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A STUDY OF THE DOMINANCE HIERARCHY IN FOUR MBUNA-SPECIES : *MELANOCHROMIS JOHANNI, M. AURATUS, PSEUDOTROPHEUS « ORNATUS »* AND *P. LOMBARDOI* (TELEOSTEI : CICHLIDAE)

by

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SUMMARY

Social organization forms in fish groups have been very poorly studied. However, NELISSEN (1985) found that *Melanchromis auratus* (BOULENGER, 1897) establishes linear rank orders in aquarium tanks. This Mbuna cichlid (Lake Malawi) is closely related to all other species of the ten Mbuna genera (RIBBINK *et al.*, 1983) belonging to the very complex community (Mbuna is a community of a monophyletic species flock ; FRYER and ILES, 1972). After this study the question arose whether other Mbuna cichlids have the same kind of social organization. In order to find out about this a study of *M. johanni* (ECCLES, 1983), *Pseudotropheus « ornatus »* (not yet described) and *P. lombardoi* (BURGESS, 1979) was carried out. A few groups of *M. auratus* were also observed in order to make a comparison between the four species.

Individuals of the same species were kept in groups of 3 to 6 members. The colour patterns and their changes were described, the length of the individuals was measured and the agonistic acts (full display, chasing, circle fighting, mouth fighting, quivering, avoiding and fleeing) were recorded. These recordings of aggression and aggression inhibition were converted into interaction matrices for analysis.

All three species establish a linear rank order in aquaria similar to the dominance hierarchy formed in groups of *M. auratus* (see NELISSEN, 1985). In these rank orders interactions are ordered :

— the interactions depend upon the status of the animals in question.

— neighbouring animals in the hierarchy interact more frequently with each other then with other group members.

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In these linear rank order α is always the most active animal, while ω is the least aggressive animal. The ω-fish does not necessarily serve as an « aggression-sink ». The coloration of *P. « ornatus », M. johanni* and *M. auratus* are status dependent and the darkness of stripes in the colour patterns changes with the aggressive motivation of the animal in all four species. The length of the individuals seems to be an important status determining factor in groups of *P. « ornatus »* and *M. johanni*. For individuals of *P. lombardoi* it is apparently more important to be yellow than to be larger for becoming dominant.

Key-words : Mbuna-cichlids, aggression, aggression-inhibition, intraspecific dominance hierarchies.

INTRODUCTION

The dominance hierarchy is a social organization form which exists in many species. WILSON (1975, p. 583) defines dominance hierarchies as follows : « The physical domination of some members of a group by other members, in relatively orderly and long lasting patterns ». Social hierarchies can only exist when individuals live in groups. In fish this subject is poorly studied. Most investigators studied pairs of fish and the factors influencing those dominance relationships (BARLOW and BALLIN, 1976 ; BARLOW and WALLACH, 1976 ; FIGLER *et al.,* 1976 ; DE BOER and HEUTS, 1973 ; ZAYAN, 1974 ; FREY and MILLER, 1972 ; BAKKER and SEVENSTER, 1983 ; MCKAY, 1971 ; KUWAMARA, 1984 ; GORLICK, 1976 ; SCHWANK, 1979 ; ERCOLINI *et al.,* 1981 ; ERICKSON, 1967 ; MILLER, 1964). Besides these investigations, dominance is often considered in relation to territoriality (MYRBERG, 1972 ; ERICKSON, 1967). The study of rank orders in groups is in most cases restricted to flocks of birds or groups of mammals considering density effects, recognition, etc. (for example : BLACK and OWEN, 1987 ; SACHSER, 1986 ; KEIPER and SAMBRAUS, 1986 ; EWBANK and MEESE, 1974 ; CHASE and ROHWER, 1987 ; CUNNINGHAM *et al.,* 1987). The investigation of the hierarchy formation and the description of the behavioural processes resulted in models to describe the dynamics in rank orders, for example the « jigsaw puzzle » approach (CHASE, 1980, 1982, 1985).

Hierarchy structures can vary from linear (an α-animal dominates all group members, a β-animal dominates all group members except α, and so on until the ω-animal which is subordinate to all group members) at one extreme, to the other extreme where one group member dominates all other group members, that are equal in rank (despotism). It is found that many rank orders in rather small groups (usually with a low number of individuals) of animals are linear (CHASE, 1980).

The establishment of a rank order always involves agonistic acts. A stable dominance hierarchy (when individuals have not changed « rank place » for several days) offers some important advantages. In such a rank order agonistic acts will be replaced in most cases by agonistic signals. In this way agonistic communication prevents injuries, and time and energy loss will be minimized (more time to get access to resources). Such communication can consist of acoustic, tactile, chemical and visual signals (SCHWARZ, 1974 ; TODD, 1971 ; BARNETT, 1977). A hierarchy can only exist when each individual knows the dominance capacity of the other group members. Differences in capacities may be caused by genotype, age, sex, health, feeding, ... (GORLICK, 1976 ; HENDERSON and CHISZAR, 1977).

Mbuna-cichlids (Lake Malawi) form a monophyletic species-flock in which all species (ten genera ; RIBBINK *et al.*, 1983) are maternal mouth brooders (FRYER and ILES, 1972). The Mbuna live in a rocky shore habitat and feed on « Aufwuchs » (algae and micro-organisms). The flock can reach a density of seven animals or more per square meter (RIBBINK *et al.*, 1983). NELISSEN (1985, 1986) found that a representative of the Mbuna, *Melanochromis auratus* establishes a linear rank order in aquarium tanks (other experiments performed with this species : ANDRIES and NELISSEN, 1987 ; NELISSEN and ANDRIES, 1988). The questions are whether other Mbuna-species have the same kind of social organization and whether there are some kind of interspecific behavioural relationships or even interspecific rank orders. A first step in answering these questions is an intraspecific study of three Mbuna-species. Therefore we investigated groups of *M. johanni, Pseudotropheus « ornatus »* and *P. lombardoi* and compared them with *M. auratus*.

MATERIAL AND METHODS

All fish used in the experiments were imported directly from Lake Malawi and were half to full grown.

We performed observations in groups of *P. « ornatus », M. johanni* and *P. lombardoi*. Each group consisted of three to six conspecifics, picked out arbitrarily. Groups were kept together for at least five days (to obtain a stable hierarchy) before observation started. In each group each individual was identified with a random code number, independent of the later rank number. All fish could easily be recognized by the observer with the aid of the patch patterns on fins and flanks. Whenever a member of the group died or when mating occurred the observation was finished for this group (to reduce possible influences on the rank order during the observation).

All groups were placed in aquarium tanks of 1.200 l (1.5 × 1.0 × 0.8 m), 256 l (1.28 × 0.4 × 0.5 m) or 154 l (0.77 × 0.4 × 0.5 m). The temperature of the water was constantly kept at about 27 C°. The bottom of the tanks was covered with gravel or sand ; short plastic tubes and stones were placed to provide shelters. The animals were fed daily with dried flake food.

To investigate whether a linear dominance hierarchy was established we made behavioural records of the following agonistic acts (between brackets the record abbreviation is given) ; the aggressive acts : full display (A), chasing (V), circle fighting (C), quivering (T), mouth fighting (M) and the inhibition of aggression : avoiding (O) and fleeing (W).

The recordings were made with the aid of a tape recorder, for each individual separately during ten minutes. After the whole group had been observed in this way we obtained one behavioural record. For each group we made six records. All records for each group were stored and processed with the aid of a computer. The processing of the records had the following output :

Interaction matrices.

