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Adaptive Behavior of Astyanax fasciatus (Cuvier) (Pisces: Characidae) and of Brachyrhaphis rhabdophora (Regan) (Pisces: Poecilidae) Associated with Subterranean Waters

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Abstract

A freshwater fish community formed by populations of two species (Astyanax fasciatus and Brachyrhaphis rhabdophora) were found at Palo Verde in 1) a pool, under the tree canopy, directly connected with a cavity which is a source of subterranean waters; and 2) another pool, located in an open area, and connected to the first one by a water canal. The schooling and feeding behavior of the fish in these nearby communities was different. In the first pool (associated with subterranean waters) the fishes formed small schools during short periods of time and did not react to some visual stimuli produced above the water surface. In the second pool, the fishes formed large schools almost all the time and strongly reacted to the same kind of stimuli with sudden changes of direction and/or breaking up of the school. Under experimental conditions, individuals of both species in the pool associated with subterranean waters took pieces of bread dropped onto the water, and carried them to the subterranean cavity where they ate them. This behavior is interpreted as an adaptation of A. fasciatus to a very peculiar environment. The well-known phenotypical and behavioral adaptation of the genus Astyanax to cave environments, and the successful adaptation of this fish to almost any freshwater and brackish conditions, and its high genetic variability are discussed in order to support that interpretation.

Introduction

Astyanax is a characid fish genus with a broad distribution in the New World. It extends from Argentina to Texas. It has overcome the Central American filter-barriers sooner than any other New Southern members of the icthyofauna from their South American origin (Bussing, 1976). Bussing also explains that unlike other species groups of the New World, only the Astyanax fasciatus species complex and the genus Synbranchus (Synbranchidae) have reached the southern United States and southern Mexico respectively. In spite of this extensive distribution, neither has been subjected to considerable speciation. Curiously, these two families of southern origin are the only ones that have blind cave representatives: A. mexicanus (sometimes considered as a synonym of A. fasciatus; Wilkens, 1971) in central Mexico, and Furmastix infernalis (Hubbs) (Synbranchidae) in the Yucatan Penisula. (Note: There is also a blind characid associated with subterranean waters, but not in caves, in Brazil: Stigichthys typhlops; see Brittan and Bohlke, 1965).

The Mexican species (form?) closely related to A. fasciatus can be found as a surface, eyed form in the rivers and as a cave, blind form. These forms interbreed in both natural and experimental conditions (in the lab), producing fertile hybrids with a phenotypic intermediate form in the F_1 generation, and a F_2 generation (after $F_1 \times F_1$) whose individuals range from an almost completely blind, depigmented form to an almost "normal," surface (eyed) form (Sadoglu, 1957; Peters and Peters, 1973; and others). Genetic and electrophoretical studies have revealed that there is not convincing evidence to support the assignment of the cave fish and the surface fish to separate genera, nor indeed to different species (Avise and Selander, 1972). Both forms are not only different in their phenotypic characteristics, but also in their behavior: the surface form schools, is very aggressive, and is active all the time (Breder, 1942, and others). The blind form displays memory and little social interaction (Romero, unpubl. data). This differential behavior between both forms is interpreted as a clear adaptation of each population of the same species to different environments (lack of competitors, loss of circadian rhythms in caves). It seems that this high adaptability is due, at least in part, to the high heterozygocity of the Astyanax complex. Avise and Selander (1972) determined that populations of Astyanax mexicanus inhabiting rivers and arroyos are among the most polymorphic organisms yet studied. The mean value of 11.2% heterozygous loci per individual has been equalled only by Drosophila pseudoobscura, D. willistoni, and Mus musculus. Bussing (pers. comm.) has found a very high phenotypic variability of A. fasciatus in Costa Rica.

