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Article I.—THE SOCIAL BEHAVIOR OF THE JEWEL FISH, *HEMICHROMIS BIMACULATUS* GILL[1]

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Plate I; Text Figures 1 to 6

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The jewel fish, *Hemichromis bimaculatus*, is a well-known favorite of the tropical fish enthusiast. Numerous accounts of it have appeared in the various aquarium journals. In general, its habits agree with those of other cichlid fishes which as a group are especially noteworthy for the parental care they bestow upon their eggs and young. During the breeding season both sexes of the jewel fish and of many other cichlids heighten their colors. In birds where both sexes develop epigamic adornments there is usually a mutual courtship (Huxley, 1921), and Lorenz (1935) describes the jewel fish as practicing the same type of courtship found in these birds. Nevertheless, Lorenz gives few details to support his view and no experiments have been performed to analyze the social behavior of this fish.

As part of a program to study the neurological basis of social behavior in vertebrates it became desirable to analyze the social behavior of the jewel fish. In this fish, as in pigeons, the corpus striatum serves as the integrating mechanism for complex social patterns (Noble, 1936*b*). These patterns in the pigeon are well known (Carr, 1919) but a detailed comparison between them and similar patterns in the jewel fish has not been made.

Early in our work on the jewel fish our attention was directed toward the rôle of sexual selection in enhancing the sexual dimorphism of this form. Sexual selection had never been proved in any fish but, as stated in a preliminary note (Noble and Curtis, 1935), it may be shown to operate under certain conditions in this form. Nevertheless other factors were found which tended to produce a similar coloration in the two sexes. To study these factors it became necessary to work out the ontogeny of social behavior in the jewel fish. The present paper covers, therefore, more than a report on the patterns of social behavior of the adult. It attempts to analyze the ontogeny of these patterns and to show how they are modified by particular environments.

Throughout our work we have received advice from various aquarium experts, especially from Mr. E. A. Candidus. We are indebted also to Mrs. Rae Borne for much technical assistance and careful observation on various fish under her care.

MATERIALS AND METHODS[1]

More than 500 breeding jewel fish were employed in this study. The largest stock was purchased from William Tricker, Inc., Saddle River, N. J., but many were reared from eggs in our own laboratory. The fish were maintained in tanks ranging from 5 to 140 gallons capacity in a greenhouse provided with a Helioglass roof. Thermostats held the temperature between 80° and 85° F. throughout most of the year. Dry shrimp and oatmeal, earthworms and, rarely, other live food were given at regular intervals.

Our jewel fish, even out of the breeding cycle, varied considerably in coloration. Two typical color patterns of breeding fish have been published in color by Innes (1935). Unripe jewel fish, kept in tanks with little vegetation, are much paler, usually a sandy gray in body tone, and neither the red ventral colors nor bluish "jewels" on the sides of the body are visible. The fish were identified either by isolating pairs in smaller tanks or more often by cutting out spines from dorsal or anal fins according to a prearranged plan.

The tanks were provided with abundant aquatic vegetation and equipped with standard 4-inch flower pots to serve as sites for egg laying. Since a series of tanks of each size was available, both flower pots and fish could be readily interchanged with a minimum disturbance to the latter. Special apparatus employed in the experiments will be described below under the appropriate headings.

THE SCHOOLING BEHAVIOR OF RECENTLY HATCHED CICHLIDS

It is well known from the home aquarium journals that the jewel fish rears its young in one of the typical cichlid ways. The fish hatch from eggs attached to some solid

[1] Assistance in the preparation of these materials was furnished by the personnel of Works Progress Administration Official Project No. 465-97-3-67.

object which had been previously cleaned by the parents. After emerging from the egg capsules two to four days after laying, the young may remain attached to them or to surrounding objects by their adhesive organs for 24 hours. The parents usually pick up the young in their mouths a few hours after hatching and spit them out in depressions which they had previously prepared. Some young may, however, fall to the bottom of the tank before being rescued by the parent fish. The young are moved from one pit to another at varying intervals until the yolk is sufficiently absorbed for them to rise as a cloud of very active "wrigglers" above the hollows in the sand. This usually requires from 2 to 4 days. The young are now carefully guarded by both parents for over a week and frequently until the parents are ready to spawn again. In most pairs it is the female and in some the male which is more industrious in caring for the young. This is essentially the account which may be gathered from the writings of Franke (1921), Enders (1922), Hall (1927), Hildebrand (1930), Solberg and Brinley (1933) and Werner (1935) on the jewel fish but it is characteristic also of all the cichlids except the mouthbreeders and the dwarf species; the latter relegate the care of the young entirely to the female.

Numerous writers have referred to the parent cichlids as putting their young to bed at night. Both Leber (1933) and Dünnebier (1927) have noted, however, that young without parents' help spend the night at the bottom and close together. We have frequently noted that young cichlids moved into a dark room sink to the bottom of the tank and remain there until some illumination is provided. In the jewel fish, if the parents are removed, the young fail to retire at night into as compact a group as when the parents are present. This is largely due to the active herding by the parents, the straggling young being often sucked up and spat out into the school. It is also due to the active "call movements" of the parents. Fischer (1924) refers to the parent jewel fish as giving these movements to attract young to food. There is an abrupt raising and lowering of the fins, especially the dorsal and pectorals. Stoye (1933) has described these movements in *Nannacara taenia* as a signal for the young to avoid danger, Liebig (1920), in *Cichlasoma biocellatum*, as serving either to attract or to disperse the young, according to their tempo. In *Aequidens latifrons*, Breder (1934) refers to them only as a warning with the result that the "young fish consequently drop to the bottom." In the jewel fish these movements are given by either parent under the strain of excitement. Merely approaching an aquarium too closely will often cause the parents to give these call movements. The effect upon the young may not be immediate but it usually results in their crowding nearer the "calling" parent. Jewel fish that have recently spawned and some that are about to spawn will sometimes give these "call movements" to young in an adjacent tank. Hence the sight of moving young is sufficiently stimulating to spawning fish to induce the movements.

Young cichlids exhibit a definite fright response which is not to be confused with either their reaction to call movements or to darkness. If an aquarium of schooling young is smartly tapped the school breaks and the young scatter through the tank. The same reaction is caused by a large fish making vigorous movements in the vicinity of a school, especially snapping movements while devouring the young. In striking contrast, a black cloth thrown over a tank will cause young jewel fish to drop to the bottom and to remain motionless. A white cloth has no effect, indicating it is not merely a sudden change of illumination but the degree of darkening which causes the drop to the bottom of the tank.

Blinded jewel fish fail to school, indicating that in this species, as in other fish (Lyon, 1904), schooling behavior is primarily a visual response. Nevertheless, a further study of the schooling behavior of the young fish at various ages has revealed that, besides the reaction of young to (a) movement, (b) light and darkness, (c) sudden disturbances of the water, there are other reactions, both instinctive and learned, which regulate the formation of schools. These other responses have never been described by previous observers of cichlid behavior, chiefly because they require experimental procedure to reveal their presence.

The response of young jewel fish to the call movements of their parents is not very specific. It is possible to wave objects having no resemblance to a fish in such a way as to attract the young away from their parents. For example, in Exp. 1, three 5-gallon tanks were placed in a row with the broadest sides in contact. A brooding female jewel fish was placed in the first tank, her school of young, 9 days after hatching, was placed in the second and a series of 2-inch disks introduced into the third. When one of these disks, painted deep red (between Nopal red and scarlet red of Ridgway, 1912), was held with a forceps and waved back and forth in the water of the third tank all the young left the side of their tank nearest their parent and gathered on the side of the waving disk. The same experiment repeated with a yellow disk (light cadmium of Ridgway) and an unpainted disk (made of tin) of the same size and material induced no response. A dark blue disk (dusky green blue of Ridgway) attracted no young while a black disk induced an incipient flight movement. At the beginning of this experiment the young were in a school approximately 1 inch from the parent's side of the middle tank. When the disk was waved the young swam toward the mother with swift, jerky movements.

Each disk was waved for a period of 5 minutes. On a second trial all the young had come toward the red disk within 30 seconds. None were again attracted by the other opaque colors although a few moved toward the yellow and then away from it. It was clear that these young jewel fish which had been swimming near their parent, reddened with nuptial colors, for 9 days were definitely attracted by red disks but not by disks of other colors.

The same experiment was repeated (Exp. 2) with another family of jewel fish. The mother was found to attract her young to her side of the center tank in less than 5 minutes after they were introduced. These young had been kept with the mother 7 days beyond hatching. Some of the young responded to the red disk in 35 seconds, and all had come to the side of the red disk in 1 min. 25 secs. Again none were attracted by the blue, yellow or metallic disks; and again the black disk seemed to excite. The test periods were of 5 minutes' duration. On a second trial the red disk attracted a few young in 40 seconds and all within 1 min. 20 secs. The other disks again failed to attract.

There are several species of cichlids which assume not red but bluish black or black nuptial colors when brooding young. We were interested to test two of these species in the apparatus described above. The results stood in striking contrast to those obtained with the jewel fish. In the case of young *Cichlasoma bimaculatum*, 10 days old (Exp. 3), the young were all attracted to the side of the black disk within 1 minute. The dark blue disk attracted the school in 1 min. 45 secs. Few were attracted by either the metallic disk or the yellow disk. However, most of the young had moved to the side of the red disk within 2 minutes. Hence, while black and dark blue attract, red in this type of experiment is effective but to a less extent. One of the reasons for this was that the mother failed to actively compete with the disks by giving call movements and the young scattered more in the tank.

Experiments with *Cichlasoma cutteri* gave more clear-cut results. The young, 8 days old (Exp. 4), were all attracted to the side of the black disk in 1 min. 30 secs. and to the side of the blue disk in 1 min. 20 secs. Only 2 of the 40 young came toward the red disk in a 3-minute period. The others, however, had moved near it before the 5-minute period was over. The yellow disk attracted a few for a short period but the metallic disk attracted all within 2 minutes. Hence in *C. cutteri*, although motion attracts, the response to black or bluish black objects is greater than to red or yellow ones.

After we established that there was a difference in the responses of young of red-throated and of black-throated cichlids to disks of the same color, the question arose as to what extent this difference was inherited. In the preliminary experiments it was difficult to keep the tempo of movement constant. We therefore devised a mechanical arm which would carry two disks of different color at the same young at either end of the tank recorded. Since the disks were frequently transposed, the difficulty of place habits was avoided. The same colors employed above were utilized again with, in addition, a lighter red (scarlet of Ridgway) and a green (Scheele's green of Ridgway). The two reds and the black and blue-black disks were an approximation to the nuptial colors of brooding fish; the green, yellow

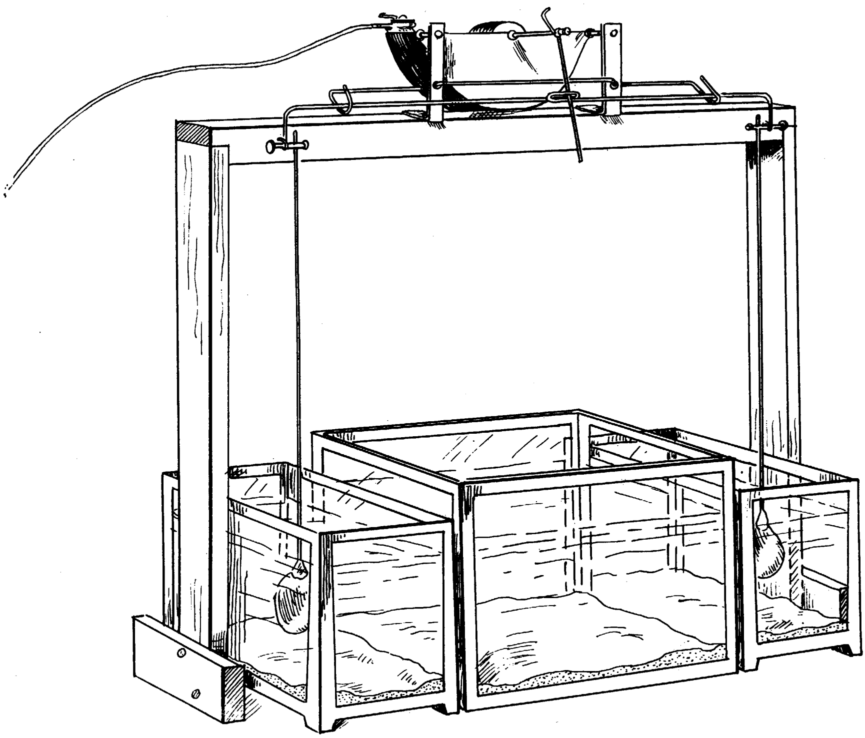

Fig. 1. Color discrimination apparatus for young cichlid fishes. The disks in the tanks are removable permitting the contrasting of disks of different colors. The windshield wiper (above) moves the arm to which both disk rods are attached.

time. This apparatus, as shown in figure 1, consisted merely of a windshield wiper activated by either an electric motor or by compressed air. The colored disks were attached at either end of a single moving arm bent to hang the disks freely in 2-gallon aquariums, one at either end of a central tank, 14 inches in greatest length. The young to be tested were placed without their parent in this central tank and after a period of 5 or 10 minutes the number of and metallic disks were selected to serve as a control. The disks were circular and cut in three sizes: 3, 2 and 1 inch in diameter. They were moved at approximately one swing a second.

Significance of Size of Stimulus Disk

The young *Cichlasoma bimaculatum*, which were found to be the least satisfactory species in our preliminary tests, were tested first in this new apparatus. When 10 young, 8 days old (Exp. 5), were placed in the center test tank and deep red contrasted with black on 3-inch disks, the results were clear-cut. All the young moved to the end near the black disk in 35 seconds and remained there during the 5-minute period. When the disks were reversed the entire school moved to the opposite end. Covering the black-disk tank with brown paper and swinging the red disk caused the school to move toward the red disk but it never crowded close to that end of the tank during a 5-minute period.

When the experiment was repeated with 2-inch disks, the school at first moved toward the red disk but turned back to the black. Within 2 min. 5 secs. the school had reached the side of the black disk. When the disks were transposed the school swung over to the side of the black disk in 35 seconds and remained there for the test period.

The experiment repeated with 1-inch disks gave positive results in slightly longer times. The school did not move toward the black disk for 2 minutes but remained there the remainder of the test period after reaching that side. When disks were reversed it again required nearly 2 minutes of waving before the school again moved toward the black disk. It is therefore clear that these young *C. bimaculatum* which had been reared by their parents for 8 days were attracted more by black disks than red disks when moved at exactly the same tempo. Further, the response to 3-inch disks is quicker than that to 2- or 1-inch disks.

Significance of Color for Young *Cichlasoma bimaculatum*

In our preliminary tests it was found that young *C. bimaculatum* would move toward the red disks but more rapidly toward the dark blue or black. When these tests were repeated in the new apparatus where there was a choice between red vs. black, the school moved almost invariably toward black. Again black or blue black was selected when yellow was the alternative. In Exp. 6, with 30 *C. bimaculatum* which had been reared 20 days by their parents, the entire school moved to the blue disk in 55 seconds on the first test and 1 min. 35 secs. on the second test with disks transposed. All the fish ignored the yellow disk.

Experiments with Schools of Two Species

In the above experiments it could not be stated what part of the reaction was due to an attraction of a particular disk and what part to the attraction of other moving young. In order to bring out more clearly the attractive powers of a particular disk we mixed equal numbers of young *Hemichromis bimaculatus* and *Cichlasoma bimaculatum.* In experiment 7 young of both species were 8 days after hatching and 10 of each species were selected. In the first test the 20 fish were placed on the side of the red disk. Within 50 seconds all the young *C. bimaculatum* had moved to the side next to the black disk and remained there for the 5-minute period. All the young jewel fish remained on the side of the red disk. When the disks were transposed the two schools swam in opposite directions and within 45 seconds all the *C. bimaculatum* were opposite the black disk in its new position and all the jewel fish at the opposite end of the tank. This experiment, as well as others that followed, gave clear evidence that the attraction is greater toward a moving disk of proper color than toward a school of other young fish. It follows that young jewel fish are more attracted by movements of their reddish parents than by the movements of the school.

