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Food-finding ability in cave fish (Astyanax fasciatus)

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SUMMARY

When competing under cave similar conditions, such as darkness and food scarcity, cave fish find much more food than their epigean relatives. The cave fish not only react much faster to food but also their food-finding ability is four times higher compared to that of the epigean fish. Several morphological and ethological alterations in the cave fish, described by other authors, seem to be responsible for this adaptation to the cave conditions.

INTRODUCTION

It is generally held that food scarcity in caves often acts as a forceful selective agent. Besides an efficient food utilization and a reduced food demand, because of reduced activity and/or reduced metabolic rate which results in greater resistance to starvation, a higher food-finding efficiency is an obviously adaptive response to environments poor in food (Culver, 1982, 1985; Mitchell, 1969; Peck, 1973; Poulson, 1963, 1964; Poulson & White, 1969). For example, the cave crayfish *Orconectes inermis* is better able to detect live prey compared to the epigean *Orconectes limosus* (Cooper, 1969), and the cave salamander *Proteus anguineus* shows a higher performance in prey detection than the closely related epigean salamander *Necturus maculosus* (Durand et al., 1981, 1982). Similarly the cave salamander *Haideotriton wallacei* and the spring cavefish

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Chologaster agassizi both have a relatively high feeding success (Peck, 1973; Hill, 1969). Sensory improvement in compensation for the absence of vision has been shown in all the cave animals investigated.

The characid fish *Astyanax fasciatus* (Cuvier, 1819) is widespread in South and Middle American freshwaters and also inhabits several limestone caves in North Mexico, Tamaulipas and San Luis Potosi states (Michell et al., 1977). It represents a special case: epigean and hypogean fish of this species are completely interfertil (Sadoglu, 1956) although they are clearly separable with regard to several morphological features. In a few caves the hypogean fish live associated with epigean ones, which sometimes are washed into the cave by floodings. In such cases interbreeding seems to occur in caves where food is abundant, as in the Chica cave, where food is provided by bat guano (Avise & Selander, 1972; Mitchell et al., 1977; Wilkens, 1972). In caves where food is scarce, e.g. the Micos cave, hybridization does not occur. Epigean fish washed into a cave with little food look undernourished within a short time and seem to be unable to compete with the cave fish (Mitchell et al., 1977; Wilkens & Burns, 1972). In the Micos cave epigean fish have very low condition factors compared to different kinds of cave fish and also in comparison to epigean fish caught at the surface (Wilkens & Hüppop, 1986). The condition factor, i.e. the relationship of body mass and body lenght, is a good measure of the nutritional state of a fish.

Besides having reduced eyes and a reduced melanophore system based on the loss of function in darkness, the hypogean *A. fasciatus* can be separated from their epigean relatives by several adaptive features. These are the enlarged and predominantly ventrally spread gustatory areas in the skin covering the head (Schemmel, 1967, 1974) and the difference in the angle of the body when searching for food (Schemmel, 1981). The aim of this investigation was to compare the efficiency of the cave fish in finding food with that of the epigean ones under cave similar conditions (food scarcity, darkness). Former observations on food-finding efficiency of hypogean *A. fasciatus* were made only with the hybrid and not food restricted fish from the Chica cave (Glaser, 1968; Thines et al., 1966).

MATERIAL AND METHODS

Six epigean fish from the Rio Teapao and six hypogean fish from the Pachon cave, three females and three males each, were taken randomly out of groups that had been held for at least one and a half years in the laboratory. The fish were transferred to a 200 l aquarium, maintained at a temperature of 25 °C in a dark and silent room. The fish were allowed to acclimatize to the cave similar conditions for about two weeks and were fed every other day. Disturbance was held to a minimum and all handlings and observations during the experiments were made with an infrared-night-sight apparatus.

After acclimations twenty experiments with twenty pieces of beef-heart muscle each (about 10 mm^3 in size) were made every other day. This rate of feeding kept the fish hungry enough to search intensively for food. The single pieces of meat were carefully put into the water where they sank to the bottom immediately. The next piece of food was not given until the former one was found and eaten by a fish. This made it easy to observe whether an epigean fish or a hypogean one found and ate the food. After all twenty pieces of food were eaten, the fish were fed with beef-heart and with dry food ad libitum, enabling the epigean fish to finally find enough food as well.

RESULTS

About 80% of all food particles were found and eaten by the cave fish, whereas the epigean fish were successful at finding only 20% (Fig. 1). Furthermore, the epigean fish did not improve; food-finding was not higher at the end of the experiments than at the beginning. If habituation to the cave conditions took place it happened in the first weeks during the acclimation time, and was obviously insufficient.

