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Author(s): Benoni H. Seghers

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# SCHOOLING BEHAVIOR IN THE GUPPY (*POECILIA RETICULATA*): AN EVOLUTIONARY RESPONSE TO PREDATION

BENONI H. SEGHERS<sup>1</sup>

*Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada*

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Many marine and freshwater fish move about their environment in a cohesive group called a school and the question, "why do fish school?", has often been raised (e.g., Cushing and Harden Jones, 1968; Weihs, 1973). In numerous species schooling is thought to have evolved primarily as an antipredator strategy but few experimental data are available to refute or support this hypothesis (Brock and Riffenburgh, 1960; Manteifel' and Radakov, 1961; Williams, 1964; Breder, 1967; Shaw, 1970). This report presents a new source of evidence favoring an antipredator role for schooling.

Because most evolutionary changes occur initially at the population or subpopulation level, studies of intraspecific (geographic) variation may yield valuable clues to the adaptive significance of schooling behavior. Natural populations of a small tropical freshwater fish, the guppy (*Poecilia reticulata*), provide excellent material for studying behavioral responses to predation. In the Northern Range Mountains of Trinidad, West Indies, several geographically isolated (no interconnecting freshwater) and semi-isolated populations of guppies are exposed to different intensities of predation by other fish species (Haskins et al., 1961; Seghers, 1973; Liley and Seghers, 1974). In some rivers predation by large characid and cichlid piscivores, notably *Hoplias malabaricus* and *Crenicichla alta*, is severe. In other rivers these predators are absent and a smaller, carnivorous cyprinodontid fish, *Rivulus hartii*, is the major predator. In a few rivers *Rivulus* density is very low and guppies enjoy virtual freedom from fish predation. (Detailed measurements of other environmental variables are in Seghers, 1973, and Liley and Seghers, 1974.)

I made observations on the schooling tendencies of 5 populations in the Northern Range area (Table 1). The tendency for fish to remain together was estimated semi-quantitatively. These observations were supplemented with observations on wild fish placed in aquaria and outdoor pools. Schooling is poorly developed in the Upper Aripo and Paria R. The most common social groups involve fish engaged in courtship activity (e.g., three males following and displaying to a female). These groups do not persist for more than a few

seconds as the males move off to court other females. Contrariwise, populations of guppies in the Guayamare and Lower Aripo R. exhibit well-developed schooling behavior. These fish are normally nonpolarized facultative schoolers as defined by Breder (1967) and Shaw (1970). Local differences in water velocity may influence the configuration of the school but fish remain together even when not feeding or courting. Large schools may exceed 200 adult fish of both sexes.

Other evidence linking schooling behavior to predation intensity is the behavior of guppies above and below a waterfall which prevents upstream movement of characids and cichlids. The schooling behavior of guppies above the falls (Upper Aripo) is much less pronounced than at sites below the falls (Lower Aripo). Apart from predation, I could detect no major biotic or abiotic differences between these two sites.

To determine if these population differences are heritable I measured the schooling tendencies of predator-naïve laboratory stocks of guppies derived from each of the five natural populations. Laboratory stocks were started with a random wild-caught sample of at least 25 males and 50 large gravid females. Each stock was cultured for 3-4 generations under identical controlled environmental conditions.

The schooling experiments were conducted in a bare, rectangular, blue-green wooden tank (48 × 110 cm) filled to a depth of three cm with aged tap water (25 ± 2 C). Uniform illumination was provided by a 40 watt, cool white fluorescent tube mounted 60 cm above the water surface. The shallow water flattened the school to a depth of one or two fish. A reference grid of 10 squares (528 cm<sup>2</sup>) was marked on the bottom of the tank to record the position of each fish. To avoid disturbing the fish, observations were made through a small peephole in a blind covering the top of the tank. The fish were viewed in a mirror (suspended under the blind) 35 cm above, and at a 45° angle to the water surface.

All recordings were made on groups of 10 mature fish, five of each sex, chosen randomly from stock aquaria. The size distributions of all test fish were the same. They were fed before and discarded after testing. The testing schedule was randomized with respect to the day and time of day (0845-1745) each stock was tested. Ten replicates for each of the five stocks were com-

<sup>1</sup> Present address: Department of Zoology, University of Western Ontario, London, Canada.