Experiments with Fish Reared in Isolation

The attraction of red for young jewel fish need not, however, be a learned response induced by the red coloring of the parents' ventral surfaces. In our stock tanks we invariably placed brick-red flower pots and this color of their early place of attachment might conceivably have an influence on their later preferences. In order to eliminate both the rosy tones of the jewel fish's early days as well as those of the schooling period we removed a series of eggs from the flower pots before the embryos had formed and reared these in paper-covered aquaria isolated from all other fish until tested in our apparatus. The results were very different from those reported above.

In experiment 8 the eggs were scraped off the flower pot and reared for 7 days in isolation. When given the choice between scarlet and black the fish were slow to respond. The first trial was run with 2-inch disks after giving the fish 20 minutes to adjust themselves in the new tank. The entire school of 15 fish came to the red in 33 seconds and remained there for the 10-minute period. But when the disks were reversed they remained on the side of the black for the second 10-minute period.

When the test was repeated with 3-inch disks similar results were obtained. Within 49 seconds, 14 of the 15 fish had moved to the side of the scarlet disk and the last one came over in 5 min. 39 secs. When the disks were transposed the school of fish remained on the side of the black disk for the following 10-minute period.

The 1-inch disks gave a negative result, the entire school remaining in the center of the tank or aimlessly swimming about during two 10-minute periods. It may, therefore, be concluded that jewel fish which have never seen red tones are nevertheless attracted by a moving red disk. They fail, however, to avoid a black one and hence are strikingly different from young jewel fish which had been reared by red parents.

In Exp. 8a the test was repeated with young jewel fish which had been scraped from the red flower pot the day before they hatched and then reared in isolation for 4 days. These fish were more attracted by the red disk than the fish in Exp. 8. When deep red and black were opposed on 3-inch disks, 6 of the school of 10 came to the red disk in 50 seconds to remain the test period. One fish went to the black and remained there. When the disks were transposed 9 out of 10 fish swam to the side of the red disk in 1 min. 15 secs.

With 2-inch disks 5 out of 10 fish came to the red side in 55 seconds and 3 more followed in 2 min. 10 secs., and one more after 5 minutes. Only one remained opposite the black disk for the entire test period. When the disks were transposed it required only 40 seconds for the entire school to swim across the tank to the red disk.

Influence of Black Nest Site on Schooling of the Jewel Fish

In order to determine if a black nesting site would have any influence on the schooling of young jewel fish, pairs were induced to lay on black flower pots. In experiment 9 the parents were removed from the tank immediately after egg laying and aërators provided to keep the eggs alive. Six days later when the young were free swimming, 15 were tested in the standard apparatus. These had, of course, never seen a parent fish.

When tested with 3-inch disks the school broke in the typical flight response. After 4 min. 8 secs., 9 of the 15 had come to the side of the scarlet disk and were definitely attracted by it. After 7 min. 3 secs., the remainder had joined them. When the disks were transposed 10 of the 15 moved to the opposite side, attracted by the red disk. After 6 min. 53 secs., 4 more had joined them. The last one came to the red side in 9 min. 13 secs. and like the others showed a definite interest in the swinging disk.

This experiment was then repeated, substituting first the green and then the blue disks for the red ones. A 3-inch black disk contrasted with a green one attracted the entire school from the center of the tank in 33 seconds. They remained near the disk for the 10-minute period. When the disks were transposed the school changed sides. Two fish came over in 1 min. 7 secs., the remainder in 5 min. 21 secs. A 3-inch disk of dark blue attracted 3 out of 15 fish in 4 min. 5 secs. and held them for the 10-minute period. The opposite black disk attracted the other 12 in 3 min.

42 secs. When the disks were transposed 2 more came over to the side of the black disk in 1 min. 11 secs. The bulk of the school drifted to the center of the tank and showed no interest in either disk.

After a short rest period the same school was tested again with the light red vs. black. Within 55 seconds the entire school, except one, had come to the side of the 3-inch scarlet disk. The single exception remained opposite the black disk for the 10-minute period. When the disks were transposed the entire school came to the scarlet side in 1 min. 3 secs. and remained there interested in the moving disk for the 10-minute period.

These experiments with eggs reared in isolation on black pots as well as those experiments with young reared from eggs scraped off the pots clearly show that young jewel fish are born with an inherent interest in red, moving objects. Black objects that move may also attract and there is not the clear-cut restriction of interest seen in fish which have been reared by red parents. The question arose at what stage the restriction of interest might be induced. Experiments were, therefore, planned to elucidate this point.

Influence of Red Surfaces on Later Schooling of Jewel Fish

In order to make sure that the black flower pot had no influence on the later schooling of young jewel fish, it was necessary to repeat the above experiment employing a red instead of a black flower pot. The scores made by isolated fish from red flower pots were essentially like those reared on black flower pots. Experiment 10 was a typical case. The eggs laid on a red flower pot were isolated from the parents. At 86° F. the eggs hatched in 2 days and the young were free swimming the next day when the pot was removed. Ten days later the fish were tested for some effect of this short influence of red. When a 3-inch scarlet disk was contrasted with a 3-inch black one, the entire school of 15 fish moved from the center of the tank to the side of the red disk in 53 seconds. When the fish were replaced in center of the test tank and the disks transposed none approached the red during a 10-minute period but 3 moved toward the black disk and remained there for the test period.

The experiment repeated with 3-inch scarlet vs. green disks and with the same size scarlet vs. dark blue failed to give any clear-cut results. Only one young fish showed any attraction and that was toward the blue.

The fish were then given an hour's rest and tested again but this time 15 *Cichlasoma bimaculatum* which had been reared for the same time as the young jewel fish by their own parents were run in the same tank to make sure that the indifference to the signals was not due to some unknown condition in the tank. In the first test, scarlet was contrasted with black on 3-inch disks. Within 43 seconds all of the young jewel fish, but not a single *C. bimaculatum*, had moved to the side of the red disk. In striking contrast all of the latter species separated from the central school and in 1 min. 3 secs. had reached the opposite side of the aquarium.

When the disks were transposed 9 of the *C. bimaculatum* swam to the opposite end of the test tank in 2 min. 8 secs. and remained showing an interest in the black disk for the remainder of the 10-minute test period. The remaining 6 of that species formed a school in the center of the tank. This unusual result was probably due to the disturbance caused by the school of 14 jewel fish which swam away from the black disk and formed a school in the middle of the tank. The exceptional jewel fish swam the length of the tank in 1 min. 55 secs. and remained opposite the moving red disk for the remainder of the test period.

When the test was repeated, contrasting scarlet with green, the entire school of jewel fish swam to the side next to the red disk in 43 seconds and remained there for the 10-minute test period. Three out of the 15 *C. bimaculatum* joined the jewels but their interest did not hold them the 10 minutes. No fish was attracted by the green disk. When the red and green disks were transposed no definite results were secured, the combined school of the two species remaining near the center of the tank.

After another rest period the first experiment was repeated with this combined school of jewel fish reared in isolation plus parent-reared *C. bimaculatum*. In 1 min. 5 secs. all the *C. bimaculatum* separated out of the central school and were schooling as near as possible to the black disk. In striking contrast none of the jewel fish went to the red disk. On the contrary, 2 of them joined the group of *C. bimaculatum*.

The disks when transposed brought a rapid migration. All of the *C. bimaculatum* had reached the opposite end of the tank in 3 minutes where they remained throughout the test period. The jewel fish, on the other hand, soon swam toward the red disk. Thus, although the jewel fish which had never seen parent fish had a decided tendency to move toward a swinging red disk, this tendency was not nearly as marked as in jewel fish which had had the benefit of parental care (Exp. 7). By contrast, the attraction of a black disk for parent-reared *C. bimaculatum* was very obvious.

Effect of Parental Care on Color Preferences of Young Jewel Fish

That the parental care of jewel fish actually has a marked influence on the color preferences of schooling young is well shown by comparing the scores of parent-reared young (Exp. 7) with those of young removed from the parents soon after hatching. For example, in Exp. 11 the young were removed in the wriggler stage from a depression at the base of the nesting pot. The next day they were free swimming and after 3 days of isolation they were tested in our standard apparatus. When deep red was contrasted with black on 3-inch disks, 12 of the school of 15 jewel fish came to the side of the red disk in 52 seconds to remain there for the 10-minute test period. The 3 remaining fish were attracted by the black disk. When the young were again grouped in the center and the test repeated with disks transposed all of the fish moved to the side of the red disk in 25 seconds and remained there for the test period. This is obviously a better score than that made by fish which had never seen adults (Exp. 8) but not as good as that of fish which had received continuous parental care (Exp. 7).

When the red disks are only an inch in diameter this preference is entirely lost. The same fish employed in Exp. 11 were tested the same day in Exp. 12 with different sized disks. A 3-inch black disk contrasted with a 1-inch deep red disk brought over all the young jewel fish in 31 seconds. When the fish were moved to the center of the tank and the disks transposed they came to the black disk in 37 seconds.

When the test was repeated with a 3-inch deep red disk and a 1-inch black disk, 13 of the 15 fish came to the side of the red disk in 29 seconds. On transposing the disks they all came to the red disk in 40 seconds. Hence, it is not merely color in motion which attracts but a moving red patch more than an inch in diameter. In the absence of such a large red patch a black patch of adequate size is attractive to young jewel fish which have had only a very brief experience with parent fish.

These same fish employed in Exp. 12 were tested for color preference with other disks. When red and blue were contrasted on 3-inch disks all the fish came to the side of the red disk in 27 seconds and remained for the test period. When yellow and red were contrasted on similar disks all the fish again swam to the side of the red disk in 23 seconds and remained there for the test period. Further tests with transposed disks gave a similar decisive preference for red. This experiment may be contrasted with the one where young fish reared on a black pot had received no parental care (Exp. 9). Their interest in moving red objects was much less than in the present case.

In Exp. 13 young jewel fish were again removed from their parents during the "wriggler stage" but in this case held in an isolated tank for 10 days and then tested with disks of different size. That is, the young reared on a red flower pot had been subjected to the visual impression of their parents for a period of approximately 3 days. When tested with deep red contrasted with black on 3-inch disks the young appeared to be frightened at first, but within 4 min. 3 secs., 8 out of 10 fish had moved to the side near the red disk. The two laggards moved to the opposite end and seemed attracted by the moving black disk. When the disks were transposed the 8 that had remained for over 5 minutes opposite the red disk moved across the test tank and within 2 min. 20 secs. had joined the other two which had remained in place for 3 minutes. These two, formerly attracted by black, moved out and followed the black to the opposite end where they remained for the next 5 minutes.

Repeating the test with 2-inch disks gave other discrepancies. Nine young came toward the red disk in 2 min. 20 secs., and one after remaining near the black for 3 min. 10 secs. joined the others. When the disks were transposed, 6 of the 10 moved across the tank to reach the opposite end in 35 seconds. Another joined them in 4 min. 5 secs. The remaining 3 were attracted by the black.

One-inch disks painted the same colors gave less significant scores. Three out of 10 fish moved to the red on the first test while 7 remained nearer the black disk. On the next test with reversed disks only 1 went to the red, the other 9 remaining nearer the black. This was further evidence that red disks only one inch in diameter are not attractive to young jewel fish.

In experiment 14 the lighter red was employed on the 3-inch disks and contrasted with black before older jewel fish. These had hatched from eggs on a black flower pot. The parents had been removed the day after laying and since the young had been free swimming 16 days their schooling response should have begun to wane. Nevertheless these young jewel fish which had never been exposed to any red color during this 16-day period showed a definite preference for the scarlet disk. On the first test the entire school swam to the side of the red disk in 32 seconds. When the disks were transposed 13 of the 15 moved across the tank to reach the opposite side in 43 seconds. In both tests the young fish having reached the side of the red disk remained there for the remainder of the 10-minute test period.

On a second test the black disk was contrasted with a blue disk of the same size. Within 22 seconds 14 of the 15 fish had swam to side of the black disk to remain there for the test period. A transposal of the disks failed to give a positive result, for the school remained near the center of the tank for the test period.

This unexpected result was not due to fatigue because testing the fish again with scarlet vs. black disks gave a fair response. In 1 min. 8 secs., 12 of the 15 fish had moved to the side of the red disk while 3 moved to the black in 53 seconds to remain there for the test period. Transposing the disks brought the entire school to the scarlet side in 1 min. 5 secs. These scores although not as good as most of those made by jewel fish which had been reared by parents are better than some of those scores made by fish which had been guarded by their parents for a short period (Exp. 13). This suggests that the young jewel fish may vary in the strength of their inherited preference for red objects in motion.

Effect of Parents of a Different Species on the Schooling of Young Cichlids

There is, however, no doubt that in spite of this inherited preference for red in the jewel fish and black in the case of certain other cichlids that rearing by foreign parents of a strikingly different color has a profound effect on the reaction of the young to the colored disks. This was well shown in Exp. 15 where a school of 15 *C. bimaculatum* was reared by a broody jewel fish from the time that the eggs were laid. Two days after these young cichlids were free swimming, that is, 7 days after the eggs were laid, the fish were tested in our standard apparatus. When scarlet was contrasted with black on 2-inch disks, 14 of the 15 fish came to the side of the red disk in 43 seconds. Four then moved to the side of the black disk but immediately returned to that of the red. In 9 min. 43 secs. they moved as a school to the black and then returned to the red. When disks were transposed the entire school moved as a group to the red in 23 seconds and remained there for the rest of the test period.

On a test with 3-inch disks the young *C. bimaculatum* when placed on the side of the black disk remained there for the 10-minute period. When the disks were transposed the school remained on the side of the red disk for 1 min. 37 secs. They then swam to the side of the black disk but 6 min. 28 secs. later returned to the red. This result with *C. bimaculatum* reared by jewel fish stands in striking contrast to the experiments with the similar young reared by their own parents (Exp. 6). The young had learned from the red tones of their foster parents to become attracted by red objects in motion. Nevertheless, their inherited interest in black moving objects had not been lost. The result was that these young fish had an interest both in moving red and black objects.

Again repeating these experiments with 1-inch disks of scarlet vs. black failed to give a definite result. The young fish either schooled in the middle of the test tank or moved at frequent intervals from one side to the other.

Fortunately while these experiments were in progress a school of young jewel fish of exactly the same age as the *C. bimaculatum* was available. These had been reared by their parents and thus offered a splendid control to the *C. bimaculatum* which had been reared by foster jewel fish parents. When scarlet was contrasted with black on 2-inch disks all the young swam to the side of the red disk in 27 seconds. When the disks were transposed they moved across the tank to the opposite side in 53 seconds and remained there for the remainder of the 10-minute test period (Exp. 16).

Repeating the experiment with 3-inch disks gave even better results. The entire school moved to the side of the red disk in 12 seconds. Transposing the disks brought the entire school to the opposite side in 14 seconds. In both tests the young fish remained near the red disk for the rest of the 10-minute period and by their active movements showed that they were definitely interested in it. The contrast between the scores secured from experiments 15 and 16 shows clearly that exactly the same parental care may have very different results when the hereditary preferences of the offspring are different.

The young jewel fish employed in experiment 16 were so sensitive to moving red objects that a test was run with 1-inch disks. These had been repeatedly shown to be ineffective in other tests but gave positive results with these fish. On the first test it required 3 min. 22 secs. for all the young fish to come to the red signal. On the second test with reversed signals only 42 seconds were required for the fish to move to the side of the red disk. It thus seems that although 1-inch disks are less effective than 2-inch or 3-inch ones, especially sensitive fish will respond to them.

Finally in order to further contrast the behavior of the *C. bimaculatum* and jewel fish reared by jewel fish parents the two lots of young employed in experiments 15 and 16 were mixed and tested together in the standard apparatus (Exp. 17). When tested with 2-inch disks all of the jewel fish swam to the side of the red disk in 37 seconds. The young *C. bimaculatum* trailed but in 1 min. 45 secs. had reached the same position, none having moved toward the black disk.

When the disks were transposed, the combined school being left on the side it had moved toward, 12 of the 15 jewel fish left the school and moved to the opposite end of the test tank in 32 seconds. All of the *C. bimaculatum* remained behind on the side which was now nearest the black signal and three of the young jewels continued to school with them.