All data are recorded in interaction matrices (for example matrix 1). On top are the reactors (those individuals who receive the acts) and on the left side are the actors (those individuals who perform the acts). The group members are ranked according to their dominance status. On the right side and on the bottom the number of interactions performed and received are respectively given. The diagonal of each matrix contains zeros, as an animal does not interact with itself. The first value in each matrix cell is the observed number of acts (O). The second value is the expected number of acts (E) (for calculation of E : EVERITT, 1977), the frequency we would expect if the interactions are independent of the rank status. The third value is the relative deviation (RD), which indicates how the observed value differs from the expected value (RD = (O - E)/E). If RD is positive the individuals interact more with each other than expected, if it is negative they interact less than expected. Interaction matrices are obtained for all agonistic acts separately (A, V, C, T, M, O, W), for the aggressive acts taken together (AVCTM) and for the aggression inhibiting acts taken together (OW). Matrices for all acts taken together are also constructed, in which O and W are taken inversely (AVCTM(OW)). This means that aggression inhibiting acts will be considered as aggressive acts performed by the reactor (e.g. 1 W 3 becomes 3 (W) 1).

Likelihood Ratio Criterion.

In order to find whether the observed values differ significantly from the expected ones, the « Likelihood Ratio Criterion » (χ^2) is used (EVERITT, 1977, p. 79) :

$\chi^2 = 2 \Sigma O \times \log (O/E)$ $[r - 1][c - 1]$ degrees of freedom
r = number of rows, c = number of columns.

The calculated χ^2 will be compared with the tabled χ^2 for the same degrees of freedom.

Symmetry test.

A symmetry test with the following formula (EVERITT, 1977, p. 114) :

$\chi^2 = \Sigma (Oij - Oji)^2/(Oij + Oji)$ $\frac{1}{2}r(r - 1)$ degrees of freedom.

can indicate whether the values above the diagonal differ significantly from those under the diagonal. If all group members would behave in the same way, irrespective of the dominance position, the values above the diagonal would not differ significantly from those below the diagonal, in other words the matrix would be symmetrical.

The standard length of the individuals is measured and expressed in millimeters. To find out whether body length is correlated with dominance the « Kendall rank correlation coefficient » (τ) was calculated (SIEGEL, 1956). This coefficient (between -1 and 1) gives a measure of association between two sets of ranks : a rank according to length and a rank according to dominance status. The significance of τ is tested.

To get an insight into the action level patterns (total number of acts performed) of the groups, the total number of acts performed in six records is divided by the number of group members. This means that we calculated the mean number of acts/individual in a group. In this way we could make a comparison between groups even when they did not have the same number of group members. The differences between these mean numbers were tested for significance with a « One-Way Analyses of Variance » test.

Comparisons were made between groups of the same species (taking the number of group members in account) and between groups of different species and this for the following acts : full display (A), chasing (V), circle fighting (C), quivering (T), mouth fighting (M), avoiding (O), fleeing (W), AVCTM, OW and AVCTM(OW).

RESULTS

P. « ornatus ».

Colour patterns.

There are two major colour patterns in this species, which can be called dominant and subordinate respectively, as the pattern depends upon the rank status of the animal.

The dominant pattern is bright blue with six to eight dark blue vertical bars which become less clear near the tail of the body. On the head (between and above the eyes) two blue horizontal stripes are seen. All fins have black and light blue stripes and a light blue edge. The caudal fin always shows at least one egg spot.

The subordinate animals are light blue or grey and in most cases the dark bars on the flanks are barely visible. Beneath the upper lateral line, a dark coloured horizontal stripe can be seen. All fins are very lightly striped or transparent. Only the dorsal fin has a black edge.

The two patterns can shade off into one another rather rapidly (in a few minutes). Females as well as males (sexed by dissections) can show the dominant colour pattern. On the other hand some individuals (mostly those who have been subordinate for a long time) will always keep the subordinate pattern, regardless of their sex. Many individuals demonstrate an intermediate pattern.

Dominance hierarchy.

a) In all groups a linear dominance hierarchy was established. In this rank order a subordinate will never act aggressively towards a dominant fish when the hierarchy is stable. The dominant animal will always display the dominant colour pattern, while all others will show the subordinate patterns, regardless of the colour of the individuals before they were put together.

MATRIX 1

Example of a matrix of P. « ornatus » *for AVCTM(OW) in a group of 5 individuals (the highest RD-value of each row is underlined)*

	1	2	3	4	5	
1	0.00 0.00 0.00	56.00 42.36 0.32	61.00 58.79 0.04	55.00 63.97 −0.04	32.00 38.87 −0.18	204 204.02
2	1.00 2.26 −.56	0.00 0.00 0.00	38.00 31.91 0.19	31.00 34.72 −.011	20.00 21.10 −0.05	90 89.98
3	1.00 0.61 −.01	1.00 10.21 −0.19	0.00 0.00 0.00	29.00 15.42 0.88	5.00 9.37 −0.47	36 36.00
4	1.00 0.61 0.65	1.00 6.17 −0.84	1.00 8.56 −0.88	0.00 0.00 0.00	18.00 5.66 2.18	21 21.00
5	1.00 0.12 7.12	2.00 1.25 0.60	1.00 1.74 −0.42	1.00 1.89 −0.47	0.00 0.00 0.00	5 5.00
	4.00 4.00	60.00 59.99	101.00 101.00	116.00 116.00	75.00 75.00	356.00 356.00

note : — from top to bottom : the acting fish ranked according to their dominance position,
— from left to right : the reacting fish ranked according to their dominance position,
— first value in each matrix cell : observed frequency of acts,
— second value : the expected frequency of acts,
— third value : the relative deviation,
— at the bottom and right : column and row totals.

b) Table 1 deals with the correlation between body length and dominance ; the correlation coefficient τ and its significance (P) are given. This table shows that a lot of groups have a τ of 1 or very close to 1, in other words the length of the individual is strongly correlated with its dominance position. The low significance value of τ is due to the low numbers of group members. To find out if there is any relation between τ and the standard deviation of body length in the group (this standard deviation gives an idea of the existing length difference among the group members) the rank correlation coefficient between those two was calculated ; $\tau = 0.441$ with a significance of 0.008. This means that there is a great chance that the importance of « size » increases when length differences between group members become larger.

TABLE 1

Length in mm. of the individuals ranked according to dominance order, τ and its significance (P).

group	dominance hierarchy	τ	P
10	73 → 64 → 64 → 58	0.913	0.044
9	61 → 61 → 54 → 53	0.913	0.044
7	73 → 64 → 59 → 58 → 58	0.949	0.014
3	86 → 60 → 55 → 51 → 48	1	0.014
6	66 → 66 → 68 → 51 → 42	0.527	0.172
13	77 → 65 → 55	1	0.118
8	76 → 74 → 70 → 74 → 68	0.738	0.056
14	71 → 66 → 64	1	0.117
5	73 → 70 → 60 → 60 → 55 → 48	0.966	0.045
11	71 → 62 → 69 → 55	0.667	0.174
C	75 → 74 → 77	−0.333	0.606
F	87 → 81 → 83 → 79	0.667	0.174
B	68 → 69 → 68	0	1
A	78 → 73 → 63	1	0.117
E	76 → 75 → 66	1	0.117
12	77 → 70 → 61 → 57	1	0.041

c) Table 2 shows which animal performs most of the acts, who performs the least acts, who receives most of the acts and who receives the least of the acts. This was noted for each group and the number of times that an animal belonged to one of these four categories is given. For example in table 2, second column under P for A, α(11x) means that in 11 groups α was the most active animal.

