of this form from the southern tip of Florida. In 1934, with Mr. and Mrs. H. G. M. Jopson, we saw another specimen at the Miami Aquarium. But the striking discovery was to find that some of the students around Gainesville, Florida, had also taken two or three specimens at that place.

[1] Cope, E. D., *Proc. Acad. Nat. Sci., Phila.*, 205 (1867).
[2] Bishop, S. C., *Jour. Elisha Mitchell Sci. Soc.*, **43**, No. 3–4, 157 (1928).
[3] Weller, W. H., *Proc. Junior Soc. Nat. Sci., Cincinnati*, **1**, Nos. 5–6, 6 (1930).
[4] Cope, E. D., *Am. Nat.*, **15**, 878 (1881).
[5] Pope, C. H., *Am. Mus. Novitates*, No. 306, 6–10, Apr. 14 (1928).
[6] Netting, M. G., and N. Richmond, *Copeia*, No. 3, 101–102, July 1 (1932).
[7] Taylor, E. H., *Univ. Kan. Sci. Bull.*, **20**, No. 11, 243–245 (1932).
[8] Wright, A. H., *Proc. Biol. Soc. Wash.*, **37**, 143 (1924).
[9] Baird, S. F., *Proc. Acad. Nat. Sci., Phila.*, 253 (1858).
[10] Bailey, V., *North Amer. Fauna*, No. 25, 40–42 (1905).
[11] Stejneger, L., *Proc. Biol. Soc. Wash.*, **29**, 228 (1916).
[12] Cope, E. D., *Rept. U. S. Nat. Mus.*, 254–255, 349, 797–799, 1098 (1898, 1900).
[13] Taylor, E. H., *Proc. Biol. Soc. Wash.*, **44**, 129–132 (1931).
[14] Stejneger, L., *Proc. U. S. Nat. Mus.*, **39**, 34 (1910).
[15] Brown, A. E., *Proc. Acad. Nat. Sci.*, 58, Jan. (1901).
[16] Ortenburger, A. I., *Univ. Mich. Memoirs*, I, 178 (1928).
[17] Yarrow, *Bull. U. S. Nat. Mus.*, No. 17, 41 (1880).
[18] Cope, E. D., *Proc. U. S. Nat. Mus.*, **11**, 388 (1888).
[19] Barbour, T., *Copeia*, No. 84, 68–69 (1920).
[20] Brady, M., *Proc. Biol. Soc. Wash.*, **46**, 153–154, Oct. 26 (1933).
[21] Brown, A. E., *Proc. Acad. Nat. Sci., Phila.*, 492–495 (1901).
[22] Schmidt, K. P., *Copeia*, No. 148, 87–88 (1925).
[23] Brown, A. E., *Proc. Acad. Nat. Sci.*, **53**, 612–613 (1901).
[24] Blanchard, F. N., *U. S. Nat. Mus. Bull.*, **114**, 247–249 (1921).
[25] Barbour, T., *Proc. N. Eng. Zoöl. Club*, No. 7, 1 (1919).
[26] Brown, A. E., *Proc. Acad. Nat. Sci., Phila.*, 199 (1890).
[27] Taylor, E. H., *Univ. Kan. Sci. Bull.*, **20**, No. 11, 243–245 (1932).
[28] Stejneger, L., *Jour. Wash. Acad. Sci.*, **15**, No. 20, 463 (1925).

STUDIES OF PROTECTIVE COLOR CHANGE. III. EXPERIMENTS WITH FISHES BOTH AS PREDATORS AND PREY

BY F. B. SUMNER

SCRIPPS INSTITUTION OF OCEANOGRAPHY, UNIVERSITY OF CALIFORNIA, LA JOLLA, CALIFORNIA

Communicated April 12, 1935

In an earlier issue of these PROCEEDINGS[1] I described some experiments designed to test the protective value of concealing coloration to organisms equipped with the mechanism for adjusting their color-scheme to that of the background. Small fishes (*Gambusia patruelis*) were chosen for this purpose, a fish-eating bird (penguin) being selected as the predator. These results afforded unmistakable evidence that fishes which are not well adjusted to the color (more strictly the *shade*) of their background are captured in preference to those which are better adjusted. The numbers of fishes used were considerable and the differences in survival rates were great.