TABLE 1. *Relationship of fish predation to the development of schooling behavior in five natural populations of guppies.*

| Population      | Major fish predator(s) <sup>1</sup> | Schooling behavior |
|-----------------|-------------------------------------|--------------------|
| Guayamare       | characids and cichlids              | well-developed     |
| Lower Aripo     | characids and cichlids              | well-developed     |
| Petite Curucaye | <i>Rivulus</i> (high density)       | intermediate       |
| Upper Aripo     | <i>Rivulus</i> (med. density)       | poorly-developed   |
| Paria           | <i>Rivulus</i> (low density)        | absent             |

<sup>1</sup> Characids and cichlids exert heavy predation pressure on all life stages of the guppy whereas the major impact of *Rivulus* falls on immature guppies. Relative *Rivulus* density: low, < 10 adults caught in one to two hr; high, > 50 adults caught with the same effort.

pleted for a total of 50 groups or 500 fish. Each group was placed in the test tank for 10 min. After this the position of each of the 10 fish was recorded at one min intervals for 30 min. When the fish had explored the tank for an additional five hr, a second 30 min recording was made. For each test I calculated an "index of cohesion" as follows. At each one min observation the maximum density for any of the 10 grids was recorded. The index is the mean maximum density for 30 consecutive observations. It has a theoretical minimum of 1 (one fish in each of the 10 squares) and a maximum of 10 (entire group in the area of one square or less). Though all stocks did spend more time in the four corner grids, inspection of individual recordings revealed no tendency for any stock to be relatively more attracted to corners.

Within each stock I found a significant decrease in the index from the first test to the second (Fig. 1), i.e., all stocks were less cohesive once they had explored the tank. The degree of dissociation was greater for Petite Curucaye, Upper Aripo, and Paria than either Lower Aripo or Guayamare.

More noteworthy were the differences (at both test periods) among the five stocks. The trend in the mean index score from a maximum at Lower Aripo to a minimum at Paria closely parallels the variation I observed in nature (Table 1). Thus stocks derived from natural populations subjected to intense predation have a significantly higher score than those obtained from populations exposed to low predation. Statistically, Petite Curucaye is inseparable from Guayamare or Lower Aripo though in the second test there is greater overlap with Upper Aripo and Paria. This intermediate position may not be due to *Rivulus* predation alone because Petite Curucaye is separated from a population exposed to characid and cichlid predation by only 1.6 km of river. The absence of major physical barriers and the continuous distribution of guppies between the two regions may provide an avenue of considerable gene flow. Upper Aripo and Paria, however, are separated from populations exposed to characid and cichlid pre-

dation by physical barriers, a waterfall and mountain range, respectively. Presumably the mixing of these gene pools is almost impossible.

The results of the experiment, therefore, confirm the hypothesis that differences in the tendency to school are controlled by underlying genetic factors and are correlated with predation pressures exerted by other fish species. Nevertheless, this discovery does not reveal the proximate mechanism(s) whereby schooling protects. More work is needed to determine if schooling evolved as a "selfish" cover-seeking response to peripheral predation (Williams, 1964; Hamilton, 1971; Vine, 1971, 1973), or developed primarily as a mechanism for detecting (Manteifel' and Radakov, 1961; Pulliam, 1973) and confusing (Manteifel' and Radakov, 1961; Eibl-Eibesfeldt, 1962; Hobson, 1968; Neil, 1970) predators. It is unlikely that schooling protects guppies simply by reducing the probability of a predator encountering a prey (Brock and Riffenburgh, 1960) because in this system predator and prey live very close together, often within each other's visual range.

If a well-developed schooling response does reduce the risk of predation, "schoolers" should survive longer than "non-schoolers" when both types are presented in equal numbers to a natural predator. I have confirmed this for both wild-caught guppies and their laboratory descendents (Seghers, 1973). For example, in three days a *Crenicichla* ate 48 guppies of an initial laboratory population of 50 Lower Aripo and 50 Paria females; of these 16 were Lower Aripo, 32 were Paria, showing clearly that Lower Aripo fish had a survival advantage ( $\chi^2_{1df} = 9.01, p < .01$ ). In a similar test 16 Lower Aripo and 34 Upper Aripo were eaten ( $\chi^2_{1df} = 11.56, p < .001$ ). However, for Lower Aripo vs. Petite Curucaye, and Lower Aripo vs. Guayamare, the differences were not significant ( $p > .05$ ). (In all experiments fish were of similar body size; females were used to control for population differences in coloration which are phenotypically expressed only in males.)

Although these results indicate that fish having a greater tendency to school are relatively less