It is clear that the α-animal is the most aggressive individual in the group. None of the other group members performs aggressive acts towards α and it is the most avoided animal. The ω-individual is the less aggressive member, the others do not avoid it. With the exception of α there is no distinction between the rest of the group members for receiving aggressive acts ; this means that the ω-individual, which is the lowest in rank does not always receive most of the aggression.

d) Table 3 gives information on the symmetry, the significance between the expected and observed value of acts and the relative deviation values in matrices of AVCT(OW). The table shows that in all groups the matrices are asymmetrical and that we usually find a significant difference between observed and expected values. In most groups (in 18 out of the 23 groups) we notice that the highest RD-values for each row lie next to the diagonal (in 18 groups RD-*d* is Yes). This

TABLE 2

Performing and receiving acts in 16 groups

acts	P	*p*	R	*r*
A	α (11x)	ω (16x)	ω (11x)	α (16x)
V	α (15x)	ω (16x)	ω (7x)	α (16x)
C	/	/	/	/
T	α (12x)	/	/	α (16x)
M	—	—	—	—
O	ω (8x)	α (16x)	α (14x)	ω (16x)
W	ω (4x)	α (16x)	α (12x)	ω (16x)
AVCTM(OW)	α (15x)	ω (16x)	ω (9x)	α (16x)

P = performs most of the acts
p = performs the least acts
R = receives most of the acts
r = receives the least acts
/ = no difference between the individuals
— = the act is not performed frequently enough

indicates that most interactions occur between neightbouring animals in the rank order. The RD-values of α with the other group members (in 20 groups RD-α is Yes) decreases with the rank order of the animal in question, in other words the highest RD-α-value is with β and the lowest RD-α-value is with ω. This means that α interacts the most with β, second most with γ, and so on.

e) In Fig. 1 the mean amount of acts/individual (for AVCTM(OW)) is shown for each group together with a 95 % confidence interval, which means that there is a 95 % chance that the real mean amount of AVCTM(OW)/individual lies within that interval. The plot for 95 % confidence intervals for the factor means of AVCTM(OW) (Fig. 1) demonstrates clearly that the action levels (total amount of acts/ind. in a group) of different groups with the same size can vary enormously. A one way of variance analyses test among the groups shows that there is a significant difference ($P < 0.001$) in number of acts/individuals. However if the mean intervals are plotted according to the number of group members (Fig. 2) we notice that there is a significant difference ($P < 0.001$) in number of acts/individual among groups of 3, 4, 5 and 6 members. There seems to be a tendency for an increase of the action level with an increasing number of group members. If the intervals for factor means for each act separately is plotted, the same type of plots (the proportions of the action levels between the four types of groups are the same) appear as in Fig. 2. Only for mouth fighting [$P = 0.696$], is there no significant difference between groups consisting of 3, 4, 5 or 6 individuals. This is probably due to the fact that the number of these acts is very low. Out of these data one can conclude that aggression in groups of *P. « ornatus »* increases with the number of group members and this is so for all considered acts.

TABLE 3

*Results of the Likelihood Ratio criterium (χ^2), the symmetry test and relative deviation position (RD-α and RD-d) in the AVCTM(OW)-matrices for the different groups (Y = yes, N = no, ex.2/3 = 2 out of the 3 RD are in the right position, namely next to the diagonal for RD-*d *or decreasing with the status of the reactor for RD-α)*

group	S-AS	χ^2	RD-α	RD-*d*	group	S-AS	χ^2	RD-α	RD-*d*
gr.Y	AS	Y	Y	N2/3	gr.10	AS	Y	N4/5	Y
gr.12	AS	Y	Y	Y	gr.15	AS	N	Y	Y
gr.2	AS	Y	Y	N3/4	gr.14	AS	Y	Y	Y
gr.B	AS	N	Y	Y	gr.1	AS	Y	N4/5	N3/5
gr.F	AS	Y	Y	Y	gr.8	AS	Y	Y	Y
gr.A	AS	Y	Y	Y	gr.3	AS	Y	Y	N3/4
gr.D	AS	N	Y	Y	gr.5	AS	Y	Y	Y
gr.E	AS	N	Y	Y	gr.7	AS	Y	Y	Y
gr.11	AS	Y	Y	Y	gr.13	AS	N	Y	Y
gr.C	AS	N	Y	Y	gr.6	AS	Y	Y	Y
gr.4	AS	Y	Y	N2/4	gr.16	AS	N	Y	Y
gr.9	AS	Y	N2/3	Y					

S-AS = symmetry or asymmetry

χ^2 = significant difference between O and E

RD-α = RD of α towards the other group member decreases with the rank order of the reactors

RD-*d* = the highest RD values of each row lie next to the diagonal

Remark : in all the experiments the α-β relationship is present, this means that in all groups α interacts the most with β.

Fig. 3 gives the proportion between the different kinds of acts performed in all the groups of *P. « ornatus »*. These acts are always the mean amount/individual performed in one behavioural record. This figure shows that avoiding (A), chasing (V) and fleeing (W) are the most frequent acts, whereas circle fighting (C) and quivering (T) are very rare. Mouth fighting (M) is almost never shown in this species. Chasing and fleeing show approximately the same frequency, because they are complementary to one another.

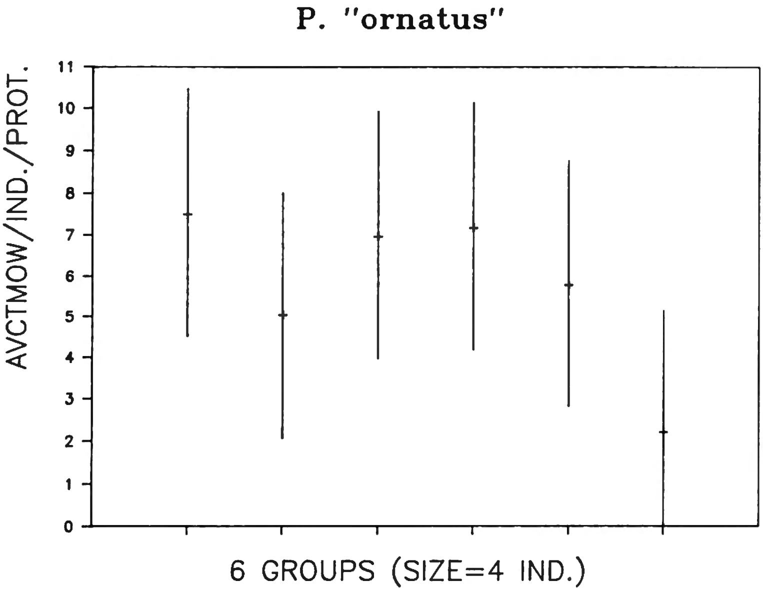

Fig. 1. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *P. « ornatus »*.

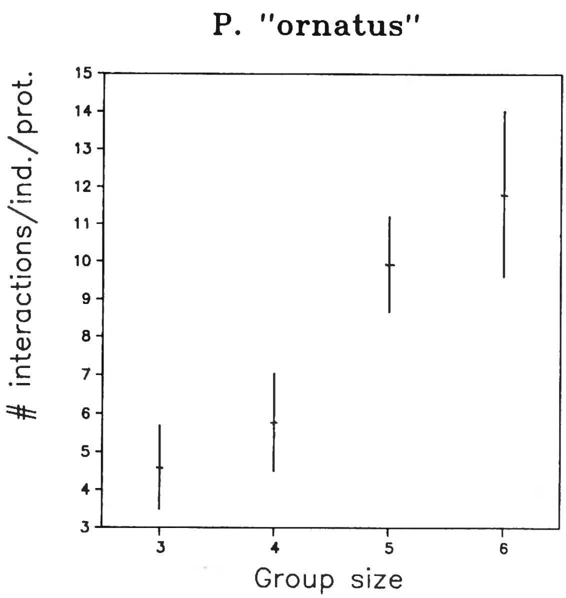

Fig. 2. — 95 % confidence intervals for the factor means for AVCTM(OW) of *P. « ornatus »* for groups of 3, 4, 5 and 6 group members.