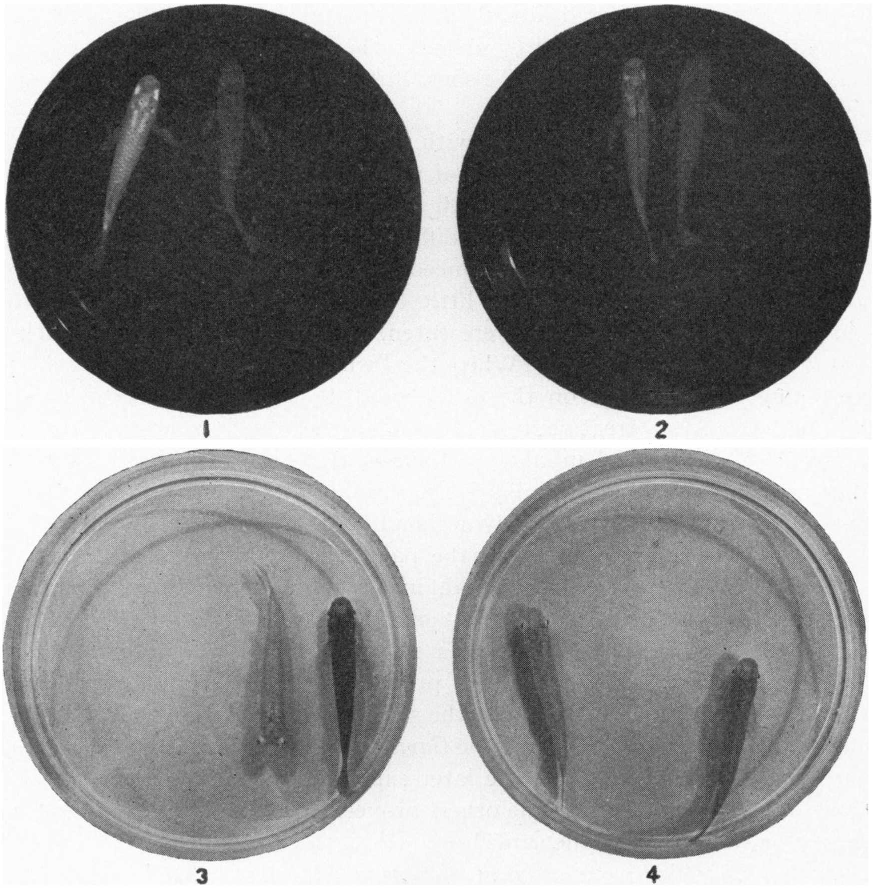
Since conducting these earlier experiments with penguins another fish-eating bird, this time a wader, was used as the predator, while the former birds were again employed in a supplementary series of experiments. These results, just published,[2] furnish additional evidence of the protection afforded by relative inconspicuousness when fishes are preyed upon by birds. This selective predation on the part of birds was still evident, even after the initial difference between the two lots of fishes had been greatly reduced by sojourn upon a common background. It was also demonstrated that the differential mortality of the two lots did not result from any difference in their ability to outswim their pursuers.

At the time of performing these experiments, I realized that smaller species of fish are probably preyed upon to a greater extent by larger fishes than by birds. Any test of the effectiveness of the mechanism for concealment must therefore take into account this more numerous class of predators.

A few preliminary experiments with the large-mouthed black-bass (*Micropterus salmoides*) were undertaken. But several features of my procedure at this time rendered the results of these experiments worthless, and this test was therefore deferred to a more favorable opportunity. Later, two specimens of a supposedly voracious Chinese species (*Channa fasciata*) were secured, and the attempt renewed. But these fishes were not very successful in catching the *Gambusia*. It is worth recording, however, that about twice as many "whites" as "blacks" were devoured in the course of a few trials in the black tanks.

