Ontogenetic Change in Phototactic Responses of Surface and Cave Populations of *Astyanax fasciatus* (Pisces: Characidae)

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Differences among three blind cave populations and one surface population of the teleost *A. fasciatus* in responsiveness to light were studied under natural and experimental conditions. For all populations, scotophilia increases with length and during development; this trend was confirmed by additional experiments in which three small groups of fish were studied in an interval of 8 mo after which they showed increased scotophilia. The level of scotophilia differs among populations: the eyed surface form was the most scotophilic while the captive-bred and the Pachón populations (both totally blind and depigmented) were less scotophilic. The La Cueva Chica population, which is the result of hybridization between surface and cave populations, was intermediate in its level of phototactic responses.

The phototactic responses of cave populations probably represent a behavioral relic from the ancestral surface populations rather than a behavioral adaptation to the cave environment. These results do not support the contention that scotophilia of cave populations represents an adaptation to prevent fish leaving the cave.

DEVELOPMENT of phototactic responses in fishes has been reviewed by Noakes (1978) who concluded that there is a marked transition from scotophilia (preference to remain in the shaded area of an experimental tank) to scotophobia (preference to remain in the light area) in some fishes, although other fishes are scotophilic in their adult stage (Ter-

ami and Watanabe, 1980; Ercolini and Berti, 1977, 1978).

Only recently have implications of ontogenetic changes in phototactic responses been investigated (Carey and Noakes, 1981; Helfman et al., 1982). To that end, it is necessary not only to describe such changes, but also to interpret them from an ecological and evolutionary standpoint. This topic is especially attractive when addressed for species in which individuals spend their entire lives in total darkness. It has been shown, for example, that some cave animals exhibit phototactic responses (Thinès, 1969; Vandel, 1965) but the evolutionary significance of such responses is uncertain. Given that for some cave animals it is possible to identify their surface ancestor, it is feasible to infer the evolutionary sequence of change, especially when both surface (epigean, i.e., eyed and pigmented) and cave (troglobitic, i.e., blind and depigmented) populations are conspecific.

A frequently cited example of such conspecificity is the freshwater teleost *Astyanax fasciatus mexicanus* (Characidae). Due to the blindness and depigmentation of the cave form, Hubbs and Innes (1936) described it as a new genus and species, *Anoptichthys jordani*. These forms interbreed under both natural and experimental conditions to produce fertile F_1 hybrids that are phenotypically intermediate and with F_2 individuals which range from an almost completely eyed and pigmented form to an essentially blind and depigmented one (Peters and Peters, 1973; Sadoglu, 1957). Karyotypic and electrophoretic studies also indicate that cave and epigean forms are conspecific (Avise and Selander, 1972; Kirby et al., 1977). These two forms differ not only in morphology, but also in their behavior: unlike the epigean form, the blind one does not school, is active all the time and is not aggressive (Breder, 1942; Breder and Gresser, 1941; Erckens and Weber, 1976). These contrasting behaviors can be seen between other cave fishes and their ancestors (Thinès, 1969).

More than 30 caves support subterranean populations of *A. fasciatus* in the San Luís de Potosí area of east central Mexico. Not all cave populations of this area display the same degree of morphological divergence from the surface form: some are fully blind and depigmented while others are only partially so; other caves contain only individuals with eyes identical to those of the surface populations. Mixed populations of blind and eyed forms and their hybrids can also be found (Mitchell et al., 1977; Romero, 1983).

Breder and Rasquin (1947) described differential photoresponses among cave populations of *A. fasciatus*. The La Cueva Chica population was reported to be scotophilic, the La Tinaja population was scotophobic and three others were nearly or totally unresponsive to light. Hybrids of different populations were intermediate not only in their morphology, but also in the nature of their phototactic responses. They suggested that there were two photosensory organs mediating light reception, the pineal organ and the optic cyst. Tabata (1982) stressed the role of the former as photoreceptor in this fish. Breder and Rasquin (1947) also suggested that scotophilia would inhibit cave fishes from exiting their cave environment toward the exterior and speculated that no change or reversal of phototactic responses occurs during ontogeny. However, no convincing explanation was given for either scotophobia or unresponsiveness to light among other populations.

