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Social Behavior: How Do Fish Find Their Shoal Mate?

Dispatch

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Fish form social aggregations called shoals which often consist of fish with similar morphologies. Experiments using zebrafish pigment variants demonstrate that fish can select shoal mates solely on the basis of their color patterns, and that early experience plays a key role in determining these shoaling preferences.

A great diversity of social groups can be found throughout the animal kingdom. One particularly dramatic example of a social group of animals is a school of fish swimming in a highly synchronous and polarized manner. Although not all fish form these highly specialized schools, many do form groups called shoals that are held together by social attraction [1]. As reported recently in *Current Biology*, Engeszer *et al.* [2] have now shown, using pigment variants of the zebrafish *Danio rerio*, that fish can select shoal mates on the basis of their learned preference for particular color patterns.

Many benefits of group living have been proposed, and shoaling behavior in fish is proving to be an excellent experimental system in which to test many of these hypotheses [3]. Shoaling can provide a defense against predators by mechanisms that include increasing predator detection, diluting the chance of capture, and confusing predators. Further down the food chain, shoaling enhances the ability of the fish to find their own prey, and can lead to an increase in foraging success. Shoaling may not only increase the chance that a fish finds food, but may also increase the chance that a fish finds a mate. Finally, fish may particularly benefit from being a member of a shoal through an increase in hydrodynamic efficiency.

One common feature of shoals is the strong phenotypic resemblance between the fish in a shoal. Much experimental work has been done in small fish that exhibit shoaling behaviors, such as killifish, minnows, guppies and sticklebacks, to identify the factors that contribute to shoaling preferences. Some of the key traits used by many fish to choose shoal mates include size of the shoal, species type, body size, parasite infection status, kinship and familiarity [3]. In the wild, fish probably use a combination of these cues to optimize predator avoidance and/or foraging success. Some experimental work has begun to address the relative roles of these different factors in shoaling preferences [4–6]. But it is first necessary to isolate individual factors to begin to dissect their relative contributions to shoaling preferences.

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One trait that may influence the choice of a shoal mate is the dazzling array of colors and pigment patterns found in fish species. Differences in pigment patterns may, however, be associated with other morphological or behavioral differences between fish, making it difficult to isolate the specific role of coloration in shoaling preferences. Engeszer *et al.* [2] took advantage of the zebrafish pigmentation mutant *nacre*, in which a point mutation in the *mitfa* gene leads to a dramatic loss of the black-pigment-containing melanophores on the body of the fish [7].

By comparing the shoaling preferences of homozygous *nacre* mutants with heterozygous siblings that have the wild-type zebrafish pigmentation — stripes — Engeszer *et al.* [2] were able to control completely for traits that might influence shoaling preferences such as differences in morphology and behavior, as well as kinship. They found that zebrafish exhibit strong color shoaling preferences: wild-type fish prefer to shoal with wild-type fish, and *nacre* fish prefer to shoal with *nacre* fish (Figure 1). Shoaling by color has previously been observed in mollies, where black and white morphs preferentially associated with fish of matching color [8]. But in this case genetic background effects could not be as carefully controlled as in the zebrafish study [2], highlighting the power of using single gene mutants for analyzing shoaling preferences.

Fish cannot know their own color, so how do they acquire this shoaling preference for fish of the same color? To address this question, Engeszer *et al.* [2] assessed whether zebrafish have an innate or a learned color preference. Because wild-type and *nacre* siblings can be distinguished at 60 hours post fertilization, the authors were able to raise fish in different environments, starting at a very early stage. They reared zebrafish of the two color phenotypes in three ways: with siblings of the same phenotype, with siblings of the different phenotype, or in isolation. Fish raised in isolation showed no shoaling preference for either color. Fish raised in groups, however, showed a very strong shoaling preference for fish with the same pigment pattern as those they were reared with, regardless of their own phenotype (Figure 1). This result suggests a strong role for learning and early experience in the acquisition of color shoaling preferences in zebrafish.

