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On the ontogeny of behaviour of the cichlid fish *Cichlasoma nigrofasciatum* (Günther)

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SUMMARY

This paper's aim is fourfold: (1) to describe the ontogeny of the behaviour in a stock of *Cichlasoma nigrofasciatum*, (2) to relate the ontogenetical sequence into the biology and group behaviour, (3) to construct a plausible motivational model which is consonant with the observations and also adaptively functional, and (4) to draw attention to the consequences of the ontogeny/phylogeny interrelationship.

The present limited knowledge of the ecology and biology in nature is reported (I.a), and some data on the biology in the laboratory presented (III.B). It is concluded that parental care leads to enhanced survival of the brood, influences the composition of the microbial flora on the eggs, and raises the level of activity of the larvae.

The reproductive cycle - pair formation, territorial defence, preparation of the spawning-site, and parental care - is briefly described (I.d). In particular, the mode of selection of the partner and the spawning-territory depends on the population density and this apparently partly in relation to the number of sheltered sites available to the fishes. The behavioural elements of the adults (I.c) and juveniles (II.c) are listed. Parental care consists of activities to activate, to feed, to group, and to defend the young. The parental elements of Aerating, Retrieving, and especially Findigging, and the juvenile elements of Undulating, Approaching-parent, and Swimming-in/to-Findigging appear to be of the greatest adaptive significance to the integrated family structure of parents and swarm.

The development of the behaviour of the individual (II) is described chronologically and in detail. For descriptive purposes the juvenile behaviour is split into the categories of responses: to the parents, to the swarm-fellows, to some simple applied disturbances, and other behaviour. The early repertoire contains fewer motor patterns and is associated with fewer objects and stimuli in the immediate surroundings than the later repertoire. By the 5th day of freely swimming, the feeding behaviour of searching and biting at the bottom has developed into the typical adult pattern. At about the 20th day the number of manipulatory behaviours directed to the substrate increases suddenly, as does the number of agonistic behaviours at about the 30th day.

The significance of the developmental stage of the behaviour of the juveniles to the behaviour of the swarm is discussed (IV.b). At about the stage where the juveniles rapidly expand their manipulatory repertoire, and where the causes for or occurrence of social fleeing continue markedly longer in their influence on the immediately subsequent behaviour, the parental element of Findigging loses its controlling influence on the travel of the swarm over the bottom.

The causal implications of the changes in the behaviour during the ontogeny are discussed (IV.a.i-v). Some behavioural changes are clearly due to morphological changes. For the rest, consideration of the motor patterns, the objects and stimuli reacted to, and temporal relations between the elements, leads to the construction of an hypothesized model of the motivational structure during the ontogeny. This model is then interpreted and presented in terms of drive concepts to explain the behaviour. Firstly, simple stimulus-response chains of behaviours are distinguished from those where continuing internal factors influence subsequent behaviours. The hypothesis is that there develops during the ontogeny internal causal linking between some behaviours but not others, and that those which are linked, are linked in different groups. At the same time as this within-group linking proceeds, a linking between

groups causes the construction of new behavioural elements and, because more external and internal events become linked causal agents for the overt behaviour, there is a correspondingly great increase in the behaviourally effective environmental complexity. The division of the behaviour into drive complexes changes through the ontogeny. It is suggested that there always remains an amount of behaviour which is only loosely - if at all - linked with the rest by internal causal binding. The behaviour can be interpreted such that (1) in the beginning, major drives for schooling and substrate-feeding exist, (2) later, a major drive for manipulation develops within the substrate-feeding major drive whilst some aggressive behaviours result partly from both the schooling and the substrate-feeding major drives, (3) still later, major drives for schooling, attack, fleeing, manipulation, and feeding can be distinguished but have at the same time undergone partial integration (IV.(a).iv.1).

The relationship between the hypothesized motivational structure and some other theories is then discussed (IV.(a).iv.1.b), and the role of attention and orientation is emphasized. It is contended that considering the manners and degrees of the integrations of major drives will be more fruitful in research than focusing on the conflicts between their component drives.

An interpretation of the causation of some selected behaviours is briefly presented. For them (IV.(a).v), and generally (IV.(a).vi), the overall functional adaptedness of the motivational structure is discussed.

The importance, for inter-specific and phylogenetic studies, of heterochrony in the behavioural development is commented on (IV.(a).vii).