Although further studies (Boucquey et al., 1965; Gertychowa, 1971; Schlagel and Breder, 1947) have provided additional information about phototactic responses in cave populations of *A. fasciatus*, no study on the ontogeny of phototactic responses has been done.

The aim of this paper is to test the following null hypotheses: (1) phototactic responses do not change during development in fish from both cave and surface populations of *A. fasciatus*; and (2) there are no differences in phototactic responses between natural and artificially bred populations of this fish. My predictions were that these fish are more scotophilic during the latest stages of development than they are as juveniles and that natural populations are less scotophilic than the artificially bred fish. On the bases of my results, I argue that scotophilia in the subterranean populations of *A. fasciatus* is a behavioral relic rather than a defensive mechanism to avoid exiting the cave.

MATERIALS AND METHODS

Four populations of *A. fasciatus* were used in my studies of phototactic responses: (1) surface (eyed and pigmented) individuals from the Río Coy (near the cave area of San Luís de Potosí, Mexico); (2) hybrid fish from La Cueva Chica (pool II; sensu Breder, 1942), all of which showed an incomplete degree of blindness and

depigmentation (Romero, 1983); (3) morphologically homogeneous (blind and depigmented) fish from La Cueva el Pachón; and (4) a commercial stock (captive) of artificially bred fish which are blind and depigmented and were obtained from a pet shop in Miami, Florida.

Fish from natural populations.—Head lamps were used for collecting in caves since preliminary studies had shown that these fish do not respond to such light. All fish were caught by unselective netting and their standard lengths were immediately measured using calipers. Measurements were recorded to the nearest 0.1 mm. Fifty-four fish were divided into nine size-groups of six individuals each; i.e., one group contained the six smallest fish, another the six largest ones and seven intermediate groups each contained six fish of very similar size.

A group size of six was selected because six is the minimum sample size suitable for many non-parametric statistical tests. Nine groups were formed to achieve reasonably fine-grained size categories given the overall range in fish length.

Each group was placed, after capture, measurement and sorting, into a separate, opaque plastic container connected to a portable air pump. The containers were then transported from the caves and rivers to the field laboratory site near the collecting areas where the fish were moved into larger opaque containers connected to filters and air pumps. Tests took place in the field laboratory within 15 days of collection. Fish were fed with commercial fish food twice per week, but no experiments were performed on the days that fish were fed.

Tests were performed to ascertain the extent and direction of phototactic responses. A glass aquarium (50 × 25 × 25 cm high) half covered with movable, opaque-black, polyethylene sheeting formed a light/dark choice chamber. The aquarium was filled to a depth of 20 cm with water from the natural environment (either cave or river) of the fish. Minnow nets were used to place fish into the aquarium.

To avoid heating the water, the light source (either infrared or white) was kept 50 cm above the aquarium. Incandescent lamps used to observe phototactic responses were "white" light General Electric Industrial reflectors, 125-watt (wavelength between 2,000–3,000 nm) and a red/infrared Norelco 2,000 h red flood, 100-watts. Lamps were turned off between experiments. Nearby, a weak red/infrared incandescent lamp (60-watt) was on continuously during the experiments.

Because temperature can affect phototactic responses (Brett, 1979), it was maintained at the level of the native habitat (±1 C) by means of a fan placed about 1 m from the aquarium at a level between the aquarium and the light. A thermometer was placed in a corner of the tank. Since chemicals released by fish during an experiment may affect the behavior of the fishes in subsequent experiments, water filters (Dynaflow) with activated charcoal were used for 30 min between experiments and the aquarium was thoroughly rinsed and the water changed after three experiments.

Each group of six fish was tested three times alternately for red/infrared (control) light (R) and "white" light (W) in the following order: R W W R W R. Tests with red/infrared light were performed before, between and after tests with white light to detect any preference of the fish for any side of the aquarium as a result of their exposure to light. Every test per group took place alternately in each side of the aquarium, so at least one test per kind of illumination took place in the opposite side from the other two.

