Measurement of Consociation Among Fishes
and Comments on the Evolution of Schooling

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Measurement of Consociation Among Fishes and Comments on the Evolution of Schooling

The schooling phenomenon presents the student of animal behavior with a paradox. On the one hand, schooling is superficially a simple phenomenon and would seem to lend itself readily to quantification and casual analysis. On the other hand, there has been a notable lack of success in relating schooling to general biological principles, and there are no really convincing ethological, ecological, or evolutionary explanations. I believe that this deficiency can be ascribed to the absence of any immediately apparent "purpose" for schooling. There is no vital function to which it seems to make an efficient contribution, and it can not be immediately assigned to reproductive, defensive, or any other category of adaptive behavior.

Certain school-like groups, such as that formed by several male guppies chasing the same female, can readily be discussed in functional terms, but for most schools that would be recognized as such, there have been only some rather weakly supported explanations, which I will attempt to evaluate later in this paper. The explanation which suggested the experiments described here is one that relates schooling to the category of defensive hiding. It proposes that a fish places itself among others of its kind to make itself less conspicuous and to place the others between itself and sources of danger. According to this view, schooling behavior (the individual reaction) is adaptive, but a school (the statistical consequence) is not.

In the design of experiments to bear on this possibility, the central consideration is that the vicinity of conspecific individuals constitutes a hiding place and that such usage can be demonstrated by removing all other hiding places. Fishes of open-water habitats in nature have nowhere to hide effectively from predators. This might furnish a partial explanation for the pre-

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valence of schooling in pelagic waters. Fishes that inhabit locali-
ties with abundant cover can be placed experimentally in cover-
deficient environments, and if schooling is a form of cover-seeking, such treatment might induce schooling even among species that do not show this behavior in their usual habitats. The ex-
periments described here gave a clear demonstration of this expected effect. They were also designed to provide an objective measurement of the intensity of schooling behavior in homotypic groups of various size, and in heterotypic pairs.

There are other theoretical standpoints from which schooling may be studied, besides that of ecological adaptation. Breder (1959) analyzed schooling from the point of view of information theory, and reviewed several aspects of physiological causation. He also discussed the theory proposed by Parr (1927), that schooling results from a force of social attraction that is replaced by repulsion when individuals approach to within a critical dis-
tance. This distance would be a point of stable equilibrium at which there would be neither attraction nor repulsion. This con-
cept is useful in explaining some of my observations.

**TERMINOLOGY**

Animals often convene because each independently seeks some localized conditions. A gathering of people beneath a shade tree on a hot day is a good example. Other groups result from mutual attractions among the members themselves. Spooner (1931) proposed that the term school be used for any socially motivated fish grouping, but not for groups formed by forces other than social attractions. Nikolsky (1963) indicated that current Soviet usage recognizes two kinds of social groupings, called school and shoal in the Birkett translation. A school is defined as a group that is sufficiently small for every fish to be aware of every other fish. A shoal would be a larger group in which a fish could sense and be attracted only to the individuals in its neighborhood, often only a small proportion of the whole. The word shoal is more common than school in the European literature and is seldom used by Americans. Breder (1929, 1959) and Atz (1953) confined the term school to social groupings in which all the indi-
viduals are oriented in one direction. They used the term aggre-
gation for disoriented social groups and did not propose a ter-
minological distinction between social and non-social groups.
I have been unable to discern, either in my own work or in the reports of others, any importance of such orientation in a school, other than indicating that it is in motion, relative to the water. The locomotor machinery of almost all fishes is such that to move in a given direction they must point their bodies in that direction. I have observed that whenever a moving (and oriented) school stops moving, the unanimity of orientation ceases, and then reappears when a school again moves away. It may be of some value to distinguish between these two phases of activity, but the difference between social and non-social groupings is in greater need of a terminological distinction. I will therefore use the term *school* to refer to any contagious distribution that owes its persistence to social (but not sexual) forces. *Aggregation* will refer to groups that arise by individuals independently seeking the same localized conditions. This use of the term aggregation is widespread, as is its use to cover both social and non-social groupings (see various general texts on ecology and behavior).

A school, therefore, is to be recognized on the basis of its cause rather than its appearance. There are situations in which appearances may reliably indicate cause. For instance, when one observes a dense concentration of fish of the same species moving about in a pelagic or other uniform habitat, and can be reasonably sure that the fish are not all chasing the same moving object, he is probably safe in calling it a school. Social attraction would be the most reasonable explanation for the cohesion of the group. Schools and aggregations can not be as confidently distinguished in heterogeneous environments, and it must often happen that groups are formed that owe their cohesiveness to both schooling and aggregation in mutual reinforcement (*heterogeneous summation* of Tinbergen, 1951).

**METHODS**

To demonstrate schooling one must show that a species has a contagious distribution in the absence of any factor that could cause aggregation. I believe that this requirement can be met by satisfying the following conditions:

1. The experimental environment should be visually and topographically uniform.
2. An experimental fish should verify this uniformity by its behavior. Singly or with companions, it should not show any tendency to prefer one part of the tank to another. The amount of time spent in any region should be in direct proportion to its area.

3. In groups (two or more) the fish should show a contagious distribution in the experimental environment.

Figure 1. Essential features of the experimental apparatus.

To satisfy the first requirement I used a cylindrical steel tank 153 cm in diameter and 30 cm deep, filled to a depth of 17 cm (Figure 1). The inside of the tank was painted white and coated with paraffin, with a thick fill of paraffin to eliminate the corner between the side and bottom of the tank. When algal and fungal growths on the paraffin made it difficult to maintain as a uniform white field, I provided the tank with precisely fitting, bowl-shaped liners of bleached cotton muslin, which were easily removed and laundered after each use. A wooden scaffolding supported an overhead platform with a hole through which
observations and photographs could be taken. The sleeve of white muslin hung around the tank below the platform to complete the visual uniformity for the fish inside. A ring of six 200-watt bulbs hung from the white underside of the platform. A fish in the tank could see nothing but nearly uniform whiteness in any direction, except for the light bulbs and the hole in the ceiling directly overhead.

The experimental fish came from various sources, as indicated in the discussion of each species. I kept most of them in 10- to 30-gallon aquaria when they were not under investigation, and fed them commercial, dehydrated fish food, with occasional meals of live or fresh foods. After an experiment, I put the fish into a different aquarium from the one they had previously occupied, so that the post-experimental behavior and condition of each specimen could be observed, and to avoid the too-frequent use of the same individuals. To minimize the effect of their previous learning, I allowed at least three weeks between experiments with the same specimens.

