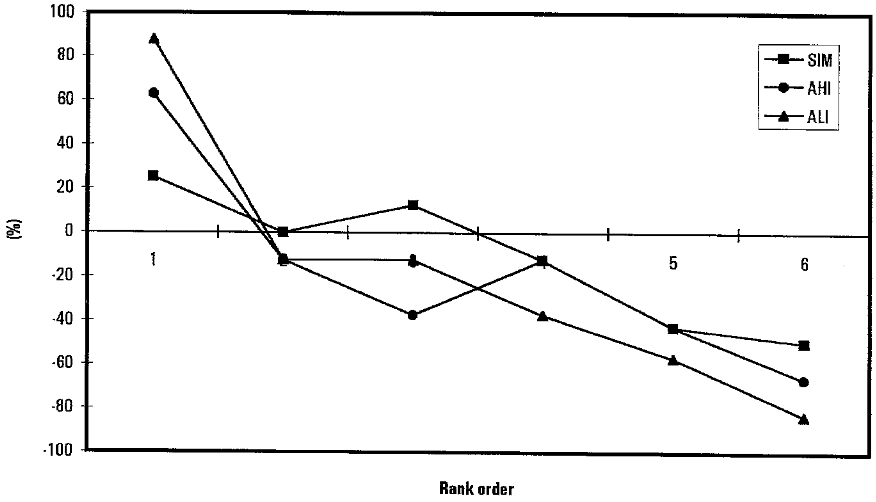

Fig. 3. — Proportion of groups in which the observed values for each position in the rank order (1, 2, ..., 6) were significantly different, larger (+) or lower (–), from the expected ones.

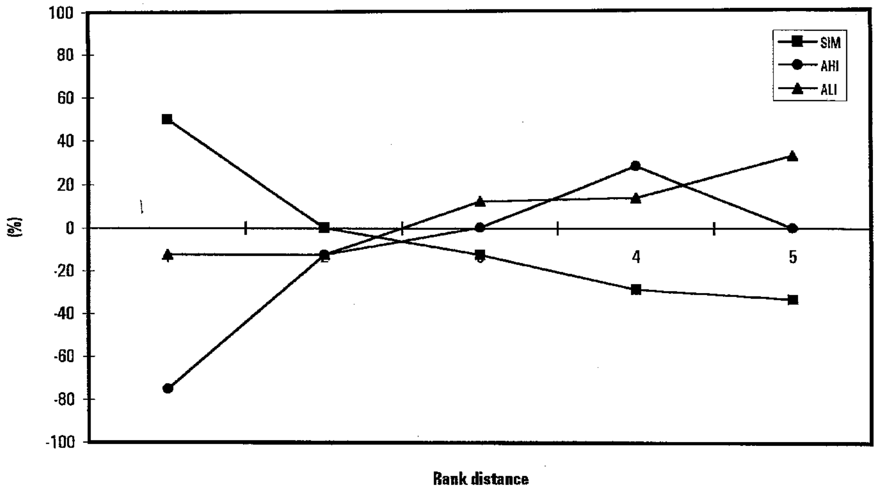

Fig. 4. — Proportion of groups in which the observed values for each rank distance class (1, 2, ..., 5) were significantly different, larger (+) or lower (–), from the expected ones.

asymmetrical interactions (both AHI and ALI) than would be expected. As already shown in the previous section these results indicate that the alpha individuals were involved in a disproportional high number of agonistic encounters.

Conversely the omega individual participated in less interactions (for all three types) than expected. For ALI interactions the second lowest individuals in the rank order also showed a low number of interactions. These results raise the possibility that low-ranking individuals may somehow avoid getting involved in agonistic interactions.

Rank distance

Data presented in Table 5 indicates that 6 out of 8 groups showed a non-random pattern of agonistic interactions according to the rank distance between the participants (for SIM, AHI and the total of all interactions) and 4 out of 8 for ALI interactions.

Inspection of Fig. 4 shows that rank order neighbours had lower than expected AHI interactions and higher than expected SIM interactions. This finding confirms the conclusion expressed in the preceding section that, in the groups studied, the dominance relationships were maintained through frequent assessments of the competitive abilities of the individuals.

DISCUSSION

There is no single measure capable of expressing the various facets of the social interactions in a group (Tomback et al. 1989 and references therein) and the neglect of this issue can lead to considerable misunderstanding (see Bernstein

1981, FRANCIS 1988 and DREWS 1993). One such example is the classification of hierarchies either as being linear, non-linear or despotic (e.g. WILSON 1975). The data presented in this paper provide evidence that captive groups of *O. mossambicus* tend to form linear hierarchies in which the alpha individual participates in a disproportionately high number of agonistic interactions, a result that agrees with findings in studies of other cichlids (NELISSEN 1985, ANDRIES & NELISSEN 1990). Thus, linearity is combined with some degree of despotism. Indeed, measures of dominance are basically aimed at ranking individuals and are not adequate to express the relative involvement of each individual in the total set of interactions that occur in a group.

