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Cave Colonization by Fish: Role of Bat Predation

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Abstract: Freshwater fishes found in a tropical pool regularly enter a subterranean source of water. They do so mostly when fishing bats are active in the evening. If fish are experimentally attracted to the pool during this period, fishing bat activity increases. Laboratory studies demonstrate that avoiding open areas in the evening is characteristic of these fishes. Predation by fishing bats can be a selective pressure favoring cave dwelling, an alternative hypothesis on the origin of cave colonization to entrapment and directional evolution.

Introduction

Although many examples exist of obligate (troglobitic) and facultative (troglophilic) cavernicoles for which a surface (epigean) ancestor can be presumed, the origin of cave colonization remains puzzling. Some theories of the evolution of cave populations assume accidental entry into caves followed by permanent entrapment of the organisms. Others propose some directional ("regressive") evolution on the assumption that cavernicolous animals represent "dying phylogenetic lines" which seek refuge in caves (*see* Barr, 1968, for a review of these theories). Neither assumption has experimental confirmation.

A ubiquitous freshwater teleost, *Astyanax fasciatus mexicanus* (Characidae), is frequently cited as an example of cave adaptation from an epigean ancestor. It is found as an eyed and pigmented surface form and as a blind and depigmented cave one. Although Hubbs and Innes (1936) described the cave form as a new genus and species (*Anoptichthys jordani*), breeding experiments (Peters and Peters, 1973; Sadoglu, 1957), as well as cytogenetic (Kirby *et al.,* 1977) and electrophoretic studies (Avise and Selander, 1972), indicate that these two forms are conspecific. These forms differ not only in their morphology but also in their behavior. In contrast to the behavior of the eyed form, the blind one does not school, lacks periodic activity cycles (*i.e.,* does not have rest periods like the epigean one), is not aggressive and, although it produces an alarm substance, does not react to it (Breder, 1943; Pfeiffer, 1966; Schemmel, 1980).

Several species of tropical bats capture fish such as *Astyanax fasciatus* from surface waters (Bloedel, 1955; Reeder and Norris, 1954). The echo-locating *Noctilio leporinus,* for example, is known to prey on *A. fasciatus* and on the cichlid *Cichlasoma urophthalmus* (Simmons *et al.,* 1979; Suthers, 1967; Villa-R., 1966). The distributions of *N. leporinus* and *A. fasciatus* are very similar, the former ranging from central W Mexico to Argentina, the latter from southwestern USA to Argentina.

At the beginning of the wet season (May) of 1982, I studied a two-species assemblage of about 120 fishes, ca. 60% *Astyanax fasciatus* and 40% the poeciliid, *Brachyraphis rhabdophora*. This assemblage colonized a shaded pool, fed by subterranean waters, that was constructed in 1976 close to "La Hacienda de Palo Verde," Guanacaste Province, Costa Rica. Diurnal observations on these fishes suggested that both species show an affinity for the subterranean habitat, evidenced by their behavior and distribution. Both species carry food into the subterranean cavity prior to eating it (Romero, 1984).

Casual observations indicated that fishes move into the subterranean source of water at dusk—the time that fishing bats begin foraging (Bloedel, 1955)—and that they reappear in the pool after the bats cease flying over it.

Methods and Results

To examine whether the subterranean cavity serves to protect fish during the time of active foraging by bats, a laboratory experiment and four field manipulations were performed.

The field observations were made from 1800-2130 hr for 9 consecutive days, with an interval of 2 days between the same kind of experiment. In addition to direct observations, a TV camera was placed on a platform directly over the center of the pool at