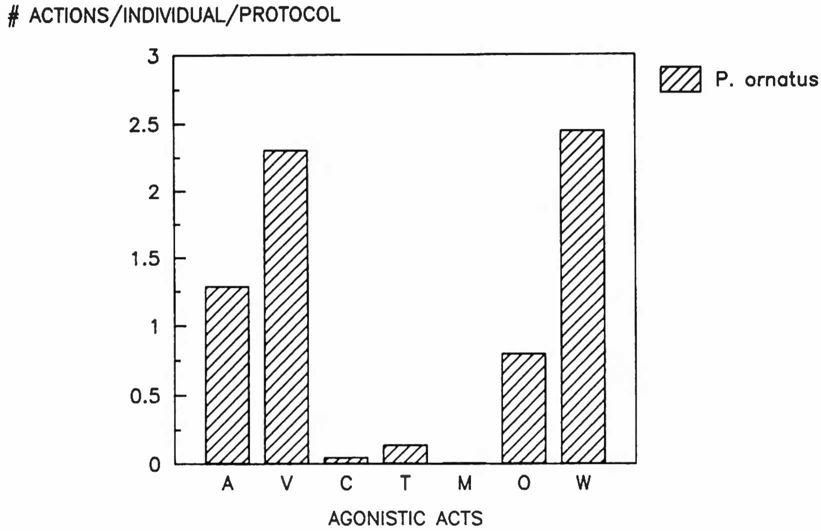

Fig. 3. — Mean amount of acts/individual in all groups of *P. « ornatus »* in one behavioural record (A = full display, V = chasing, C = circle fighting, T = quivering, M = mouthfighting, O = avoiding and W = fleeing).

P. lombardoi.

Colour patterns.

In nature *P. lombardoi* seems to live in small groups consisting of females, juveniles and non-territorial males (Ribbink, *et al.*, 1983). In this species we notice two colour patterns : « yellow » and « blue » individuals. The first ones are yellow or orange with brown vertical bars which disappear during aggressive motivation. The fins are « bluish » transparent.

The blue animals are bright blue with dark blue vertical bars that continue in the dorsal fin. The darkness of those bars depends upon the aggression motivation of the animal. With a strong aggressive motivation the bars will become very dark.

The « yellow » animals will always be dominant when a group is put together. When only « blue » fish are put together we notice that after a long period (several weeks) the dominant animal, which was blue at first, will become yellow. An intermediate colour pattern (sandy) is seen in this period. Many individuals show this « sandy-coloured » pattern. Dissections revealed that most of the yellow individuals are males and most blue fish are females. Nevertheless, there are also females with a sandy-coloured pattern and blue males.

Dominance hierarchy.

a) In all groups a linear dominance hierarchy was established. In most groups group members never experienced aggression from an individual lower in rank. In some groups we noticed a few exceptions to this rule. When a « yellow » individual was present in the group it always became α no matter how small it was regarding to the other individuals. A group with two « yellow » individuals was very difficult to keep because of the high aggression level of these two animals. If such a group came to a stable hierarchy the two individuals became α and β, the β-animal gained the intermediate colour pattern with brown vertical bars.

MATRIX 2

Example of a matrix of P. lombardoi *for AVCTM(OW) in a group of 5 individuals (the highest RD-value of each row is underlined)*

	1	3	2	4	5	
1	0.00 0.00 0.00	13.00 9.32 0.40	84.00 71.84 0.17	77.00 85.11 −0.10	87.00 94.74 −0.08	261 261.05
3	2.00 0.91 1.20	0.00 0.00 0.00	15.00 11.44 0.31	17.00 13.56 0.25	7.00 15.09 −0.54	41 41.00
2	1.00 2.61 −.62	1.00 4.26 −0.77	0.00 0.00 0.00	45.00 38.87 0.16	42.00 43.27 −0.03	89 88.93
4	1.00 1.32 −.24	1.00 2.16 −0.54	1.00 16.61 −0.94	0.00 0.00 0.00	39.00 21.91 0.78	42 42.01
5	1.00 0.17 5.03	1.00 0.27 2.69	2.00 2.09 −0.04	1.00 2.47 −0.60	0.00 0.00 0.00	5 5.00
	5.00 5.00	16.00 16.00	102.00 101.98	140.00 140.01	175.00 175.01	438.00 438.00

(for explanation see matrix 1).

b) Table 4 (deals with the correlation between dominance position and body length ; for explanation see Table 1) shows that in many groups τ is rather low and in some groups even negative. It seems that « being yellow » is more important than « being big » to become dominant. Small yellow animals often dominate large blue fish. This explains that the rank correlation coefficient between τ and the standard deviation (τ = 0.095, sign. = 0.587) is very low.

TABLE 4

Length in mm. of the individuals ranked according to dominance order, τ and its significance (P).

group	dominance hierarchy	τ	P
9	66 → 60 → 66 → 60	0.408	0.363
11	60 (y) → 55 (y) → 68 → 61	−0.333	0.497
5	71 (y) → 66 → 60 → 50	1	0.041
4	46 (y) → 57 → 54 → 51 → 49	0.200	0.624
6	64 (y) → 54 → 63 → 61 → 56 → 60	0.333	0.348
7	66 → 61 → 60 → 61	0.548	0.228
2	46 (y) → 49 → 48 → 45	0	1
1	57 (y) → 57 (y) → 57 → 54 → 51 → 54	0.701	0.027
3	57 (y) → 57 → 54 → 48 → 45	0.949	0.013
8	66 (y) → 72 (y) → 55 (y) → 68 → 60 → 51	0.467	0.188
10	72 (y) → 55 (y) → 68 → 60 → 61 → 51	0.467	0.188
13	72 (y) → 70 → 64	1	0.117
A	78 → 77 → 80 → 72	0.333	0.497
B	74 → 78 → 70	0.333	0.601
D	84 (y) → 81 → 82	0.333	0.601
12	58 (y) → 72 → 66	−0.333	0.601

y = a yellow animal.

c) Table 5 shows that in most groups the α-animal is the most aggressive animal, is avoided most frequently and receives no aggression. The ω-individual is the less aggressive group member and is never avoided or fled from. But ω is not always the one who receives most of the aggressive acts.

d) The symmetry, the highest RD-positions in the matrices and the results of the Likelihood Ratio Criterium tests for *P. lombardoi* are shown in table 6 (for more explanation see Table 3). The matrices for all the acts together are always asymmetrical and the Likelihood Ratio Criterium shows us that in most groups there is a significant difference between the expected and observed value. In most matrices the RD-diagonal (all highest RD-values of each row lie next to the diagonal) is complete or almost complete (only one value is missing for a total RD-diagonal) and the interactions of α with other group members is in almost all cases status dependent.

TABLE 5

Performing and receiving acts in 16 groups
(for legend table 2)

acts	P	*p*	R	*r*
A	α (14x)	ω (16x)	ω (11x)	α (16x)
V	α (16x)	ω (16x)	ω (10x)	α (16x)
C	/	/	/	/
T	α (9x)	/	/	
M	/	/	/	/
O	ω (12x)	α (16x)	α (13x)	ω (16x)
W	ω (10x)	α (16x)	α (16x)	ω (16x)
AVCTM(OW)	α (16x)	ω (16x)	ω (11x)	α (16x)

TABLE 6

Results of the Likelihood Ratio criterium (χ^2),
Symmetry test and position of the Relative Deviation
in the AVCTM(OW)-matrices of the groups

group	S-AS	χ^2	RD-α	RD-*d*	group	S-AS	χ^2	RD-α	RD-*d*
gr.13	AS	Y	Y	Y	gr.D	AS	N	Y	Y
gr.12	AS	N	Y	Y	gr.C	AS	Y	Y	Y
gr.A	AS	N	Y	N2/3	gr.E	AS	N	Y	Y
gr.11	AS	Y	Y	Y	gr.B	AS	N	Y	Y
gr.9	AS	Y	Y	N2/3	gr.14	AS	N	Y	Y
gr.1	AS	Y	Y	N2/5	gr.10	AS	Y	N4/5	N4/5
gr.3	AS	Y	Y	Y	gr.8	AS	Y	Y	N4/5
gr.4	AS	Y	N	N1/4	gr.6	AS	Y	Y	N2/5
gr.2	AS	Y	N2/3	Y	gr.7	AS	Y	Y	N2/3
gr.5	AS	Y	Y	N2/3	gr.15	AS	N	Y	Y
gr.16	AS	N	Y	Y					

e) Fig. 4 shows that the variation in the total number of aggression among groups of the same size is large ($P < 0.001$). A plot of the 95 % confidence levels of the intervals for factor means (Fig. 5) also shows that the level of aggression