While NELISSEN (1985) and ANDRIES & NELISSEN (1990) found that for Mbuna cichlids individuals that are closest in rank (i.e. rank distance = 1) "interact more frequently with each other than with other group members", the reverse was found in *O. mossambicus*. Hierarchical neighbours despite showing more symmetrical interactions than could be expected by chance, exhibited lower frequencies of high intensity asymmetrical interactions which comprise more than half of the total number of interactions. Thus, the lower than expected high intensity asymmetrical interactions indicates that fishes that are neighbours in rank also engage in less agonistic interactions in total than expected by chance. The high frequency of symmetrical interactions is easy to explain if one assumes that individuals that are neighbours in rank are those that are more similar in their competitive ability and are therefore more likely to retaliate when challenged. However, the finding that neighbours in rank engage in less agonistic interactions than expected is more difficult to explain.

FREEMAN et al. (1992) based on costs-benefits considerations suggested that red-deer stags are likely to fight less often with rank neighbours and with individuals that are far apart in the hierarchy, and to fight more often with stags two places apart in the hierarchy. They further suggested that data presented by APPLEBY (1983) fitted this scheme. In a subsequent paper APPLEBY (1993) not only critized the very limited sample used by FREEMAN et al. (1992) but also pointed out that it is unlikely that non-primate animals have detailed information on the precise ranks, both of their own and of other group members. As a more parsimonious hypothesis APPLEBY (1993) suggested that animals may perceive other members of its own group as being either dominant or subordinate towards it, and that in some species some variation may exist in this evaluation with the status of some individuals being perceived less clearly. In this context, if the costs of retaliation are high, individuals could avoid confrontation with other group members when their relations are unclear, especially, if the aggressive acts are initiated by dominant group members to maintain their status (APPLEBY 1993). This is the case in *O. mossambicus*. Indeed, the more dominant member of each dyad initiated significantly more of the dyads interactions than the more subordinate member. Although the present results are encouraging from this point of view, further investigation is needed to clarify this situation in *O. mossambicus* since acoustic signals, which were not controlled in our study, are known to occur during agonistic interactions (RODMAN 1965, LANZING 1974). Another possibility that needs to be investigated is that similar rank fishes may space themselves out minimising the likelihood of agonistic encounters.

Another interesting feature of *O. mossambicus* groups is that the omega individuals participated in less agonistic encounters than would be expected. This finding may be due to the fact that the lowest ranking individuals are females and females tend to be smaller and less aggressive than males in this species. It would be important to investigate whether females actively avoid the proximity of males thus reducing the likelihood of agonistic encounters, or, if some male traits are specially effective in eliciting aggression by other fishes (e.g. colouration and/or sounds, NEIL 1964, RODMAN 1965, LANZING 1974).

Alpha individuals were consistently both males and the largest members of their groups, a result which agrees with the available data for other cichlids (NELISSEN 1985, ANDRIES & NELISSEN 1990). It was also demonstrated that agonistic interactions were especially common among males. Since, in *O. mossambicus*, males tend to be larger than females of the same age (OLIVEIRA & ALMADA 1995) further work is needed to evaluate the specific contributions of size and sex to the pattern observed. Due to the mating system of *O. mossambicus* it is to be expected that one crucial function of aggression is related to the establishment and defence of breeding territories in the arenas. Thus, it is predicted that agonistic behaviour will be especially developed in males.

In any case the finding that the females tend to occupy lower ranks and interact less frequently than expected may be biologically relevant in this species. The fishes were observed soon after the onset of sexual maturity, when males tend to congregate and establish territories in areas from which females are excluded except when they are ready to spawn (BRUTON & BOLTT 1975). The pattern of interactions observed in these groups raises the hypothesis that agonistic interactions may play an important role in the sexual segregation observed in nature.

The dominance index (V/V+D) was shown to be a very good predictor of rank order. This measure has the practical advantage of being straightforward to calculate and not needing the construction of sociometric matrices for ranking individuals. Moreover it may be a biologically more realistic measure of relative competitive ability than rank orders for organisms in which social interactions are not determined by complex cognitive processes. Ranks are human abstractions, as has been noted by other authors (e.g. BERNSTEIN 1981, APPLEBY 1993), and, for many species it is to be expected that overall agonistic behaviour may be based on much simpler decision-making factors, for instance the balance of effects of prior victories and defeats and the subsequent adjusting of the level of aggressive motivation accordingly.

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