On the other hand, Bussing (1976) attributed the unique, broad distribution of Astyanax among freshwater fishes of South American origin to a "combination of generalized ecologic requirements, salt tolerance, large populations, a strong migratory proclivity, and little ostariophysian competition." Bussing and Lopez (1977) showed that A. fasciatus in Costa Rica is a eutropic species, is found under varying ecological conditions, and forms large schools. Its relative biomass in comparison with other species is very high. These studies were made in the same ichthyological province (Chiapas-Nicaraguan) (Bussing, 1976) as my research site. Although A. fasciatus has this broad distribution and some ecological studies involving this species have already been done, we know very little about its behavior that may help to understand the species' ecological success.

The species found in both pools in this study, Brachyraphis rhabdophora, is a small poecilid species which is abundant in flowing waters, especially in zones under tree shadow. It is one of the few species that can be found in headwaters of rivers (which fits perfectly with the conditions of this research site), although this species is resistant to conditions of drying pools and can also be found in shallow waters of the margins of large rivers (Bussing and Lopez, 1977).

The Site

Between July 14 and July 17, 1981, I found a fish community formed by two small populations of the species A. fasciatus and B. rhabdophora in a 19.45 m^2 pool about 100 meters from "La Hacienda de Palo Verde" (Dr. Rafael Lucas Rodriguez Caballero Wildlife Refuge and Palo Verde National Park), Province of Guanacaste, Northwestern Costa Rica. Palo Verde extends over 9,466 hectares of the north bank of the Tempisque River. The topography of the refuge is flat, slightly rolling with a transition to hills. The run-off profiles are prominences of superficial waters, except in the lowest points in which run-off water is accumulated during the rainy season (Boza and Mendoza, 1981).

The place where the fishes were found is a boot-shaped pool that receives its water from two sources: 1) from an underwater source below the level of the surface of the pool, and 2) from a very small waterfall, also of subterranean origin, two meters up the pool. This pool is occasionally used by the people who live in "La Hacienda" as a source of potable water. A man-made well is there but it was not used either several months before or during my observations. The water goes from this pool through a canal to a little marsh on the road to "La Hacienda." In these two places, as well as in the canal, individuals of both species were observed. The deepest place of the boot-shaped pool is 1.17 m and almost all the bottom is covered by a very soft mud of fine grain. Below it, there are some rocks (not visible from the surface), especially around the well. Some bubbles could be seen coming from the bottom of the pool and also from the well. They are probably related with a phenomenon of subsidence. Some leaves from understory and canopy plants were seen on the bottom. There is also a platform over the pool, with a water pump. This platform was used for most of my observations (see Figs. 1 and 2).

The Fishes

Individuals of both species rarely form schools in the boot-shaped pool, and these schools were small (no more than 6 individuals) and the duration of the school was limited (no more than 2 minutes). The fishes of the other pools that receive water from the boot-shaped pool through the canal, formed large schools almost all the time.

The fishes of the boot-shaped pool were almost always very close to the surface of the water. The number of individuals and their body size were greater close to the exit of the subterranean waters. The abundance of fishes was determined using quadrats of 50 cm^2 in three different places of the pool. These quadrats were established with cords supported from the banks of the pools and from the platform. The quadrats were set up one day before the experimental observations in order to avoid disturbed behavior.

The results of the observations of the quadrats confirmed the initial impressions that the fishes were more abundant close to the entrance of the cavity than elsewhere. Also, the fishes were more active after the beginning of the experiments (with the dropping of the first object on the water) (see Table 1). The only nonmicroscopic aquatic animals seen in addition to the fishes mentioned before were crayfish (Crustacea: Decapoda: Natantia: Palaemonidea), the species of which has yet to be determined.

Experimental Behavioral Studies

A. fasciatus is an omnivorous species while *B. rhabdophora* is a carnivorous one (Bussing, pers. comm.). Because some leaves were found on the bottom, I dropped leaves from several species of understory and canopy plants on the surface of the water of the first pool. The initial reaction of the fishes was to go to the place of dropping and swim around the leaves until they submerged in the water. They never bit the leaves, and after seven leaves had been dropped in a period of five minutes, the fishes displayed a lack of interest in further leaves that were dropped. The same results were obtained using mud and living and dead myriapods (Chilopoda: Epimorpha: Scoropendromorpha), which are very common in this site.