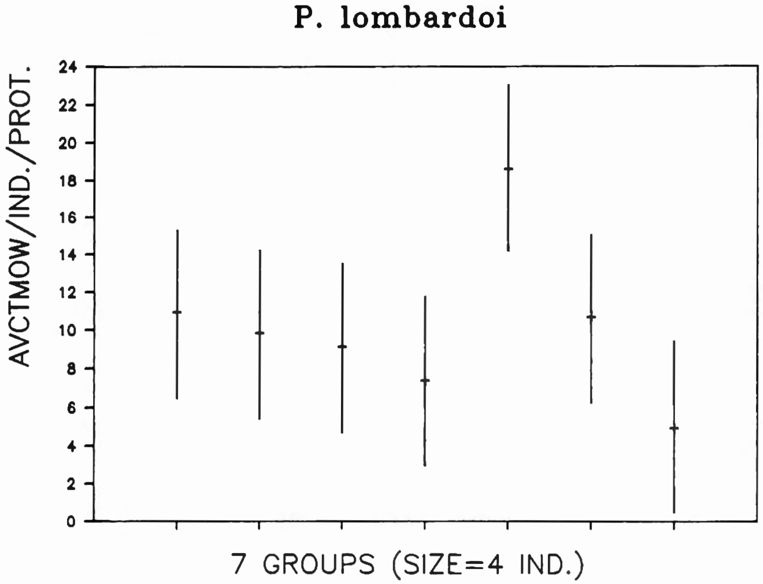

Fig. 4. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *P. lombardoi*.

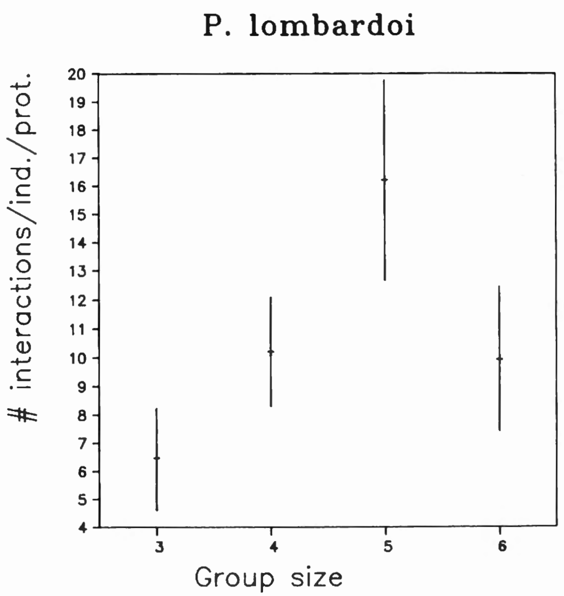

Fig. 5. — 95 % confidence intervals for the factor means for AVCTM(OW) of *P. lombardoi* for groups of 3, 4, 5 and 6 group members.

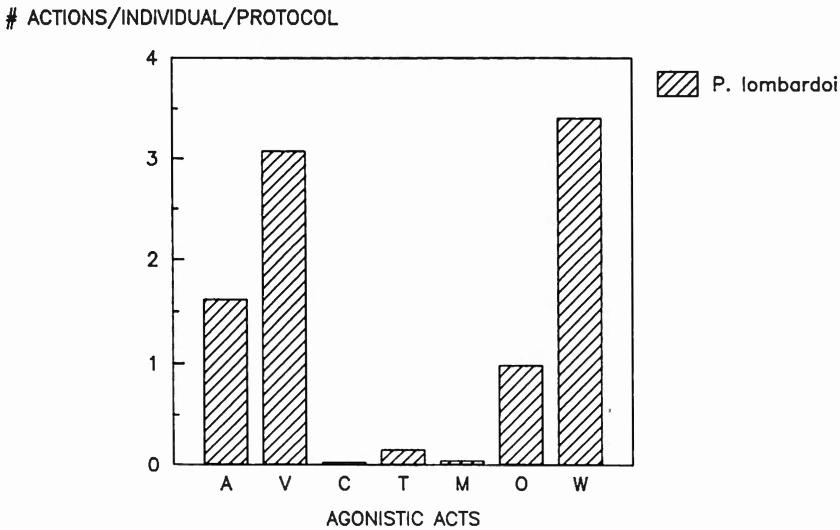

Fig. 6. — Mean amount of acts/inidividual in all groups of *P. lombardoi* in one behavioural record (expl. symbols see fig. 3).

increases with the number of individuals in a group (to 5 group members). However, in groups with 6 fish the aggression is lower. There is no significant difference between groups with 4 and 6 individuals. Plots for all the acts separately show the same kind of action levels as in Fig. 5, except for circle fighting (C), quivering (T) and mouth fighting (M), and indicate that there is no significant difference (P = 0.076, P = 0.383, P = 0.420 respectively), probably because these acts occur very rarely.

Fig. 6 shows that avoiding (O), chasing (V) and fleeing (W) are the most frequent acts. Circle fighting (C), quivering (T) and mouth fighting (M) are rarely shown.

M. johanni.

Colour patterns.

In litterature the two major colour patterns are often considered to be sexually determined, which is not absolutely true. The patterns depend upon the status of the animal.

Dominant animals are usually black or dark blue with two light blue horizontal stripes. In most cases the lower stripe is very vague and the other is often not continuous (the stripe consists of blocks). The head shows one light blue stripe between the eyes and one above the eyes. The dorsal fin, the caudal fin and the pelvic fins have a black and light blue edge. We always notice one or more egg spots. The caudal fin is light blue and black striped according to the fin rays.

Subordinate animals are greyish or yellow with or without brown horizontal stripes. The dorsal fin has a dark stripe, the rest of the fins are transparent (occasionally with dark spots). The change from yellow or grey to black can happen rather quickly (± 24 hours), while the change from dark to grey or yellow takes some more time.

Dominance hierarchy.

a) A linear dominance hierarchy was always established in a group of *M. johanni.* The α-individual (and sometimes also the β-animal) gains the dominant colour pattern, no matter what its colour was before the establishment of the group.

MATRIX 3

Example of a matrix of M. johanni *for AVCTM(OW) in groups of 5 individuals (the highest RD-values of each row are underlined)*

	1	2	3	4	
1	0.00 0.00 0.00	37.00 22.11 0.67	13.00 15.87 −0.18	6.00 18.02 −0.67	56 56.00
2	1.00 1.49 −.33	0.00 0.00 0.00	15.00 11.94 0.26	11.00 13.56 −0.19	27 26.98
3	1.00 1.36 −.27	1.00 15.23 −0.93	0.00 0.00 0.00	27.00 12.42 1.17	29 29.01
4	1.00 0.15 5.73	1.00 1.66 −0.40	1.00 1.19 −0.16	0.00 0.00 0.00	3 3.00
	3.00 3.00	39.00 39.00	29.00 29.00	44.00 44.00	115.00 115.00

(for explanation see matrix 1).

b) In groups of *M. johanni* we normally find a high correlation coefficient between size and dominance (Table 7). The correlation between standard deviation and the rank correlation coefficient ($\tau = 0.272$, $P = 0.117$) indicates that even small differences in length of the group members are important for determining dominance.

