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Geometry of a Selfish School: Defence of Cichlid Young by Bagrid Catfish in Lake Malawi, Africa

W. D. Hamilton has proposed that gregarious behaviour evolves because of 'pruning of marginal individuals' by predators at the edge of an aggregation; this pruning leads to the formation of true herds, flocks, and schools (W. D. Hamilton, *J. theor. Biol.*, **31**, 295–311, 1971). One advantage of schooling has been shown to be reduced predation (D. V. Radakov, *Schooling in the Ecology of Fish*, New York: Wiley, 1973). Fish schooling resembles cover-seeking in that an individual remaining near another fish is, under certain conditions, less likely to be taken by a predator (G. C. Williams, *Publ. Mus. Mich. St. Univ. Biol.*, **Ser. 2**, 351–358, 1964). Juveniles of the eleotrid fish *Gobiomorus dormitor*, for example, have a lower probability of being taken by predators when schooling than when solitary (K. R. McKaye et al., *Copeia*, 542–544, 1979). Hamilton's anti-predator model of consociation can be used to explain the adaptive significance of kidnapping foreign young and the evolution of interspecific brood care in fishes (K. R. McKaye in: *Proceedings of a Symposium on Natural Selection and Social Behavior*, R. Alexander, ed., Newton, Mass.: Chiron, in press). If the 'selfish herd' hypothesis is correct, one might expect to find cases of interspecific brood care in which parental fish keep their own young within the centre of the school and allow the adopted young to remain only on the periphery. We report that three pairs of parental *Bagrus meridionalis*, a predatory catfish, were observed defending young cichlid fishes, and that the pairs apparently manipulated the geometry of the interspecific school in the manner predicted above from Hamilton's theory.

The three catfish nests with cichlid young were among 30 nests observed at the transition between a sandy and a rocky substrate between depths of 25 and 30 m off West Thumbe Island, Cape Maclear, Lake Malawi (34°50′E, 14°05′S). Mixed broods such as these are relatively rare since the cichlids of Lake Malawi are mouth-brooders. In two broods the unidentified cichlid young appeared to belong to a single species, but in one brood the young of two species of cichlids, tentatively identified as '*Haplochromis*' *pictus* and '*H.*' *pleurostigmoides*, surrounded the bagrid (Plate I, Fig. 1). The catfish parents chased away possible predators that approached to within 1.5 m of their brood but left the cichlid young alone unless these young ventured into the area where the bagrid fry were gathered. The parents' own young remained beneath the head of the larger fish of the pair, presumed to be the female. The juvenile cichlids formed a circular school about 0.5 m in radius, and the juvenile catfish were in a smaller, concentric circle. In the case of the photographed brood, two adult cichlids, one of each species being tended by the catfish, circled the brood at a distance of 1 m. These two fish did not feed. Their coloration, behaviour, and orientation to the broods suggest that they were mouth-brooding females that had released the young from their mouths to allow the young to feed on plankton.

Cichlids of the genera *Rhamphochromis*, '*Haplochromis*', and *Pseudotropheus* made predatory strikes upon the broods. During a 10-min watch of a pure brood of catfish, an individual of *Pseudotropheus* sp. took one juvenile catfish. At the nest with the mixed brood, individuals of an undescribed three-spotted '*Haplochromis*' species and of a *Rhamphochromis* sp. (both of which are visible in Fig. 1) directed strikes at the juvenile cichlids but captured none. Such associations persisted over two 10- and 14-day periods in two separate years.

The occurrence of this behavioural interaction between a bagrid catfish and two cichlids, fishes belonging to different orders, suggests that it is unlikely that a non-adaptive mistake (caused by the foster parents' supposed failure to recognize that the adopted young are not their own (as suggested by J. A. Coyne & J. J. Sohn, *Am. Nat.*, **112**, 447–450)) can be invoked to explain this phenomenon. The distinctive shape of the school, caused by the active exclusion of cichlid young from the centre, demonstrates that the catfish parents can clearly distinguish between the cichlid young and their own larger young, as well as between the cichlid young and predators upon the catfish brood. Thus, since a neutral or accidental explanation for this behaviour is inadequate, a more complex hypothesis involving adaptation is required.

The observed behaviour might be adaptive for the cichlids only, or for both the catfish and the cichlids. It is possible that the catfish simply distinguish among (i) their young, which they guard; (ii) predators, which they attack; and also (iii) other small fish, which they ignore unless those fish approach too closely to the catfish young. The association may be beneficial to the cichlids, who gain protection, but of neutral value to the catfish. Until decompression or saturation diving can be safely conducted in Lake Malawi, the necessary observational and experimental data on relative reproductive success of catfish with and without this cichlid ring around their brood cannot be collected. This hypothesis, therefore, cannot be dismissed.

We speculate, however, that the interaction is mutualistic, both catfish and cichlids deriving benefit from the school. Predators on fish broods attack from the sides, or occasionally from above. Cichlid fry were more vulnerable to attack from any direction than the catfish young and would probably be the target of any intruding predator (Fig. 1). Nevertheless, the cichlid fry were actively protected by the parent catfish. There was no altruism in this defence since the catfish young, in turn, enjoyed reduced exposure to predation because of the surrounding cichlids.