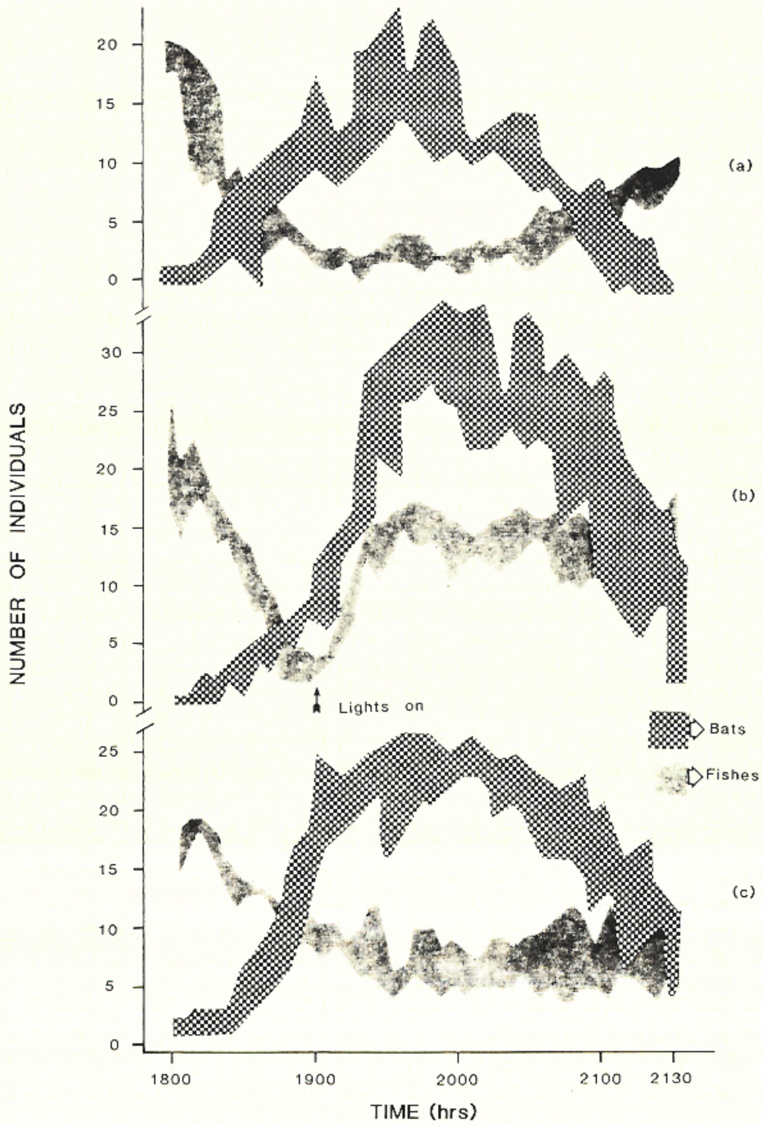

Fig. 1.—Fishing bat activity and fish density. (a) Normal control levels observed under red/infrared light; there is negative correlation between fish density and fishing bat activity (Kendall's tau = -0.8131, $p<0.001$). (b) When white lights are used to attract the fishes from their subterranean shelter to the pool, there is a significant positive correlation between fish density and fishing bat activity (Kendall's tau = 0.1333, $p<0.15$). (c) The entrance of the subterranean cavity was covered with a cotton sheet to prevent fishes from entering the cavity; bat activity viewed under red/infrared light follows the same temporal pattern as in the control

ca. 2.5 m from the surface of the water. The field of view covered was ca. 70% of the pool's surface, including the entrance to the subterranean cavity. The camera's output fed a videorecorder, yielding videotapes that were later analyzed frame by frame in the laboratory. Sunset took place approximately at 1830 hr during the days of observation. Illumination was supplied by six tungsten lamps, two 125-w red/infrared or four 125-w clear floods suspended from the platform at about 1.25 m from the water surface. Two 50 cm x 100 cm matte aluminum ceiling sheets were placed on the bottom of the pool and near the entrance of the subterranean cavity to obtain better video contrast. Relative density was determined by counting the number of fish observed in the field of view every 5 min. The number of bats passing through the field of the camera was counted for 5-min periods. Results are combined for all nights, the maximum and minimum for each 5 min plotted and the area between them shaded.

Fish density in the pool and fishing bat activity above it were recorded in the evening under red/infrared illumination. Figure 1a shows a drastic decrease in this control level of fish density while the number of fishing bats passing above increases. The negative correlation of fish density with bat activity is significant.