Fish were maintained in the aquarium for 5 min to adjust to the new environment. Fish behavior was either observed directly or videorecorded by placing a videocamera in front of one of the large walls of the tank. For experiments with red/infrared light, a "total darkness-camera" was used; for experiments using white light, a low-light camera was used. Cameras were connected to a portable videorecorder. Tapes were re-recorded on a laboratory slow-motion videorecorder for frame-by-frame analysis.

Each test took 30 min. The number of fish present in the light compartment was counted at 1-min intervals from the beginning of the test. A fish was counted as in the light compartment if its head was visible.

Preliminary results had shown that there are no significant differences in the total level of phototactic responses when *A. fasciatus* groups of six are tested individually or together, using either red/infrared light or white light, when following the experimental procedures described above. [Eight tests (four groups in two conditions) comparing counts of all six fish from each group when tested separately vs together. Counts compared using a one-sample χ^2_{adj} test for each experiment (Sokal and Rohlf, 1981:

711). The maximum difference was observed under red/infrared illumination: 77 counts for six fish tested individually and 90 for that group together. $\chi^2_{adj} = 0.86$ with a critical value for overall $P < 0.05$ of $\chi^2 = 7.441$ for eight replicate tests of one overall hypothesis (Rohlf and Sokal, 1981; table 15).]

For each test of the nine groups from each population, an index of phototactic response was derived by dividing the total count of fish scored in the light compartment by the number of samples per experiment (30) and subtracting 3 from the resultant ratio:

$$INDEX = (counts\ of\ fish\ in\ the\ light\ compartment/30) - 3.$$

Thus, $+3$ = maximum scotophobia (all of the six fish in the light area every sample), -3 = maximum scotophilia (none of the six fish in the light area every sample) and 0 = unresponsiveness to light (a mean of three fish in the light area over the 30 samples). This index was plotted against the mean length for fish in each group for the four populations.

The one-sided hypothesis is that these fish under either red/infrared or white illumination will not respond negatively to light. Therefore the lower 90% confidence limit to the null expectation of 90 counts was calculated using the normal approximation to the binomial probability distribution. Index values above this value signify that the null hypothesis cannot be rejected ($P > 0.10$). This value was transformed to the one-sided 90% confidence limit below an index of zero as follows: 30 min × 6 fish scored each minute × (½) = probability of scored fish being in lighted half of test aquarium = expected count of 90 = 180 scores × (½) = np = μ. q = 1 − p = probability of score not being counted in lighted half. Confidence limits: lower limit = $90 - Z_{90\%}\sqrt{npq} = 90 - Z\sqrt{45}$. From a normal probability area curve $Z_{90\%,1-sided}$ = 1.282. The lower limit is therefore 90 − 1.282· $\sqrt{45}$ = 81.400 which is tranformed into an index of -0.287.

The commercial (captive) fish stock.—Since most experimental studies on the blind cave form of *A. fasciatus* are performed using either commercially bred stocks of these fish or fish that have been maintained for long periods of time under laboratory conditions (Breder and Rasquin, 1947; Kuhn and Kahling, 1954; Sadoglu, 1967), it is important to know if fish subject to

such artificial conditions display different phototactic responses. To that end, similar experimental procedures were used for testing the Miami pet shop fish, with the exception that these fish were kept on a 12L:12D photoperiod (lights on at 0600 h) until two weeks before the experiments, at which time they were changed to a regime of total darkness to reduce any possible effects of circadian rhythmicity.

To see if growth and changes in phototactic response were correlated, six groups of six fish each were tested. Grouping by length was performed as for the fish from natural populations. Each group of fish was placed in a different tank. The first set of experiments was conducted in April 1982, using the three smallest and the three largest groups. In Dec. 1982, the same experiments were conducted on the three smallest fish groups; these were now designated medium in size due to their growth. So, although only six natural groups of the commercial fish stock were used, results in Fig. 1 for this population show the results of nine length groups because each of the three smallest ones was tested on two different dates separated by eight months of growth.

The phototactic responses exhibited by each of these three commercially bred fish groups tested three times each and then again after an eight-month interval were compared by using a Wilcoxon, matched-pairs, signed-rank test on the phototactic index. Matching for test order and combining the results for all groups yields a test of nine pairs of results.