When there was a temperature difference between the experimental tank and the aquarium from which the fish were taken, I allowed time for acclimation by floating the fish in aquarium water in a glass jar in the experimental tank with the lights turned on. This gave the fish an opportunity to adjust to the visual environment for several minutes before being released in the tank. The tank was on a floor where, most of the year, it kept a temperature of about 18°C. For tropical species, I heated the water with electric heaters to at least 22°C. before introducing the fish. The heaters had to be removed for the experiment, but the overhead lights kept water from cooling appreciably, and would raise the temperature from 18° to more than 20° in six hours. No experiments were conducted at the higher temperatures of the summer months.

After releasing the fish in the experimental tank, I allowed a few minutes of additional time for their adjustment to the unusual conditions before starting to photograph. I usually used a 36-frame roll of 35-mm. film and took pictures, nine consecutively, at 30-second intervals. I continued in this pattern until all 36 frames were exposed, and then left the fish in the illuminated tank for from five to eight hours (usually about six) and exposed another roll of film in the same way as the first. In this way each group of fish provided two series of 36 observations.
By comparing the two series I could note any effect of the amount of time spent in the experimental tank.

Most of the data came from photographs taken through the observation port. Moving pictures were used initially, but snapshots proved adequate, and only the three native minnows, the first species studied, were investigated with moving pictures.

The camera (Kodak Cine-Special or Ansco Memar) was on a wooden frame, permanently fixed to the overhead platform so that the relationship of film to tank was the same for every frame. The shallowness of the water assured that the fish were always about the same distance from the camera, and that distances measured on the film bore a nearly linear relationship to horizontal distances in the tank. Also, there were detectable landmarks in each picture, the circular water-edge, the seams in the tank-liner, and the reflections of the six light bulbs and of the observation hole, which showed as a small circle in the center of the field. I used the middle of this circle as the origin for measuring distances of fish from the center of the tank. The fixed position of both camera and tank meant that lines on a photograph drawn through the central circle parallel to the sides of the picture defined geometric quadrants that corresponded to fixed equal areas in the tank.

Measurements on moving-picture records were made with a meter-stick on single-frame projections, and on snapshot negatives by an optical micrometer in a low-power microscope. Photographs of a meter-stick floating in the experimental tank served to indicate conversion factors for obtaining tank distances from the measurements.

The intensity of schooling is determined by comparing the size of a group formed by a certain number of individuals with the size that would have been shown if each individual had moved at random. Area would undoubtedly be a suitable measure of group size, but I believe that the perimeter is more convenient and useful. Perimeters of irregular polygons, which small groups of fish usually form, are easily calculated as simple sums of individual measurements. The calculation of areas of such figures is tedious. Since the study involved recording several thousand school sizes, ease of calculation was of prime importance. The perimeter has other advantages over area, however, besides that of convenience. The perimeter of a school of a few individuals corresponds more often to an intuitive judgment of group size.
than the areal measurement would (Figure 2). Moreover, the perimeter is a linear measurement of distances between individuals, while area is a power function of such measurements, and therefore much more variable. The perimeter is, in fact, a special case of the traditional distance-to-nearest-neighbor measurements. It merely requires the restriction of such measurements to peripheral neighbors.

The measure of central tendency used throughout the work is the median. This usage is also justified partly on the basis of convenience. The median of a series of measurements is more rapidly calculated than is any kind of mean. It is superior to the mode in that it is a precise value for any distribution, while a modal value depends partly on an arbitrary decision as to what class limits should be recognized for the independent variable. The school-perimeter frequency distribution for a group of schooling fish is often highly skewed. Most of the time the fish will school, and show a small group-perimeter. Occasionally, however, one or more individuals will leave the school and move about independently, thereby greatly and variably augmenting the perimeter. So the frequency distribution shows a low modal value but includes some values of several times the mode. A number of statisticians (e.g. Yule & Kendall, 1950:115-6) have urged the advantage of the median over a mean as a measure of central tendency in such asymmetrical distributions, of which annual per-capita income is the usual example.

For graphical and mathematical comparisons of species it proved convenient to express all median perimeters as a proportion of the maximum that a group of fish could possibly show in the tank. This maximum is the perimeter of an inscribed regular polygon.

\[ 2N \sin \frac{\pi}{N} \]

where \( N \) is the number of fish.

THE PARAMETERS OF RANDOM MOVEMENT

I take random movement in the experimental tank to mean that a fish shows no tendency to prefer one region to another and that the movements of a fish have no influence on those of its fellows. Bias for certain regions could be on any pattern or scale: a preference for the northern half over the southern; a
preference for the point of introduction and avoidance of areas a few centimeters away; a tendency to move along a set itinerary; etc. The observed movements of the fish were such, however, as to rule out any small-scale bias. The fish could and often did travel through widely separate regions in a few seconds. I assume that counts of occurrences in large areas are a sufficient test of regional bias. Constant geometric quadrants could be defined on the photographs, and if a fish moves at random it should be found about equally often in each of the four quadrants. It should also occur about equally often in equal central and peripheral areas. In other words, its median distance from the center should be about \( \frac{1}{\sqrt{2}} = .707 \) of the tank radius.

Figure 2. Area vs. perimeter as a measure of schooling intensity. Of the two triangular schools, the upper has a much greater perimeter but lesser area than the lower. The perimeter measurement accords with the intuitive impression that the lower group is a more cohesive school. Note also that a slight movement of any fish in the upper school would greatly increase the area but have slight effect on the perimeter or apparent cohesiveness of the group.

The distribution of a group of fish with no regional bias and with independent movement should be the same as that of a numerically similar group of points scattered at random within a circle. Descriptions of distributions of points in terms of devi-
lations from randomness, either in the direction of clumping or of overdispersal, are available (Clark and Evans, 1955). They are not, however, appropriate to the present study. They relate to single distributions of large numbers of individuals in large spaces, for example, trees in a forest. The treatment of schooling required a statistical summary, the median perimeter, of the smallest convex polygons circumscribed about small numbers of points repeatedly scattered in a circular area.

I have been unable to deduce the medians of the perimeters of such polygons, and have therefore estimated them empirically. The technique is to draw a circle of unit radius on graph paper, and then to use a random number table to choose \( x \) and \( y \) coordinates of two decimal places for a point within the circle (disregard the point if it falls outside the circle). When the requisite number of points are thus located, the perimeter of the smallest enclosing polygon can be measured. The median of a large number of such perimeters then serves as the value for random distribution (Table 1).

The perimeter for two points was defined as twice the distance between the points. For three points the polygon is always a triangle. For more than three points (e.g., twelve, as in Figure 3) the polygon will have a point at each corner and a variable number of points scattered inside.

