On the (In)stability of Dominance Hierarchies in the Cichlid Fish *Oreochromis mossambicus*

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Dominance hierarchies were studied during 8 weeks in eight heterosexual captive groups of *Oreochromis mossambicus* at the onset of sexual maturity. Linearity was assessed for each group on a weekly basis based on the Landau's index (h) and on the procedure described by Appleby [Appleby MC (1983): Animal Behaviour 31:600–608]. Week-to-week stability of the hierarchical structures was measured using the Burk's stability index (b) and Spearman rank correlation coefficients for the ranks of fishes in consecutive weeks. The two measures of stability showed a high level of concordance but the Spearman rank correlations were more conservative in detecting cases of stability. Although most dominance structures were linear they were unstable from week to week. Dominant individuals were less likely to experience rank reversals than subordinates. Rank reversals were especially likely among hierarchical neighbors. Dominance hierarchies did not stabilize in the time span of this study.   © 1996 Wiley-Liss, Inc.

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INTRODUCTION

There is a very extensive literature on dominance hierarchies in animal groups [see Gauthreaux, 1978; Dewsbury, 1982 for references in different taxa]. Many studies have focused on the dominance structure, i.e., linear vs. nonlinear [e.g., Chase, 1974, 1982, 1985; Appleby, 1983; Jackson, 1988; Jackson and Winnegrad, 1988; Iverson and Sade, 1990; Rothstein, 1992]. There are, however, fewer studies that deal with the temporal variation of these hierarchical structures in nonprimate animals [e.g., Guhl, 1968; Cain and Baenninger, 1980; Elwood and Rainey, 1983].

Attempts to quantify the stability of social groups have used different approaches. One such approach is to measure correlations between the ranks of the individuals that comprise a group in successive time periods [e.g., Keiper and Sambraus, 1986]. Burk [1979] developed an index of stability based on the number of observed reversals over the total number of observed reversals over the total number of possible reversals in a given group, and found that in laboratory groups of male crickets, although the structure of the groups was linear on each observation day, the groups were unstable from day to day. Oliveira et al. [1995] used the concordance index of Kendall [see Siegel and Castellan, 1988] to establish the agreement among the rank orders measured on successive days during hierarchy formation in male *Oreochromis mossambicus*.

Other workers have approached this problem by studying the extent to which the same hierarchy can be replicated after group disruption (e.g., by separating and reuniting the group members) [Guhl, 1953; Fishelson, 1983; Dugatkin et al., 1994], although this is more a measure of resilience than of stability. The results of these studies are not clear, since in a large proportion of cases [i.e., 2/3 in domestic fowl, Guhl, 1953; and 4/10 in cockroach, Dugatkin et al., 1994] the hierarchies were not fully replicated.

These studies raise several general problems. One concerns the relationship between linearity and stability. Indeed these two properties are not necessarily related. Landau [1951a], based on theoretical considerations, has stated that dominance reversals in dyads do not lead necessarily to changes in the group structure, as expressed by linearity measures. This conclusion has been supported empirically by the above-mentioned work of Burk [1979] on crickets, and by the work of Bekoff [1977] on the ontogeny of social behavior in coyotes.

This finding leads to the second issue. Since stability and linearity are not necessarily related, the image of a given social structure may be affected by the time scale used in sampling.

A third issue is related to the inherent biological characteristics of the group members. When individuals are undergoing rapid ontogenetic changes, e.g., during sexual maturation, the relationships among them may change very rapidly. Similar problems may arise when the individuals experience cyclical behavioral changes, e.g., cyclical reproductive territoriality.

Finally, group instability may not affect all ranks equally. For instance, Dugatkin and Wilson [1992] presented data that show that dominant individuals are more stable than subordinates.

In this paper we have studied the relationship between stability and linearity of dominance structure and the effect of rank order position in the likelihood of reversals in captive heterosexual groups of *O. mossambicus* at the onset of sexual maturity. In a previous study, the existence of linear dominance hierarchies was demonstrated for *O. mossambicus* at this developmental stage [Oliveira and Almada, 1995]. In groups of adult mature males, it was demonstrated that a dominance structure was established a few hours after group formation and was highly consistent over 5 consecutive days, the time that the experiment lasted [Oliveira et al., 1995].