The real test with a predaceous fish was made with the blue-green sunfish (*Apomotis cyanellus*). Twenty-five specimens of this species were caught in a pool which had been stocked some years ago.[3] These ranged from 7 to 14 cm. in length, but it is probable that at least half of the specimens were too small to devour the *Gambusia*. The latter, for the most part, ranged in length from 3 to 5 centimeters. Before the commencement of the experiment they had been kept for 72 days in cement tanks painted black and white, respectively. As stated in my earlier accounts these two lots differed glaringly when first compared upon a common background. The difference decreased perceptibly within a minute or two, however, and was greatly reduced during the first hour or less (Figs. 2, 4). But some degree of difference commonly remained discernible to the human eye for several days. At no time in the course of the experiments here reported was any real difficulty encountered by me in distinguishing fishes having these contrasting histories. Commonly recognition was immediate.

For the feeding tests a cement tank was used, having a bottom area of 187 × 55 centimeters. Running fresh water was passed through this tank, and kept, in most of the experiments, at a level of 30 cm. The walls and bottom of the tank were painted a pale yellowish gray, approximating Ridgway's "light olive gray" or "light grayish olive." For those experiments in which a black background was required, the interior of the tank was not itself painted, but a tight-fitting, black wooden box was inserted as a lining.



Figures 1 and 2.—Two specimens of *Gambusia* which had been kept for nearly four months in black and white tanks, respectively, then photographed upon black background. Figure 1, after 10 seconds; figure 2, after 2 hours.

Figures 3 and 4.—Two specimens of identical history, photographed upon pale gray background, very similar to that of tank used in experiments. Figure 3, after 35 seconds; figure 4, after 10 minutes.

(Photographs by Nelson A. Wells and the writer.)

The sunfish were kept in this experimental tank[4] and the *Gambusia* were introduced as occasion demanded. Commonly, 25 each of the "blacks" and "whites" were poured in simultaneously, but the procedure was varied to suit the requirements of the experiment. The food-fishes were left in for a period of from one minute to several hours before being removed and counted. Since most of the feeding occurred within the first few minutes, this period, in a large majority of cases, was less than fifteen minutes.

The data derived from these 29 experiments are recorded in table 1. The more essential results of these studies may be stated briefly as follows:

(1) In four experiments with the black tank, both "white" and "black" *Gambusia* were transferred directly from their customary backgrounds to the experimental tank. Thirty-seven of the 200 food-fishes were eaten, i.e., 18.5 per cent. Of these 37 fishes, 8 (22%) were "blacks," 29 (78%) being "whites."

(2) In four other experiments with the black tank, the "white" fishes were kept for a preliminary period of varying length in a black container before being transferred (along with the "blacks") to the experimental tank. This was in order that the differences in appearance between the two lots might be considerably reduced. Such treatment, for periods up to two hours, seems to have had little effect upon the outcome. In two experiments thirty-four fishes were eaten, of which 8 (24%) were blacks and 26 (76%) were whites. When the "whites" had been subjected to darkening for 23 hours, on the other hand, 9 "blacks" and 4 "whites" were eaten. After treatment for two days the numbers were 6 and 4, respectively, the initial number of each in this last case being only 13. This heavier mortality of the black fishes, under these conditions, is hard to account for. It may be purely accidental.

(3) In nine experiments with the pale gray tank, both "black" and "white" *Gambusia* were transferred, in equal numbers, directly to this tank without preliminary treatment of the "blacks." Of the 430 fishes used, 208 (48%) were eaten. This much heavier consumption of the *Gambusia* in the pale tank cannot probably be regarded as significant. It depends partly on the fact that the sunfishes had, by this time, become more fully accustomed to eating the *Gambusia* in the presence of observers, partly upon my selection, in the later experiments, of the smallest food-fishes available. (Many of the others proved to be too large to be readily caught or swallowed by the sunfish.)