Neither the epigean nor the hypogean fish responded to the food pieces as they sank to the ground. Only if direct contact near the mouth occurred, did the fish snap and try to catch it. However, when a piece of food laid on the ground there was a clear difference in behaviour between the epigean fish and the hypogean fish. The latter reacted to the presence of the piece of food already after 5 to 10 seconds. After one cave fish began to search, the other cave fish followed within a few seconds. They searched for it exclusively on the ground swimming at an angle of about 45° subtended to the ground as described by other authors (Glaser, 1968; Schemmel, 1967, 1980; Thinès, 1955). The epigean fish, on the other hand, not only reacted very slowly to the food but also showed little propensity to search for the food on the bottom. Often all six cave fish were looking for food on the ground before any epigean

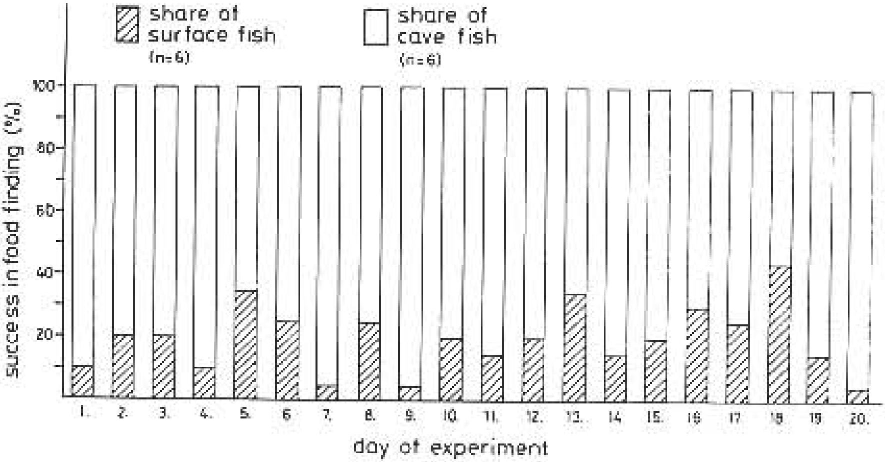

Fig. 1 - Food-finding success in cave-fish and in surface fish (*Astyanax fasciatus*), when competing under cave similar conditions.

fish showed a reaction. Only a coincidental approach towards the piece of food to a distance of less than 3 to 5 cm released food searching behaviour in the epigean fish. They then swam at a very steep angle (see also Schemmel, 1967, 1980). However, food searching was not very successful since the movements were excited and violent. The epigean fish could often not find the food particles, after having pushed them away while rotating around their body axis. Once the epigean fish started to look for food, they did it exclusively on the ground like the cave fish. Therefore they could find enough food at the end of each experiment when food was given ad libitum. The same behaviour has been observed in artificially blinded fish (Schemmel, 1967, 1980; Thinès & Capon, 1975). Epigean fish can find food in total darkness, but they need much more time compared to the cave fish.

DISCUSSION

For cavernicoles with epigean ancestors that forage nocturnally food scarcity rather than the darkness is the main selection factor for the evolution of a superior ability to locate food (Cooper, 1969). For cavernicoles with diurnal ancestors, as *A. fasciatus*, both factors act together as important selective agents. The epigean fish usually take up floating food particles by optic orientation from the open water and almost never take up food from the ground. Since optic orientation is not possible in darkness, the cave fish evolved a more efficient food searching behaviour: they search only on the ground, as do most of the nocturnal feeders. This behaviour is supported by the morphological and ethological alterations mentioned above which enable the cave fish to preferentially register and localize food lying on the ground (see also Schemmel, 1967). They are also able to feed at the surface, another twodimensional area.

The fact that the cave fish reacted much faster to food does not imply an improvement in tasting ability, that is a lowering of tasting thresholds. Earlier investigations have never shown this (Breder & Rasquin, 1943; Humbach, 1960). Little is known of the nasal organ, however, no improvements in cave fish seem to exist (Breder & Rasquin, 1943; Schemmel, 1967). Chemicals may bring more and different informations to cave fish than to epigean ones which normally feed by optic orientation, independent of threshold effects. The same holds for disturbances caused by food particles dropping into the water. Additionally, my results may support earlier findings (Lüling, 1954) that characteristic food searching movements of the cave fish on the ground cause specific water turbulences. It might be possible that these turbulences contain more information for cave fish than for epigean ones. As a consequence, the cave fish, stimulated by the characteristic turbulences after one cave fish released them, would be searching for food on the ground long before the epigean fish. This would increase the possibility that a cave fish and not an epigean fish finds the food.

Intensive food searching behaviour on the ground as an adaptive trait in cave fish has also been observed in the hypogean form of *Poecilia sphenops*, and is possibly related to morphological alterations of the mouth, the belly, and the caudal peduncle (Gordon & Rosen, 1962; Walters & Walters, 1965). The hybrid Chica cave fish of *A. fasciatus* also show this form of food searching (Thinès et al., 1966). However, the Chica cave is rich in food and the observations were not quantitatively compared to the pure epigean fish. If the Chica cave fish are really better in food finding than epigean ones, this adaptation would be a compensation for the loss of vision only.

In food scarce caves where cave fish and inwashed epigean fish may occur together, as in the Micos cave (Mitchell et al., 1977; Wilkens & Hüppop, 1986) the cave fish have an advantage when competing with the epigean fish. The inferiority of the epigean fish under cave similar conditions, which is accelerated by their higher metabolic rate and their higher body mass loss during starvation (Hüppop, 1985, 1986), explains their undernourished appearance in such caves.

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RESUME'

Quand ils se trouvent en compétition dans des conditions identiques à celles existant dans les grottes, telle la rareté de la nourriture et l'obscurité, les poissons cavernicoles trouvent beaucoup plus de nourriture que leur parents épigés. Non seulement ils réagissent plus vite pour se nourrir mais aussi leur possibilité pour trouver leur nourriture est quatre fois supérieure à celle des poissons épigés. Plusieurs modifications morphologiques et éthologiques propres aux poissons cavernicoles, décrites par d'autres auteurs, semblent être responsables de cette adaptation aux conditions du biotope souterrain.

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