MATERIALS AND METHODS

Synopsis of the *O. mossambicus* Mating System

O. mossambicus is an African maternal mouthbrooding cichlid in which males form dense nest aggregations (arenas) in shallow water during the breeding season. Males

establish territories within these aggregations where they dig pits (nests), to which they attract a succession of females. Spawning takes place in the nest. The female quickly takes eggs and sperm into her mouth where fertilization takes place, and leaves the arena [Bruton and Boltt, 1975]. In the wild, the embryos and fry are brooded in the females' mouth during 20–22 days [Bruton and Boltt, 1975].

Subjects and Procedures

The fish used in the present study came from a single brood from a stock kept in our laboratory which is derived from the Vasco da Gama Aquarium stock, that originated from individuals collected at Incomati River (Mozambique) in the early 1970s. Individuals were reared in three stock tanks until they were 9 months old (males ranging from 80.7 to 36.6 mm standard length, and females ranging from 71.4 to 34.3 mm standard length), when the experimental groups were formed. At this age the onset of sexual maturity was detected as revealed by the first appearance of dark individuals and nest beginnings in the stock tanks. Eight groups of six individuals were established in standard aquaria ($62 \times 34 \times 39$ cm^3) and were observed weekly for 8 consecutive weeks. Although we tried to keep the sex ratio at 1:1, difficulties in sexing the fish at this stage led to some variation in sex ratio among the groups (3 groups had 3 males:3 females and five groups each had 4 males:2 females). To confirm the sex of each fish, individuals were sacrificed at the end of the experiment with an overdose of the anaesthetic quinaldine (Sigma). Sexing was achieved by direct inspection of the gonads, and the aceto-carmine coloration method proposed by Guerrero and Shelton [1974] was used when necessary. Fish were fed commercial food flakes, and were kept at $24 \pm 2°C$ with a photoperiod of 12L:12D.

Behavioral Observations

In each group, fish were recognized individually by natural markings and by relative size differences. Behavioral observations were conducted following a behavioral sampling procedure [see Martin and Bateson, 1993] for agonistic interactions, in periods of 5 min each. Six such observations were performed per group per week, comprising an observation effort of 30 min per group each week. Observations were conducted between 11 a.m. and 6 p.m.

We considered that an agonistic interaction had occurred when one or more of the following behavior patterns was seen: approach, charge, butting, biting, chasing, lateral and frontal display, circling, mouth fighting, pendelling, fleeing, and submission. A detailed description of these behavior acts may be found in Baerends and Baerends van Roon [1950] and in Neil [1964]. We also recorded the identity of the participants and the outcome of the interactions. An individual was considered a loser in an agonistic interaction when he retreated, adopted a submissive posture, or fled from the opponent.

Data Analysis

Two dominance indexes were computed: a) V/V+D, number of victories over the total number of interactions in which the fish participated; b) V-D, the difference between the number of victories and defeats for each fish. The former index was demonstrated to be highly correlated with the rank order of the individuals determined from the analysis of sociometric matrices [Oliveira and Almada, 1995] and has often been used by other authors [Barlow and Ballin, 1976; Winberg et al., 1991; Gómez-Laplaza

and Morgan, 1993]. This index, however, has the disadvantage that it generates a high number of ties, because individuals that do not win any agonistic encounters have a zero score independently of the number of agonistic acts received. To overcome this problem we used the second index (V-D) because we found that the two indexes were highly correlated ($r_s = 0.956$, $P < 0.001$, $n = 48$).

Linearity was measured according to Landau's linearity index [Landau, 1951b], with the correction proposed by Nelissen [1986] for ties. The significance of the linearity of the dominance structures was assessed by computing the number of circular triads (d) (i.e., A dominates B, B dominates C, but C dominates A) for each group and then consulting Table I of Appleby [1981].

Stability of dominance structures between consecutive weeks was measured by Spearman rank correlations and by Burk's index (b) [Burk, 1979]. The agreement between the two measures of stability used was accessed by Cohen's K [Cohen, 1960], and its significance was estimated according to the procedure described by Siegel and Castellan [1988].