Previous work in other fish suggests that prior exposure to potential shoal mates — familiarity — makes an important contribution to shoaling preferences [3]. Engeszer *et al.* [2] did not directly test the role of familiarity in shoaling preference, because their stimulus fish were reared separately from the experimental fish. Importantly, olfactory and auditory cues should not be a factor in the shoaling preferences seen in their experimental design. So they were able to isolate color as the sole trait that the fish use to determine shoaling preference. It would be an interesting follow-up to this study to determine if morphological cues, such as color, might be one of the

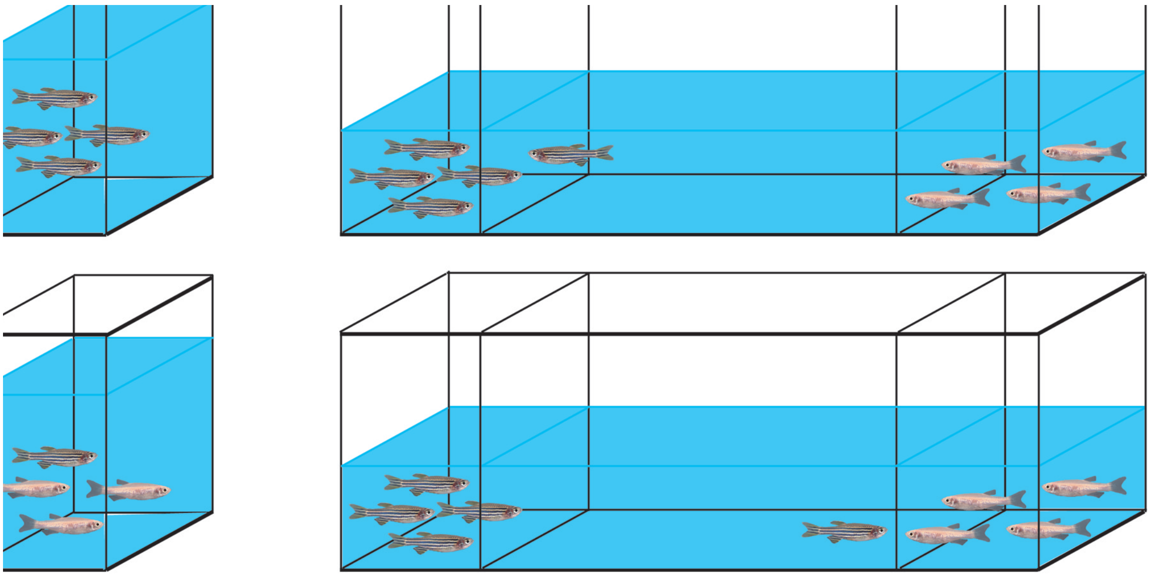

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Figure 1. Learned shoaling preferences in zebrafish.

(A) Wild-type zebrafish reared with wild-type siblings prefer to shoal with wild-type zebrafish; *nacre* zebrafish reared with *nacre* siblings prefer to shoal with *nacre* zebrafish. (B) Wild-type zebrafish reared with *nacre* siblings prefer to shoal with *nacre* zebrafish; *nacre* zebrafish reared with wild-type siblings prefer to shoal with wild-type zebrafish.

mechanisms that underlie the preference for shoaling with familiar fish.

To explain why there is often phenotypic matching between fish in a shoal, several hypotheses have been put forward. One popular theory, called the 'oddity effect' posits that rare, phenotypically distinct individuals within a shoal are more likely to be targeted by predators. Two studies using minnows as prey fish and bass as predators provides the strongest experimental evidence in support of this hypothesis [9–10]. Color mutants in zebrafish provide an opportunity to test this hypothesis further using fish that are identical in all respects except pigment pattern, to see if predators really do target odd-looking fish within a shoal.

Many mutations affecting pigment patterns have now been isolated in zebrafish, and they often resemble pigment patterns found in other *Danio* species [11]. Ultimately, it will be necessary to do more work on the ecology and evolution of these different *Danio* species in their natural environment. Then it will be possible to have an integrated view of the cellular and developmental basis of pigmentation with the adaptive significance of these pigment patterns in the wild. Currently, the ability to genetically manipulate zebrafish enables an analysis of the effects of a single or relatively few genetic changes on behavioral phenotypes. Future studies using additional zebrafish pigmentation mutants are sure to yield interesting results in laboratory studies of social behaviors such as mate choice and shoaling.

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