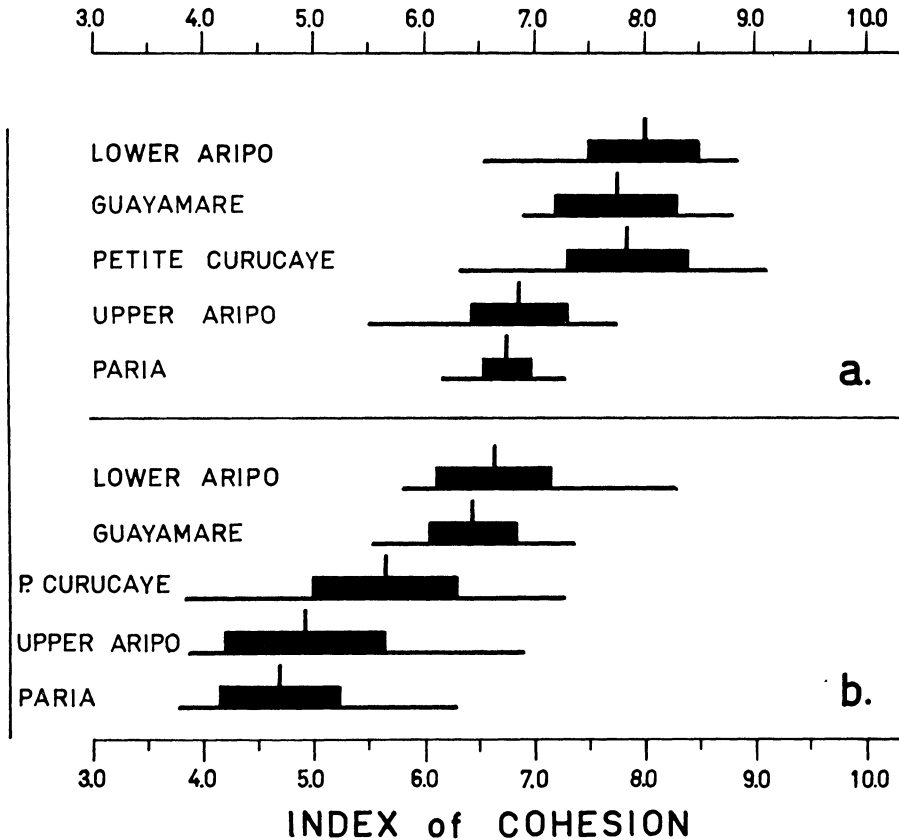


FIG. 1. Index of cohesion for five laboratory stocks of guppies. The stocks were derived from five natural populations exposed to a wide range of predation pressure. Vertical lines show the means of 10 replicates per stock; horizontal lines show the ranges; rectangles are  $\pm 95\%$  confidence limits. (a) Cohesion during the first 30 min test. (b) Cohesion during the second test five hr later.

vulnerable to predators, schooling per se was probably only partially responsible for the differences—populations of guppies also differ quantitatively in other important antipredator devices including reaction distance to predators, alarm threshold, and microhabitat selection (Seghers, 1970, 1973, 1974).

Schooling behavior in the guppy is thus viewed as one component of a coadapted complex of antipredator adaptations. A precise measure of its efficacy is difficult to obtain because the tendency to school is linked to other behavioral traits also serving to reduce predation.

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#### POLYMORPHISM IN CRICKET FROGS: AN HYPOTHESIS

WILLIAM W. MILSTEAD, A. STANLEY RAND, AND MARGARET M. STEWART

University of Missouri—Kansas City; Smithsonian Tropical Research Institute, Canal Zone;  
and State University of New York at Albany

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On each of five continents there are small frogs inhabiting the water's edge of ponds and sluggish or intermittent streams. These ecomorphs, called "cricket frogs," represent five different origins but are strikingly convergent in appearance as well as in ecology and behavior. Five genera are involved, one on each continent: *Acris* in North America (Hylidae); *Pseudopaludicola* in South America, and *Crinia* in Australia (Leptodactylidae); *Phrynobatrachus* in Africa, and *Rana* (*R. limnocharis*) on the Indian subcontinent (*Ranidae*). All are ecological equivalents in the cricket frog niche (Milstead, 1972), and all are polymorphic for color and pattern. Their dorsal ground color varies from light to dark gray or from light tan to dark reddish-brown. The dorsum may be of uniform ground color or have darker blotches on the back and on the limbs. A light mid-dorsal stripe may be present. When present, the stripe may be cream to yellow, light reddish-brown to bright reddish-brown, or pale green. In *Phrynobatrachus*, at least 33 species are polymorphic for a mid-dorsal stripe or band (Stewart, 1974).

These color and pattern variations, especially regarding the mid-dorsal stripe, have attracted the

attention of those studying cricket frogs. Some early workers, e.g., Abbott (1882), thought that the entire dorsum was capable of metachrosis, but Cope (1889), Darnell (1902), Ditmars (1905), Dickerson (1906) and others believed that the ground color was capable of color change, but that the vertebral stripe was not. Later, Pyburn (1961a) concluded that metachrosis involved the green but not the red vertebral stripe, and Gray (1972) reported that both the red and green stripes can undergo metachrosis.

In *Rana limnocharis*, the presence of the vertebral stripe results from the expression of a dominant allele of a single gene (Moriwaki, 1953). In *Acris crepitans* and *A. gryllus*, however, stripe color results from the interactions of a series of multiple alleles of a single gene (Pyburn, 1961a, 1961b).

Pyburn (1961a) found seasonal variation in numbers of individuals with a stripe of any given color. His findings suggest that selection favors different color and pattern morphs depending upon amounts of bare mud or grass at the water's edge, and upon colors of the vegetation during the four seasons. Presumably, the varying shades of