For the first manipulation, white floodlights were turned on after dark from 1900-2130 hr. When these lights were turned on, fish density nearly returned to the

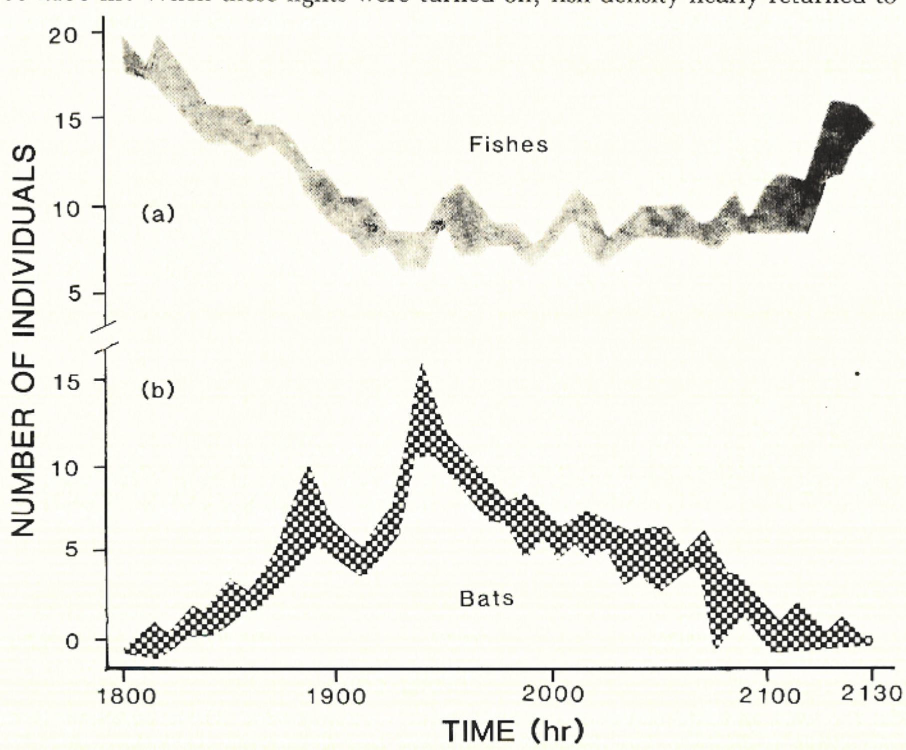

Fig. 2.—Changes in fish density and fishing bat activity when detectability of the other animal group is decreased. Three nights when fish density is examined in the absence of bats alternate with 3 nights when bat activity is examined when fish are blocked from surfacing. The observation procedures are as for Figure 1. Results for all 3 nights are combined and the maximum and minimum of bats or fish density each 5 min are plotted and the area between them shaded. (a) The entire circumference around the pool was blocked using opaque plastic sheets; fish density is greater than control levels of Figure 1a. (Wilcoxon's $p<0.001$). (b) A cotton sheet was stretched across the pool just covering its surface; fishing bat activity is less than the control levels of Figure 1a. (Wilcoxon's $p<0.001$)

earlier levels, with fishes swimming very close to the water surface (Fig. 1b). Bat activity follows the same temporal pattern as in the control, but the overall level of bat activity is significantly greater.

The second manipulation consists only of covering the entrance of the subterranean cavity with a cotton sheet, preventing fishes from entering the cavity. When the entrance of the subterranean cavity is obstructed, fish density is higher than the control level (Fig. 1c). The slight reduction of fish density was due to the fact that many fishes moved toward the borders of the pool, with many escaping from the observation area. Fishing bat activity also increased compared with the control observations.

To determine if fishing bats passing over the pool influence fish density, a third manipulation consisted of obstructing the flight path over the pool using vertically oriented, opaque plastic sheets, thereby preventing bats from passing over it. The overall fish density in the pool was significantly greater than the control level (Fig. 2a).

Because fishing bats find their prey by detecting the disturbance that swimming fish create on the surface (Simmons *et al.,* 1979), a fourth manipulation was performed by stretching a cotton sheet across the pool of water so as to cover its surface. Although only ca. 65% of the surface was covered, a marked decrease in bat activity was observed (Fig. 2b).