Of the 208 which were eaten in these nine experiments, 137 (66%) were "blacks," 71 (34%) being "whites." These figures imply a lower degree of selectivity on the part of the sunfish in the pale-tank experiments than in those with the black one. It is of interest that this same relation held in the experiments with penguins, and, indeed, that the proportions of "black" and "white" fishes eaten in the two tanks agree fairly closely

TABLE 1

NUMBERS OF "BLACK" AND "WHITE" *Gambusia* DEVOURED BY *Apomotis* UNDER VARIOUS EXPERIMENTAL CONDITIONS

	NO. OF EXPERIMENT	DATE 1935	NO. OF "BLACKS" OFFERED	NO. OF "WHITES" OFFERED	PREVIOUS SOJOURN ON COMMON GROUND	DURATION OF TEST	NUMBERS EATEN "BLACKS"	NUMBERS EATEN "WHITES"	PERCENTAGES "BLACKS"	PERCENTAGES "WHITES"
Black tank	1	2/13	25	25	0	1 hr. 45 min.	1	5		
	2	14	25	25	0	2 hrs.	2	7	22	78
	3	15	25	25	0	5 hrs.	3	5		
	4	18	25	25	0	15 min.	2	12		
	5	20	25	25	16 min.	2 hr. 40 min.	4	9	24	76
	6	25	25	25	2 hrs.	20 min.	4	17		
	7	27	25	25	23 hrs.	4 hrs. 30 min.	9	12	48	52
	8	28	13	13	48 hrs. (±)	35 min.	6	4		
Gray tank	9	3/6	25	25	0	10 min.	6	5		
	10	7	25	25	0	5 min.	17	12		
	11	9	25	25	0	3 min.	18	11		
	12	11	25	25	0	2 min.	16	10		
	14	13	25	25	0	1¼ min.	24	10	66	34
	18	18	15	15	0	66 sec.	15	3		
	19	18	25	25	0	3 min.	14	11		
	23	22	25	25	0	30 min.	10	2		
	28	4/1	25	25	0	3 min.	17	7		
	16	3/15	16	32	0	1 min.	13	8	67	33
	24	23	16	32	0	3 min.	9	3		
	13	12	25	25	1 hr. 20 min.	5 min.	10	14		
	15	14	25	25	30 min.	2 min.	14	12		
	17	16	25	25	15 min.	2 min.	9	10	49	51
	25	27	25	25	10 min.	3 min.	5	0		
	26	28	20	20	10 min.	12 min.	4	6		
	27	30	25	25	10 min.	3 min.	8	10		
	20	20	15 ur. 15 con.			1½ min.	15 ur. 3 con.			
	21	20		25 adr. 25 con.		2 min.		25 adr. 2 con.		
	22	21		25 adr. 25 con.		?		22 adr. 2 con.		
	29	4/2	25	25 adr.		2 min.	5	20		

in the two cases. It is likewise a result which an observer might readily have forecast. It is much easier for the human eye to see one of the "white" fishes in the pale tank than to see one of the "black" fishes in the black tank.[5]

(4) Two of the experiments (9 and 19), conducted in the late afternoon when the light was dim, seemed to indicate that selection on the basis of visibility was less intense at such times.[6] But the numbers are few.

(5) In a number of the foregoing experiments, in which equal numbers of the "black" and "white" *Gambusia* were offered to the sunfishes, all or most of the "blacks" were devoured, while a majority of the "whites" remained uneaten. This means, of course, that in the later stages of such an experiment the "whites" greatly outnumbered the "blacks" in the tank. Despite this fact, the sunfish continued to pursue the latter and largely to ignore the former.

As a further test of this tendency, two experiments were performed (numbers 16 and 24) in which twice as many "whites" as "blacks" were introduced at the outset. It is of interest that of the 33 fishes eaten 67 per cent were "blacks" and 33 per cent "whites." These percentages, it will be recalled, are almost precisely the same as those obtained when equal numbers of "blacks" and "whites" were offered. Furthermore, if we consider for each lot the proportion of the number offered which was eaten, we find this to be 69 per cent for the "blacks" and 17 per cent for the "whites." Thus "availability," in the spatial sense in which this word seems to be chiefly employed by McAtee, has had little to do, in the present case, with the choice made by the predators.