When pieces of bread were dropped far away from the entrance of the subterranean cavity, only the small poecilids and some small individuals of Astyanax paid attention to them.

When the bread was dropped gently on the surface of the water, it was not noted as food by the fishes in a period of 8 minutes, even when several individuals swam close to the piece of bread. But when, at random, some of the fishes (of either species) swam very close to the bread and touched it (or almost touched it; further analysis of the photographs taken during this process will give more details), that fish bit the food and vibrated its body in a different way than for swimming. Then many of the fishes came immediately to the piece of bread. In consequence, vibrations of feeding fish (and also of food being dropped?) as opposed to smelling, seem the basic signal for the group in order to know of the presence of food.

Another observation was that neither of the species formed schools after the first dropping of objects. Both before or after the experiment, I moved my hand and shook some clothes close to the surface of the water, but there was almost no reaction by the fishes. But when I repeated the same visual stimuli with the fish community of the other pool (about 50 m away from the first one) where these fishes form large schools, they did react with sudden changes in their swimming directions, and by dispersing into 2 or 3 smaller schools. The second pool lacked canopy trees around it, and these fishes were believed to be more exposed to predation by birds.

During the night fish activity was also noted, but because I lacked good artificial illumination (dorsal coloration in both species closely matches the bottom substrate of the boot-shaped pool), no experimental observations were made.

Crayfishes were observed walking on the bottom of the pool as well as on the well walls. I counted as many as 5 individuals at the same time in the first pool. They were usually looking for food on the bottom. Sometimes, when food was taken by a crayfish, a solitary individual of Astyanax went directly to the piece of food carried by the crayfish. As soon as this happened, the crayfish abandoned the food and swam backwards rapidly. Aggressivity is the norm in Characid fish behavior (e.g., piranhas belong to the same family) and aggressivity (agonism) has been already noted in the literature (Myers, 1966) for Astyanax.

Bread Experiments

Little pieces of molded bread (which float on the water) were dropped 10 times, one piece each 15 minutes. This experiment was repeated two times daily, in the morning starting at 7:30 AM, and in the afternoon starting at 1:15 PM, over three days. The weather was generally sunny during these days, and no heavy rain occurred at night. The flow of water to the pool and the level of it seemed constant during the period of observation.

All of the times (except one) when the pieces of bread were dropped from the platform into the quadrat #1, the fishes (especially the little ones) took this food and, swimming quickly, they pushed it to the entrance of the cavity until the piece of bread could not be seen anymore from the platform. The fishes had to swim against the current in order to carry the food. After that, no trace of bread was observed and after five minutes the violent swimming behavior and general activity of the fishes close to the entrance of the cavity ceased and the fishes seemed to return to their normal distribution and swimming behavior in the pool.

When pieces of bread were dropped out of the quadrat (but no more than 20 cm away), similar results were obtained. During the days of the experiments, a little floating log was put between the quadrat and the entrance of the cavity. In this case the fish also pushed the bread toward the cavity, five times jumping over the log and two times doing so under the log (2 cm diameter). Saltatory capacity in Astyanax fasciatus has been observed during its migration; Lopez, 1980). These data as well as the data of time spent carrying the bread to the cavity are shown in Table II. As it can be seen, the mean time spent between the moment that the food was taken and the moment that it was introduced into the cavity is a little shorter in the morning than in the afternoon.

Discussion

The differences in behavior between the two communities of the fishes Astyanax fasciatus and Brachyrhaphis rhabdophora, connected by water but under different ecological conditions, cannot be considered too surprising because more striking differences have been observed between cave and surface populations of Astyanax in Mexico and also because the high heterozygocity of this genus is presumably reflected in behavioral characteristics as well as in phenotypic ones. If we add to these factors the fact of high ecological adaptability of this fish, then we can consider this adaptive behavior as an additional proof of this wide adaptability.