Upensky (1937:257-8) has calculated that the mean perimeter about pairs of points randomly located in a circle is about 1.82 radii, slightly less than my empirical estimate of the median. This difference is to be expected, because the distribution of distances from the center, which influences the distance between points, is skewed in the direction of larger values. The mean distance from the center (a problem formally similar to finding the center of gravity by integration, as treated in elementary texts) is two-thirds, slightly less than the median, \( 1/\sqrt{2} \).

Having obtained paired values, number of points and associated median perimeters (Table 1), one can fit the data to an equation that describes median perimeter as a dependent function of the number of points. Unfortunately, there is no set of principles that dictates the form that this equation should take, and there is no limit to the number of kinds of equations to which a given set of data can be fitted. Fortunately, there are some intuitive and aesthetic guides to the selection of an equation. A simple function is preferred to one that is more complex. A
function that could conceivably hold over a wide range of the independent variable is preferable to one that would give patently erroneous or meaningless values outside the investigated range. For the present study, for instance, it would be undesirable to use an equation that could give negative perimeters or perimeters that exceeded that of the enclosing circle. It is highly desirable that equations of the same form as that used for random distribution be applicable to observed fish distributions. Such equations would differ only in the values of constants that would furnish a basis of quantitative comparisons of each species with other species and with random distribution. One further consideration is that the number of fish (or points) be treated as a logarithmic rather than arithmetic function. We would expect the difference between two and three fish to be more closely comparable to that between twenty and thirty than to that between twenty and twenty-one. A logarithmic function emphasis proportionate, rather than absolute differences. An equation of the form

\[ P = \sum_{m=0}^{\infty} G \ \text{d}m \]

satisfies these conditions. \( P \) is the median perimeter, \( m \) the independent variable, and \( G \) the normal-curve ordinate of the parenthetical expression with constants \( a \) and \( b \). The function \( G \) is, of course, mathematically quite complex, but the complexity has a ready resolution in standard statistical tables.

For the independent variable, it was convenient to use, not the number of points or fish, but the number minus one (companion number). This has an intuitive justification in that the smallest possible school is that formed by two individuals. Here

<table>
<thead>
<tr>
<th>Number of Points</th>
<th>Polygons Measured</th>
<th>Medians</th>
<th>In Radii</th>
<th>Proportion of Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>300</td>
<td>1.93</td>
<td>0.480</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>100</td>
<td>2.84</td>
<td>0.547</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>70</td>
<td>3.93</td>
<td>0.688</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>40</td>
<td>4.51</td>
<td>0.737</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>32</td>
<td>4.80</td>
<td>0.783</td>
<td></td>
</tr>
</tbody>
</table>
the companion number is one, and this is a convenient origin on
a logarithmic scale. The observed perimeter should be expressed
as a proportion of the maximum possible perimeter that the
group of points or fish could show (right-hand column in Table
1) . With this selection of parameters the equation (1) plots as
a straight line on log-probability paper. The fit is very good
(see Figure 4) for random distribution, and certainly close
enough for observed school perimeters. The function (Equation
1) also has the advantage of being readily visualized : As com-
panion number increases, the observed perimeter approaches
the maximum possible perimeter. The rates of approach for school-
ing fish and for randomly scattered points are, understandably,
quite different, and the differences have a quantitative expression
in the constants $a$ and $b$.

Median perimeter as a proportion of the theoretical maximum
is most easily visualized for two points. The maximum perimeter
for these points (double the distance between) would be four
radii and would occur when the points are at diametrically op-
oposite positions on the edge of the circle. If observation showed
that a group of two fish had a median perimeter of one radius,
the plotted value would be 0.25.

OBSERVATIONS

Nine species were investigated in varying detail, and there
was clearly evident schooling in all but two. The experimental
animals formed a closely cohesive group most of the time and
moved about the tank together. The schooling of the eel and the
male guppy was weak and intermittent, and its demonstration
requires a detailed analysis of distribution patterns. The male
guppy proved too small to be clearly photographed at the 2.8-
meter distance between camera and experimental tank. The eels,
however, were clearly visible in photographs at this distance and
therefore lent themselves to a photographic study that led to un-
foreseen complications. I will consider the eel first, therefore, to
illustrate my statistical techniques for demonstrating and meas-
uring schooling, and to indicate the intensity of this behavior at
what is probably its lowest development among the species
studied. The remaining species will be considered in a phylo-
genetic order.
The eels were collected from seawater near Woods Hole, Massachusetts, by Dr. Carl J. George, now of the American University, Beirut. He netted them in August, 1958, as elvers, newly arrived from the sea. I conducted experiments with them in late 1958 and early 1959, when they averaged about 80 mm. in standard length. There was a steady mortality before, during, and after the period of experimentation, until the last of the original 33 died 15 months after collection. The behavior of this species may, therefore, have been influenced by the poor condition of some or all specimens.

In the experimental tank the eels moved listlessly near the bottom most of the time. They seldom remained completely still for more than a moment, but continuously made at least minor shifts of position. A contagious distribution was at least suggested most of the time, and was mediated by vision. When the lights were turned on after a few minutes of total darkness the fish appeared randomly scattered, but would usually come together in loosely cohesive groups in a minute or two. Sometimes, however, the fish would engage in rapid dashes about the tank, and such movements seemed independent. Groups of two to nine eels always lost cohesion when they started moving actively about. Their mutual attraction seemed weak at best.

As indicated above, a single fish can be said to move at random if it shows about the same frequency of occurrence in each quadrant of the tank and a median distance from the center of about 0.707 of the tank radius. Apparently neither requirement was met by the animals tested. Consider first the addiction to Quadrant II (under "single fish" in Table 2). The deviations from the expected 18 occurrences in each quadrant are highly significant ($X^2 = 17; n = 3; p < .01$). The test, however, is based
on the assumption of the independence of each count. The observations were clearly not independent events. In one experiment, for example, there were eleven consecutive observations in Quadrant II. The fish was sufficiently quiescent to stay in that quadrant for a long time. The degree of dependence of consecutive observations can be evaluated and suitable corrections made, but the problem can be more directly attacked in another way. The preference of single fish for a certain quadrant can cause a contagious distribution only if the majority in a group show the same quadrant preferences. To investigate this possibility I noted the quadrant distributions of each fish when in groups of two and three, the only group sizes for which I have photographic records (Table 2, last column). A preference for Quadrants I and II, the western half of the tank, is clearly apparent. The fish were in this half six-tenths of the time, and the 95 per cent confidence intervals for this proportion and sample size extends only from about 0.55 to 0.63 (Wilks, 1949:101).