(6) As in the case of the black tank, a number of experiments were performed with the gray one, in which the food-fishes offered had been subjected to treatment which greatly reduced their initial differences. The treatment in the present case consisted in keeping the "blacks" upon a white background for a varying period before they were poured (in company with the "whites") into the experimental tank. This period ranged from 10 to 80 minutes. In the present experiments the convergence proved to be sufficiently great within even the ten-minute period to completely nullify the difference in survival rate. Of the 290 *Gambusia* offered to the sunfishes in the course of six experiments, 102 (35%) were eaten. The proportions of "blacks" and "whites" were nearly identical (49% and 51%, respectively).

This result may seem surprising, in view of the evident difference to the human eye between the two sets of fishes, even after keeping the "blacks" on a pale background for ten minutes (Fig. 4). The result is likewise quite different from that obtained in the later penguin experiments,[7] in which a marked degree of choice was still evident after keeping both sets of fishes in the pale tank for 20 to 27 hours.

However, the penguin experiments differed from those with sunfishes in certain important respects. First, the entire lot of *Gambusia* employed in the latter experiments had been kept for more than a month in a nearly white tank before transferring them to white and black tanks, preparatory to the experiments here described. Because of this history, it seems likely that these later "blacks" would more readily pale when transferred to a pale background.

In the second place, the pale tank used in the sunfish experiments was somewhat darker than that used in the experiments with birds. The fact that, after a period of "bleaching," an originally black *Gambusia* still appeared distinctly darker than this background, to the human eye, is not decisive as to its appearance to the sunfish. The human observer views these fishes from above, or nearly so. The piscine predator views them from the side or even from below. It may well be that, against the background here used, the "whites" and the (bleached) "blacks" were equally visible (or invisible) to their pursuers.

(7) Four experiments (20, 21, 22, 29) were performed for the purpose of determining the influence of motion versus quiescence upon the chances of survival of these little fishes. Numerous authors (e.g., Young[8] and Cuénot[9]) have pointed out the importance of quiescence in protecting helpless organisms from predators. Cuénot describes an experiment of his own in which certain shrimps proved to be safe, regardless of their color, so long as they remained motionless, though they were promptly seized by fishes as soon as they moved. My experiments dealing with this subject make it plain that the situation is altogether different in the case of *Gambusia* and *Apomotis*.

In the first of these experiments (No. 20), 15 black *Gambusia* were subjected to a 1% solution of urethane until they were completely narcotized. This drug has the effect of anesthetizing the fish and likewise of maintaining it in a condition of maximum blackness. These 15 fishes, after rinsing, were introduced along with another 15 "blacks" into the gray experimental tank. The *Gambusia* were poured in at one end while the sunfishes were at first kept at a distance by the insertion of a wooden partition. When the latter was removed, the sunfishes promptly attacked the anesthetized *Gambusia* and consumed the entire lot within one and a half minutes, at which time only three of the active ones had been taken.

In a second experiment, 25 "whites" were subjected to a 1:2000 solution of adrenalin. This drug, likewise, narcotizes the fish but its effect upon the chromatophores is opposite to that of urethane. The fishes retain their high degree of pallor. In this experiment, the sunfishes devoured all of the 25 anesthetized *Gambusia* within two minutes, during which time only two of the controls had been eaten.

Another experiment was conducted with "white" fishes subjected to adrenalin. In this case, the water was diminished in depth from 30 centimeters to 13. In the two experiments first described, in which deeper water was used, the anesthetized fishes mostly sank to the bottom while the controls swam actively near the surface. The reduction of the water level was for the purpose of bringing the two lots into closer association. The result of the feeding test was, nevertheless, almost identical with the others. Twenty-two of the anesthetized fishes and only two of the controls were devoured during the period of the experiment.

