A causal analysis of the behaviour of Pseudotropheus zebra (Boulenger) (Pisces, Cichlidae)

Vodegel, Nance

Publication date:
1978

VI. SUMMARY

A brief description is given of the behaviour of Pseudotropheus zebra, a mouth-breeding and sexually dimorphic Cichlid species from Lake Malawi. Although the two sexes have different roles in the organization of the territorial society, both were found to use the same behavioural repertoire. This repertoire has been quantitatively analysed in order to obtain better insight into the organization of behaviour over time. Various analytical techniques have been used for this purpose, including a cluster-analysis and factor-analysis. The results of the different analyses were compared and critically discussed. Each method was found to have a limited value for such an analysis of behaviour because of its specific restrictions and deficiencies. A combination of different techniques gave the best result, because artifacts in the results due to these deficiencies could then be recognized.

Two of the behavioural groups resulting from these quantitative analyses consisted of elements only occurring in the presence of another individual or dummy. They were therefore called Communicative behaviours. One group was mainly performed in response to ripe females by territorial males, and is called Courting Behaviour. The other group occurred in response to all other types of conspecifics and is called Agonistic Behaviour.

In order to analyse the motivation underlying Communicative Behaviour fish dummies were presented to isolated individuals of both sexes during several months. The size and colour pattern of a fish apparently influence its chance to win interactions with rivals and to establish a territory, which may account at least partly for the division of roles between the sexes within a territorial society. Size and colour-pattern of the dummy were therefore varied in the experiments in order to manipulate the communicative behavioural system.

A large individual variation was found both in the amount of activities directed towards the dummies and in the type of behaviour shown. Since the effect of dummy-size on these aspects of the behaviour was found to be dominant over the effects of colour-pattern, the former is analysed and discussed most extensively. An increase of dummy-size was found to result in an increase of the total amount of (mainly communicative) activities shown in response to the dummies (= degree of stimulation) and in a change of the type of behaviour performed.

It was postulated that two interfering tendencies account for the ob-

served behaviour. These tendencies were identified as a tendency to attack (A) and a tendency to escape from the dummy (E). The resultant of the different effects of these two tendencies on the behaviour is called the Relative Aggressiveness (RA) of the response.

The RA was measured according to three different criteria in order to estimate the correctness of the postulation mentioned above. These different measures resulted in highly similar arrangements of individuals and of their responses to differently sized dummies in orders of decreasing RA. These results did not give reason to reject the initial postulation. They can be summarized as follows: The more stimulated an individual is by a dummy of a particular size, the lower is the relative amount of Butting performed in response to that dummy, the longer is the latency-time between Approach to the dummy and the first incidence of Butting, and the more activities are performed at a larger distance from the dummy and/or less oriented towards it; in short, the lower is the RA of the individual's response to that dummy. An increase of dummy-size results in an increase of its stimulus effect on all test fish and consequently in a decrease of the RA of their responses.

A decrease of the RA of the response results in a replacement of Butting by various displays, such as Frontal Display, Lateral Display or Courting, and finally even by Fear-Indicating Behaviour. A method is presented to measure the extent of this replacement by different activites. The type of behaviour replacing Butting with an increase of dummy-size, was found to depend on the individual's average RA.

Next the organization of behaviour over time has been analysed in more detail. The type of behaviour shown to a particular dummy was found to change over time. The structure of a sequence of communicative activities was found to vary with the RA of the average response to the dummies. The RA was found to affect the extent to which two particular activities preceded or followed each other in a behavioural sequence. Bout analyses showed that the bout length of various communicative behaviours vary with their orientation to the dummy, with the RA of the entire response, and with the type of behavioural sequence in which they occur.

The results of this experiment are explained by a mathematical model which postulates that both A and E are positive functions of the stimulus effect of a dummy on an individual. This stimulus effect is a function of 1. dummy-size, 2. individual susceptibility to stimulation by a dummy, 3.the distance at a particular moment between fish and dummy, 4. the time passed since the first moment of perception of the dummy by the fish (= the effect of habituation), and 5. the type of behaviour performed in that time. E is more affected by this stimulus effect than A.

A threshold value (Tr) is introduced into the model in order to explain the differences in attention to the dummy shown by an individual at different moments and at different distances from that dummy. Tr is thought to be positively affected only by activated behavioural systems other than those affected by the dummy.

This model makes it possible to simulate the behaviour of a hypothetical individual of P.zebra in response to differently sized dummies. An example of such a simulation is presented and compared with the data actually obtained.

The model is, in addition, used to explain the results of the quantitative analysis of behaviour on the basis of temporal relationships. Each object in an aquarium is thought to be the centre of at least two gradient fields, one of attraction of which A is an example and one of repulsion, e.g. E. The gradient of the latter is larger than that of the former field. In other words, the ratio $\frac{\text{attraction}}{\text{repulsion}}$ decreases with a decrease of the distance to the centre of the fields. Both gradients decrease exponentially over time. One stimulus can be the centre of more than one attractive field. Overlapping fields around different stimuli affect each other's sizes negatively.

The effect of dummy-colouration on the behaviour is less clear than the effect of dummy-size. More experiments on more individuals are required to study these effects. Some trends were found in this experiment. Speculations have been made about possible mechanisms responsible for these trends. They are the following:

1. The blue colour of the dummies (representing the male's colour) seems to be both more stimulating and more intimidating than the brown coloured dummies (resembling females or juveniles). The difference between the effects of these two colours seem to be larger in the female test fish than in the males. These trends can be explained by the mathematical model by assuming that a blue coloured dummy has a stronger stimulus effect on the fish than a brown one. The differences between males and females may be due to differences in experience with the two colours.

2. The presence of bars on the dummies, representing the territorial

colour pattern, tends to result in a lower amount of activities shown to the dummies and in lower relative amounts of Butting and Courting than plain coloured dummies. Since the plain colouration is most frequently shown by ripe females, these trends are explained by the presence of a stronger gradient field for the performance of sexual behaviour around a plain dummy than around a striped one. The presence of such a gradient field means a strengthening of the attractive force of the gradient field for attack, which results in a decrease of the average distance at which the fish responds to the dummy with DAB; this explains the data on Butting and on the total amount of activities shown in response to the dummy. In addition, the presence of such a gradient field for sexual behaviour can explain the data on Courting. More data are required to find out how far these speculations are correct.

Finally some properties of the model are more extensively discussed in relation to some classical ethological theories. Some of the model's characteristics are compared by analogy with those of physical or mechanical systems.