THE LATERAL DISPLAY OF FISHES: BLUFF OR HONESTY IN SIGNALING?

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ABSTRACT

The adaptive significance of the pattern of aggressive threat display in fishes has been interpreted to suggest that they bluff their rival to believe that they are larger than they really are. Theoretical considerations and the color patterns of body and dorsal fins suggest that in fact the threatening fish may transfer, by its lateral display, information concerning its real size. Hence, the threatening fish influences the reaction of its rival by being honest rather than by bluff.

Key words: fishes; display; bluff; honesty.

Many fish species utilize the lateral threat display, in which the side of the body is turned to the opponent and the dorsal fin is erected. It is customary to suggest that a fish that erects its dorsal fin increases its apparent body size (Baerends and Baerends, 1951) and, consequently, can better intimidate its rival. Hailman (1977a) could find little comparative evidence for the notion that threat displays make the signaler appear larger, but even he admitted that 'one of the best ostensible examples' might be the lateral display of fishes (Hailman, 1977b). If the functional significance of raising the dorsal fin is to make the fish appear larger, the display is a bluff (Maynard-Smith and Parker, 1976), hence, it constitutes deceit rather than honesty in signaling. I shall argue that the evolution of bluff is unlikely on theoretical grounds, for common threat displays, that a simpler explanation of the fish lateral display is possible, and finally, that the two hypotheses can be discriminated by differences in the color patterns they predict.

The assumption that it is possible to evolve a strategy to win by bluff (Maynard-Smith and Parker, 1976) or through clever manipulation (Dawkins and Krebs, 1978)

seems unreasonable. Why should animals continue to react to signals that harm them? Any mutant behaving according to all other available information, except the false signal, would be more adaptive than an animal attending also to the false signal. Reacting to deceitful signals should therefore be eliminated by natural selection. I do not mean to say that cheating is absolutely impossible. Under certain circumstances failing to react to a false signal will be more harmful than reacting. But this cannot be the explanation to common adaptations such as the lateral display of fishes. The 'stupidity' of the cuckoo host which continues to react to signals emitted by the cuckoo nestling has been reinterpreted by similar reasoning (Zahavi, 1979).

Dawkins and Krebs (1978) and Zahavi (1977) suggested that the receivers of signals should evolve responses to honest signals. It is reasonable to assume that most signals display honest information. I suggest that in the side display of fish the length of the fish is displayed honestly. It is also easier to detect the border between the dorsal fin and the body when the fin is spread and hence the true body height. When the fin is folded there is a certain amount of ambiguity as to the real size of the body. This ambiguity decreases when the fin is spread.

I also suggest (1977) that in order to deliver a reliable threat signal the threatening individual should expose itself to a risk which is not reasonable to a fish which is not ready to fight. By exposing its flank to its opponent, the threatening fish advertises its readiness to sustain the first strike and, hence, its confidence in its chances of winning. Furthermore, the spread dorsal fin decreases its option to make a sudden move (to flee or attack), hence, it is more vulnerable to attack by its rival. Fishes fold their dorsal fin when in quick motion and fishes preparing to move fold their fins. While preparing to fight, a fish with a folded dorsal fin would have advantage over its otherwise equal rival whose fin is spread.

It is interesting to note that subordinate fishes which are cornered, but are still threatening, neither spread their dorsal fin nor expose their flanks. They face their opponents with folded fins and open jaws to bite. Analogous postures have been described by Lorenz (1966) for dogs which are frightened but are still aggressive. They also face their rivals ready to bite unlike confident dogs which expose their flanks to their rivals in a side display.

The size-bluff and honesty hypotheses make different predictions concerning the color of the dorsal fin. Under the size-bluff hypothesis, the dorsal fin should be colored like the body in order to enhance the deception of size, whereas in the honesty hypothesis the dorsal fin should be of a color different from the body in order to demarcate the true size of the body. Even a passing familiarity with non-cryptic fish species that use color extensively in signaling, makes it clear that the latter prediction is overwhelmingly supported by comparative evidence (see plates in Smith, 1961; Lythgoe, 1975; Carcasson, 1977; and similar handbooks).

It is also not reasonable to assume that fishes cheat one another about their real body size by spreading their fin, because sooner or later the movement of the fin against the body should disclose the true nature of the fin. It is thus interesting to note that butterfly fishes (*Chaetodon* spp.), most of whose dorsal fin is permanently fixed to their body, display a color pattern common to both body and fin except the distal moving portion of the fin whose color pattern is distinct from the rest of the body.

In sum, it would require extraordinary circumstances for a deceitful signal such as an aggressive size-bluff to become evolutionarily stable, and the actual comparative evidence does not support the old ethological notion that threat displays give the animals the illusion of being larger. The most convincing possible example of this phenomenon, the lateral display of fishes, can be interpreted under a simpler hypothesis of honestly displaying both the readiness to take the risk of fighting and the true size of the body.

Finally, the evidence from color patterns enhancing display postures strongly supports the simpler interpretation of honesty in threat display.

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REFERENCES

Baerends, G.P. and J.M. Baerends-Van Roon. An introduction to the study of the ethology of cichlid fishes. Suppl. *Behaviour*. 1950, 1.

Caracasson, R.H. A Field Guide to the Coral Reef Fishes of the Indian and West Pacific Oceans. London: Collins, 1977.

Dawkins, R. and J.R. Krebs. Animal signals information or manipulation. In Davies N. and Krebs J.R. (Eds.), *Behavioural Ecology*, Blackwell, London 1978.

Hailmen, J.P. Communication by reflected light. In T.A. Sebeok (Ed.), *How Animals Communicate*, Bloomington and London: Indiana University Press, 1977a.

Hailman, J.P. Optical Signals: Animal Communication and Light. Bloomington and London: Indiana University Press, 1977b.

Lorenz, K. On Aggression. London: Methuen and Co., Ltd., 1966.

Lythgoe, J. and G. Lythgoe. Fishes of the Seas. Garden City, N.Y.: Doubleday, 1975.

Maynard-Smith, J. and Parker. The logic of asymetric contests. *Animal Behaviour*. 1975, 24, 159–175. Smith, J.L.B. *The Sea Fishes of Southern Africa*. Cape Town: Central News Agency Ltd., South Africa, 1961.

Zahavi, A. Reliability in communication systems and the evolution of Altruism. In Stonehouse, B. and Perrins, C. (Eds.), *Evolutionary Ecology*. London: Macmillan Press Ltd., 1977.

Zahavi, A. Parasitism and nest predation in parasitic cuckoos. American Nature. 1979, 113, 157-159.