Singly, the eels showed a median distance from the center of about 0.56 radii, about 0.79 of the expected random value of 0.71. About seven-tenths of the distances from the center were less than the random value. This fraction does not include 0.5 in its 95 per cent confidence interval. So individual eels not only deviated from random movement in their quadrant distribution, but also in their bias for the central and away from the peripheral parts of the tank. In groups this bias for the center was even more pronounced. In pairs, the median distance from the center was only 0.54 and in groups of three only 0.49 radii. The fish in groups spent about half the time in the central 25 per cent of the tank area. These observations can be interpreted as favorable to the schooling hypothesis by assuming that the presence of other eels near the center of the tank increases the attractiveness of that region of each eel. So their concentration in the center can be ascribed to the heterogeneous summation of schooling and aggregation.

Of the two kinds of departure from random distribution, the quadrant preference is the less serious. If each eel had a probability of 0.5 of occurring in each half of the tank, two eels would occur in the same half about half the time. If the probabilities were (as the data indicate) 0.4 and 0.6 for the two halves, the probability of two fish being in the same half or two different halves merely changes to 0.52 and 0.48, respectively. This
slightly greater likelihood of occurring in the same half could scarcely have a very important effect, by itself, on the median distances between individuals. If, however, as the data suggest, the median distance from the center is only about three-fourths of the expected random value, the median distance between two fish would also be reduced to about three-fourths of what it would be if they moved at random.

### Table 3

<table>
<thead>
<tr>
<th>Date</th>
<th>Companion Number</th>
<th>Experiment</th>
<th>Median Perimeter Observed/Random</th>
</tr>
</thead>
<tbody>
<tr>
<td>27 Jan. 1959</td>
<td>1</td>
<td>early</td>
<td>0.50/1.87 = 0.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>late</td>
<td>1.16/1.87 = 0.62</td>
</tr>
<tr>
<td>6 April 1959</td>
<td>1</td>
<td>early</td>
<td>0.60/1.87 = 0.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>late</td>
<td>0.43/1.87 = 0.23</td>
</tr>
<tr>
<td>30 May 1959</td>
<td>2</td>
<td>early</td>
<td>3.00/2.84 = 1.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td>late</td>
<td>1.28/2.84 = 0.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean</td>
<td>0.49</td>
</tr>
</tbody>
</table>

*Expressed as a proportion of tank radius. For perimeter in mean fish lengths, multiply by 9.5.

Under these circumstances a demonstration of schooling would necessitate median perimeters well below three-fourths of the value expected from random movement. This requirement was certainly met in three of the six experiments (Table 3). In one experiment (on 30 May), the median perimeter was greater than the random value. This should not be regarded as over-dispersal caused by repulsion between individuals, because it resulted from the unusual behavior of one of the three fish, which spent nearly the whole time circling rapidly about the edge of the tank. Thus it showed, in contrast to the other specimens, a bias for the peripheral regions. The effect of this was to increase the perimeters resulting from independent movement. Six hours later this specimen had joined its fellows in the more central parts of the tank, and the resulting median perimeter was less than half the value calculated for independent motion.

For a group to show, in a series of 36 observations, such median perimeters as 0.23 and 0.27 of the calculated random value, it had to show a consistently contagious distribution, much stronger than could be attributed to slight tendencies to prefer certain regions of the tank. I conclude that the eels were schooling on these occasions. Obviously, however, they do not always
school, because on at least two occasions they showed median perimeters not very different from what would have been expected on the basis of complete independence. The inconsistency is especially apparent from the observations made in June, when the same group that failed to school in the morning showed the most intensive schooling recorded for this species in the afternoon. The January observations indicate that the difference cannot be resolved by taking account of the amount of time the fish spend in the experimental tank. I would conclude, therefore, that the species sometimes forms schools of low cohesion compared with other species that were investigated, that at other times it does not school, and that this inconsistency cannot at present be explained.

*Hyphessobrycon flammaeus* Myers

Twelve "flame tets," probably *Hyphessobrycon flammaeus* (Family Characidae), were purchased from Pets Aquarium in Lansing, Michigan. I made no quantitative study of this species, but have no doubt that it schools. The twelve moved about the tank as a group that seldom presented more than what I would judge to be a third of the perimeter that random movement would have produced. A few usually dashed about in a frenzied manner when first introduced, but once they joined a school their behavior seemed normal. When the lights were switched on after a few minutes of darkness, the fish gave the appearance of random scattering, but soon started to school. The formation of a school, in this and other species of comparable size, seemed contingent on chance approaches of individuals to within about 20 cm of each other. Pairs formed of such encounters then swam about, in a seemingly undirected manner, until other individuals or small groups were closely approached and joined. Pairs always formed within a few seconds of sudden illumination, but sometimes a minute or two would pass before all of the small groups would coalesce into one school. Such a school of twelve would occasionally break up into two or three smaller groups, and sometimes a single individual would wander off for a brief period. Most of the time, however, the fish moved about in a single school.

The behavior of isolated individuals was quite different. One stayed immobile for 25 minutes where it had been placed in the tank. When eleven others were added, they formed a school
that was joined by the first, although not for about four minutes. Another single individual showed marked disorientation when placed in the tank. It alternated between a head-up and head-down position for a few seconds and then sank, head downwards, to the bottom, where it rested immobile on its snout. I was convinced that I had done the fish some physical injury in transit from its aquarium. When I replaced it, however, it quickly entered a plant thicket and in a few minutes was swimming about normally. I saw similar but less extreme indications of disorientation in Xiphophorus on transfer to the experimental tank.

Hyphessobrycon, Xiphophorus, and also Colisa, indicated what seems to be distress caused by the all-white environment in another way. Some or all of them would rush to the net, instead of fleeing from it, when I undertook their removal at the end of an experiment. It would appear that the experimental fish were so cover-starved that a net, from which they would ordinarily flee as from a predator, was entered as if it were a haven.

Notropis atherinoides Rafinesque

Three emerald shiners, all about 55 mm long, were borrowed from exhibition tanks of the Department of Fisheries and Wildlife at Michigan State University and were returned a few days later. I made no quantitative study of this species, but observed them from time to time during their 19-hour stay in the experimental tank, and found that they school about as consistently and intensively as the following two native minnows.