Other results were statistically treated as follows: (1) the phototactic responses of the three smallest groups were compared with those of the three largest groups for each of the four populations by performing four independent, two-sample exact randomization tests (Sokal and Rohlf, 1981:788) on the same phototactic response test results (three tests per three groups of six fish each). The three scores between 0 and 180 for each group were added to form a single score for each size-group; and (2) the correlation between phototactic index and size for each of the four populations was analyzed using a Kendall rank-order correlation coefficient. All the indices were negative, so absolute values were used to obtain a scotophilic correlation.

To assess the origin of these commercially bred fish, I sacrificed six individuals selected at random after the experiments were performed. These fish were stained using the method described by Dingerkus and Uhler (1977) in order
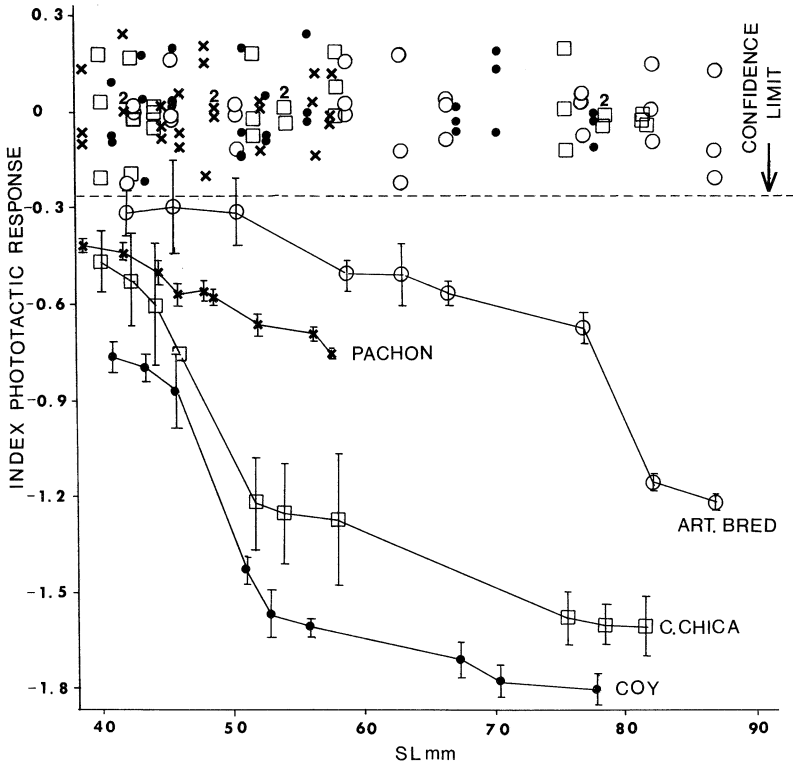
Fig. 1. Phototactic index of each fish group from four populations of *Astyanax fasciatus* plotted against mean length of each group. Symbols: (●) Río Coy (surface, eyed, pigmented) population, (□) La Cueva Chica (hybrid cave) population, (X) El Pachón (homogeneously blind, depigmented) population and (○) commercial (blind depigmented) fish stock. Symbols above the 90% confidence limit represent results of tests with red/infrared light (one original and two replicates per fish group per population). Number 2 on symbols means that the same result for the same fish group was obtained twice. Symbols below the confidence limit represent means for an original and two replicate tests per group per population using "white" light. Vertical lines represent standard deviation.

to observe bone and cartilage tissue. Circumorbital bones were examined using a dissecting microscope, since each cave fish population has a characteristic orbital bone arrangement (Álvarez, 1946).

RESULTS

When tested under the red/infrared light, all fish groups fell within the confidence limit, demonstrating that their distribution in the tank was not scotophilic in this type of light. Under the white light, all populations proved to be significantly scotophilic (Fig. 1).

The phototactic index of the three smallest groups of the commercial fish stock, when compared with its phototactic index after eight months of captivity, was significantly different (Wilcoxon's $T = 0$, $N = 9$ (no ties), $P < 0.01$).

When the groups of the three smallest vs the three largest fish of each population were compared using the exact randomization tests, in each population the three groups of small fish had higher scores than the large fish, with no overlap. The randomization test results are $P = 0.10$ that there is no size-related difference for each population. These four probabilities were then combined using Fisher's method (Sokal and Rohlf, 1981:799) to yield a low probability ($0.010 < P < 0.025$) of there being no overall differences in phototactic response test scores between large and small fish.