It is plain that active locomotion, far from exposing these food-fishes to greater hazard, was of vital importance in enabling them to escape their pursuers. In order to evaluate the relative efficacy of these two methods of protection (concealment and flight) in the present circumstances, one decidedly inadequate experiment was performed (No. 29). Twenty-five "white" *Gambusia* were subjected to adrenalin, while 25 "blacks" were left untreated. In the course of two minutes 20 of the motionless "whites" were devoured and only 5 of the active "blacks." One cannot be certain, however, that the results would have been the same had the *Gambusia* used been smaller. By this time most of the specimens were too large to serve well as living prey for the sunfishes.

The foregoing experiments, in the aggregate, make it plain, first, that relative conspicuousness in a given environment, far more than availability in the spatial sense, determines the survival or non-survival of small fishes under attack by piscine predators; and, second, that total quiescence is a handicap rather than an advantage to such fishes in escaping capture. These statements are subject, of course, to the customary qualification: "at least for the species used, and under the conditions of these experiments." But the species used are believed to be representative, each of a vast array of species with similar habits; while the conditions of these experiments are not believed to be such as to enhance the selectivity in feeding, but rather to diminish it. For the chances of capturing an inconspicuous fish are probably greater in an experimental tank than in a large natural body of water.

Granting these facts, the utility of the chromatophore mechanism by which these color changes are effected is hardly open to doubt. And since there exist wide differences in the perfection of this mechanism, between individuals as well as between species, it seems probable that natural selection has played an important part in its evolution.

[1] *Proc. Nat. Acad. Sci.*, **20**, 559–564, October (1934).

[2] *Am. Nat.*, **69**, 245–266 (1935).

[3] This species is not native to California.

[4] It is of interest that the sunfish itself undergoes color changes nearly or quite as marked as those undergone by the *Gambusia*. The sunfish, especially when young, is

doubtless preyed upon by larger species. Perhaps, also, we have to do here with the concealment of the predator from prospective prey.

[5] This relation did not hold for the night-heron, however. In the case of this bird, the intensity of selection was somewhat greater in the pale tank.

[6] In the second of these experiments, the curtains were drawn and the light so dim that newspaper print could be read only with difficulty.

[7] See footnote 2

[8] *Jour. Exper. Zoöl.*, 20, 457–507 (1916).

[9] *Annal. Sci. Naturel.* (Ser. Bot. et Zool.), T. 10, 123–150 (1927).

SUMMATION OF MULTIPLE FOURIER SERIES BY SPHERICAL MEANS

BY S. BOCHNER

DEPARTMENT OF MATHEMATICS, PRINCETON UNIVERSITY

Communicated May 8, 1935

Let $x = (x_1, \ldots, x_k)$ be a point in the k-dimensional Euclidean space, and $f(x)$ a function of the Lebesgue class L having the period 2π in each variable, and let

$$f(x) \sim \sum a_{n_1 \ldots n_k} e^{i(n_1x_1 + \ldots + n_kx_k)} \tag{1}$$

be its Fourier series. If $\varphi(t)$ is a fixed function in $0 \leqq t < \infty$ for which $\varphi(0) = 1$, then, under unessential restrictions about the behavior of $\varphi(t)$ at ∞, we may form the "partial sums"

$$S_R(x) = \sum \varphi\left(\frac{v}{R}\right) a_{n_1 \ldots n_k} e^{i(n_1x_1 + \ldots + n_kx_k)}, \qquad v^2 = n_1^2 + \ldots + n_k^2. \tag{2}$$

and consider conditions under which $S_R(x) \longrightarrow f(x)$ as $R \longrightarrow \infty$. For instance, if $\varphi(t) = e^{-t}$ we have (spherical) Abel-Poisson summation, and for

$$\varphi(t) = \begin{cases} (1-t)^\alpha, & 0 \leqq t \leqq 1 \\ 0 & 1 < t \end{cases} \tag{3}$$

we have the important case of summation (R, α) (summation by spherical Riesz's means of order α).

The spherical partial sums (2) have a great advantage over the usual rectangular ones. In the case of rectangular partial sums it is necessary (and natural) to consider, for $k \geqq 2$, the behavior of the given function $f(x)$ in a "cross-neighborhood" of the given point x. This complicating feature is eliminated entirely in the case of spherical partial sums (2), as is evident from the formula