Replacing the disks by 3-inch ones again brought a quicker response from the jewel fish. In 11 seconds all of this species had moved to the side of the scarlet disk. The *C. bimaculatum* which had been left on that side by the previous test remained there for the 10-minute period. Transposing the disks brought 12 of the 15 jewel fish to the opposite side in 10 seconds. The entire school of *C. bimaculatum* remained behind close to the black disk and 3 straggling jewel fish eventually schooled with them. It is obvious, therefore, that either black or red disks will attract *C. bimaculatum* reared by adult jewel fish while young jewel fish reared by similar parents are attracted only by red. Some exceptions occur when two or three stragglers become attracted by a school of young fish remaining at the opposite end of the tank. But these exceptions fail to obscure the fact that there is a marked hereditary difference in the preferences of young cichlids of different species.

This experiment with young *C. bimaculatum* reared from the egg stage by jewel fish parents was repeated many times. In Exp. 18 with fish free swimming for 10 days approximately 75 per cent were attracted by the red disk and none by the black. In Exp. 19 with *C. bimaculatum* which had been free swimming only 5 days there was a greater tendency to be attracted by the black. With 3-inch disks 7 out of 10 came to the deep red and 3 to the black on the first test. With disks transposed 8 went to the red and 2 to the black. As a control for Exp. 19 a series of young *C. bimaculatum*, the same age as the above but reared by their own parents, was tested in the same apparatus. With 3-inch disks the entire school moved to the side of the black disk in 55 seconds and remained there for the test period. With disks transposed the entire school swam across the tank in 1 min. 20 secs. to the black disk now on the opposite side. A third test with disks again transposed brought the school across the tank in 45 seconds to remain near the black disk for the test period.

As a further control to Exp. 19 a series of jewel fish reared by their own parents for exactly the same period was run in the above apparatus for the same test period. The contrast to the *C. bimaculatum* was striking. On the first test the entire school came to the red disk in 15 seconds, on the second test in 10 seconds. In both cases the school remained opposite the red disk for the test period. Since this school was very reactive to the red disks, a 3-inch black disk was opposed to a 1-inch red disk. On the first test the school required 1 min. 25 secs. to reach the side of the red disk. On the second test the entire school swam across the tank to the small red disk in 15 seconds and remained there for the test period.

Some attempt was made to determine if early training by natural parents could be overrridden by the later influence of foster parents. In Exp. 20 young jewel fish were left with their parents during the wriggling stage and then reared by adult *C. bimaculatum* for 5 days. When tested with deep red and black opposed on 3-inch disks the school came to the red in 40 seconds. With 2-inch disks they swam across the tank to the red disk in 25 seconds. When the disks were transposed they remained with the black disk for 2 minutes and then swam to the side of the red disk where they remained for the test period. Hence, while the school had a greater interest in the red disk their reaction to it was slower than that of jewel fish reared by jewel fish parents.

A second test of this same lot of fish, placed in the test tank with the same number of *C. bimaculatum* which had been reared by their own parents, failed to reveal that this influence of brooding by foster parents had had much effect upon the young jewel fish. Tested with deep red vs. black on 3-inch disks, the two species separated, all the jewel fish moving to the side of the red disk in 30 seconds and the *C. bimaculatum* to the black-disk side in nearly the same time. Transposing the disks brought a cross migration of the two schools. Within 40 seconds each school had taken up its position on the opposite side. Repeating the experiment opposing a 1-inch red disk with a 3-inch black disk brought all the jewel fish to the red side in 10 seconds and the *C. bimaculatum* to the black side in 30 seconds. This surprising record suggests that the interest of jewel fish in moving red objects is strengthened by the presence of red parents during the wriggling stage. Later care by black parents may have no marked influence on their response to moving disks of different colors.

These results on the ability of young jewel fish to learn during a critical period of their life cycle stand in striking contrast to the results secured by Peters (1937) with *Haplochromis multicolor*. Jewel fish are hatched with an inherent interest in red which may be modified by early training of the young fish. *Haplochromis* hatch with an inherited tendency to move toward moving objects having a certain shape and with eyes in a particular position. Under ordinary circumstances this object is the parent fish which will take the young into its mouth. Peters could find no difference between the responses of young fish reared in isolation from those taken from the parent's mouth. Our work has revealed a marked difference between the responses of jewel fish toward moving red objects when the fish have been reared in isolation as compared with those reared by parents. It is surprising that the inherited responses in two such closely related species should be so different at such an early age.

The Problem of Color Vision in the Schooling Fish

Although the black and red colors used in these tests were an approximation to the nuptial colors of *C. bimaculatum* and the jewel fish, respectively, the response of the young fish may well have been to the brightness values of the disks rather than to the wave lengths of the reflected light. The difficulties of determining the existence of color vision in fish are very great (Warner, 1931). The purpose of the above experiments was to show that there was a difference in the inherited dispositions of the different cichlids and to show that this difference could be modified by training. Young cichlids which have been reared by their parents will respond to disks of colors not found in the brooding dress of these parents. This was well shown in Exp. 21 where young *C. bimaculatum* were reared for 10 days by their parents and then tested in our standard apparatus. With 3-inch blue vs. yellow disks opposed, the entire school of 10 came to the side of the blue disk in 10 seconds and remained there for the 5-minute test period. When the disks were transposed the school immediately swam across the tank and reached the opposite side in 30 seconds to remain for the test period. Two-inch disks gave comparable results. All came to the side of the blue disk in 1 min. 15 secs. to remain for the test period. A reversal of the position of the disks brought the school across the tank again in 30 seconds. Even 1-inch disks were found to be effective in this case, the entire school moving to the side of the blue disk in 1 min. 50 secs.

The nuptial colors of *C. cutteri* may be bluish black but the response of the young to black disks was as well marked as that of young *C. bimaculatum.* For example, in Exp. 22 a group of 10 young reared for 10 days by their parents was tested in the standard apparatus with deep red and black opposed. The entire school came to the 3-inch black disk in 55 seconds. Transposing the disks brought the school across the tank in 1 min. 10 secs. to remain opposite the black for the 5-minute test period. With 2-inch disks the school came to the black disk in 1 min. 10 secs. on the first test and 50 seconds on the second. One-inch disks attracted no fish. Another test (Exp. 23) with 30 young *C. cutteri* which had been reared by their parents gave comparable results. Even though the school was larger than in Exp. 22 the times for moving to the side of the black disk were 50 secs. and 1 min. 40 secs. for 3-inch disks and 1 min. 20 secs. and 45 secs. for 2-inch ones. In this case 1-inch disks had some attractive effect.

This attraction of moving disks of different colors for young cichlids fades as the fish grow older. Thus in 4 different lots of young jewel fish over 24 days of age no attraction of one colored disk in preference to another could be demonstrated. The age at which this change occurs in *C. bimaculatum* was not determined accurately but in one lot of young reared by jewel fish parents for 30 days it had definitely faded.

THE SCHOOLING BEHAVIOR OF OLDER YOUNG

Although jewel fish no longer respond differentially to the red disks after 24 days of age they, like all other cichlids which we have studied, continue to school throughout life. The schooling response is moreover induced by a variety of external conditions. Large objects waved before the tank will produce flight movements followed by schooling. A sudden lowering of the temperature or radical change of the pH will do the same. Jewel fish placed in a new tank usually school. In all these cases irritation produced by unfamiliar or mildly injurious environments calls forth the schooling which may be considered a defense reaction. In larger tanks of 75 or more gallons capacity jewel fish school without any obvious provocation. Our first approach to the problem of schooling in older fish was to test a series of individuals in large tanks where the inducement for schooling was probably the mere unfamiliarity of the fish with their surroundings.

It is well known that species differ enormously in their tendency to school. For example, a series of 10 *Danio malabaricus* and 10 *Hemichromis bimaculatus* which we reared together in a 15-gallon tank for one month, when placed in a 50-gallon tank, almost immediately separated out into separate schools. This would seem to be due in part to the different method of swimming of the two species, the danios dipping over and under one another much more than the jewel fish. Danios also swim nearer the surface than schooling jewel fish. Guppies, *Lebistes reticulatus*, when frightened by swirling water, invariably rush to the surface and form a school. It is possible by picking danios and guppies of the same size to form a mixed school near the surface of the water which may maintain itself for long periods. A mechanical mixing device which will produce a constant current in the aquarium may be used to advantage to keep the group intact. Jewel fish of the same size swim to the bottom or to protecting weeds when such a water disturbance begins. There they form an aggregation which may move as a school as much out of the current as possible.

Schooling is usually considered a visual response. Certainly many schooling fish will follow closely the moving stripes in a rotary nystagmus apparatus (Hosch, 1936; Janzen, 1933). Both jewel fish and other cichlids, such as *Tilapia macrocephala*, which we introduced into such a tank, followed the moving stripes for long periods. The record the *Tilapia* made was as good as that of such close schooling species as *Danio malabaricus*. Blinded fish have been frequently reported not to school. We have noticed, however, that in the best schooling species there is a response of one fish to another of the same species even when both are blinded. In one experiment we tested 5 blinded *Tilapia macrocephala* in their responses to other fish in a 60-gallon tank. When one of these blinded *Tilapia* came in contact with a *Pterophyllum scalare* it gave an avoidance response. On the other hand, when it contacted a normal *Tilapia* of the same size it turned toward this fish and followed it for a short distance. Hence, blinded fish may show a species discrimination in spite of the fact that lack of vision prevents any real schooling. What sensory modalities enter into this species identification is not clear.

Two species of cichlids usually form separate schools when placed together in large tanks. In the case of *Tilapia* and jewel fish a difference in the speed of movement and manner of schooling may be observed. The reasons for the separation of schools of jewel fish from *Cichlasoma tetracanthus* of the same size, which regularly occurred in our tanks, were by no means obvious.

Since we had been able to modify the inherited tendency of certain cichlids to school toward moving disks of particular colors it occurred to us that it might be possible to modify the disposition of older fish to school together if we gave them a long period of training. For this purpose we selected the jewel fish and *Cichlasoma cutteri*, since preliminary tests had proved that these two species will normally separate out into distinct schools. Many tests were run and the results were essentially alike. In Exp. 24, for example, 10 *C. cutteri* young which were 23 days old and beginning to lose their early schooling reactions were placed in a separate tank with one jewel fish of the same age. Thirty-seven days later the jewel fish and 4 of the *C. cutteri* in this tank were removed to another tank and 4 additional jewel fish of the same age added. This involved a change from pH 5.5 to 7.0 and induced schooling. The experimental jewel schooled at once with its own species and showed no tendency to follow the *C. cutteri*.

In other experiments, as for example Exp. 25, the jewel fish reared with *C. cutteri* would swim toward its former tank associates but would school only with its own kind. In this case the jewel fish had been placed with the *C. cutteri* when only 5 days of age and had been reared with them for 77 days. Again there was no hesitation in the experimental jewel fish schooling only with its own kind.

In another variation of this experiment a single jewel fish only 5 days old was introduced into a tank of *C. cutteri*, 19 days old, and separated from them by glass for 5 days in order that no injury would come to it (Exp. 26). Then 30 days after being introduced into this tank, 4 *C. cutteri* from this tank and 4 jewel fish of the same age were placed in a new tank and the experimental jewel fish added. Again the new tank and the change of pH induced schooling but the experimental jewel fish went only with its own species. It is therefore clear that even a prolonged stay of young jewel fish in a tank with many cichlids of another species will not prevent the jewel fish from schooling with its own kind on the very first opportunity. This represents presumably a fine sense of visual discrimination since blinded fish fail to school.

A jewel fish placed in a tank with a school of the same species is usually accepted at once into the school by the resident fish. A *Tilapia*, however, will be approached and mouthed. This is essentially a hostile gesture which tends to ward off the newcomer. It shows that jewel fish can readily distinguish their own kind from foreign species which approach them too closely. Jewel fish at an early age also learn to distinguish one another as individuals. A well-marked dominance-subordination hierarchy is formed similar to that of the domestic hen as described by Schjelderup-Ebbe (1935). Noble and Borne, who first discovered this dominance behavior in another group of fishes, have considered the jewel fish so fully in their report (unpublished) that it is unnecessary to duplicate their observations here.

THE SEXUAL BEHAVIOR OF THE JEWEL FISH

The breeding behavior of *Hemichromis bimaculatus* has been frequently described in aquarium journals. The general pattern may be gleaned from the writings of Apel (1932), Baake (1927), Boug (1934), Dünnebier (1927), Enders (1922), Fischer (1924), Franke (1921), Hall (1927), Hildebrand (1930) and others. Both sexes when ready to spawn assume a reddish tone on the sides and lower surfaces of the head and this extends over more or less of similar regions of the body. The fish start to clean a nesting site from which they drive other fish. Both sexes of the pair quiver, either while in the horizontal position or when the head is pointing down and the body is more or less vertical to the substratum. The nest site is usually a stone or some solid object and it is cleaned by both sexes nipping off with their mouths mould or other undesirable material adhering to it. Genital tubes protrude from both sexes and they rub their ventral surfaces over the nest site. At first there may be more or less slapping of one another with their tails especially if disturbed but this gives way to nest cleaning and finally to laying movements (pseudolaying) as the moment of spawning approaches. Laying lasts one-half to two hours, the male synchronizing with the female by dragging his genital tube over the egg mass at frequent intervals during the laying. Usually the female leaves the mass after laying a short row of eggs and the male takes her place to inseminate these and other eggs, but both sexes may hover over the egg mass at one time. The eggs, with capsules, measure from 1 to 1.5 mm. in diameter and are guarded alternately by both parents, one or the other assuming most of the duties. During this period the eggs are usually fanned by the parent remaining on guard. Development is rapid, hatching occurring in about 48 hours.

SEX RECOGNITION

No attempt has been made by previous observers to determine how the jewel fish recognizes the sex of a partner which, as stated above, courts the same way whether male or female. In the fighting fish, *Betta*, and the sunfish, *Eupomotis*, the two sexes behave differently and sex recognition is accomplished in a simple manner (Noble, 1934). In the cichlid, *Aequidens latifrons*, Breder (1934) describes a "peculiar quiver" of the dorsal and anal fins of the gravid female. This combined with the general disposition of males and non-spawning females to fight, Breder believes to be the sole basis of sex recognition in this form. He adds, however, "An item for which no explanation is offered is that after spawning has once occurred the pair seldom fight again, but generally live in peace spawning repeatedly thereafter." We have critically observed the spawning of over 200 jewel fish and find that the mechanism of sex recognition is far more complex than previously described in any fish. It has in fact many resemblances to that of birds.

Territory

As in many birds the first evidence of breeding in the jewel fish is that the male dons his nuptial colors and begins to defend a particular territory. This area consists of a stone, flower pot, bare corner of the tank or other suitable substratum on which to attach the eggs together with the surrounding region for a distance of 8 to 15 inches. The male will attack any fish which enters this territory. Unripe fish of either sex usually flee before this attack. Other males ready to breed may fight back. The gravid female stands her ground and retaliates merely by raising her dorsal and spreading her caudal in a feeble gesture of defiance. If the male's attack is particularly vicious the female may flee but soon returns even though seriously bitten by the male. It is for this reason that in any large tank containing many jewel fish most of the deaths occur among the gravid females for they are the fish which, with an avenue of escape open, will most often stand their ground. We have observed such behavior many times in our large tanks.

In the sunfish this differential response of the sexes to the attack of a territory-guarding male seems to serve as the sole basis of sex recognition but in the jewel fish other elements enter. If no ripe males are present in the tank, a ripe female may take up territory and attempt to drive other fish from it. Unripe males and females flee before this territory-guarding female. Other ripe females will fight back and often dash far beyond the limits of the territory in their struggles. Ripe males stand their ground and very soon, without any battle become dominant to the former holder of territory.

Both sexes, therefore, as the gonads ripen and nuptial colors appear, may defend a possible nesting site in a typical territory defense. It is remarkable that in some cases very young fish not yet capable of breeding may do the same. Thus in one instance we found that a female only 105 days old and with a total length of only 4.2 cm. had assumed nuptial colors and was holding territory. Sections of her ovary showed the eggs still in a rudimentary condition. These exceptional territory holders are found only in very young fish and probably owe their existence to a rapid growth of the gonads. Certainly in all mature fish territory guarding is a sign of sexual ripeness.

The Cues Employed in Sex Recognition

From the behavior of gravid females when holding territory it is impossible to escape the conclusion that the females are capable of recognizing sex, that is, of differentiating between two aggressive fish which approach her when she is guarding a territory. Numerous attempts to discern any difference in the approach of such aggressive fish of opposite sex resulted only in failure. Nevertheless, a difference very probably exists, for a gravid female can identify the sex of another jewel fish even when in an adjacent aquarium.