Temporal changes in linearity and stability measures were studied using analysis of variance (ANOVA) repeated measures procedure. One-way ANOVA followed by a Tukey HSD multiple comparisons test was performed to access the relative stability of different rank order positions. For each individual we computed a dominance index (V-D) for the total observation period and attributed a rank order position accordingly (ranging from 1 = alpha individual to 6 = omega individual). We also counted the total number of reversions per individual, which we used as the dependent variable in the one-way ANOVA.

All ANOVA procedures, including the tests of its assumptions, were run on a PC computer with STATISTICA for Windows version 4.0 [copyright Statsoft Inc., 1993] software package.

To assess the extent to which reversals occurred differentially between fishes that are neighbors in rank or at greater rank distances, a goodness-of-fit χ^2 test was performed. Expected values were calculated according to the respective number of possible changes between neighbors and nonneighbors in the dominance hierarchy.

RESULTS

All groups studied yielded linear dominance hierarchies in 50% or more of the weeks: four groups in all 8 weeks, two groups in 7 of 8 weeks, one group in 6 out of 8 weeks, and one group in 4 of 8 weeks. A hierarchy was considered linear when its Landau's index was equal or greater than 0.9, as proposed by Chase [1974], and when its significance was confirmed by Appleby's procedure [Appleby, 1983].

In Figure 1 we present data on the temporal variation of the Landau's indexes (h) along the 8 weeks of study. Although the weekly h average increased slightly with time (Fig. 1), this variation was not significant (ANOVA repeated measures: $F_{7,49} = 0.977$, $P = 0.458$).

A dominance structure was considered stable between 2 consecutive weeks if the index of Burk (b) was equal or less than 0.2 [Burk, 1979]. When using Spearman rank correlations we adopted a criterion for stability of an r_s equal or greater than 0.7, since it explains about 50% or more of the total variance. This use of r_s was not intended to give actual probabilities, and should be viewed as a descriptive measure. It has the
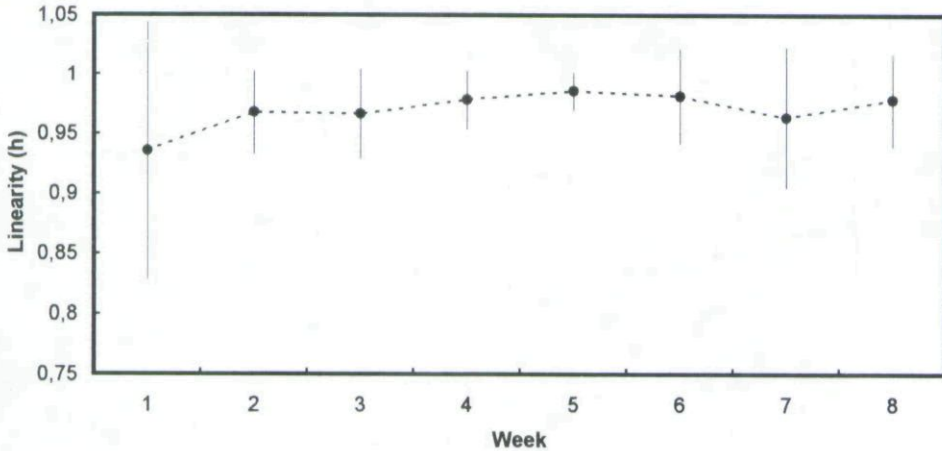
Fig. 1.   Variation of the Landau's index of linearity (h) (mean ± SD for the eight groups) along the 8 weeks of study.

advantage of allowing one to define cut off values that can be related in a simple way to specific percentages of the variance explained, which facilitates comparisons between studies.

The two measures of stability used were found to yield similar results (Cohen's K: concordance observed = 89.3% of the cases, n = 56, K = 0.780, $P < 0.001$), although the Spearman rank correlations were more conservative than the b index (number of stability cases [S] detected by each of the measures: $S_{rs} = 21/56$; $S_b = 25/56$). In face of these results we decided to adopt the more conservative r_s, and the data presented hereafter are based on this measure.

