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Motivational influences on individual and species differences in response to conspecifics in three *Haplochromis* species (Pisces: Cichlidae)

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Document Version

Publisher's PDF, also known as Version of record

Publication date:

1981

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Carlstead, K. (1981). *Motivational influences on individual and species differences in response to conspecifics in three Haplochromis species (Pisces: Cichlidae)*. s.n.

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SUMMARY

This paper reports on differences in behavior to conspecifics among individuals of the same and of closely related species. The purpose is to determine through which motivational mechanisms selection for responsiveness to stimuli in the environment may have had, indirectly, consequences on the evolutionary development of attack and display behavior.

The behavior of three species of cichlid fish, *Haplochromis elegans*, *H. angustifrons*, and *H. squamipinnis*, all endemic to Lake George in Uganda, was studied intensively in the laboratory. The first and major part of this study is devoted to unraveling the causal organization underlying the response to a territorial intruder. Spatially isolated territorial males, physically but not visually isolated from conspecifics, were presented with an equally-sized conspecific intruder, restrained in a glass tube small enough to prevent it from responding behaviorally to the actions of the test fish. The experiment thus employs a constant external stimulus situation in which differences in the behavioral responses among individual test fish, as well as changes over time in the behavior within individuals, can be attributed to changes in the internal controlling factors for the behavior. Various measurements of the behavior were taken from video films of the experiments, and later analyzed using univariate and multivariate statistical techniques, in order to deduce the existence and define the influence of certain causal mechanisms.

In a first experiment, principal components analysis was used to reduce the large number of behavioral variables to a few response dimensions along which individuals mainly vary. Four components were extracted that explain 77.4% of the total variance of the original variables. These were concluded to reflect individual variation in 1) the *relative attention* paid to the intruder versus other stimuli, 2) *avoidance* responding to the intruder, 3) *responsiveness to disturbance of the surroundings*, and 4) *persistence* of responding to all selected external stimuli. Scores for each individual on each of these response dimensions were calculated so that each fish could be characterized relative to the others on these properties of the response.

Correlations of individual component scores with aspects of the movements and stereotyped behavior patterns performed to the intruder were analyzed. They indicated that two of the components are associated with a tendency to approach

the intruder, and two with a tendency to stay out of its vicinity. The ratio of movements towards and away from the intruder was found to be associated with the strength of these two tendencies.

In the same experiment an attempt was made to manipulate one or more factors underlying the components by presenting a frightening stimulus, a bright light. The light was presented halfway through the observation period while the response to the intruder was ongoing. The behavior in the period with the light on was compared to the behavior before it came on, and to behavior in a similar control period later in time but without the light.

The light increased the scores of individual fish on the components for *avoidance* and *responsiveness to disturbance*, and it removed the changes in the scores on *persistence* that had occurred over time. The results also indicated that there are mutual influences between the components. Scores in the initial period of the test for *responsiveness to disturbance* were found to explain a substantial amount of the variance in *avoidance* later in time whether the light was on or not. Initial scores on *avoidance* and *responsiveness to disturbance* had an inhibitory effect on scores on *persistence* when the light was on.

It was concluded that the light potentiates a system for fear, encompassing the *avoidance* and *responsiveness to disturbance* components. This fear system exerts a control over the persistence of response to external stimuli.

A second experiment was performed to examine the relationship between measurements of the response to the intruder and the response to another constant external stimulus. The response to juvenile fish, residing in the same aquarium with the test fish, was recorded before and after intruder presentation. Response to the experimenter entering the room to place and remove the intruder was also recorded. In the post-intruder period the degree to which decrements occurred in the responsiveness to juveniles or to disturbance was found to be positively related to the amount of response evoked by the intruder. It was concluded that a system exists which controls the attentional mechanisms for responding to territorial intruders by excluding responding to other stimuli.

An attempt was made to explain these phenomena in a model for the arrangement of state variables and integrative systems controlling this behavior. It proposes that the response to the intruder at any given moment is controlled by two mechanisms integrating the output of three systems: a system for responding

to stimuli that disturb aspects of the surroundings (D), a system for responding to territorial intruders (TI), and a system for fear responses (F). The former two systems compete for control of selective attention, and each controls the appropriate motor patterns for responding to the selected stimulus (in the behavioral final common path). Another input to this control originates from the fear system. The model also postulates a factor controlling in general the persistence of the response to all selected external stimuli by influencing the output from systems D and TI.

The discussion of Part I deals with the mechanisms through which responsiveness to external stimuli might have an effect on the form of attack and display behavior, and with the literature on fear behavior in animals.

The second part of this study deals with differences in underlying motivational factors of the response to external stimuli among the three species. The responses were studied of twelve individuals of each species to restrained territorial intruders while at the same time the experimenter was sitting in front of the tank in view of the fish. It was found that *H. angustifrons* is the species most responsive to disturbance afforded by the experimenter. This has the effect of reducing its responsiveness to intruders. *H. elegans* is the most responsive to intruders and least so to disturbance. *H. squamipinnis* has the highest level of a general persistence factor, responding persistently to both disturbance of the surroundings and to territorial intruders. These differences are discussed concerning the environmental forces that might have selected for these motivational specializations in view of what is known of the natural habitat of each species.

Differences among the species in the display associated with spawning activities with females were found to correspond to differences in the display following an approach/withdrawal conflict to restrained male intruders. The divergence of courtship displays in relation to selection for responsiveness to environmental stimuli is discussed.