Notropis stramineus (Cope)

Dennis W. Strawbridge (of Michigan State University) and I collected 23 specimens of sand shiner in October, 1956, from Little Long Lake, Kalamazoo County, Michigan. Most of them died within a month of collection, but five survived through the following October, when I initiated experiments on them. The experimental specimens ranged from 50 to 58 mm in standard length. Three were tested singly, two of them on two different occasions. Observations at 120-frame (about 7.5 second) intervals on motion-picture film gave occurrences in Quadrants I to IV of 23, 32, 35, and 34, respectively. Deviations from the expected 31 in each quadrant are not significant (X² = 2.8; n = 3; p = .41). The median distance from the center was 0.662 radii, which
is not sufficiently smaller than the 0.707 expected of random movement to cause appreciable aggregation. I assume that a single individual moves at random, although the number of observations is insufficient to demonstrate any but very marked deviations from randomness.

Groups of three individuals of 51-58 mm showed median perimeters of 0.47, 0.78, 1.20, and 1.30 radii in four experiments. The largest of these values is less than half of the 2.84 radii expected of independent movement. I conclude that this species schools consistently, although with variable intensity.

Pimephales notatus (Rafinesque)

Blunt-nosed minnows were collected at the same time and place as Notropis stramineus and had a similar history in captivity. There were fewer initially, but mortality was lower. One lived for more than three years in captivity. Four isolated individuals of this species were recorded 31, 41, 35, and 47 times in Quadrants I to IV, respectively ($X^2 = 3.84; p = 0.28$ with 3 degrees of freedom). So the deviations can reasonably be attributed to chance, especially since the extremes are in adjacent quadrants. The four showed median distances from the center of 0.60 to 0.86 radii, with a mean of 0.72, almost precisely the estimated random value. Individual movement, therefore, can be regarded as random.

Two groups of three fish (58 to 69 mm standard length) showed median perimeters of 0.41 and 0.86 radii, which average 0.64, a small proportion of the 2.84 radii expected from random movement, and a smaller value than the comparable measure for Notropis stramineus, although the difference is not significant. The blunt-nosed minnow seems to show schooling behavior to a marked degree.

Xiphophorus hybrid

I borrowed nine "black platies" from exhibition aquaria maintained by the Department of Natural Science, Michigan State University, and returned them shortly after the experiments. Their source and fate are unknown. The females were about 35 mm and the males about 30 mm in standard length.

I observed them in homo- and heterosexual groups of three and four individuals. One repeatedly jumped into the air im-
mediately after introduction to the experimental tank, and two others jumped at least once after introduction. Of all the species tested, this seemed the most ill at ease. Even after several hours in the experimental tank, some individuals would hover immobile near the bottom, bent into a slight arc at the tail region. Fish more than a half meter apart would ignore each other, but at closer intervals, one would sometimes approach the other and station itself a few millimeters away. When one member of such a pair moved a short distance away, the other would follow. These were the main indications of schooling. The typical appearance of schooling behavior, that of two or more fish swimming about together, was seldom seen.

*Poecilia reticulata* Peters

The experimental guppies came from Pets Aquarium in Lansing, Michigan. There was a steady mortality, of perhaps 10 per cent per week, with no overt cause. Whatever was killing the fish might have influenced schooling behavior.

I observed males in a group of five on one occasion, long enough to convince me that schooling behavior was indicated. All five swam about as a group for a few seconds, and at other times two or three swam together for brief intervals. The schooling of the male guppies, however, was obviously intermittent and of low intensity. They were too small for a photographic study, but females were large enough to photograph clearly from the observation port. Unlike the males, they schooled most of the time. Two females tested singly gave 14, 18, 19, and 19 occurrences in Quadrants I to IV, respectively. Deviations from the expected 17.5 in each quadrant are not significant (p = .82 for $X^2 = .972$ with three degrees of freedom). They gave median distances from the center of 0.53 and 0.69 radius, which indicate that the species might have a tendency to aggregate in the center, but not enough to cause a markedly contagious distribution.

I tested female guppies in groups of two, three, five, and twelve (Table 4 and Figure 4). All median perimeters were markedly below the values expected from random movement. With respect to the general equation for the relationship of school perimeter to companion number, female guppies show a value of $b$ of about 0.09 and a value of $a$ of about 0.68. The low
value of $b$ (it is about 0.80 for random distribution) indicates strong social attraction among small numbers of individuals. The high value of $a$ signifies a steep slope, much greater than with random movement (in which $a = 0.35$). The regression line for female guppies would, if continued, cross that of random distribution. Extrapolation on the graph gives a crossing at a companion number less than one hundred. The extrapolation is, of course, an uncertain basis for prediction, but it has a theoretical justification to be discussed later.

**TABLE 4**

<table>
<thead>
<tr>
<th></th>
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<tbody>
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<td>Early Late</td>
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<td>3.78</td>
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</tbody>
</table>

*Multiply by 24 to obtain median perimeters in mean standard lengths.

**Lepomis cyanellus**  Rafinesque

Two green sunfish of about 100 mm standard length were borrowed from exhibition tanks maintained by the Department of Fisheries and Wildlife at Michigan State University. Their origin and fate are unknown. They schooled intermittently during their twenty minutes in the experimental tank. I estimate the median perimeter to be about a third of that calculated for random distribution.

**Colisa lalia**  (Hamilton-Buchanan)

The dwarf gouramis were purchased from Pets Aquarium in Lansing, Michigan. They always seemed normal and healthy, and mortality was negligible. The larger males frequently built and defended nests and courted the females. Spawning may have occurred, but reproduction could scarcely be successful with several pairs of fish in each aquarium and with frequent disturbance by nets.
This species was my primary experimental subject, chosen because it offered a number of advantages. I judged its size to be an optimum compromise between the need for photographic clarity and for small size relative to the experimental tank. It also satisfied my desire for a species that would not ordinarily be thought of as a schooler. If such a fish schools in the experimental tank, it is obviously capable of schooling and inclined to do so in the special environment provided by the tank. Its disinclination to school in a planted aquarium must be attributed to an absence of the proper stimuli in such surroundings. This species also has the advantage of being readily obtainable and of having easily distinguished sexes. The males ranged from 35 to 42 mm in standard length, and the females from 33 to 38 mm.

Figure 4. Median perimeters of schools of guppies and of dwarf gouramis compared with perimeters expected of random movement.

Two females tested singly each gave a median distance from the center of 0.86 radius in early observations. In late observations they gave 0.88 and 0.90. All these values are higher than
the 0.71 calculated for random distribution. If they are representative, the independent movement of different individuals would result in an over-dispersed distribution (median perimeters larger than those calculated for randomness). The difference, however, hardly justifies consideration. The same females showed frequencies in Quadrants I to IV of 33, 29, 37, 32, respectively. Deviations from the expected 32.75 in each quadrant are not significant (p = 0.80 for $X^2 = 1.0$ with three degrees of freedom).