Detailed analysis of the pictures taken during the experimental observations will reveal the exact role (if there is some difference) played by each species during the "take food to cavity" behavior. On the other hand, further video and/or subaquatic recording of this behavior would give additional information, especially for the mathematical analysis of it. Also genetic studies may result in some conclusions concerning the genetic differentiation between the populations of both pools, as well as on the genetical basis of the differential behavior in these species.

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Literature Cited

Avise, J. C. and R. K. Selander. 1972. Evolutionary genetics of cave-dwelling fishes of the genus Astyanax. Evolution 26 (1): 1-19.

Boza, M. A. and R. Mendoza. 1981. The National Parks of Costa Rica. Incafo, S.A.: Madrid.

Breder, C. M., Jr. 1942. Descriptive ecology of La Cueva Chica, with special reference to the flind fish, Anoptichthys. Zoologica 27: 7-15.

Brittan, A. and J. E. Bohlke. 1965. Stygichthys typhlops, a new genus and species of characid in subterranean waters in Brazil. (Source not given)

Bussing, W. 1976. Geographic distribution of the San Juan Ichthyofauna of Central America with remarks on its origin and ecology, in Thorson, T. B. (editor), School of Life Sciences, University of Nebraska, Lincoln, pp. 157-175.

Bussing, W. A. and M. I. Lopez-S. 1977. Distribucion y aspectos ecologicos de los peces de las cuencas hidrograficas de Arenal, Bebedero y Tempisque, Costa Rica. Rev. Biol. Trop. 25(1): 13-37.

Lopez-S., M. I. 1980. Migracion de la sardina Astyanax fasciatus (Characidae) en el rio Tempisque, Guanacaste, Costa Rica. (Source not given).

Myers, G. S. 1966. Derivation of the freshwater fish fauna of Central America. Copeia 1966 (4): 767-773.

Peters, N. and G. Peters. 1973. Genetic problems in the regressive evolution of cavernicolous fish, in Schroder, J. H. (editor), Genetics and Mutagenesis in Fish, Springer-Verlag: N.Y., pp.. 187-201.

Sadoglu, 1957. Mendelian inheritance in the hybrids between the Mexican blind cave fishes and their overground ancestor. Verh. dtsch. zool. Ges. Graz. (Vol. ?), 432-439.

Wilkens, H. 1971. Genetic interpretation of regressive evolutionary processes: studies on hybrid eyes of two Astyanax cave populations (Characidae, Pisces). Evolution 25: 530-544.

Table 1. Number of fishes/quadrat/time (5 minutes) before and after the first dropping of any object. The number of fish/quadrat was determined by observing how many fishes entered through each side of the quadrat.

	Before	After
Quadrat I	148	197
Quadrat II	28	31
Quadrat III	4	5

Table 2. Behavioral data relating to the experiment in which bits of bread were dropped every 15 minutes into the water of the boot shaped pool with the subterranean cavity.

	Day 1		Day 2		Day 3		
	AM	PM	AM	PM	AM	PM	Total
Number of pieces of bread dropped	10	10	10	10	10	10	60
Number of pieces of bread dropped into the quadrat	7	7	7	7	7	7	42
Successful "take food to cavity" behavior	10	10	9	10	10	10	59
Mean interval from taking food to introducing it to cavity	16	19	15	19	16	23	18 min(mean) 15.7 min (AM) 20.3 min (PM)
Number of pieces of bread dropped 1.5 m from Quad. I.	4	2	2	2	6	.0	16
Successful "take food to cavity" behavior in latter experiment	1	0	0	0	0	0	1

FIGURE 1

Q= quadrat; W=well; E= entrance of the subterranean cavity; 2S= secondary source of water; EW= exit of exceeding water; C= canal.