The field manipulations had an overall effect on both fish density and fishing bat

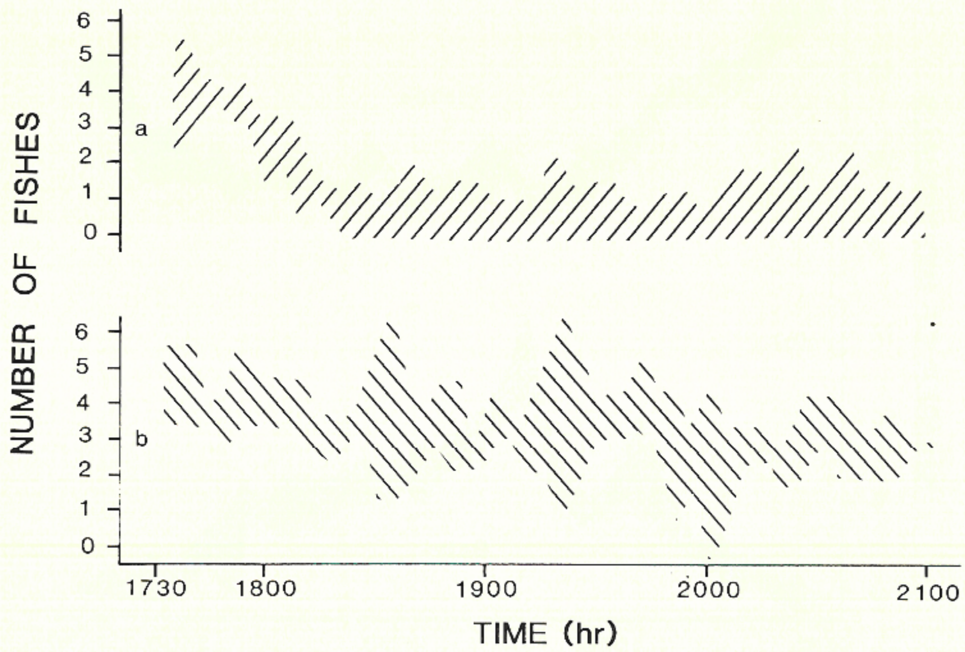

Fig. 3. — Dark and light preferences of fishes from two populations. These laboratory studies used one group of six fishes (two *Astyamax fasciatus* and four *Brachyraphis rhabdophora*) taken from the pool described above, and another identical group taken from a second pool located in an area without shading canopy ca. 50 m from the study pool. Fishes were held in the laboratory for 9 months under a 12L:12D photoperiod (lights on at 0600 hr). Observations were conducted during 3 consecutive days between 1730 and 2130 hr. The fishes were placed in a 200 x 100 x 60 cm tank which formed a light/dark choice chamber. The number of fishes present in the light compartment was counted at 1-min intervals. Number of fish represents the number of individuals present in the visible half of the experimental tank. (a) Fishes from the study pool; (b) fishes from the pool without a subterranean connection. There is a significant difference between the light and dark preferences of both groups (Wilcoxon's $p < 0.001$)

activity (Kruskal-Wallis one-way ANOVA on fish $p<0.005$, on bats $p<0.001$).

To compare the behavior shown by these fishes with that of the same species from a nearby area without subterranean connections but also under bat predation, laboratory observations were made on light and shade preferences in the evening. Using fish captured 9 months earlier during the fieldwork, I found the proportion situated in the shaded area of an aquarium tank to be greater for fish from the study pool than for fish from another pool without any subterranean connection (Fig. 3). It thus appears that light avoidance, even when bats have been absent for 9 months, still occurs in the evening hours when such behavior may be part of predator avoidance. Previous results on schooling behavior of this and other fish populations substantiate this suggestion (Romero, 1984).

DISCUSSION

Considering the low level of nutrients, cave-dwelling as a habitat has often been assumed to have little advantage (Barr, 1968). Results presented here, on the other hand, reveal that entry into one subterranean cavity can be linked to fishing bat activity. Using the underground area of the pool may be advantageous here and wherever bat activity is high, as is the case over most of the range of *Astyanax fasciatus*.

Of course, predator avoidance is not the only explanation possible for cave colonization in an animal that has successfully colonized caves in other regions as well. However, these results suggest that not only is it unnecessary to argue for "accidental" or directional evolution in cave-dwelling organisms, but also that it is possible to identify specific potential advantages and test whether they are reasonable.

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