The apparatus which we employed to demonstrate this surprising conclusion is shown in figure 2. It consists merely of a 15-gallon aquarium surrounded on three sides by 2-gallon aquaria. A space a centimeter wide is left between the aquaria to avoid any contact vibrations. A small flower pot is placed in the large aquarium directly before the center of each small aquarium. A gravid female is placed in the large aquarium and other gravid females or males placed in the small aquaria. A female if sufficiently advanced will lay her eggs on one of the pots. We assume that the fish opposite the flower pot she selected was the one she had picked out as a mate even though this fish was separated by two panes of glass and an air space. In every case proof of this pairing off when separated by glass was obtained by releasing the occupants of the three small aquaria in the large tank with the female and her eggs. In every case she permitted only the fish which had formerly occupied the tank opposite her eggs to come near them.

The first series of tests was carried on with gravid females which had at least one previous spawning record. These fish ranged from 7.6 cm. to 8.2 cm. in total length. Ten of these gravid females were removed from the tanks where they had become ripe, as shown by their genital tubes and pseudolaying, and placed on different days in the central tank of the apparatus. In six tests they were given one male and two females of the same size as the males to choose between. In four tests the females were given one female, one ripe male and one male, which had recently spawned, between which to make a selection. In every one of these ten tests the female laid her eggs on the flower pot in front of the ripe male.

In the second series of tests we selected 10 gravid females which had never previously spawned. Six of these had been under constant supervision and the other four came from stock tanks where no spawning had been recorded. They ranged in size from 5.5 cm. to 6.9 cm. with an average length of 6.2. These fish were given the opportunity of selecting between a ripe male and two females of the same size. Six times these females laid before the ripe male but four times in front of one of the two females. Hence, females spawning for the first time are not as successful as more experienced females in distinguishing between the sexes when separated from them by glass. Whether the perfect record of the latter group was due to learning or merely to maturation of their mechanisms of discrimination was not clear.

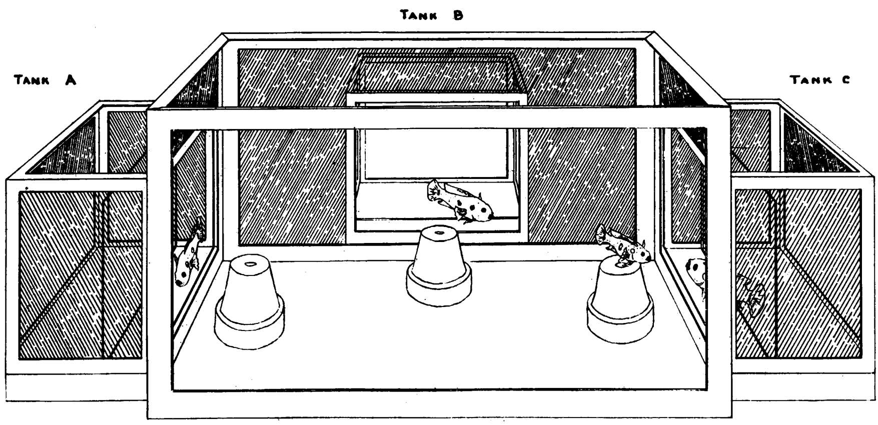

Fig. 2. Sex recognition apparatus. A male and two female jewel fish are placed in the outside tanks. The experienced female placed in the central tank will invariably lay her eggs opposite the male.

It was obvious from these experiments with fish in different tanks that vision could be the only sensory modality entering into sex recognition because all others would be excluded under these circumstances.

Wunder (1934) assumes that the male three-spined stickleback, *Gasterosteus acu-*

leatus, selects among several possible females the one with the greatest girth. We injected several spent jewel fish with saline solution but found that a territory-guarding male would not accept them. Apparently neither size nor shape enters into the mechanism of sex recognition. Both sexes vary considerably in color and as no constant difference between them could be found, color cues did not seem to be involved in the problem. Hence, by a matter of elimination, we were forced to conclude that there were small differences of movement which were serving as the cues for sex identification.

In order to prove this point experimentally we equipped some of the fish with "blinders." These consisted of small triangles of ambroid painted with black lacquer. The points were cut off the triangles and when the blinders were adjusted over the eyes the stubs of these points were pushed into the space between eyeball and socket holding the blinders in place. Fish with these blinders in place swam slowly, moving their dorsal and caudal fins in a cautious manner. All responsive movements which are normally produced by the approach to, or contact with, another fish were entirely eliminated.

Some preliminary tests proved that these blinders caused the fish little discomfort. Further, when three males were equipped with unpainted and hence transparent blinders they were readily distinguished from females of the same size by a series of territory-guarding males. Two other males equipped with blinders in each of which a small hole, 1 mm. in diameter, had been punched were also immediately distinguished from females of the same size. Hence their black-eyed appearance had in no way delayed the identification of their sex.

Eight territory-guarding males were selected and given preliminary tests to prove that they could distinguish between a ripe male and a gravid female of the same size. Blinders were then fitted to the eyes of these pairs which had just been tested and the experiment was repeated. In not a single case could the territory-guarding fish distinguish between the two blindfolded fish. In seven tests the guarding males attacked both blindfolded fish with equal vigor, in three tests both fish of each pair were treated with indifference. When the blinders were removed the territory-guarding males again distinguished at once between the two fish of each pair.

Five gravid females with previous spawning records were then tested in the sex discrimination apparatus described above. The small middle tank was left vacant and one ripe male was blindfolded and placed in one end tank and a female of the same size was blindfolded and added to the other end tank. In three cases the female in the control tank laid on the flower pot opposite the blindfolded female; in two other cases on the pot in front of the empty tank. Since all females with a spawning record which had been previously tested in this apparatus had selected the ripe male, we may conclude that blindfolding a jewel fish will prevent the identification of its sex. The reason for this is that blindfolding slows down swimming activity and eliminates all responsive movements to the approaches of another fish.

Although blindfolding prevents sex identification, blinding does not, and apparently because the blind fish soon adjust themselves to the new conditions. We enucleated two pairs ready to spawn. Eight days after the operation the male of one pair fought a male introduced into his tank but not a female. The fight came only after the blind fish had touched the introduced fish and apparently it was the different responses of the introduced male and female which made possible this recognition of sex. Fourteen days after the operation the blind male made a feeble head stand before both blind and normal females. This was obviously an attempt at courtship which never proceeded further. The other blind male also attacked males and head stood before introduced females while assuming a full breeding color. When a spawning female was introduced into one blind male's tank he succeeded in finding the eggs and fertilizing about one-third of them. There was no synchronization in the spawning act and no brooding of the hatching young. A blinded female, which laid her eggs in the presence of a normal male, scattered them over an area about three times as long as usual and half as wide. Then she proceeded to rest closely over the eggs and would not synchronize in brooding with the normal male which had fertilized them. This female attempted to gather the hatching young and searched repeatedly for them. The few she was able to find she picked up and spat out without reference to the nest the normal male had made. It is therefore clear that sex recognition and fertilization can occur in the absence of vision but neither a complete courtship nor a synchronization with the partner in fertilization or brooding can take place in the absence of sight. Vision remains, therefore, the chief sensory modality of social behavior although other sensory modalities may play a secondary rôle.

It has been frequently observed by aquarists that the courtship of the jewel fish may not proceed smoothly. After a preliminary period of gesturing the male may attack his mate viciously. In our own experiments it was usually not difficult to find some cause for this maladjustment. For example, 10 territory-guarding males were selected at random and 42 pairs of fish introduced into these tanks. In 32 cases the territory-guarding male accepted the introduced female at once and attacked the male. In 10 cases the male attacked the introduced female. Checking the records of these 10 females showed that 4 of them were still guarding eggs or young in their own tank when introduced into the new quarters. They were therefore not gravid. In 4 other cases the introduced females had engaged in a long period of courtship with their males and hence a bond had been established between them. Under such circumstances a gravid female is responsive only to the male she has courted with. The other two cases of failure to adjust may have been caused by the excitement of netting the fish. In all cases, however, it was the female which was unresponsive and actually responsible for the maladjustment which soon led to the male's attacking.

The Recognition of Mates

An examination of a group of breeding jewel fish in a large aquarium will soon convince one that after a pair has courted for an extended period these two fish recognize one another as individuals. If, for example, all the fish in the tank are driven toward the territory occupied by such a pair, the male will accept his mate but drive other gravid females which appear identical to her. Before courtship had occurred he would accept any gravid female but now every other gravid female except his mate is a trespasser in his territory and something to be driven out. Similarly, the female, which before courtship had occurred would accept the challenge of any male in a passive manner, now will attempt to drive all males except her mate from her chosen territory. During courtship bonds are formed and fish which before were treated like other fish of that sex are now readily distinguished from them.

A close parallel to this state of affairs is found among birds. There is evidence in some species that mates identify one another by small features of the head (Heinroth, 1911; Noble, 1936*a*). No attempt has been made previously to determine what cues fish might utilize to distinguish their mates from other individuals of the same sex.

Before modifying the appearance of the fish it was necessary to develop a standard procedure for proving mate recognition. After various trials the following tests were found to be most satisfactory.

Test 1.—Two parents guarding eggs or young and therefore well beyond courtship are cut off from other fish in the tank by an opaque screen. The male or female of the pair is removed and a stranger of the same size and sex of the retained fish placed in the screened territory with this fish. If the latter attacks the stranger but after the screen is lifted accepts its true mate, the fish is stated to have passed the first test.

Test 2.—Two parents are separated as in test 1, but the substitute is of the same size, sex and, so far as possible, color pattern of the fish removed. This is a very critical test. It may fail, however, if the introduced fish is a gravid female ready to spawn. Such a fish will sometimes induce the male to start a new breeding cycle with her. Noble and Kumpf (1936) have shown that a succession of female jewel fish ready to spawn may reduce the castrate male's interspawning period to a single day. By introducing only females which had recently spawned this difficulty was avoided.

Not all jewel fish that spawn can be proved to identify mates. This may be due to their indifference resulting from ill health or to fright inadvertently produced by the experimenter. No pairs which had not passed our two standard tests for mate recognition were carried further in our experiments. Since jewel fish will readily lay their eggs on red flower pots turned upside down in an aquarium, it was a simple procedure to secure pairs of fish guarding eggs on flower pots placed near the glass sides of a series of tanks. After such fish had been proved to be aggressive in mate recognition by our standard tests two small aquaria were placed outside the tank directly opposite the eggs of this pair. Then one member of the pair was placed in one of the outside tanks and another fish of the same size was added to the tank next to it. The small tanks were adjusted until their two surfaces of contact were exactly opposite the midpoint of the group of eggs. This assured that the fish remaining in the main tank with the eggs would be able to see the two fish in the outside tanks equally well.

Five mother fish guarding their eggs, when tested in this apparatus, were able to distinguish their mates from stranger males. In each case the guarding fish attempted to attack the strange male through the glass sides of the aquarium. She would erect her fins and opercular covers and attempt to bite only this stranger.

In two cases egg-guarding females confused their mates with males of similar size and color pattern but readily distinguished them from males of a different size. These seven egg-guarding females were each tested several times and the two fish in the outside tanks frequently transposed in order to make sure that reflections or other extraneous factors were not responsible for the result. Since under the conditions of the experiment all sensory modalities except vision were ruled out, we may conclude that jewel fish recognize their mates by visual cues.

One of these seven females which was very quick in mate recognition was then tested again in the same apparatus but screens were adjusted between the large and small tanks in such a way as to obscure part of the bodies of the two fish in the outside tanks. This female was found to be able to identify the anterior but not the posterior half of her mate's body. She could also distinguish between her mate and a stranger when the screens were adjusted until only the anterior thirds of their bodies were visible. To less an amount she made no response.

Since sex recognition was found to be a matter of the visual recognition of differential movement, it occurred to us possible that some movement would also be essential for mate recognition. To test this hypothesis we selected 3 female jewel fish which had passed our two standard tests for mate recognition. The mate of each female and the stranger male which had been employed in test 2 were then anaesthetized and moved into the territories guarded by the females. Two of these females attacked both their motionless mates and the motionless strangers. When both anaesthetized mates and strangers were moved on wires to simulate the approach of a fish to its nest they were still both attacked with vigor. When, however, both began to come out of the anaesthesia the guarding females distinguished at once between them, attacking the stranger and accepting the mate.

The males of four pairs were then blindfolded with the ambroid blinders described above. Four foreign males of the same size were similarly blindfolded. Fish treated in this manner swim slowly and make no responsive movements to other fish at a distance. In each of these four tests the guarding fish was able to discriminate between the blindfolded mate and the blindfolded stranger, directing its attack only against the latter no matter which outside tank it occupied. The seven experiments considered together show that some movement is essential for mate recognition in the jewel fish. Artificial movements made by an anaesthetized fish on a wire are inadequate. Responsive movements of the mate are not essential because a slow moving blindfolded fish can also be identified by a nest-guarding jewel fish.

Since jewel fish can identify mates when swimming slowly, it occurred to us possible that the slow movement of a parent approaching its nest might be the sole basis of mate recognition. A mated pair is held together by a common interest in their territory. If all territorial influence could be removed would mates still recognize one another? To test this question a mated pair of jewel fish was removed from a tank and the female of this pair induced to adopt a set of eggs of *Cichlasoma biocellatum* in another tank. A male jewel fish, stranger to the female, was then introduced. The female guarding eggs of another species in a foreign territory drove him but immediately accepted her mate when he was introduced. Here was a case where a female immediately recognized her mate in a tank unfamiliar to both of them and in the presence of eggs which the male had never seen previously.

For a further test of the ability of egg-guarding female jewel fish to recognize their mates when the territory factor is removed, we selected two pairs of fish which had passed our standard tests for mate recognition and were brooding eggs one day old. Each female was then placed in the tank with the eggs of the other. Each soon adopted the eggs and began to fan them in characteristic brooding fashion. The males were then returned to their own tanks. Each found a strange female brooding his nest of eggs in his own territory. Each male moved toward his own nest slowly but forcefully and was met by the foster mother with a furious attack. When the beaten males were removed and the mates of the foster mothers added to these tanks they were immediately accepted. Here were two other cases, then, where females brooding foreign eggs in a foreign territory distinguished at once between their mates and stranger males. Further, they made this distinction when the stranger males were returning slowly in a confident manner toward their own eggs.

These three experiments show clearly that neither a familiar territory nor a familiar nest of eggs is indispensable for mate recognition. Females may distinguish their own mates from stranger males even in a strange tank when the male is approaching eggs unknown to him.

In view of these facts it seemed highly probable that mate recognition was accomplished by distinguishing differences in the form or color pattern of the fish themselves even though these differences had no significance for the fish unless they were moved in the manner of a living fish. In order to test this hypothesis a group of fish was selected and proved by our standard tests to be able to recognize their mates. One member of each pair was then painted in various ways and returned to its original tank with its mate. It was found:

(a) A male jewel fish guarding eggs one day old will readily distinguish its mate from a female of the same size. When both females have their melanophores strongly contracted with an injection of 0.1 cc. of adrenalin chloride they are attacked equally vigorously by the male although both swim slowly. Hence an extreme contraction of the melanophores may prevent mate recognition.

(b) A male jewel fish guarding eggs is readily identified by his mate when the whole posterior half of his body is painted with chrome yellow mixed with stopcock grease. He is also recognized when his entire body exclusive of the head is painted with the same substance. When the same paint is applied only to the forehead, gill covers and under the eyes, the entire body being free of paint, he is immediately attacked by his mate which fails to recognize him. The same areas of the head covered with stopcock grease alone call forth no attack.

(c) A male jewel fish is readily distinguished from another male of same size by his egg-guarding mate. Three large spots (1 cm. wide) of black lacquer painted along each side of body cause the female to hesitate but she soon accepts him. When the lacquer has been cleaned off the body and three spots, the same size, are painted on the head he is still distinguished from a stranger male of same size. Extending the spots to cover the whole top and sides of head with black lacquer does not prevent her from attacking a larger male while accepting him. The female also accepts for a time a male same size as mate indicating some confusion in the identification.