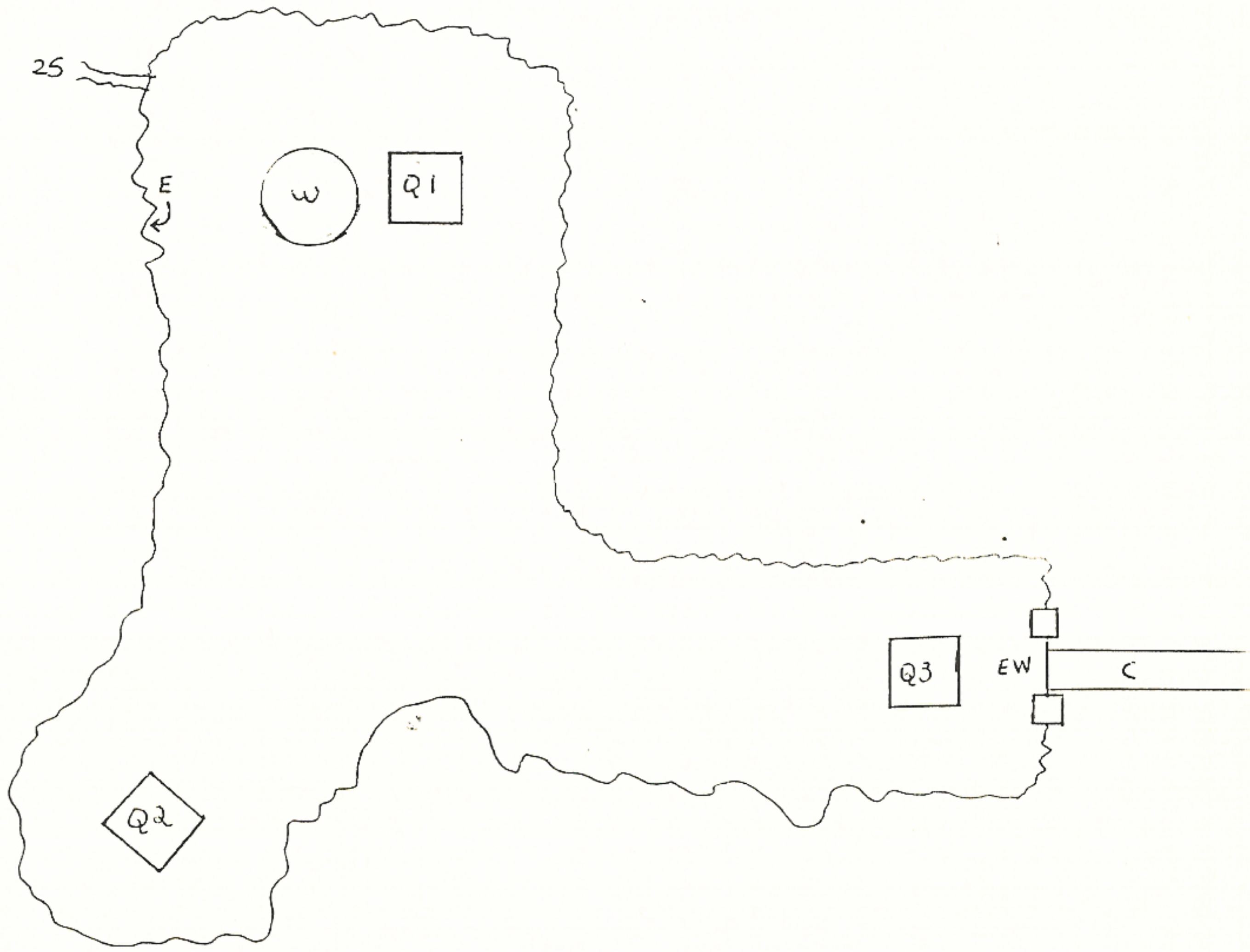

FIGURE 2

LW = Level of water; E = entrance to the cavity; Cv = cavity;
W = well; P = platform; 2S = secondary source of water.