Two males similarly tested gave median distances from the center of 0.77 and 0.74 radius for early observations, and 0.64 and 0.63 for late. The mean of 0.695 is quite close to the random value. Occurrences in Quadrants I to IV were 30, 30, 29, and 21, respectively. Deviations from the expected 27.5 are not significant (p = 0.63 for $X^2 = 2.1$ with three degrees of freedom). I assume that both sexes move at random in isolation.

Both sexes showed pronounced schooling in all groups tested (Tables 5 to 8, Figure 4). It apparently makes little difference whether the school is composed of males or females or both. Hence the only variable considered in the graph is companion number. All experiments with the same companion number were averaged to obtain the plotted points. Such means of medians scarcely deviate from a straight line on the graph and thereby indicate the suitability of the graphic procedure. The schooling constants a and b are about 0.54 and 0.095, respectively, and indicate that social forces in this species are less than those of female guppies. Further consideration of these points will be undertaken in the discussion.

**Gouramis and Guppies in Heterotypic Pairs**

Median perimeters of one-companion schools of Colisa and Poecilia are about 0.39 and 0.18 radii, respectively. If schooling were a non-specific reaction to any object of appropriate size, one might expect heterotypic pairs to show intermediate perimeters. This, however, is decidedly not the case. In eight experiments with a female guppy and male or female gourami there was never a clear indication of schooling. Occasionally there were movements that could be interpreted as the guppy attempting momentarily to school with the gourami, but these events were infrequent and uncertain. The two fish usually gave the
### TABLE 5
**MEDIAN PERIMETERS IN RADII* OF ALL-MALE SCHOOLS OF *Colisa lalia***

<table>
<thead>
<tr>
<th>Corn-Panion Number</th>
<th>Random Value</th>
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<th>Late</th>
<th>6 Dec. '59 Early</th>
<th>Late</th>
<th>15 Jan. '60 Early</th>
<th>Late</th>
<th>6 Feb. '60 Early</th>
<th>Late</th>
<th>7 Mar. '60 Early</th>
<th>Late</th>
<th>26 Mar. '60 Early</th>
<th>Late</th>
<th>8 Apr. '60 Early</th>
<th>Late</th>
<th>Means Early</th>
<th>Late</th>
<th>Total</th>
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<tbody>
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<td>1.38</td>
<td>1.47</td>
<td></td>
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</tr>
</tbody>
</table>

For perimeters in mean standard lengths of fish multiply by 19.

### TABLE 6
**MEDIAN PERIMETERS IN RADII* OF ALL-FEMALE SCHOOLS OF *Colisa lalia***

<table>
<thead>
<tr>
<th>Corn-Panion Number</th>
<th>Random Value</th>
<th>16 May '59 Early</th>
<th>Late</th>
<th>13 Dec. '59 Early</th>
<th>Late</th>
<th>9 Jan. '60 Early</th>
<th>Late</th>
<th>13 Feb. '60 Early</th>
<th>Late</th>
<th>30 Mar. '60 Early</th>
<th>Late</th>
<th>7 Apr. '60 Early</th>
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<th>Means Early</th>
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</table>

*For perimeters in mean standard lengths of fish multiply by 19.

### TABLE 7
**PERIMETERS IN RADII* OF SCHOOLS OF EQUAL NUMBERS OF MALES AND FEMALES OF *Colisa lalia***

| Corn-Panion Number | Random Value | 13 Nov. '59 Early | Late | 14 Nov. '59 Early | Late | 16 Nov. '59 Early | Late | 21 Nov. '59 Early | Late | 22 Nov. '59 Early | Late | 22 Jan. '60 Early | Late | 22 Feb. '60 Early | Late | 12 Mar. '60 Early | Late | Means Early | Late | Total |
|---------------------|--------------|-----------------|------|-----------------|------|-----------------|------|-----------------|------|-----------------|------|-----------------|------|-----------------|------|------------|------|--------|
| 1                   | 1.93         | 0.26            | 0.29 | 0.35            | 0.40 | 0.21            | 0.83 | 0.32            | 0.40 | 0.34          | 0.46 | 0.40            | 0.46 | 0.30            | 0.41 | 0.34          | 0.38 | 1.77   |
| 7                   | 4.50         | 1.77            | 0.29 | 0.35            | 0.40 | 0.21            | 0.83 | 0.32            | 0.40 | 0.40          | 0.46 | 0.40            | 0.46 | 0.30            | 0.41 | 0.34          | 0.38 | 1.77   |
| 11                  | 4.80         | 2.59            | 2.58 | 2.59            | 2.58 | 2.59            | 2.58 | 2.59            | 2.59 | 2.59          | 2.59 | 2.59            | 2.59 | 2.59            | 2.59 | 2.59   |

*For perimeters in mean standard lengths of fish multiply by 19.
impression of complete independence. These intuitive impres-
sions are verified by analysis of photographic records (Figure 5). 
Although the median perimeters of heterotypic pairs differ sig-
ificantly from the calculated random value and from both homo-
typic combinations, they are closer to the random value.

I attempted to match all heterotypic pairs with respect to 
size. The two specimens were always within about two milli-
meters of the same standard length.

### Table 8

<table>
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<th>Companion Number</th>
<th>Random Median</th>
<th>Means of Medians</th>
<th>Prop. of Max.</th>
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<td></td>
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<td>Late</td>
</tr>
<tr>
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<td>1.93</td>
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<td>0.36</td>
</tr>
<tr>
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<td>0.86</td>
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</tr>
<tr>
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<td>1.77</td>
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<tr>
<td>11</td>
<td>4.80</td>
<td>2.58</td>
<td>2.59</td>
</tr>
</tbody>
</table>

Figure 5. Median perimeters of homotypic and heterotypic pairs of dwarf gouramis and female guppies. A horizontal line shows the observed range, the open rectangle a standard deviation, and the blackened rectangle two standard errors on either side of the mean (central peak).

**DISCUSSION**

The proposals that have been made on the survival value of 
schooling can be put in three groups: (1) that schooling serves to 
"condition" the medium, (2) that it relates to reproduction, and 
(3) that it affords protection against predators.

It is well established that various organisms can modify their 
environments to their own benefit, but can succeed in this only 
when their population densities are high. The removal of toxic
substances from the water is of demonstrated effectiveness in aquaria (Allee et al., 1949:360), where concentrations of toxins may be high while their absolute quantity is low. In nature, such effects may be of some importance in areas of industrial pollution, but they could not have been important in the evolution of schooling in the oceans and other large bodies of water where this behavior is most in evidence.