(d) A male *Cichlasoma cutteri* has a band of black lacquer painted across the top of head back of the eyes, another spot of the same color on top of snout behind nostrils and a narrow band of the same paint in the midline of the head connecting the two. This painting does not prevent his mate from readily recognizing him. When one side of the head below the eyes is given an additional band of black lacquer this side of the head is vigorously attacked by the female. The other side induces no attack and is obviously recognized as that of the mate. Then paint is removed from the face and a broad band of black, 1 cm. wide at anterior end, is painted along each side of the body. *C. cutteri* has conspicuous vertical stripes of black and this longitudinal stripe on each side of the body brings forth a conspicuous change in color pattern. When returned to the tank the painted fish is vigorously attacked. Paint is removed; female immediately exchanges guard over the eggs with her mate and attacks a new male of the size of her mate when introduced.

These experiments, although few, clearly indicate that covering large parts of a jewel fish's head with paint usually prevents his being recognized by his mate. Covering equal or larger parts of the body may bring no confusion in mate recognition. In *C. cutteri*, a cichlid with conspicuous vertical stripes, altering the pattern with a horizontal stripe of black may also induce confusion. In both this species and the jewel fish painting only small parts of the head fails to prevent mate recognition while extending the paint to the sides of the face usually prevents mate recognition. Hence, while cichlids may secure visual cues for mate recognition from the color pattern of the body, the face would seem to have greater significance in this regard.

RECOGNITION OF TERRITORY

It has been shown in the preceding section that jewel fish recognize their mates as individuals—provided they are in motion—and that they identify them by detailed differences of the color pattern, especially of the head. If these fish have such a keen eye for detail it occurred to us that they might be paying considerable attention to the character of their nesting site. In the jewel fish, as in many other vertebrates, if the nesting site is removed the owners return again and again to the vicinity. It is obvious that jewel fish quickly learn the position of their nests. To what extent they consider the details of their nesting sites has not been previously determined.

In order to test this question we selected a series of jewel fish which were ready to spawn. The females were removed to another tank and permitted to lay eggs there on a new flower pot in a new location. The female was then removed and the male placed in the tank with the eggs. By varying the color pattern of the new flower pot it was possible to determine to what extent the new pot had to be like that in the old territory before fertilization would occur. In every case the new territory was, of course, confusing to the male but it was interesting to find that even more disturbing were color differences between the old and new nesting sites.

In 10 tests made as described above, the male fertilized eggs on the strange flower pot only 2 times. In the 8 cases where he failed to fertilize the eggs, the new flower pot was dissimilar from the old one. In 5 of these 8 failures the difference between the 2 pots was merely that one was clean and the other was stained from old algal growths. In 2 tests the flower pots differed in size. In 1 test they differed in the direction of black striping painted on them. In 1 of the 2 successful cases the new pot was identical to the old one. In the other it was merely the old pot placed in the new tank. These 2 successful cases were with males which had failed in previous tests, either because of difference in staining or of size of the pots, to fertilize the eggs in the new tank. They serve as a control to the other tests. These experiments seem to show conclusively that male jewel fish are aware of differences in staining and of size of the objects on which they are preparing to spawn. A sudden change in either of these two qualities will prevent fertilization from taking place.

It may be noted, however, that the presence of a female laying her eggs may induce the male to fertilize them even on a new type of nesting site. This was proved by other tests where, after failure of the mate to fertilize half a laying on a strange pot in a new territory, the female was permitted to continue laying in the presence of the male. Under such conditions the reserve of the male breaks down and fertilization will occur.

It might seem from the above tests that the female pays less attention to the site of egg laying than does the male. We frequently noted that a radical change in the character of a flower pot would induce the female already pseudolaying to go elsewhere to lay her eggs. The following test is typical.

Feb. 20.—A female was cleaning and pseudolaying on a flower pot from 3 to 4:30 P.M. At 4:30 P.M. the pot was turned around 80° in its exact position. The female went to the face of the pot that was in the old position. This face was stained very differently from the original one but the female continued her pseudolaying. At 5 P.M. a smaller pot ringed with black lines was placed in the exact position of the old. The female returned but would not clean or pseudolay on this pot. She turned and began to clean side of tank.

This and other experiments with differently colored pots indicate that, while the female is less sensitive than the male to sudden changes in color or size of the selected nesting site, the female will also be disturbed by marked changes and will desert sites which have been modified in this way.

Jewel fish with previous spawning records retain a decided preference for red flower pots and will always select the red when red, yellow, green or black pots are available. Older jewel fish with numerous spawning records, when given only Scheele's green (Ridgway, 1912) and black pots on which to lay, selected the green. This selection was on the basis of color and not position of the pot. After various pairs of jewel fish had taken up territory in our standard tanks with only red flower pots and were about to spawn, we placed black flower pots in the place of the red ones and moved the latter to the far end of the tanks. The jewel fish invariably followed the red flower pots to their new locations. The flower pots were painted with scarlet or black lacquers in order to give them identical textures. A pair of young jewel fish with no previous spawning record was given only a black flower pot on which to spawn. At the next laying, when both red and black pots were available, they selected the red. One spawning on black had no apparent influence on these fish.

Further experimentation revealed that there actually was an effect of this training even though the final results showed no evidence of it. This was well shown in the case of six additional pairs of jewel fish which had no previous spawning experience. These were given only black flower pots on which to lay. After two successive spawnings each pair was transferred to a new tank containing two flower pots, one painted with red enamel (Scarlet of Ridgway) and the other with black enamel. In every case when the third spawning was imminent the female took up territory on the black pot and the male on the red one. When, however, spawning took place, the female went to the male's territory. In 5 out of 6 cases the female laid on the red pot guarded by the male. The sixth pair spawned on the floor of the tank near the black pot. This occurred only after the female had made several excursions to the male's pot. These six tests show conclusively that the female actually seeks the male when spawning is imminent. The fact that each female took up territory on the black pot while the male remained on the red pot is evidence that the hereditary preference of the jewel fish for red may be modified by training quicker in the female than in the male.

Each pair of jewel fish was then left together with the red and black pots for subsequent spawnings. It was interesting to find that under these conditions the ability of the male to attract the female was not so pronounced. At least only 2 of the 6 pairs laid eggs on the red flower pot at the second spawning with pots of both colors available. One pair spawned on the floor of the tank near the red pot and two on the floor near the black pot. One pair that had spawned on the red pot the first time laid on the black one the second time. It would seem therefore that the color of the substratum has a profound effect on the female jewel fish on her first or first two layings. If she is put in a new tank she will seek a male even if he is on a pot of a color not attractive to her. But in subsequent layings she is able to induce a male, at least in some cases, to spawn on a substratum which his hereditary constitution makes unattractive to him.

Male jewel fish nearly ready to spawn will fertilize eggs which have been laid in isolation provided they are attached to a pot identical to the one the male had cleaned. If the new pot is spotted or stained with algal growths in a different manner from the original pot the male will invariably eat the eggs. If the female which laid the eggs is the male's mate and is introduced with the eggs she will at first suffer the male to pluck off a few eggs. As the eating continues most females will attack their mates with vigor. Conversely, males which have fertilized and are guarding eggs will attack their mates if they, because of a disturbance or breakdown, begin to devour eggs. Hence, if spawning has proceeded normally both sexes are irritated by any fish eating the eggs, even their mates.

From the above observations and experiments it may be concluded that jewel fish are hatched with a preference for a red nesting site over a black one. If young jewel fish are forced to lay on black surfaces they will still select red surfaces for the next laying. If a female is forced to lay her eggs on a black surface at the first two spawnings, she will retain a definite preference for black surfaces on later spawnings even if red surfaces are available to her. Both fish of a mated pair learn to recognize their nesting site by details of marking and size. If a female is ready to spawn she may be induced to accept a new nesting site, but the male will not fertilize eggs on this site if it differs considerably from the original one in staining or size. If the female continues to lay on this territory her activity may break down his reserve. If a female has laid eggs, or a male fertilized a set, neither will usually permit its mate to eat them.

SEXUAL SELECTION

The jewel fish and most other cichlids develop brilliant colors during the breeding season. The functional significance of these colors is entirely unknown. No experimental work has been directed previously toward determining their function. In other fish with conspicuous sexual adornments no experimental evidence of Darwinian sexual selection, that is of female choice, has been secured. It, therefore, seemed especially desirable to determine the factors which regulate the selection of mates in the jewel fish.

Experimental Procedure

In order to eliminate all sensory data except visual ones, the apparatus employed in the above study of sex recognition was rearranged. Preliminary observation revealed that many females develop place habits, selecting the corners of tanks to deposit their eggs instead of attaching them to suitable flower pots along the sides of the tank. Hence the small aquarium *b*, figure 2, opposite one of the long sides of the central tank, was entirely eliminated. This left tank *a* opposite the left-hand end of the central tank and tank *c* opposite the right-hand end. Since the apparatus was arranged in a greenhouse having a whitewashed roof, lighting was diffuse and uniform throughout the three tanks.

As in the sex recognition experiment a female about to lay was placed in the central tank and two identical flower pots arranged one directly opposite each end tank. Two male jewel fish which were actually courting, that is, cleaning a flower pot, head standing or vibrating in the stock tanks, were then selected for the test. One was injected subdermally along the abdomen with 0.3 cc. of a 1:1000 solution of yohimbine hydrochloride, the other was similarly injected with 0.2 cc. of a 1:1000 solution of adrenalin chloride

(Parke, Davis and Co.) which had been diluted 5 times with 0.65 per cent salt solution. Both injected fish were then returned to a stock tank for 1 to 2 hours. The result of this treatment was that the yohimbine injected fish expanded its erythrophores and melanophores to an extreme degree while the adrenalin injected one became very pale. The adrenalin also tended to make the pale fish sluggish but by the end of the hour rest period it would be usually swimming normally. If any difference in movement between the two males could be detected they were not used in the experiment. Further, if one became sluggish in the course of the test, the record was disregarded. In this way only courting males swimming normally were considered in each test.

In order to avoid any tendency of the test males to hide in corners, a glass partition was added to their tanks. This made each test male remain broadside to the female in the central tank. The males were capable of considerable movement but they had to remain near the front of the tank in full view of the female.

In later tests this apparatus was modified, and in certain tests females were added to the outside tanks. These variations in procedure and the results obtained will be discussed below under different headings.

Results Obtained with a Three-Tank Apparatus

As shown in the following table the female jewel fish invariably laid her eggs on the flower pot opposite the male which had been reddened with yohimbine. All courting males tend to become red but the injection brought these erythrophores to their fullest expansion and kept them expanded during the course of the test which might run from one hour to one day.

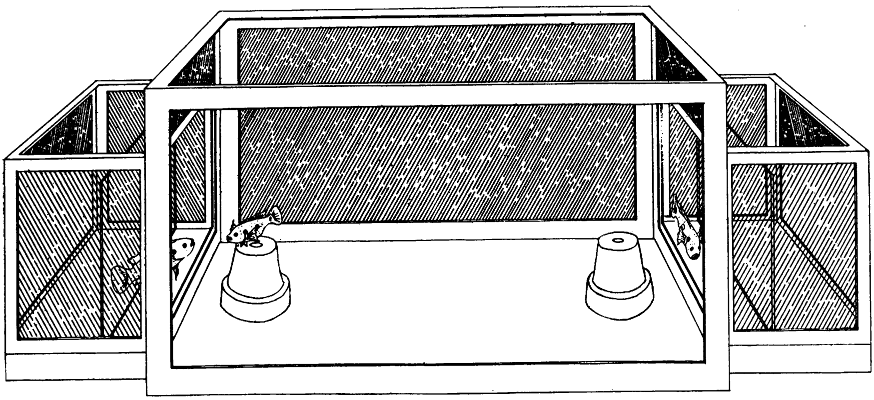

Fig. 3. Sexual selection apparatus. A courting male jewel fish is placed in each of the two lateral aquaria. One of these males has its erythrophores and melanophores expanded with yohimbine and the other has them contracted with adrenalin. The gravid female placed in the center tank will invariably lay her eggs opposite the male with expanded pigment cells.

Results Obtained with a Four-Tank Apparatus

As stated above, in any large series of jewel fish certain females are found which tend to avoid laying near the more exposed sides of a tank. This is very probably the result of conditioning in the stock tanks, the disturbance caused by the observer walking near the tanks having induced the fish to seek retreats in the far corners on frequent occasions. It was interesting, therefore, to determine if the tendency for the female to seek the most conspicuous male could be overridden by the tendency of these females to avoid the more open parts of the tank. The experiment described in the preceding section was therefore repeated but in addition a tank was placed opposite one of the long sides of the central tank and a pot placed in this tank opposite it. This returned the apparatus to the form it had in the sex recognition experiment. The only difference was that here only males were employed in the outside tanks and all of these were found courting before selection for the test. Further, they were always kept from moving away from the fronts of the small tanks by glass partitions.

SEXUAL SELECTION OF JEWEL FISH IN 3-TANK APPARATUS WITH COURTING MALES

Date	Red ♂ in Tank	Pale ♂ in Tank	Eggs Laid on Pot at	Score	Per Cent Preference for Red
7/6	*c*	*a*	*c*	+	
7/12	*c*	*a*	*c*	+	
7/21	*a*	*c*	*a*	+	
8/6	*a*	*c*	*a*	+	
8/27	*a*	*c*	*a*	+	
8/27	*a*	*c*	*a*	+	
8/31	*a*	*c*	*a*	+	
9/2	*a*	*c*	*a*	+	
9/2	*c*	*a*	*c*	+	
9/3	*a*	*c*	*a*	+	
9/3	*c*	*a*	*c*	+	
9/9	*a*	*c*	*a*	+	
9/9	*c*	*a*	*c*	+	
9/9	*a*	*c*	*a*	+	
9/16	*c*	*a*	*c*	+	
9/17	*a*	*c*	*a*	+	
10/4	*c*	*a*	*c*	+	
10/4	*a*	*c*	*a*	+	
10/6	*a*	*c*	*a*	+	
10/6	*c*	*a*	*c*	+	
10/7	*a*	*c*	*a*	+	
10/9	*c*	*a*	*c*	+	
				22+	100 per cent

As shown in the following table, in 24 tests the reddened male was placed in *b* tank opposite the long side 10 times. In 5 of these cases the female went elsewhere to lay her eggs. Thus exactly half of our females avoided the long side even though a reddened male was present. If we disregard all tests where the reddened male was in *b* tank, we have 14 other cases to be considered. In all of these 14 tests the female laid her eggs opposite the reddened male. The red fish was at one end 6 times and at the opposite end 8 times. If these 14 cases are added to the 22 in the preceding section, a total score of 36 positive cases without a single failure is obtained.

The Nature of the Attraction

It cannot be concluded from the above experiments that the gravid females were attracted by the red *per se*. It is possible that the yohimbine merely made the movements of the males more conspicuous. As shown above, some movement is essential for the identification of sex and the males with expanded pigment cells would presumably have their sex-identifying movements made more visible to the female. We frequently observed that reddened males which became sluggish for one reason or another no longer attracted females. A variety of tests was therefore carried out to determine the relative importance of movement as distinguished from color in sexual selection.

First, the four-tank apparatus was provided with non-breeding but fully adult females in the outside tanks. One of these was reddened with yohimbine exactly as the male had been. In three tests the gravid female laid opposite one of the untreated and hence much paler females. This result was in full agreement with the frequently observed fact that a courting, and hence normally reddened, female is avoided by others of her own sex.

Second, a series of males was selected from various stock tanks where no fish at the moment were courting. One male was injected with yohimbine as in the experiments reported above and two others were injected with the same amount of Ringer's solution. When these 3 fish were placed with a gravid female in the standard four-tank apparatus described above the female laid her eggs opposite the male reddened with yohimbine. This was repeated 5 times with identical results although the reddened male was moved to a different outside tank after each test. At every test there were twice as many pale males as red ones and yet only the latter were selected.

This test was repeated with the three-tank apparatus. Here each female was given the opportunity of selecting between a male reddened with yohimbine and another of the same size merely injected with Ringer's solution. In 6 tests the female laid opposite only the fish reddened with yohimbine. But in 4 other tests the eggs were laid before the paler male. When the pale and reddened fish were placed with the female and her eggs, however, it was revealed that in 2 of the latter cases there were mutual courtship movements between the female and the pale fish. Hence the pale fish must have already begun to court while the reddened fish had remained inactive. Here courtship movements were apparently in competition with swimming movements made conspicuous by the coloring.