Although each population showed a different degree of scotophilia, there was a significant

correlation between scotophilia and fish length [Kendall's Tau = 0.7627 for the commercial fish stock, 0.6034 for El Pachón population, 0.4845 for La Cueva Chica population and 0.7908 for the surface (Río Coy) population; for each population N = 27 (nine groups × three tests each); $P < 0.001$ for each of the results].

The number, relative size, configuration and distribution of the circumorbital bones in the commercial fish stock were the same in all the examined individuals. Among the several cave populations of *A. fasciatus* that have been described osteologically (Álvarez, 1946), only the La Cueva Chica population includes individuals with cranial osteologies identical to this artificially bred population. La Cueva Chica is the most accessible and best known source of cave fish to pet shop dealers. Furthermore, given the amount of intrapopulational variation found by Álvarez (1946) (six different cranial osteologies) and the uniformity reported here in the sample from the experimental stock, it is likely that the stock of fish used here is descended from a relatively small original sample, probably from La Cueva Chica.

DISCUSSION

Several conclusions can be drawn from the present study. The level of phototactic responses varies during development in both cave and surface populations of *A. fasciatus*. This factor was previously neglected (Breder and Rasquin, 1947; Schlagel and Breder, 1947; but see Gertychowa, 1971) and it may be responsible for the diversity of results previously reported for the degree of phototactic response among cave populations. For example, Breder and Rasquin (1947) reported the El Pachón population to be "almost" indifferent to light, while my results indicate that this population is significantly scotophilic. Also, the mean length of each population may play a role as a confounding variable: the unique size distribution found in the El Pachón population (no individuals >60 mm vs individuals >88 mm in other populations) demonstrates the importance of performing representative sampling on natural populations prior to any study.

The level of phototactic response differs among the populations. The El Pachón population is the least scotophilic of the natural populations. The La Cueva Chica population is intermediate in phototactic response and this is consistent with the interpretation that these

morphologically intermediate fish are hybrids between the eyed and the blind forms (Romero, 1983). Other kinds of behavior in *A. fasciatus* hybrids are known to be intermediate between those displayed by the parent populations (Schemmel, 1980). Finally, the commercial fish stock showed phototactic response levels similar to those in individuals of similar length from the El Pachón population; individuals from both populations are uniformly blind and depigmented.

It has been assumed by many authors that results obtained from commercial blind *A. fasciatus* stock can be extrapolated to natural populations (Erckens and Weber, 1976; Popper, 1970; Weissert and Von Campenhausen, 1981). For exceptions see Schemmel (1980), Wilkens (1970) and Zilles et al. (1983). The interpopulational differences that I observed suggest that the origin of the experimental fish should be considered in subsequent research.

Neither El Pachón fish nor the commercial fish stock showed the unresponsiveness to light typical of most troglobites. Their level of phototactic response is intermediate between unresponsiveness and that of the surface population. This result is consistent with the breeding, electrophoretic and karyotypic studies that indicate that there is little genetic differentiation between the eyed and blind populations of *A. fasciatus.*

My results do not support earlier contentions that cave populations of *A. fasciatus* developed scotophilia as a "defensive" mechanism in order to avoid exiting the cave to a surface environment where they would be disadvantaged relative to eyed fish (Breder and Rasquin, 1947). In fact, the results indicate less scotophilia in cave populations than in the surface form. Furthermore, field observations of the natural habitat of cave *A. fasciatus* in Mexico (Mitchell et al., 1977), indicate that these fish have little, if any, opportunity to be exposed to light, which weakens even further the suggested "defensive mechanism" explanation for scotophilia in these populations. Also, field studies conducted on an eyed, pigmented population of this species which facultatively enters a subterranean cavity in Costa Rica, suggest that entrance to the cave is driven by predation and not by photoperiod (Romero, 1984, 1985).

Finally, because the observed ontogenetic change in phototactic responses is parallel for cave and surface populations of *A. fasciatus,* the presence of this pattern in the cave populations

may best be interpreted as a behavioral relic rather than a specific adaptation to the cave environment.

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