The dominance structure of most groups was shown to be unstable from week to week: three groups yielded stable structures in three of seven week-to-week transitions, three other groups in two of seven, one group in one of seven, and one group in five of seven transitions.

In Figure 2 we present the temporal variation of the r_s along the consecutive weeks. Although the average r_s increased from the beginning of the experiment to the 7th week there is no significant variation with time (ANOVA repeated measures: $F_{6,42} = 1.342$, $P = 0.26$). Thus, in the groups studied high levels of linearity do not mean that the groups are stable.

In Figure 3 we present data on the variability of the occurrence of reversals as a function of rank order position. Inspection of Figure 3 shows a marked contrast between the first rank and the others, and a tendency to higher rates of reversals for intermediate rank positions. ANOVA results confirmed the effect of rank order position on the number of reversals (one-way ANOVA: $F_{5,48} = 7.815$, $P < 0.001$). Multiple comparisons revealed a significant difference between rank 1 and all the others ($P < 0.01$) and between rank 2 and ranks 3 and 4 ($P < 0.05$). Thus, the more dominant fish of each group are more likely to preserve their position than subordinates.

A comparison of the number of reversals between the two sexes failed to reveal any significant difference (males: n = 29, mean ± SD = 8 ± 4.13; females: n = 19, mean ± SD = 9.42 ± 2.66; t test: t = 1.327, $P = 0.191$).
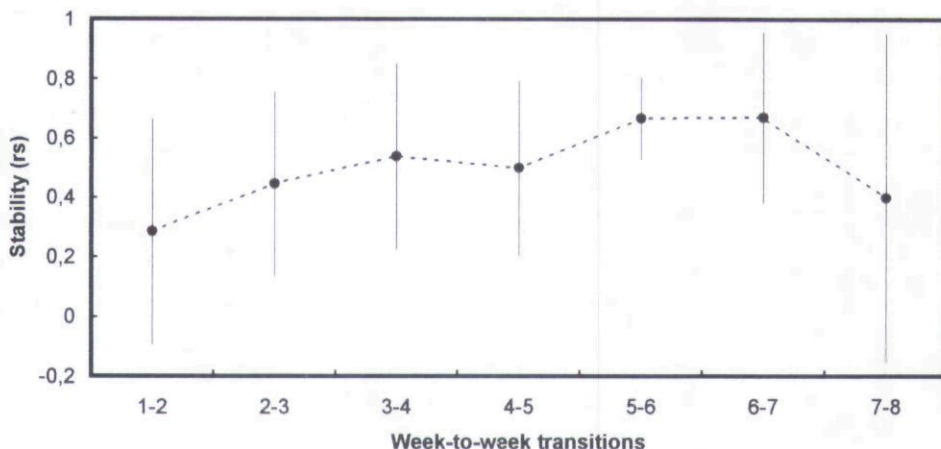
Fig. 2.   Variation of the stability measured as a Spearman rank correlations (mean ± SD for the eight groups) between successive weeks, along the 8 weeks of study.

Finally the comparison between reversals among rank neighbors and individuals separated by rank distances greater than 1 showed that there are more reversals involving rank neighbors than would be expected by chance (χ^2 goodness-of-fit test: $observed_1 =$ 120, $expected_1 = 97.6$; $observed_{>1} = 124$, $expected_{>1} = 146.4$; $\chi^2 = 8.568$, $P < 0.01$).