TABLE 7

Length in mm. of the individuals ranked according to dominance order

group	dominance hierarchy	τ	P
4	62 → 60 → 58 → 61 → 52 → 47	0.733	0.039
5	63 → 63 → 56 → 58 → 52 → 47	0.828	0.014
6	70 → 55 → 66	0.333	0.601
7	72 → 65 → 65 → 65 → 48	0.836	0.016
8	63 → 58 → 51	1	0.117
9	74 → 68 → 61 → 57 → 54	1	0.014
G	83 → 75 → 74 → 64 → 56	1	0.014
I	84 → 84 → 68 → 66	0.913	0.044
A	70 → 66 → 55 → 55	0.913	0.044
B	75 → 61 → 57	1	0.117
H	83 → 77 → 67	1	0.117
F	82 → 81 → 80 → 66 → 60	1	0.014
C	72 → 70 → 68 → 58	1	0.041

c) Table 8 points out that the α-individual performs most of the aggressive acts and it is the most avoided animal, whereas ω is the less aggressive animal. However, there is no difference among the individuals as far as the performance of aggression inhibition and the receiving of aggressive acts is concerned.

TABLE 8

Performing and receiving acts in 19 groups

acts	P	*p*	R	*r*
A	α (16x)	ω (19x)	ω (12x)	α (19x)
V	α (19x)	ω (19x)	/	α (19x)
C	—	—	—	—
T	α (12x)	/	/	/
M	—	—	—	—
O	/	α (19x)	α (18x)	ω (17x)
W	/	α (19x)	α (19x)	ω (19x)
AVCTM(OW)	α (19x)	ω (19x)	/	α (19x)

d) In Table 9 we see that all AVCTM(OW)-matrices are asymmetrical. The χ^2-test shows that only in half of the investigated groups there is a significant difference between expected and observed values. In most cases there is a complete or almost complete RD-diagonal (all highest RD-values of each row lie next to the diagonal) and the interactions of α with the other group members is status dependent.

TABLE 9

Results of the Likelihood Ratio criterium, the Symmetry test and the position of the Relative deviations of the AVCTM(OW)-matrices

group	S-AS	χ^2	RD-α	RD-*d*	group	S-AS	χ^2	RD-α	RD-*d*
gr.G	AS	Y	Y	Y	gr.J	AS	Y	Y	Y
gr.I	AS	N	Y	Y	gr.D	AS	Y	Y	N2/3
gr.A	AS	N	N2/3	Y	gr.K	AS	Y	N	Y
gr.C	AS	Y	N	Y	gr.H	AS	N	Y	Y
gr.B	AS	N	Y	Y	gr.E	AS	N	Y	N2/3
gr.F	AS	Y	Y	Y	gr.4	AS	Y	Y	N3/5
gr.7	AS	N	N3/4	N3/4	gr.6	AS	N	Y	Y
gr.1	AS	Y	Y	N2/3	gr.2	AS	N	N2/3	Y
gr.5	AS	Y	N	N2/5	gr.8	AS	N	Y	Y
gr.3	AS	N	Y	Y					

e) As shown in Fig. 7 one can notice that also in this species the variation in action level among groups of the same size is very substantial. There is no significant difference if groups with different number of group members are compared for all the acts together (Fig. 8 : P = 0.810) nor for all acts separately.

Chasing and fleeing are the most important acts. Circle fighting and mouth fighting almost never occur (Fig. 9).

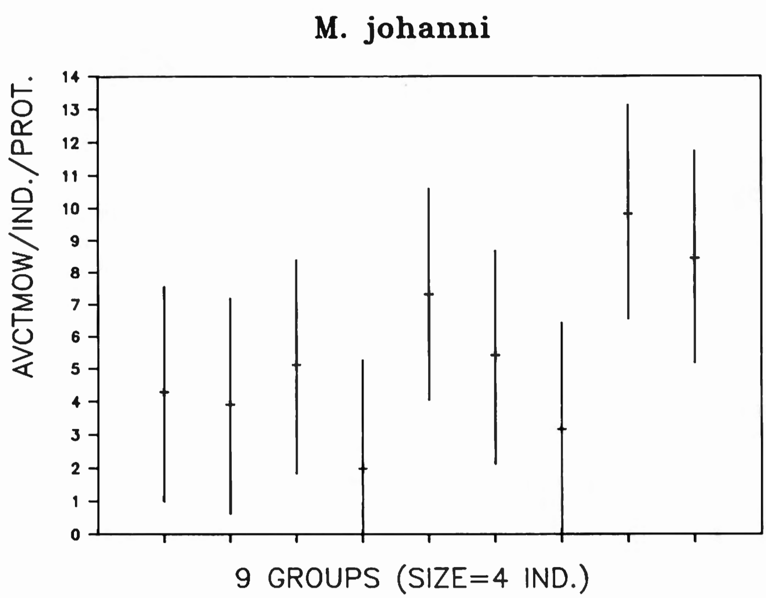

Fig. 7. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *M. johanni.*

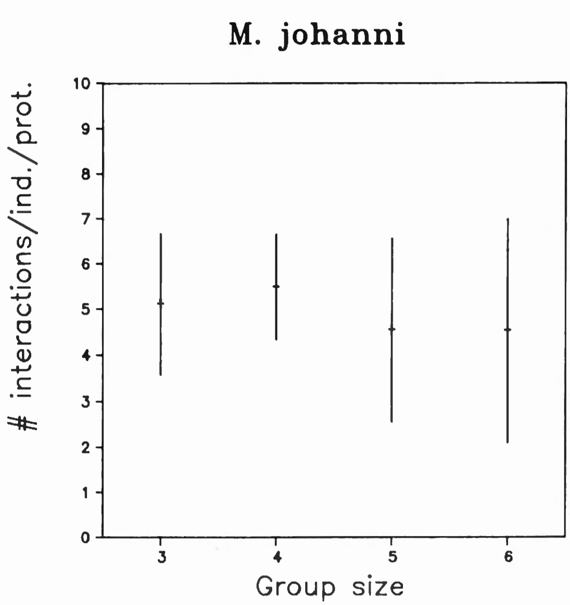

Fig. 8. — 95 % confidence intervals for the factor means for AVCTM(OW) of *M. johanni* for groups of 3, 4, 5 and 6 group members.

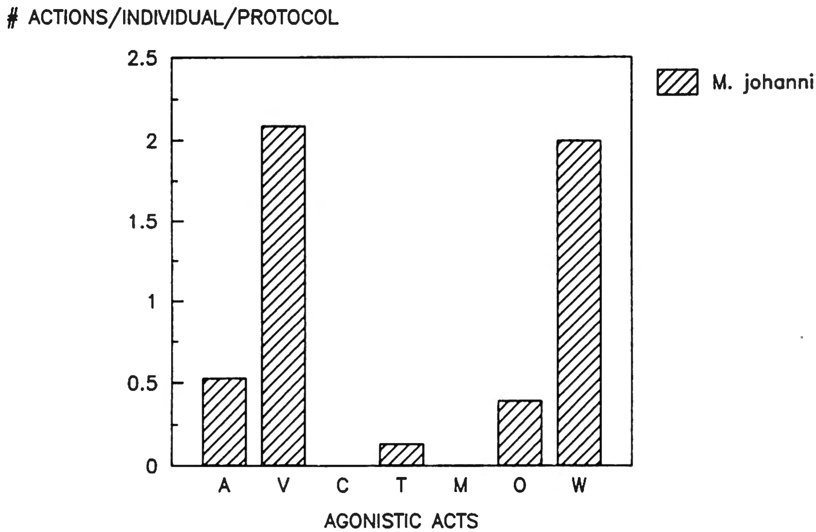

Fig. 9. — Mean amount of acts/individual in all groups of *M. johanni* in one behavioural record (expl. symbols see fig. 3).

M. auratus.

Since *M. auratus* has already been studied (Nelissen, 1985) we restrict ourselves to a brief summary of the findings in this species.