Repeating these experiments with the three-tank apparatus but injecting the pale fish with adrenalin as described above instead of Ringer's solution failed to eliminate all the errors. In 14 tests there were 10 cases where the female laid her eggs opposite the bright fish and 4 where she selected the pale male. But again it was

Sexual Selection of Jewel Fish in 4-Tank Apparatus with Courting Males

Date	Red ♂ in Tank	Pale ♂ in Tank	Pale ♂ in Tank	Eggs Laid on Pot at	Score	Per Cent Preference for Red
7/6	*a*	*b*	*c*	*a*	+	
7/7	*c*	*a*	*b*	*c*	+	
7/8	*b*	*a*	*c*	*b*	+	
7/8	*b*	*a*	*c*	*b*	+	
7/10	*a*	*b*	*c*	*a*	+	
7/26	*a*	*b*	*c*	*a*	+	
7/26	*a*	*b*	*c*	*a*	+	
8/2	*b*	*a*	*c*	*b*	+	
8/4	*c*	*a*	*b*	*c*	+	
8/5	*c*	*a*	*b*	*c*[1]	+	
8/5	*b*	*a*	*c*	*a*	−	
8/6	*b*	*a*	*c*	*b*	+	
8/9	*c*	*a*	*b*	*c*	+	
8/10	*b*	*a*	*c*	*b*[1]	+	
8/10	*b*	*a*	*c*	*a*	−	
8/11	*c*	*a*	*b*	*c*[1]	+	
8/16	*c*	*a*	*b*	*c*	+	
8/16	*a*	*b*	*c*	*a*	+	
8/18	*a*	*b*	*c*	*a*	+	
8/18	*a*	*b*	*c*	*a*	+	
8/19	*a*	*b*	*c*	*a*	+	
8/22	*b*	*a*	*c*	*c*[1]	−	
8/25	*b*	*a*	*c*	*a*	−	
8/25	*b*	*a*	*c*	*c*	−	
Total					19+ 5−	73+ per cent

[1] Laid on floor of tank near this pot.
Note: All failures occurred when red fish was in tank *b*.

possible to account for these errors by assuming that the pale fish, in spite of its injection of adrenalin, was more active than the fish treated with yohimbine. Observation of the two males after the laying showed that in the case of the failures on 4/20, 4/16 and 3/25 the pale male was decidedly more active than its rival. Only the failure on 5/28 did not reveal a greater activity on the part of the pale male. Activity is, therefore, a modifying factor which, when most evident in the pale test male, may reverse the results secured with this apparatus. It is essential to test the female only with males in the same stage of the breeding cycle and to work only with males which are equally active.

Further evidence that movement is more important than color *per se* was obtained by utilizing the blinders employed in the experiments on sex recognition. Six tests were made with the three-tank apparatus. The female was given the opportunity of laying her eggs on flower pots opposite either a sexually inactive male fitted with blinders or another of the same size and stage in the breeding cycle without blinders. The blindfolded fish expanded both its melanophores and erythrophores while the control fish, being in a new tank without vegetation, grew pale. In brief, here were two sexually inactive males, one very sluggish but very bright and the other more active but pale. In 4 of the 6 tests the female laid in front of the pale but more active male. In one of two exceptions the blindfolded fish was abnormally active although not responsive to the female. In the other, the pale fish became very pale and sluggish before the test was over.

To summarize, the nuptial colors of the male jewel fish are attractive to the female in that they make his movements more conspicuous. If these colors are artificially induced in a non-breeding male they enhance his attractiveness because they render the small movements characteristic of maleness more evident to the female. A courting male is rendered even more attractive by the nuptial colors in that, besides the movements of maleness, there are responsive movements of courtship made conspicuous to the female. The latter movements are stimulating to the female and essential for the formation of nuptial bonds. These bonds can be formed through glass and, hence, the visual stimulations require no support of other sensory modalities. A true sexual selection of the more attractive male by the gravid female jewel fish has been demonstrated above, but the nuptial colors are not adornments in the usual sense of the word. Without movement these colors have no selective value.

It has been shown in an earlier section that jewel fish are hatched with a preference for moving red objects. It seemed possible that this preference might be retained in a latent form until sexual maturity when it would operate to induce females to select redder males. The apparatus used to test the young fish was rearranged to cover a tank 12 × 24 × 12 inches and a flower pot was placed at either end. In five tests the female laid opposite the red disk 3 times and the green disk, 2 times. These tests although few gave no indication that the moving red disk was attractive to a spawning female.

Direct observation on the activity of a gravid female in the three-tank apparatus showed that if two males are both sexually inactive and one is reddened with yohimbine as described above the female will spend more time opposite him than opposite his rival. For example, the times on 4 different females before 2 such males is as indicated in table below.

This shows that a gravid female will spend nearly twice as much time before a sexually inactive male reddened with yohimbine as before one not so treated.

In the tests with the laying females various stains were employed to color one

Period Gravid Female Remained Before Injected Males

(a)	4215 secs. before red male	2205 secs. before pale male
(b)	255 secs. before red male	135 secs. before pale male
(c)	3475 secs. before red male	1780 secs. before pale male
(d)	454 secs. before red male	43 secs. before pale male

of the males. Of these stains, neutral red and mercurochrome were the most successful but since none of these stains lasted as well as the yohimbine injection the latter was finally adopted for the tests tabulated above. For shorter periods of observation in the triple tanks both stains, but especially the neutral red, were eminently successful. Again it was found that the gravid female was more attracted by the stained male. The times on different females before two sexually inactive males, one stained with neutral red, are as shown in the following table:

PERIOD GRAVID FEMALE REMAINED BEFORE MALES

(a)	454 secs. before stained male	43 secs. before control
(b)	681 secs. before stained male	249 secs. before control
(c)	562 secs. before stained male	84 secs. before control
(d)	771 secs. before stained male	177 secs. before control
(e)	910 secs. before stained male	313 secs. before control
(f)	1181 secs. before stained male	738 secs. before control
(g)	423 secs. before stained male	155 secs. before control
(h)	128 secs. before stained male	64 secs. before control
TOTAL	5110 secs. before stained male	1823 secs. before control

That is, the eight gravid females remained before the stained male more than 2 1/2 times as long as in front of the unstained control.

Repeating this experiment with males further along in the sex cycle, one of each pair injected with yohimbine and the other with adrenalin as described in our first experiments with the sexual selection apparatus, gave varying results. No attempt was made to pick out courting males with the result that now the reddened and again the pale male secured the greater attention, according to which male was further along in his cycle and responded more quickly to the female. For example, one day male 28 injected with yohimbine secured 619 seconds of the female's attention as contrasted with 173 seconds obtained by the control. The next day the same male received only 305 seconds of the test time of another female while the control received 156 seconds. Ten tests were run with different females on the 9 different pairs of males. When the males were equally active the reddened one was preferred (times other than those for male 28 were red 929, 575, 1303 secs. and pale 195, 163, 993 secs., respectively) but whenever the reddened male remained less active than the pale one this advantage fell off until there was no significant difference between them.

DOMINANCE AND COLOR IN THE JEWEL FISH

In many groups of vertebrates the chief, if not the only, function of conspicuous nuptial colors is to intimidate rival males (Hingston, 1933; Noble and Bradley, 1933; Lorenz, 1935). Male jewel fish maintain their territories more by intimidatory gestures than by actual biting. Similarly the females, when they have accepted the male's territory, drive other females from it by raising the dorsal, erecting the opercular covers and spreading the fins while making short dashes toward their opponents. After courtship has proceeded for a time, and the two fish have learned to identify one another, the defense of territory, as stated above, is directed against other fish regardless of sex. In a tank of 50 gallons or less the driving of other fish by a mated pair is usually sufficiently disturbing to prevent all other fish in this tank from breeding. On many occasions we have observed a second male attempting to secure territory in such a tank but unable to succeed because of the dashes of the territory-holding fish. Not all sexually ripe fish in a tank will breed, but only those which are vigorous enough to secure and maintain territory. If the dominant male is removed, two or more other males may fight for supremacy in the sense that each fights to drive the other from a part of the tank intended for a territory.

A dominant male placed in a new tank usually becomes subordinate to the territory-guarding male resident in the tank. The unfamiliar surroundings apparently place the newcomer at a disadvantage. If, however, the newcomer is larger than the resident male he may succeed in dominating the latter. If he is courting in his own tank and the resident male is merely holding territory in his, the newcomer may succeed in pairing with the resident male's potential mate. In which case the newcomer will become dominant in the new tank. In brief, the dominancy of either male or female in a tank is dependent on their ability to hold territory. This, in turn, is dependent on the ripeness and size of any fish. These conclusions, reached from daily observations on many individuals, made it desirable to inquire further into the selective value of size and color in the social behavior of the jewel fish.

When two males, both holding territory, are placed in a new tank with a ripe female, the larger male usually dominates. For example, a male jewel fish 7.9 cm. in total length and another 7.7 cm. long were placed, 5/28, in a tank with a ripe female. Both males locked jaws and struggled. Within two minutes the larger male had driven the smaller male to the far end of the tank. The female mouthed the large male gently and both at once attacked the small male. Here was the apparent formation of a pair with very little courtship having taken place. The female had merely joined with a dominant male in driving a subordinate one. The action continued and the first two fish became a mated pair.

This incident and several similar ones raised the question of the importance of size in sexual selection. In most pairs formed naturally in a large tank the male is the larger. We therefore tested seven pairs of males in our three-tank sexual selection apparatus. In every case one male was larger and one smaller than the selecting female. In three cases the female laid opposite the smaller, and in four cases opposite the larger male. This experiment gave little evidence of females' selecting the larger males.

There is, on the other hand, an inherent tendency for males to be larger than females regardless of any selection on the part of the latter. As shown in the following table this is due to their more rapid growth. These measurements are the total lengths of average specimens selected at random from our stock tanks.

GROWTH OF JEWEL FISH

Age in Days after Fertilization of Egg	Sexually Immature	Length in Cm. Male	Female
12	1.0		
100	4.2		
124		6.5	5.3
143		6.5	5.8
160		7.0	6.2
210		6.7	6.2 and 5.5

The nuptial colors of jewel fish are usually acquired by both sexes as they begin to hold territory. They are retained during the egg laying and brooding periods by both parents. They may be lost, however, by any fish during this long period if another fish becomes dominant within the first fish's territory. Frightening the fish by waving bright objects before the tank will also cause the fish to flee and lose color. Gonadectomy does not destroy the nuptial colors (Noble and Kumpf, 1936) which are presumably under nervous control. Since complete hypophysectomy causes the contraction of both melanophores and erythrophores, this gland may play a part in sustaining the nuptial dress for the one or two weeks of the breeding cycle. The sudden disappearance of nuptial colors, however, in frightened fish indicates that the nervous control prevails in these situations.

Although color would seem to have important functions in intimidating rivals, staining a subordinate fish red will not make him at once dominant over his rival. This is largely due to the fact that the behavior of the fish following staining does not change. Some examples will illustrate:

Exp. 27.—A male 6.8 cm. long and another 7.5 cm. long are placed in a new tank with a territory-guarding female 6.6 cm. in length. The smaller male is redder and darker than his rival. The female mouths him gently while attacking the larger and paler male. After twenty minutes of driving it appears that the smaller male is accepted by the female and the larger one is considered an intruder. The pale male is then stained with neutral red until he is brighter than the rival. Three minutes later their rôles are reversed, the female gently mouthing the stained male and driving her former partner. In six minutes she began to attack the reddened fish again when he would not respond to her gentle movements.

Exp. 28.—Two territory-guarding males, one 7.9 cm., the other 7.7 cm., are placed in a new tank with a territory-holding female. The larger male attacks the smaller and they lock jaws. The larger overpowers the smaller and the female joins the fight to attack the vanquished male. The large male gently mouths female and both again attack the small male. Ten minutes later the female headstands before large male indicating that she has definitely accepted him. In the meantime the dominant male has become red and the subordinate remains pale. Fifteen minutes later the subordinate male is stained with neutral red. During the next ten minutes the female attacks the reddened male viciously every time he swims near the flower pot even though his colors are redder than those of the larger fish. Here is a case where pairing off between the dominant male and female had proceeded so far that the coloring of the subordinate male had no influence on the female's choice.

Exp. 29.—A dark male, 6.6 cm. in length, and a lighter one, 7.2 cm. long, are placed in a 15-gallon tank with a female which had been holding territory there. She attacks the smaller and darker male almost at once and within 10 minutes has accepted the larger male which during this period has become red. Both males are removed and the smaller male is stained with neutral red until he is more conspicuous than his larger rival. When both males are returned they are attacked equally hard by the female. The larger male continues to resist the attack with gentle mouthings while holding a position near the flower pot. The smaller male when similarly attacked fails to hold his ground but escapes to the far end of the tank. Within 20 minutes she has accepted the larger and paler male because of his gentle persistence.

Once dominance had been established in a tank we never succeeded in reversing it by staining the subordinate male. In every case, except when a female was well mated with the dominant male, staining the subordinate male with neutral red brought renewed interest in this subordinate fish by the female. This fish, however, possibly disturbed by the staining process, failed to gain an ascendancy over his rival. Hence, color without threat has no value in securing dominance. The stained male attracts the attention of the female but in none of our 8 tests with different pairs of fish did the stained male show sufficient interest in the territory to win the female.

SEX RATIO AND SEXUAL SELECTION

Darwin (1871) assumed that sexual selection would occur only at times that males were more abundant than females. In our tanks of 15 to 140 gallons capacity there was undoubtedly some selection taking place regardless of sex ratio. One breeding pair in tanks of average size normally prevents all the other ripe fish from breeding. We have frequently had 20 or more ripe fish in one of the larger tanks for several months unable to breed until we isolated small groups in other tanks. Whether intimidatory display or large size were giving preference to certain males, or whether the female was actively selecting the most conspicuous ripe males, could not be stated in any one case. To what extent failure to breed in nature is due to the dominance of other breeding pairs is not known.

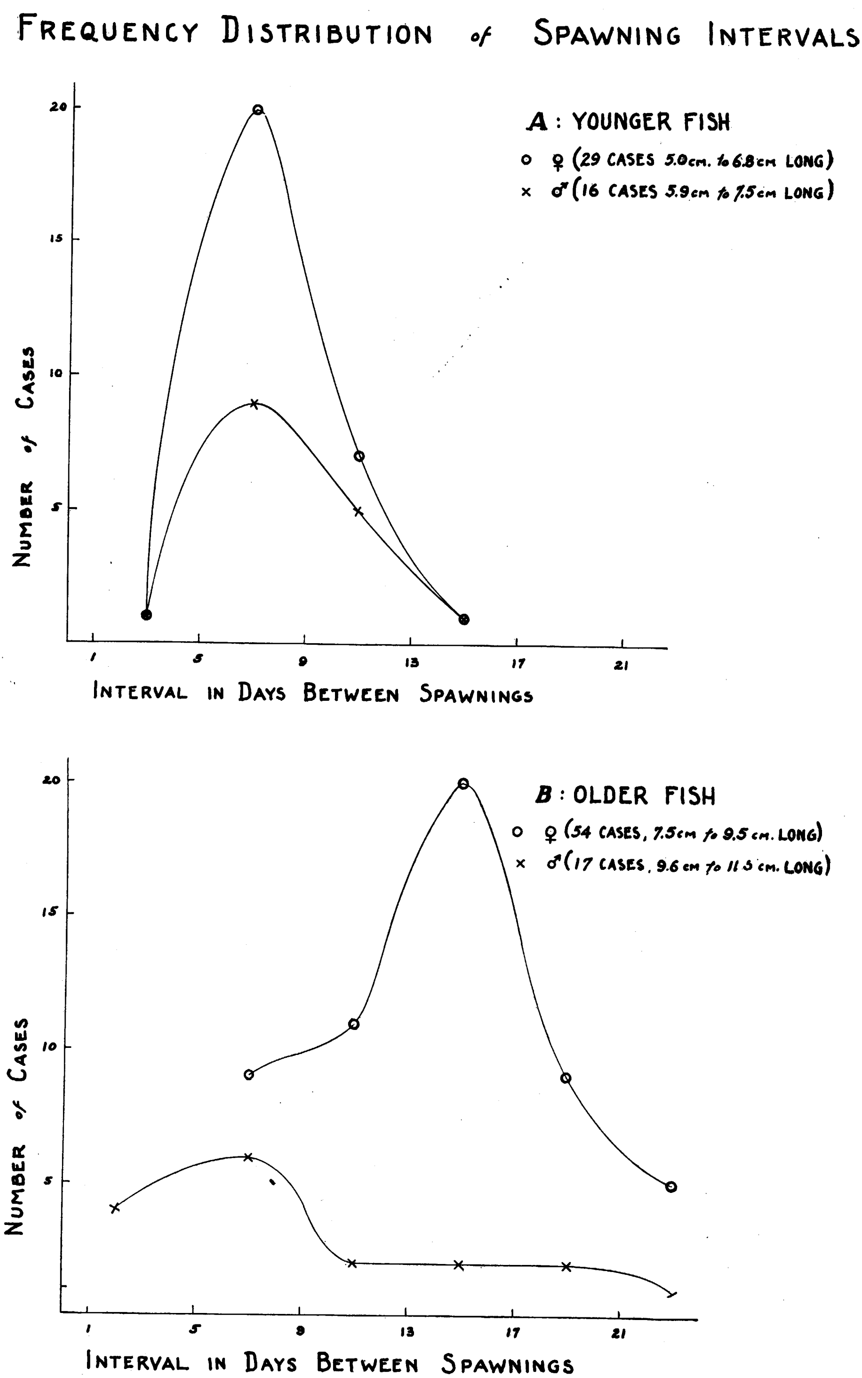
FREQUENCY DISTRIBUTION of SPAWNING INTERVALS
A : YOUNGER FISH
o ♀ (29 CASES 5.0cm. to 6.8cm LONG)
× ♂ (16 CASES 5.9cm to 7.5cm LONG)
NUMBER of CASES
INTERVAL IN DAYS BETWEEN SPAWNINGS
B : OLDER FISH
o ♀ (54 CASES, 7.5cm to 9.5 cm. LONG)
× ♂ (17 CASES, 9.6 cm to 11.5 cm. LONG)
NUMBER of CASES
INTERVAL IN DAYS BETWEEN SPAWNINGS

Fig. 4

Crowding, however, is probably less severe and hence competition less intense.