It can hardly be doubted that some schools play an important role in reproduction. The young of many species move in a school of their sibs under parental supervision. Likewise, adults of some species form spawning schools, although most of the apparent examples may really be aggregations on restricted spawning areas. In the present discussion I am not concerned with these specialized examples, but with the schools formed both in and out of the breeding season by individuals of about the same size regardless of sex.

Breder (1959:470) pointed out that schooling keeps individuals of the same species together and must therefore assure, at least occasionally, that each fish can find a mate when the breeding season arrives. This is undoubtedly true, but it can hardly be an important factor in the evolution of schooling. If it were we would expect a certain efficiency in the realization of this effect. We would expect that schooling would generally be initiated or intensified as the breeding season approaches, and we would expect it to be most characteristic of species of low population densities in which the finding of mates would be a serious problem. Neither of these expectations is realized.

A number of people have suggested that schools afford protection against predation. Allee (1951:100, Allee et al., 1949:399) maintained that schooling reduces the total area exposed to attack, or produces a "confusion effect" on the predators and thereby reduces the loss by predation. Brock and Riffenburgh (1960) proposed that predators quickly feed to satiation when they find a large school of their prey, but that such encounters are reduced in number as the schools become fewer and larger. Since any predator has a limited capacity at any one time, the reduction in the number of encounters may reduce the total predation. Knipper (1955) interpreted some very dense schools as "collective mimicry." A school of a large number of small fish presumably resembles a single large fish or other invulnerable object well enough to deceive its usual predators. These effects
are probably real in some instances, but there are known examples of predation being facilitated by the schooling of the prey. An obvious example is predation by man. To be commercially exploitable a fish must be individually so large that it is economical for fishermen to pursue a single individual, or it must form schools, so that fishermen may pursue a large number in one operation. No small fish that does not school can support an important fishery. It is likely that schooling plays a similar role in the activities of predators other than man. The long tail of the thresher shark is reputed to be used to herd fish into localized schools so as to facilitate attack (Bigelow and Schroeder, 1953). The sword of a swordfish may be a weapon specialized for attacking schools. Rich (1947) described swordfish moving through large schools and swinging their two-edged weapons so as to incapacitate large numbers of smaller fish, some of which are then recovered and consumed. Enough are missed, however, to allow fishermen to glean "bushels" of dead or maimed individuals. The wastefulness of attacks on schools by swordfish and other species seriously impugns the concept of protection by the rapid satiation of the predator. The saw of the sawfish may likewise be a specialized device for feeding on schools (references cited by Breder, 1952). The spear of the marlins apparently has no such significance (Wisner, 1958). Breder (1959: 414), Bullis (1961) and Fink (1959) gave other probable examples of the facilitation of predation by the schooling of the prey.

The normal effect of schooling on predation, either positive or negative, can not be decided by the citing of examples, real or hypothetical. Extensive and unbiased evidence is required for such an approach and is not likely to be forthcoming. The matter must be decided on the less direct evidence of relating the properties of schools to the presumed protective function. It is incumbent on those who believe that schools are protective adaptations to show that the structure and workings of a school are such as to achieve mass protection in a functionally efficient manner.

I see no evidence that schools do have such properties. On the contrary, a school typically shows no trace of any functional organization. It has no leader; it shows no division of labor; it undergoes no ordered sequence of endogenous changes. As Breder (1959:459) asserted in cybernetic terms, a school is highly re-
dundant and has a low information content. In these respects, a school shows a sharp contrast with such groups as ant colonies, in which all important features have an inescapable functional basis.

This lack of any apparent functional organization is an eloquent argument for the conclusion that the properties of schools have not been established by natural selection on the basis of their survival values. I would therefore propose that a school is not an adaptive mechanism itself, but rather an incidental consequence of adaptive individual behavior. The adaptation is the reaction of each individual to the school. The fact that the reaction contributes to the properties of the stimulus need not complicate the basic issue. A similar, but less extreme position has been suggested by Breder (1959 and earlier).

I suggest that schooling could be expected to arise in any species subject to aggregation. Even pelagic fishes would aggregate where their food is concentrated, as at zooplankton concentrations caused by convergence of surface waters. Under such conditions, the first fish to be sighted and pursued by a predator would be one on the periphery of the aggregation. Any individual that had an urge to place itself among others of its own kind would often be putting them between itself and sources of danger. Such an individual would be found within the group more often and on the periphery less often than its fellows, and would therefore be favorably selected for survival in the presence of vision-dependent predation. Genetic tendencies in this direction would accumulate until the advantages of increased gregariousness would be balanced by some disadvantage, such as the depletion of food in the center of a school.

I believe that this is an adequate explanation of the historical initiation of schooling behavior. Once started, however, other factors would become important. It would be an advantage to any fish, normally found among others of its own kind, to be able to recognize fright or distress in its companions. Such a fish would not only be using them to lure predators away from itself, but also as a distant early warning system for the detection of dangers beyond its own sensory range. Adaptations to exploit this possibility could be expected to arise.

The seeking of conspecific individuals or groups is only one way of achieving the protection of their proximity. Another way is to attract other individuals by making species-recognition
cues as effective as possible. Both species specificity and size homogeneity would be important for making a fish inconspicuous in a school. The schooling phenomenon would be based on four factors: (1) The recognition of conspecific individuals, (2) the desire to approach them, (3) the giving of species-recognition cues, and (4) the initiation of defensive reactions when such reactions are detected in other members of the school. A school and all of its properties can be explained as the statistical consequence of these individual adaptations. Nothing is implied here of any functional organization of the school as such. Such organization would be implied by the existence of any specialized warning signals, any sounds or displays that function as warnings and can not be explained as incidental to the flight reactions themselves. Flocks of birds, which give alarm notes and display conspicuous tail feathers when they take flight, do appear to be functionally organized in this respect, although these mechanisms may relate more to the survival of dependent offspring than of the flock. Evidence for such mechanisms in fish schools would invalidate my position on their lack of a functional organization.