How the young cichlids joined the catfish brood is an intriguing question. We suggest that in the case of the photographed nest the two adult cichlids circling the brood were the mothers and that they had released the young from their mouths into the catfish nest. The cichlid fry were defended from predation in a novel way that permitted them to devote their waking time to eating zooplankton (personal observation). The young cichlids could grow and mature much faster since they were no longer confined to their mothers' mouths.

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KENNETH R. MCKAYE
MICHAEL K. OLIVER

Department of Biology,
Peabody Museum,
Yale University,
New Haven, CT 06511, *U.S.A.*

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PLATE I

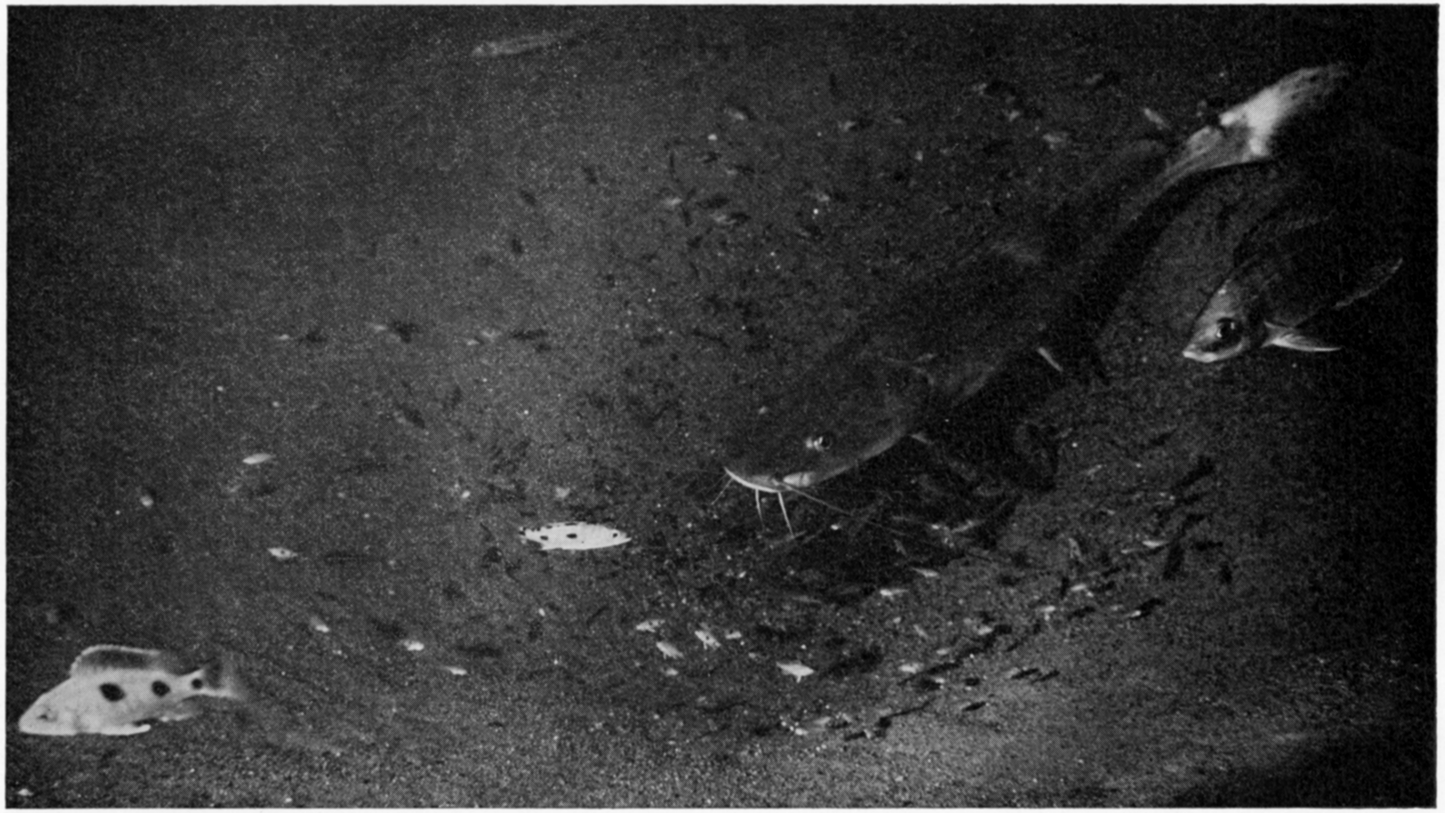

Fig. 1. This photograph, one of a series, shows a female catfish, *Bagrus meridionalis*, guarding a nest. Its own young are beneath its head, and juvenile cichlids of two species surround the catfish young. Two predators are present. The first, belonging to an undescribed '*Haplochromis*' species, is the elongate spotted fish that appears to face the catfish head on but is actually in the foreground. The second, an individual of *Rhamphochromis* sp., is the striped fish at the top. The two presumed mothers of the cichlid young are identified as '*H.*' *pleurostigmoides* (centre right, parallel to catfish) and '*H.*' *pictus* (lower left). '*H.*' *pleurostigmoides* is unique among its species group in having yellow pelvic and anal fins; in the original colour transparency this coloration is clearly visible on the putative mother and the unspotted young. The '*H.*' *pictus* individual, seen in sharper focus in other photographs, was identified through experience gained during a taxonomic revision currently in progress. Details of spot shape and placement suggest that the spotted young are conspecific with this adult fish.