If small jewel fish can escape from the dominancy of larger ones they will breed more frequently than the large ones. This was well shown by rearing isolated pairs under identical conditions. It is also shown by our graphs (figure 4) of the frequency of spawning in 116 cases. The graphs show that the frequency of spawning decreases as the females grow older, whereas that of the males does not. Some old males may breed twice as frequently as the old females. This means that regardless of the original sex ratio there may be in some cases twice as many available males as females. Noble and Kumpf (1936) have shown that introducing a succession of ripe females would induce castrated male jewel fish to shorten their cycles to as little as 1 or 2 days and more recent observations by the same workers indicate that this is also true of normal males. Hence, although the male seems to regulate the breeding cycle by occupying territory at definite intervals, which under laboratory conditions may be uniform, actually ripe males without territory are extremely sensitive to the presence of a ripe female and are able to advance their cycles several days if territory becomes available and a ripe female is present.

Hence, the graph shown in figure 4 merely indicates that under the conditions in our laboratory during the period when most of the above experiments were being conducted, the males, removed from young approximately as often as the females, bred more frequently than the older females. We observed several cases where the male lost interest in the young sooner than the female. In one case a male abandoned his mate 2 days after spawning, just as the eggs were hatching, and mated with another female which had taken up territory. Two days later he spawned with her. From these data we may conclude that the breeding cycle is regulated by the female. If there are opportunities for the establishing of several territories, males will be ready for a second spawning sooner than the older females. This state of affairs tends to prevent a pair from continuing to spawn together for any extensive period. It also places more males in competition with rivals and gives a greater opportunity for a selection to occur.

RESPONSES OF PARENT JEWEL FISH TO EGGS

The oviposition of the jewel fish has been frequently described by aquarists but little attempt has been made previously to analyze this behavior in terms of the stimulus and response. Spawning in our laboratory took place at temperatures ranging from 76° F. to 93° F. and at a pH from 6.0 to 6.8. The averages for 20 spawnings, scattered throughout the winter months from October to May, were temperature 85° F. pH 6.4. The time of egg laying in this series averaged approximately 1:30 P.M. One laying occurred at 9:30 A.M., three between 11 A.M. and noon, the remainder between noon and 4 P.M. The eggs are attached to some solid object, usually the flower pot provided for this purpose, and they form a group usually between 5 to 8 cm. in diameter. As shown in figure 5, the average number of eggs varies with the size of the female. A female of 5.5 cm. averages 550 eggs, while one of 8.5 cm. averages 1500. These counts were made on 27 layings.

Sexual maturity occurs at approximately 4 months of age, under our laboratory conditions. First spawning occurred in one lot of young at 124 days, in another lot at 144 days. Both males measured 6.5 cm., the females 5.3 and 5.8 cm., respectively. As stated above this difference between the sexes is due to the more rapid growth of the males.

Sex is not difficult to determine in the ripe fish. The females have more rotund bellies and are usually less brilliantly colored than the males. At the beginning of courtship both sexes protrude genital tubes. In an average female 74 mm. long the tube, when fully protruded, was 2.2 mm. long, and tapered slightly to a blunt tip. The genital tube of a 92 mm. male was 1.5 mm. long, narrower and more conical than that of the female. It always points backward as in that sex. In some other cichlids, such as

Cichlasoma aureum and *Aequidens portalegrensis*, the male's tube is proportionately longer than that of the jewel fish, curved and pointed forward. Since the function of the tubes is essentially the same it is surprising to find these differences.

The details of egg laying and fertilization have been described by Apel (1932), Dünnebier (1927), Fischer (1924), Hildebrand (1930), Müller (1928), Solberg and Brinley (1933) and other aquarists. The pattern is essentially the same as that of all egg-laying cichlids. The eggs are first laid in short rows which may be straight or curved. Later they are deposited by the sensitive genital tube between the rows until they form a more or less circular plaque on the surface cleaned by the parents. The fins play no rôle in either expressing the eggs or sensing available egg sites between the egg rows.

Frequent reference appears in the aquarium literature to abnormal behavior. Parent cichlids disturbed while spawning or brooding will frequently eat the eggs and often fight viciously among themselves. In our work precautions were taken to avoid these disturbances. As our experimental work continued it became clear that many parents would break down under the strain of repeated handling. For example, one female, which had been normal in mate recognition and brooding of eggs, broke down after 3 1/2 hours of our experimentation and allowed herself to be driven from her eggs by a stranger male whom she had previously dominated. When the other fish in the tank swarmed in to eat her eggs

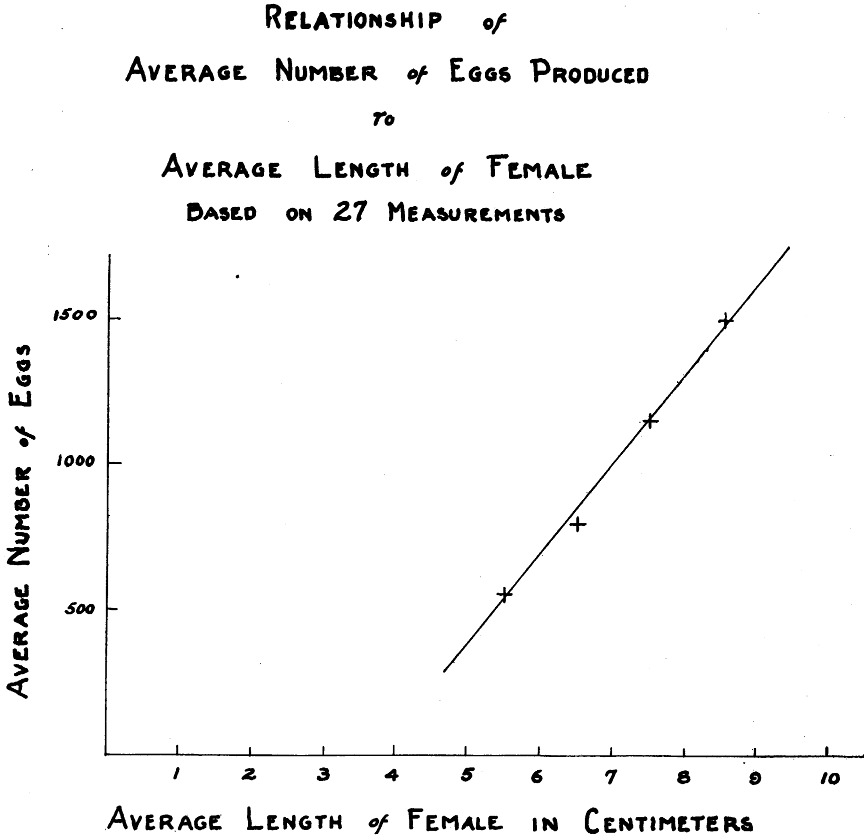

Fig. 5

she made no defense. In some cases these breakdowns may actually result in an advance in the cycle, or at least a substitution of other behavior patterns for the one which should be taking place. Similar substitutions have been described in birds (Kirkman, 1937). For example, one female broke down after four hours of our continuous testing and picked her half developed eggs off the flower pot on which they had been laid. Instead of eating them, however, she churned them in her mouth for a few seconds and spat them out on the floor of the tank. At this stage there were no pits for the retention of recently hatched young and the eggs, treated as young, died.

It has been shown above that sex recognition, mate recognition and other forms of social behavior of the jewel fish are primarily visual responses. The question remains, do jewel fish recognize their eggs by visual cues or by other types of sensory data? To test this question two identical flower pots were placed 18 inches apart in a 60-gallon tank. On one of these flower pots a pair of jewel fish was allowed to spawn. Then the flower pots were transposed. This simple experiment was carried out with four different sets of parents. Each pair was tested several times, screens being applied each time to prevent the parents from seeing the change. In every case the parents found the eggs in the new position and began to brood them within 2 to 15 minutes after the screens were raised. These results are different from those obtained by Goldsmith (1905) with a species of Goby which recognizes its shell retreat by its position rather than by its form or color. They also differ from those obtained by Breder (1934) with *Aequidens latifrons* which was apparently much further along in the brooding cycle and instead of brooding in the new location carried the eggs as if they were hatching to a depression in the sand.

Having established that the jewel fish could find its eggs in a new locality, we repeated the experiments but enclosed each flower pot in a battery jar full of water. When the pots were interchanged the test fish still had no difficulty in finding their eggs. Two sets of parents found their eggs and began to brood in from 8 to 20 minutes. Then this experiment was repeated but the flower pots were placed in glass jars with glass tops sealed with petrolatum. Here there was no possibility of odor playing a rôle. Two sets of parents again located their eggs in the new position in from 8 to 13 minutes. In a final test both sealed pots were placed in an entirely new position in the large tank. Again the fish found the eggs. The parents would assume a vertical position against the glass side of the jar and fan their fins as if brooding. This is the position a parent takes when fanning eggs on a vertical pane of glass.

Although these experiments showed that vision alone suffices for a jewel fish to identify eggs in a new situation, they did not prove that olfaction under normal circumstances has no influence. The test was therefore repeated with the pots concealed in screen cages which permitted a free circulation of the water but obscured vision. For 1 hr. 35 min. a pair remained at the original location near the pot without eggs. When the cages were removed the fish went at once to the eggs in the new location. This experiment was repeated with pairs of *Cichlasoma bimaculatum* and *Apistogramma steindachneri* without securing any evidence that olfaction aids the parents in locating their eggs..

In all these experiments the parent fish went first to the old location but not finding their eggs there, they would swim toward the other flower pot which stood out as a landmark. It seemed possible that the parents might be distinguishing their eggs by slight differences in the staining of the flower pot to which they were attached. A series of pairs was therefore selected, the pots with their eggs removed and the eggs scraped off into watchglasses. When any one pot was returned to its original tank and a watchglass with eggs placed a distance from it, the parent fish after an examination of the pot ignored it and began to brood the eggs. They would hover over the glass, fan the eggs, pick them up in their mouths and spit them out in the glass again. In a few cases they picked up the eggs and carried them to pits which they made in the sand. Although the embryos had not yet formed they treated these eggs as if they were young. Hence, removal of the eggs in some cases carried the parents forward to the next stage of their reproductive cycle. This experiment was repeated with 7 pairs of parents, each time with the same result. The eggs varied in age from 10 minutes to 25 hours and hence their being treated as young seemed very remarkable.

Experiments were performed to determine how long a jewel fish could remember its eggs. The female of a brooding pair was removed and the male tested with a strange male to determine if his own territory defense was normal. If normal, the female was returned and the male parent isolated. After varying periods the male was returned to his guard duty and tested again to see if he would defend the eggs. In 5 such tests out of 6 the father still guarded his eggs after absences varying from 24 to 28 hours. In the sixth, the father ate his own eggs after 23 hours, but in his absence the mother had moved them to a pit in the sand. In view of the 5 preceding experiments this last may be considered as a breakdown similar to the two described above. In a seventh case the mother ate the eggs during the male's absence; on his return after 48 hours he guarded the pot.

The ability of parents to discriminate between their own eggs and those of other parents or even of other species remained to be determined. For this purpose the parents' own eggs were removed from their tank and a pot with strange eggs substituted.

In these experiments, jewel fish, *Etroplus maculatus* and *Cichlasoma cutteri* parents adopted *C. cutteri*, jewel fish and jewel fish eggs, respectively, guarding them until they hatched. A pair of jewel fish which had only spawned once before adopted *Etroplus* eggs and reared the young for at least 8 days after hatching. Other observations on one cichlid brooding the eggs of another were made in the course of our study. These included:

(a) A female jewel fish adopted *Cichlasoma biocellatum* eggs.

(b) A pair of jewel fish with free-swimming young, when moved without their young to another tank, fanned and guarded eggs just laid there.

(c) A pair of jewel fish with one-day eggs on a pot was moved, without their pot, to a tank where *C. cutteri* eggs were on a wall. They stood guard over the eggs and when they began to hatch picked them off and carried them to a corner of the tank.

(d) Two pairs of jewel fish which had just laid were induced to take up guard over each other's pots, each pair being moved to the other tank. These same females, placed together in a strange tank with first one pot and then the other, each, after about 20 minutes, guarded her own eggs while ignoring the others. But it is to be noted that one set of eggs was laid on the side of a clean 3-inch pot, the other on top of a stained 4-inch pot, and it seems probable that it was these features in the nest sites that the mothers recognized.

It is obvious from these observations and experiments that cichlid parents recognize eggs wherever they find them. Sight alone suffices for this recognition. Smell is not necessary. A strong topographic sense exists, but the eggs alone when removed from the pot on which they were laid are a sufficient stimulus for guarding. A flower pot without eggs soon loses its significance to a brooding cichlid. This egg-guarding behavior is in effect as soon as the eggs are laid and may be retained by the male parent during an absence from the eggs of 48 hours. There is no discrimination between own eggs and other eggs, even those of another cichlid species.