Such a mechanism has been recognized in the Schreckstoff effect. Skinner, Mathews, and Parkhurst (1962) state that "As a means of warning other members of a school, alarmed fish communicate fright by releasing a chemical substance into the water." Investigations of the Schreckstoff effect were reviewed by Pfeiffer (1962). It has been established for many of the Cypriniformes that an injured individual gives off an olfactory stimulus that induces defensive reactions in other individuals. These reactions are obviously adaptive. The release of the stimulus, however, is explainable as an incidental effect of damage, and gives no indication of being "a means of warning other members of the school." My reasons for this conclusion are: (1) Fishes provide a wealth of examples of communication by visual and auditory social releasors, which are transmitted instantaneously between individuals, and schooling itself is a reaction to visual stimuli. Why then, for communicating a message for which speed of reception would be especially important, would fishes rely on the slow process of chemical diffusion? (2) Schreckstoff is not actively secreted into the water. It escapes from the skin as a result of mechanical injury. (3) The phenomenon is almost entirely confined to a freshwater order, and within this group it can be as easily demonstrated in
species that seldom school as in those that do so regularly. (4) *Schreckstoff* has a low specificity, and a damaged fish may stimulate alarm reactions in other genera and families. I suspect that *Schreckstoff* may be functionally a repellent, which would stimulate distaste and rapid release from the mouths of some predators. A number of observations reported by Pfeiffer suggest this interpretation.

I have assumed that schooling is a form of cover-seeking, and should be most in evidence in cover-deficient habitats. This is certainly in accordance with general observations, which indicate that schooling is a conspicuous phenomenon in pelagic oceanic waters, scarcely detectable in weedy or rocky shallows, and of intermediate development in intermediate habitats. No doubt there are species with strong innate tendencies to form schools, and other species in which such tendencies are never more than weakly developed. My experiments, however, raise the possibility that much of the observed variation is due directly to the habitats in which different species are found. It was with this possibility in mind that I designed the experimental environment to be as deficient in cover as possible. A fish in such an environment would have no possible outlet for its cover-seeking reactions other than whatever outlet could be provided by other fish. Every species observed in this tank schooled in it, at least part of the time. These species included such forms as eels and dwarf gouramies, which would not ordinarily be expected to school. The fact that they did so indicated the pertinence of schooling to cover-seeking behavior. There are many other observations that indicate that schooling is initiated or intensified when escape or cover-seeking would be appropriate (Breder, 1959:412).

Yet the great contrast in the intensity of schooling between homotypic and heterotypic pairs of the dwarf gourami and the guppy indicates that these fish show a specialized reaction to conspecific individuals. Even in these species, schooling has evolved to the point at which specific recognition cues play an important role. In nature, the schooling reaction would probably be weakly shown, because these species normally inhabit cover-rich, heterogeneous environments. Their schooling, however, would probably reinforce any aggregating tendencies, and cause a more contagious distribution than would otherwise prevail. I do not wish to imply that the reinforcement of schooling by
species recognition cues can be demonstrated in all fishes nor that I would expect them in all of the species treated in this report. I would seriously doubt their existence in the juvenile eels. Their schooling is probably in its most primitive state, a mere reaction to other objects that afford a slight amount of visual concealment.

One objective of the study was to attempt to measure schooling intensity by parameters that would be independent of the number of individuals present. The constants $a$ and $b$ in the schooling equation are uniformly descriptive over the investigated range of two to twelve individuals. This gives a minor advantage over comparing deviations from the binomial distribution of fish numbers in different halves of an aquarium (Breder and Halpern, 1946). These deviations provide meaningful data only with respect to specific numbers of individuals. No one has yet used a measure of schooling that would not be influenced by the size of the experimental container.

I have quantitative data on groups of widely different companion number in two species, and in at least one the regression of school perimeter as a function of companion number was steeper than the corresponding random function. If these slopes showed even an approximate constancy for one more logarithmic cycle, the regressions for the fishes would certainly cross that of random distribution, probably with companion numbers in the range of fifty to a hundred. This crossing is to be expected on the basis of the theory of equilibrium distance, of which Breder (1954) provides a mathematical derivation based on the observed behavior of fish as they approach each other and form a school. Similar Soviet studies are summarized by Nikolsky (1963). If schooling results from the establishment of preferred average distances between individuals it would, if distances were short, explain the small perimeters observed in my experiments. With increasing numbers in any finite container, however, it would sooner or later be impossible for the fish to avoid being forced closer together than the equilibrium distance. As this condition is approached, the fish would pass from a contagious to an over-dispersed distribution (crossing of the regressions). A hundred guppies or dwarf gouramis in the experimental tank would be over-dispersed if they maintained distances from each other equal to the median observed for pairs.
SUMMARY

Schooling (a contagious distribution due to social attraction) was apparent in all nine species investigated, including such normally territorial or solitary forms as the dwarf gourami and the eel. This behavior was attributable to the special conditions of the circular experimental tank, which provided a topographically featureless and visually uniform white background. Dwarf gouramis, female guppies, and groups of points scattered at random within a circle showed median perimeters (of the smallest circumscribed convex polygons) closely approximated by a mathematical function of fish number that plots as a straight line on a log-probability graph. Such lines and two constants are useful for comparing species with each other and with the calculated random distribution. The schooling behavior seen in homotypic pairs of either dwarf gouramis or female guppies was virtually absent for heterotypic pairs of these species.

Schooling can be expected to evolve in any population subject to aggregation (contagious distribution due to non-social forces), because peripheral or isolated individuals would be especially liable to predation. Genetic tendencies to avoid such positions by associating with other individuals would accumulate. Social releasers effective in the attraction of other individuals would evolve for the same reason. Another expected adaptation would be the ability to react appropriately to the appearance of flight or distress in other members of a school. In this way a school can be explained as the statistical consequence of the adaptations of its members. The regularities of the properties of schools are those of statistics, not of a functional organization of the whole.
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ZUSAMMENFASSUNG


Fischschwärme sind in jeder Fischbevölkerung zu erwarten, die sich normalerweise in Gruppen aufhält, da vereinzelte und periphere Einzelgänger der Plündern ausgesetzt sind. Man spricht hier vom "Zusammenbringen," das ist die gruppierende Anordnung, die nicht auf soziale Anziehung beruht. Es scheint auch, dass sich die genetischen Tendenzen, sich zu vereinigen um Plündern zu vermeiden, vergrößern würden. Ausloser, die bewirken andere Fische anzuziehen, würden sich aus dem gleich Grund entwickeln (d. i. Schutz vor Plündern). Eine andere Anpassung, die man erwarten könnte, wäre die Fahigkeit auf die Gefahr oder Flucht anderer Mitglieder eines Schwarmes entsprechend zu reagieren. Auf Grund dieser Betrachtungen kann man einen Schwarm als die statistische Folgerung der Anpassung ihrer Mitglieder erklären. Die Regelmassigkeiten eine Schwarmbildung sind auf die Statistik basiert und nicht auf die funktionelle Einordnung in den Schwarm.

Translated from the English summary by Erich Gorgias of Berkeley, California.