M. auratus shows two types of colour patterns : a black pattern in dominant animals and a yellow one in subordinate individuals. A linear dominance hierarchy is always established when groups of fish are kept in aquarium tanks. The α-animal is always the most active one and the ω-individual is the least aggressive one. The ω-animal receives most of the aggression. All matrices are asymmetrical and in most cases there is a significant difference between expected and observed values. The highest RD-values are found next to the diagonal. This means that in groups of *M. auratus* the interactions depend upon the rank status of the animals and that neighbouring animals interact more with each other than we would expect if there was no relationship between rank status and interactions among group members.

In order to make a comparison between the four Mbuna-species a few supplementary observations on groups of *M. auratus* were made. These observations pointed out that the aggression level of the groups is very variable (Fig. 10 ; also see Fig. 1 for explanation) and that there is a difference between groups of 3 and 4 individuals (Fig. 11 : $P = 0.033$). If we consider every act separately we notice that the only act where a significant difference is found is chasing. Unfortunately we had only groups of 3 and 4 individuals (because the supply of fish was limited) so it is not very clear if chasing would increase with the number of individuals.

Chasing and fleeing are the most frequent acts (Fig. 12). Mouth fighting almost never occurs and circle fighting and quivering are very rare.

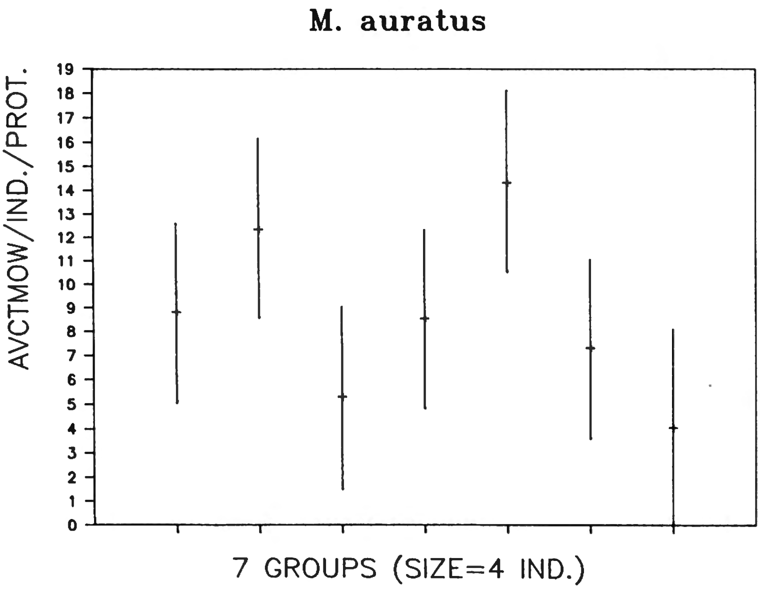

Fig. 10. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *M. auratus*.

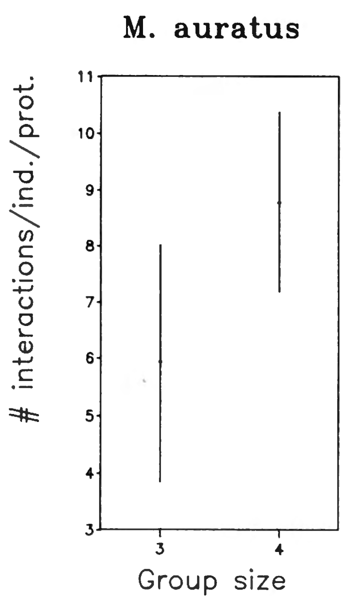

Fig. 11. — 95 % confidence intervals for the factor means for AVCTM(OW) of *M. auratus* for groups of 3 and 4 group members.

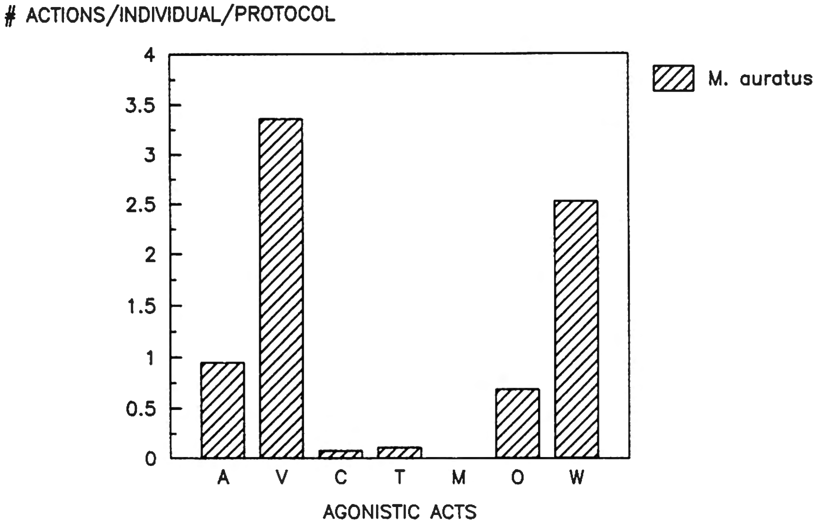

Fig. 12. — Mean amount of acts/individual in all groups of *M. auratus* in one behavioural record (expl. symbols see fig. 3).

Comparison between *P. « ornatus »*, *P. lombardoi*, *M. johanni* and *M. auratus*.

In Fig. 13 the 95 % confidence intervals for the mean amount of aggressive acts/ individual are given for the four species. It shows that the four species differ significantly when the amount of aggression is considered. *M. johanni* is the least aggressive species and *P. lombardoi* is the most aggressive one. In aggression inhibition (Fig. 14) *P. lombardoi* performs much more avoiding (O) and fleeing (V), while *M. johanni* performs it the least. If all the acts are considered separately the same pattern is found as in Fig. 13 and Fig. 14, except for circle fighting (C) and quivering (T) where there is no significant difference between the four species. In Fig. 15 it is clearly demonstrated that *P. lombardoi* performs significantly more mouth fighting than the other species.

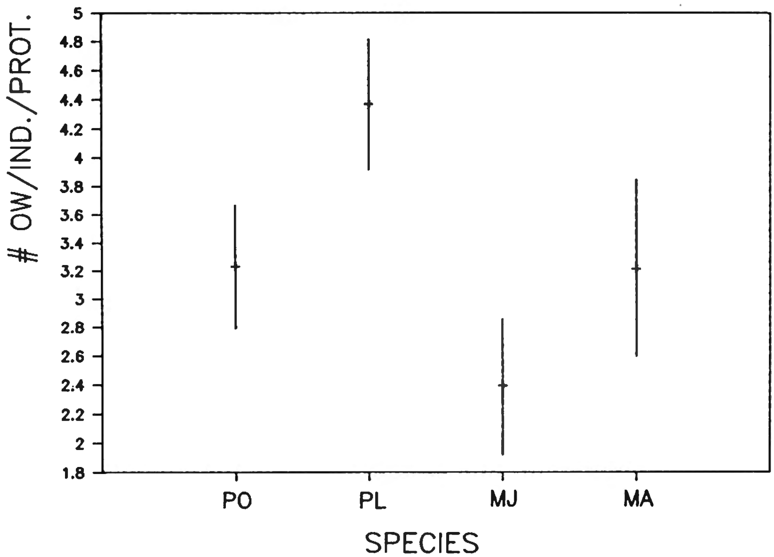

Fig. 13. — 95 % confidence intervals for the factor means of AVCTM, the aggressive acts (PO = *P. « ornatus »*, PL = *P. lombardoi*, MJ = *M. johanni*, MA = M. auratus).

