STUDIES ON THE BEHAVIOUR OF CYPRINODONT FISH
III. THE TEMPORAL PATTERNING OF AGGRESSION
IN APHYOSEMION STRIATUM (BOULENGER)

by

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(With 6 Figures)
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INTRODUCTION

Most functional systems in behaviour, such as courtships or aggressive
encounters, are structured in time, that is, the frequencies of the components
or elements comprising such systems will change during performance of the
behaviour. While this is implicit in most descriptions of behaviour there
have been rather few attempts to describe these temporal changes quanti-
tatively. One exception, however, is that of courtship behaviour in glandulo-
caudine fishes investigated by NELSON (1964) who demonstrated non-
stationarities for some species, that is changes in behaviour with time, which
were mainly of a cyclical nature. BALTHAZART (1974) also analysed the non-
stationarities in fights between males of Tilapia macrochir using a method of
dividing fights into quarters similar to that described in this paper. While
large non-stationarities were found BALTHAZART concluded that these were
mainly an artefact due to the experimental situation. The outcome of fights
could be predicted by the end of the first quarter and the remaining period
merely accentuated the differences in behaviour of dominant and subordinate
fish. If sufficient data were available it might have been more instructive
to have looked for non-stationarities within the first quarter.

One possible reason for the paucity of studies concerned with long-term
patterning of behaviour is that some of the more sophisticated methods of
analysis which have been used, such as factor analysis, are not concerned
with temporal organisation (WIEPKEMA, 1961, BALTHAZART, 1972), while
stochastic or sequence analysis derived from matrices are only valid if the
data show stationarity, that is, if the frequencies of behaviours and of
transitions between them do not change with time (DELIUS, 1969; SLATER,

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1974; Van der Kloot & Morse, 1975). This is, for reasons already discussed, probably infrequent in complex behaviour although the courtship of one of the species of characid fish studied by Nelson (1964), Corynopoma ruisei, was stationary, as were the transition probabilities between song elements in Cardinal birds (Lemon & Chatfield, 1971).

In a previous comparative study of aggressive behaviour in rivulins, evidence was presented which suggested that considerable non-stationarities existed for the individual elements comprising aggressive behaviour (Ewing, 1975). In this paper we describe how the behaviour of Aphyosemion striatum changes during the course of an aggressive encounter and suggest a mechanism which accounts for the pattern observed.

MATERIALS AND METHODS

The species of killifish used in this study was Aphyosemion striatum (Boulenger) form north-western Gabon. This species is relatively hardy and easy to breed. It is a small fish, males reaching a maximum total length of about 50 mm, females being somewhat smaller on average. Males are beautifully patterned with a bronze-green ground colour to the body along which are five rows of red spots. The caudal, dorsal and ventral fins are barred longitudinally with bands of red, yellow and blue. Wild caught fish were obtained and the fish used in this study were all the first and second generation progeny from these.

Methods of maintaining stocks of fish and for recording aggressive behaviour have been described in detail previously (Ewing & Evans, 1973; Ewing, 1975) and an abbreviated account is given here, except where the procedures differ in some major respect. Eighteen young, sexually mature males were removed from the stock tanks and kept visually isolated in partitioned aquaria 60 X 25 X 25 cm. Aggressive behaviour followed removal of the partition. The behaviour was recorded by voice on a tape recorder and subsequently transferred to paper along with a time scale. At the end of an encounter the fish were separated.

Three series of fights were recorded of which the first, consisting of eight fights, was observed after a minimum period of eight weeks visual isolation. In the second series the fish were repaired so that winners fought winners and losers fought losers from the first series. The encounters were arranged between 28 and 32 days after the first fights. Finally after a further period of 24 - 26 days separation a third series of five fights was observed of which one was between fish which had won twice previously and one between fish which had lost twice. The remaining three fights were between fish which had both lost and won one fight. No significant differences were found in the behaviour performed in the three series. The object of the method of pairing used was to try and avoid one-sided encounters. The total number of fights observed was 21.

AGGRESSIVE BEHAVIOUR

The aggressive behaviour of a number of related species has been described by Ewing & Evans (1973) and Ewing (1975) along with some evidence and speculations concerning the functions of the various elements. The qualitative aspect of the behaviour differ little between species and only a brief description is given here.

Fin clamp (FC): All the fins are folded and held against the body. Sigmoid posture (SP): The body is flexed so that the tail points towards, and the head away from, the opponent. The fins are usually folded. Full display (FD): All the fins are maxi-