DISCUSSION

Our results showed that for the groups studied, linearity and stability are not associated. Although the hierarchical structures were not stable over the observation period, linear structures tended to succeed to linear structures as time passed. That is, the hierarchical structures of the groups measured on a weekly basis were linear in most cases
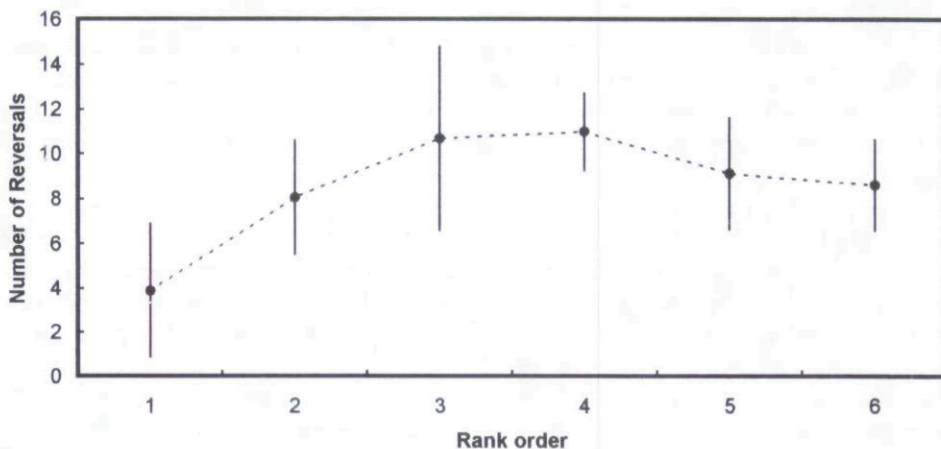

Fig. 3.   Number of reversals (mean ± SD for the eight groups) experienced by different rank order positions.

despite the occurrence of reversals in rank among group members from week to week. This finding raises the following three issues:

1. It is possible that rank orders are not the real relevant point when characterizing a social structure. The fact that an observer is able to scale individuals in an ordered sequence of ranks does not mean that animals without sophisticated cognitive systems are themselves able to categorize other group members in precise ranks. It is more likely that animals may perceive simple categories such as those that are much stronger, those that are less stronger, and those with which the relationships are uncertain [Appleby, 1993; but see also Freeman et al., 1992]. In this respect it is also likely that the most relevant difference that matters for the group members is whether the rank is high or low. Bolles [1981] pointed out that even for a human observer it is easier to "see who the alpha animal is (…) (but) it takes the careful observation and skillful data analysis of the behavioral scientist to identify the fifth and sixth dominant animals in a group of twelve, (…)."

In a previous study, we found that although a linear rank order can be defined, the dominant member of each group was involved in the great majority of the interactions that occurred in that group [Oliveira and Almada, 1995]. Cain and Baenninger [1980] also found that, in captive male groups of the Siamese fighting fish, the alpha and omega males are clearly defined in the dominance structure while midranking males are of comparable status, and that the dominant male of each group participated in the great majority of the agonistic interactions of the group.

Two findings in the present work seem to support this view: the greater stability in rank of the dominant fishes and the fact that reversals are especially frequent among rank neighbors.

2. To what extent is the presence of linearity compatible with such a scheme? The persistence of linearity in successive dominance structures can be explained if the basic changes in the structure are caused by reversals in contiguous positions in the rank order, i.e., neighbors in a hierarchy might view each other as neither clearly dominant nor subordinate, as opposed to categories perceived as clearly dominant and clearly subordinate. In fact, in a previous study we found that symmetrical fights are more common between rank neighbors [Oliveira and Almada, 1995], a result also found for other species [e.g., Nelissen, 1985; Andries and Nelissen, 1990].

3. Concerning the high level of instability found it is important to remember that the subjects were at the onset of sexual maturity, and it is likely that their relative fighting ability [or their resource holding power; see Parker, 1974] could undergo rapid changes as new fish mature. In *Xiphophorus variatus* Borowsky [1973, 1978, 1987] found that maturing males inhibit the maturation of other males that continue to grow and mature later and at a larger size, a pattern that generates a kind of a compensatory tactic among individuals.

Even in adult males of *O. mossambicus* each territorial male leaves the territory after some days of occupancy [Neil, 1964], apparently when body reserves are depleted [see Bowen, 1984], and vacated territories are quickly reoccupied by other fish [Neil, 1966]. Such shifts are also likely to lower the stability of social relationships in a group.

The processes mentioned above emphasize the importance of clearly specifying a given time scale and biological peculiarities of the species studied when collecting data

on dominance hierarchies, namely in studies in which reproductive success and rank are under investigation.

ACKNOWLEDGMENTS

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