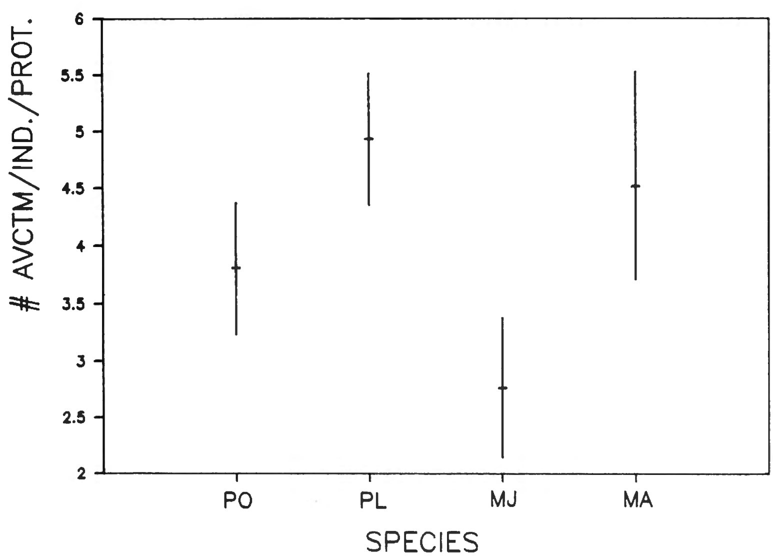

Fig. 14. — 95 % confidence intervals for the factor means of OW, the aggression inhibition.

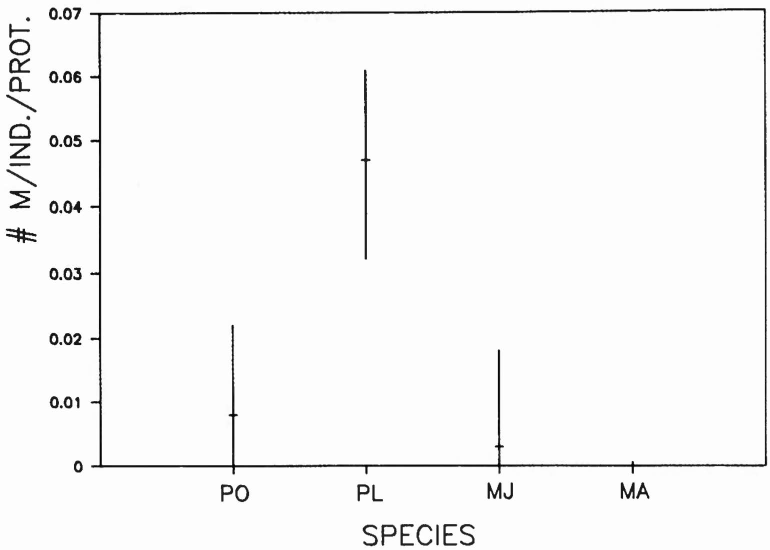

Fig. 15. — 95 % confidence intervals for the factor means of M, mouth fighting.

DISCUSSION

Because of the lack of information on the existence of dominance hierarchies in groups of fish (most experiments only involve pairs of fish and the dominance factors in such a relationship) a study was performed on three cichlid species *M. johanni, P. lombardoi* and *P. « ornatus »*. The choise of the species was based on the fact that they are very closely related to *M. auratus*. This species was investigated by NELISSEN (1985). The three species as well as *M. auratus* belong to the very closely related group of the Mbuna.

Our results show that these three species establish a linear rank order in aquarium tanks. When these hierarchies are stable a subordinate individual will never or very rarely perform an aggressive act towards a dominant animal. The very structured communication system in the dominance hierarchy of *M. auratus* found by NELISSEN (1985) also seems to apply for *M. johanni, P. lombardoi* and *P. « ornatus »*. The relations between agonistic behaviour and dominance hierarchy can be summarized as follows :

— the frequency of the aggressive acts and signals are determined by the rank number of the animals.

— neighbouring animals in the rank order interact more with each other than with the other group members.

These severe rules in a communication system minimize time and energy loss while maintaining the hierarchy. The fact that every group member takes care of its relationship with its neighbour reduces harmful fights and acts that should confirm the rank order.

In all four species the α-individual is the most aggressive animal. This means that the α-status requires a lot of energy. So it is easy to imagine that the advantages of being α must be of some importance (Phillips and Swears, 1979). The few observations of copulations show that only the α-animal (when it is a male) mates with the females. During the mating all other group members are chased into one area of the aquarium ; the α-individual is extremely aggressive towards them. As one occasional observation in a group of *M. johanni* has shown subordinate males seem to be able to « steal a copulation » by interfering in the mating act and spraying sperm over the eggs, before the α male is able to chase him away. Besides the advantage of reproduction the dominant animal seems to occupy the only or the best hiding place in the aquarium tank.

The ω-animal is the least aggressive fish in the group. However, this does not mean that it serves as an « aggression-sink » (Wilson, 1975, p. 290), since it does not always receive the most aggressive acts.

Circle fighting and mouth fighting are rarely seen in a stable hierarchy (if it does occur the dominant fish will always interrupt the fights). *P. lombardoi* seems to form an exception, because it performs mouth fighting more frequently than the other species. On the other hand it also performs relatively more full display and avoiding. One can assume that this rather aggressive species can still minimize time and energy loss by performing more aggression inhibition and aggressive signals. The aggression level of *M. johanni,* in aggression a very moderate species, seems to be independent of the group size (no significant difference between groups with different numbers of group members). However, in the other three species aggression increases with the number of group members. One could expect that when group size increases, a group will show the same amount of overall aggression simply spread over more individuals (which means that there would be less aggression/individual), or an increased amount of overall aggression but a constant aggression level per individual. However, non of this seems to happen : in larger groups there is not only a significant tendency towards more overall aggression, but also an increasing aggression level per individual. This tendency can not go on forever, which means that at a certain level of group size the overall aggression has to decrease again in order to make living in a group worthwhile. This level of group size where maximum aggression appears, seems to be five individuals for *P. lombardoi.* Apparently it is lying higher for *P. « ornatus ».* To get a full understanding about the impact of group size on the aggression level and possible density effects further investigation is needed.

All four species seem to have status dependent colour patterns, especially in *P. « ornatus », M. johanni* and *M. auratus*. In most cases a lot of intermediate patterns appear according to the aggression motivation (changes in darkness of the stripes and spots or changing colour) ; this was also found in *Coreoperca kawamebar* by Kohda and Watanabe (1982). A difference with their findings is that when the Mbuna-species are placed in isolation the previous colour pattern with stripes disappears and a neutral colour pattern is seen. The blue and the yellow colour patterns of *P. lombardoi* seem to belong to different sexes. Most blue fish are females and the yellow ones are males. On the other hand intermediate patterns often occur, in females as well as males. This means that the colour patterns in *P. lombardoi* are not strictly tied to sex. Yellow is always dominant over intermediate, which dominates blue. In contrast with the three other species individuals of *P. lombardoi* very rarely show changes in colour pattern, but the darkness of the bars is also dependent on the aggression motivation.

Size seems to play an important role in gaining a dominant position : larger fish will easily dominate smaller fish. This is especially true when size differences are increasing. *P. lombardoi* is an exception ; in this species being yellow is more important than being big, in other words small yellow fish dominate larger blue fish. Barlow and Ballin (1976) ; Barlow and Wallach (1976) and Barlow (1983) made a similar observation in *Cichlasoma citrinellum* in which gold morphs always dominate the others, even if they are smaller. According to them this was due to the fact that gold coloration inhibits attacking by stimulating fear responses. This is also a possible explanation for *P. lombardoi* because this species performs a lot of avoiding and fleeing (much more than the other three species). However, it does not explain the fact that *M. auratus* and *M. johanni* show a yellow colour in subordinate fish. In fact *P. lombardoi* is an exception among the Mbuna, because it is the only species in which yellow dominates blue (Ribbink *et al.*, 1983). Also in this case further investigation of data and observations are necessary for making a further hypothesis about this subject.

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