RESPONSES OF PARENT JEWEL FISH TO YOUNG

The recently hatched young of the various cichlids available to us differ in small details in their color patterns (figure 6). Although these differences are apparent under the binocular they are often difficult to see with the naked eye. The question arose, do cichlids recognize their own young, and if so, by what means? Although parents can distinguish their nesting site by the algal stains on its side, it by no means follows that their vision is adequate to distinguish between the color patterns on young fish only 5 or 6 millimeters in total length. No experiments have been devised previously to test this question. Breder (1934) believed he saw one pair of *Aequidens latifrons* attempt "to

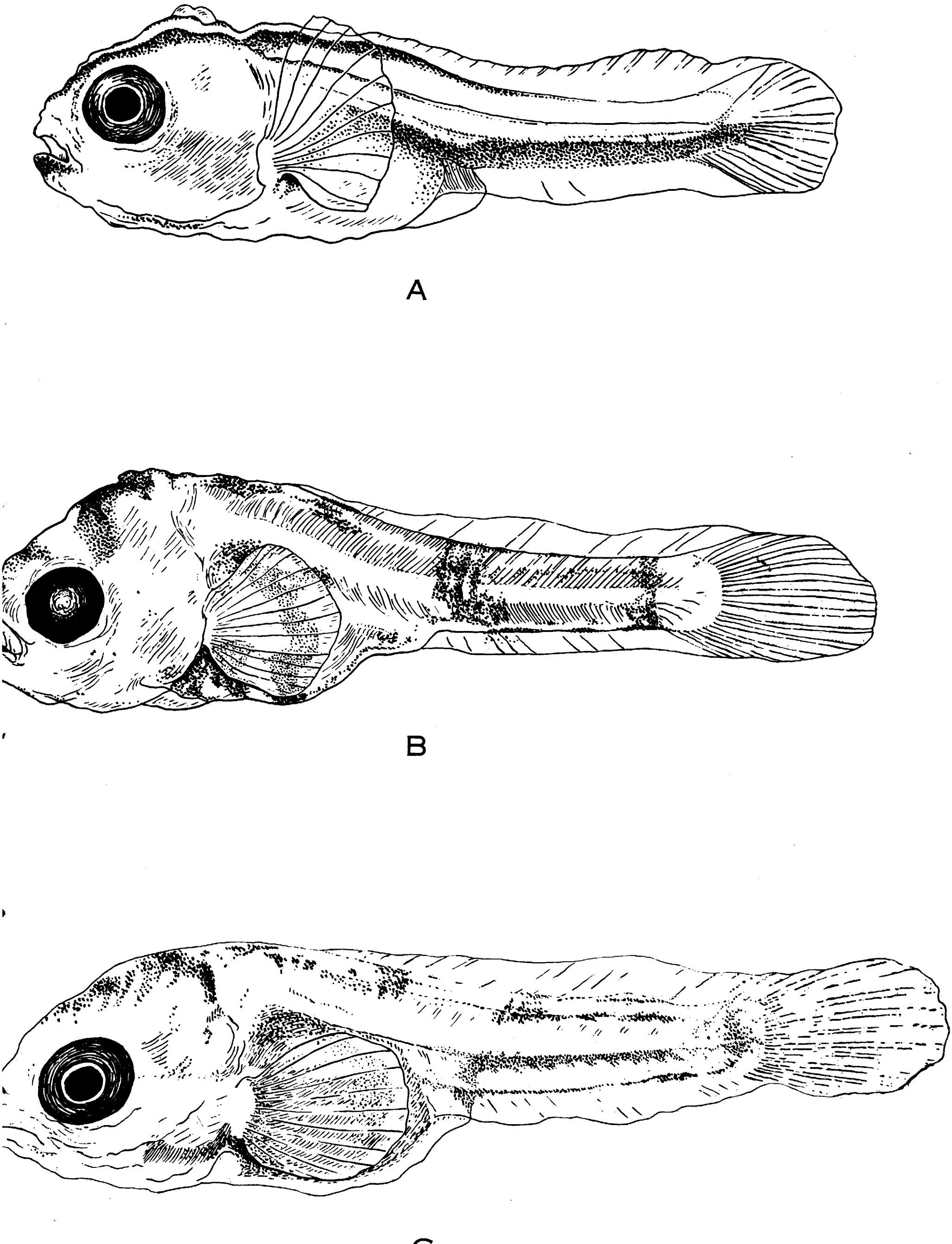

Fig. 6. Young cichlid fishes, first day of free swimming stage. ×20. A, *Hemichromis bimaculatus;* B, *Cichlasoma bimaculatum;* C, *Cichlasoma cutteri.*

herd two young *Lebistes reticulatus* together with their offspring," which would suggest that the powers of discrimination in this cichlid were poor.

We have tested a large series of cichlids, including, besides the jewel fish, *Cichlasoma bimaculatum*, *C. cutteri* and *C. biocellatum*. This work has shown beyond any doubt that cichlids can distinguish their young from those of other species. Our standard procedure was to select a pair of parents guarding young; remove some of these young in a dip tube and then introduce some young of the species to be tested into the tank. The parents will usually take the young at once into their mouths. If they spit them out among their own young it is assumed that they cannot distinguish them from their young. If they eat them at once or within a short time it is assumed that they recognize them as a foreign species. In every test, for a control, some of the parents' own young, which had been previously removed, were reintroduced.

During the "wriggling stage" the young of a foreign species cannot be distinguished from a parent's own wriggling young. This stage usually lasts from 2 to 4 days after hatching. This was shown to be true both when parent jewel fish were given wrigglers of *C. bimaculatum* and when parents of the latter species were given young jewel fish. In both these pairs when young of the foreign species were introduced during the free-swimming stage they were immediately devoured. Other tests were made by placing (1) among young jewel fish 6 days of age (counted from the time the eggs were laid), young of *C. bimaculatum* 8 days of age; (2) among jewel fish 9 days old, *C. bimaculatum* 12 days old; (3) among *C. bimaculatum* 12 days old, jewel fish 9 days old; (4) among *C. cutteri* 10 days old, jewel fish 5 days old; (5) among *C. cutteri* 10 days old, *C. bimaculatum* 29 days old; (6) among jewel fish 7 days old, *C. cutteri* 7 days old; (7) among *C. cutteri* 7 days old, jewel fish 7 days old; (8) among *C. bimaculatum* 6 days old, *C. cutteri* 9 days old; and (9) among *C. bimaculatum* 6 days old, jewel fish 6 days old. All of these tests were run several times and in every case the parent fish ate the foreign young.

When cichlids guarding wrigglers were given wrigglers of a foreign species they invariably guarded them throughout the wriggler period. This was tried with *C. cutteri* given jewel fish young, *C. bimaculatum* given jewel fish young and jewel fish given *C. bimaculatum* young. But if a parent guarding wrigglers is given free-swimming young of a foreign species, only a day or two older, the latter are invariably eaten. This was tried with *C. bimaculatum* given free-swimming jewel fish young and jewel fish given free-swimming *C. bimaculatum* young. Hence, the wriggler-guarding stage is not one of parental indifference. The foreign young must be in the free-swimming stage to be distinguishable from other cichlid young.

The ability of cichlid parents to distinguish their own young from young of other species is found only in fish with previous spawning records. Cichlids which are spawning for the first time will invariably adopt the young of a foreign species. We placed young *C. bimaculatum* 7 days old among young jewel fish 6 days old; young *C. bimaculatum* 3 days old among young jewel fish 4 days old; young *C. bimaculatum* 2 days old among jewel fish 3 days old; fresh eggs of *C. bimaculatum* in the nest of a jewel fish; young jewel fish 2 days old among *C. bimaculatum* 1 day old; young *C. bimaculatum* 4 days old among young *C. biocellatum* 1 day old; young *C. cutteri* 10 days old among young jewel fish 5 days old; young *C. cutteri* 9 days old among young *C. bimaculatum* 6 days old. In every case the parent fish spawning for the first time reared the foreign species.

Although the recognition of a foreign species is made by experienced cichlids only during the free-swimming stage, motion is not a prerequisite for discrimination. If several young of an experienced jewel fish are removed from the parents, anaesthetized with urethane and placed back in the tank with the same number of similarly treated *C. cutteri*, either parent jewel fish will seize its own motionless young and spit them into the school of young while the motionless *C. cutteri* will be seized with greater vigor and swallowed. Similarly if the *C. cutteri* have had the previous experience of rearing young, either parent will distinguish in the same manner its motionless young from motionless jewel fish.

The anaesthetized young may remain floating on the surface of the water or they may drop down headfirst to the bottom of the tank. As they fall the parents usually rush forward to seize the young in their mouths. Young lying motionless below the surface film are also identified. In this position it would presumably be very difficult for the parents to see any color pattern. Before being swallowed foreign young are often spat out several times and it is during this period their color patterns are probably seen.

Proof that it is the color or color pattern of the young and not their shape or texture which the parent recognizes is proved by staining the young in various ways. The details of one of the experiments will illustrate.

Exp. 30.—A pair of young *C. cutteri* with only one previous spawning record laid on 2/5/36. The young were free swimming 6 days later when 6 were removed and 6 young jewel fish of the same size introduced. Although these parents had had only one previous brooding period they distinguished their own young at once from the jewel fish, eating only the latter. All the *C. cutteri* introduced as a control were spat out into the school of young.

One young *C. cutteri* was secured with the dip tube and stained with Janus green B. When introduced into the tank the stained fish swam well. The mother *C. cutteri* at once dashed forward, however, and ate it. A young jewel fish stained the same way and released with the *C. cutteri* parents was immediately devoured.

The experiment was then repeated several times, first introducing a stained *C. cutteri*, then an unstained young of this species. Although the method of releasing the two fish into the tank was the same the parent fish ate only the stained young.

The marked difference between the ability of cichlids with previous spawning records and those without them in identifying young of their own species is not due to different degrees of maturation of the nervous systems of the fish but to differences in learning. This was well shown by testing the discriminative ability of young parents which had previously reared only young of a foreign species. The details of one experiment will illustrate.

Exp. 31.—A pair of jewel fish had been given eggs of *C. bimaculatum* in place of their own first spawning. They brooded eggs and young in a typical manner. There were approximately 150 young in the school which was kept in a fairly compact group by the parents. When the young were 9 days of age and had been free swimming 2 days, 15 were removed from their foster parents for further experimentation.

Two young *C. bimaculatum* were then returned to their foster parents together with two young jewel fish of exactly the same age. The mother allowed the 4 small fish to join her school. Then 2 1/2 minutes after introducing these fish she swam forward and devoured the two baby jewel fish.

The experiment was repeated but the four fish were introduced at the far end of the 15-gallon tank. The male parent at once left the school and seized one of the introduced *C. bimaculatum* in its mouth. Returning to the school he spat it out in their midst. Then he rushed back and seized the other *C. bimaculatum* to repeat the performance.

The female now moved forward and seized one of the young jewel fish; after churning it in her mouth a moment she spat it out. Then she seized it again and spat it out once more. This was repeated 4 more times before the female swallowed the young one. She then swam to the other jewel fish and sucked it in and spat it out several times before she swallowed it. Apparently the female jewel fish which had recognized the introduced young of her own species as "foreigners" when they were near her foster young had now some misgivings when they were at a distance from the school.

On the next trial and those that followed both parents showed little hesitation in making a selection. It will be recalled that these parents had never reared young previously. They had been associated with foster young only two days as free-swimming fish. Nevertheless these two days had been sufficient for the little fish only 6 or 7 millimeters long to impress their characters on their foster parents' minds. Hence, when young of the parents' own species were introduced they were devoured as foreign objects suitable for food. It is possible that these rightful young were also considered a danger to the school because both parents eventually attacked them with more vigor than they usually directed toward food.

As a control for Exp. 31, a pair of jewel fish which was engaged in its first brooding was tested. The young were exactly the same age as the *C. bimaculatum* being reared by foster parents. Again the four fish were placed near the school and the parents allowed them to mingle with the school before they swam toward them. Soon the parents became restless and rushed forward to devour the two young *C. bimaculatum.* The experiment repeated several times gave always the same result. These jewel fish parents which had brooded as long as the first pair, but only their own young, would eat only the *C. bimaculatum.*

Other tests were made with other jewel fish which were given *C. bimaculatum* eggs on their first spawning. In all cases young jewel fish introduced in the free-swimming stage were devoured as "foreigners." Similarly, a pair of jewel fish given *Etroplus maculatus* eggs on their first spawning would eat young jewel fish.

As a further test the experiment was repeated with the first-mentioned jewel fish to rear *C. bimaculatum* young. The young jewel fish and *C. bimaculatum* before being tested were anaesthetized in 1 per cent urethane. When the young were introduced they remained in contact with the surface film. Both young were seized and spat out approximately 3 times but the *C. bimaculatum* were finally returned to the school while the young jewel fish were eaten.

When this experiment was repeated and the narcotized young dropped slowly to the bottom of the tank there was instant recognition on the part of the parents. It will be noted that in both this test and the previous one the young were being propelled through water when the parent seized and swallowed them. The spitting out of the young attached to the surface film may well have served to place them in a position that the parent fish could see their color patterns.

It might be assumed that the frequent excursions in and out of the parent's mouth would revive the young sufficiently to induce some movement which would aid in species identification. To avoid this possibility, young were killed by short immersions in 10 per cent formalin. When these young were retested the parents were found still able to discriminate. For example, in Exp. 32, 20 young were removed from a school of jewel fish which had been free swimming 2 days. Two returned to the parents were immediately seized and spat out in the school. Two others, stained with aqueous methylene blue were seized by the female parent and spat out without bringing them near the school. The male parent at once seized and swallowed the stained fish. On the second test both parents seized and swallowed the stained young.

The experiment was repeated but the young were killed with 10 per cent formalin. The female spat out the unstained fish 6 times and finally let them float away. When given two young similarly killed but stained with methylene blue the female parent swallowed them without spitting them out.

On the second test the formalin-killed but unstained young were spat out into the school while the similarly killed but stained fish were swallowed. On further tests the same result was obtained indicating clearly that spontaneous movements of the young fish are not required for recognition. Since the only difference between the experimental and control young was the staining it would seem certain that color or color pattern serves as the basis of young recognition.

Staining makes the young a "foreigner" whether they are motionless or active. The jewel fish with the first-mentioned brood of young *C. bimaculatum* were given some of their own young stained with Janus green B. Although the stained young seemed to swim normally, the female parent seized the nearest one and after spitting it out once, swallowed it. The male seized the second one and swallowed it without spitting it out. The female spat out another stained jewel fish before swallowing it. The male, however, continued to devour all stained young of either species without spitting them out.

During the early part of these studies it was thought that wrigglers of foreign species were not eaten because their distinctive color patterns had not yet developed. But a series of tests with experienced jewel fish given a closely graded series of foreign young during the critical period at the end of the wriggler stage revealed that the problem was more complex. Foreign young which have been free swimming only a few hours are repeatedly sucked in and spat out many times before they are finally eaten. The way such a parent fish rushes at the foreign young would seem to indicate that it recognizes the young as something to be destroyed but as soon as the young fish has been churned a few moments in the parent's mouth it is forcefully spat out again. The whole process gives the impression that the tactile stimulation of so small a fish calls forth the spitting reflex so characteristic of the wriggler-guarding stage while the sight of the object spat out induces the parent to immediately swallow it again. The whole process is carried on with such vigor that the young are sometimes killed.

The experiments on early swimming young repeated several times with different species gave varying results according to the exact age of the young and the stage in the brooding cycle of the parent. For example, in Exp. 33, the first-mentioned jewel fish to rear *C. bimaculatum* young, as described above, was tested when its foster young had been free swimming 3 days. It was given young *C. cutteri* which, although 6 days old (from date of egg laying), were barely able to rise from the substratum. Both jewel fish parents took the tiny *C. cutteri* in their mouths and spat them out but not into the school of foster young. They seemed to recognize them as foreign objects but not as something to be swallowed.

This experiment repeated with the jewel fish pair which served as a control for the foster parents just mentioned gave identical results. The young *C. cutteri* were seized and spat out several times but never into the school of young jewel fish. The next day the young *C. cutteri* in both this tank and in the tank of foster parents had been eaten. Within a few hours they had become objects which after being seized could be swallowed.

A jewel fish recognizes its young not only by their color pattern but also by their size. A parent will readily adopt young from other broods of jewel fish if these are approximately the same age. We performed a large series of experiments to determine how great an age difference jewel fish would tolerate in their young. Where the difference is less than 2 days the foster young are adopted, and where it is more than 3 days they are eaten. But where the difference is exactly 2 days the young may or may not be eaten according to the individual peculiarities of the parents. The following represents a summary of our findings.

Young jewel fish were adopted by jewel fish parents when the latter's young were 10 days old, and the foster young the same age. They were also adopted when the ages of own and foster young were 5 and 4 1/2, 4 1/2 and 5, 6 and 4, 8 and 6 days, respectively.

On the other hand, the introduced young were eaten by jewel fish guarding their young when the ages of resident and introduced young were 4 and 6, 10 and 7, 10 and 7, 7 and 10, 12 and 14 days, respectively.

In various trials the same fish were first given foster young 1 day older or younger than their own young and then given young with an age difference of 3 days or more. These fish would invariably guard the first group and devour the second lot. There is, therefore, no doubt that parent fish are aware of the size of their young at any moment and individuals which diverge considerably from this standard are treated as foreign objects which being alive and edible are subject to being swallowed.

DISCUSSION

Although the social behavior of the jewel fish and other cichlids would seem to function well when only visual cues are available to the fish, it is possible that other sensory modalities may reinforce the visual stimulations. A jewel fish with its olfactory nerves severed will readily find food resting motionless on the bottom of the tank. Since the jewel fish has only one nasal aperture on each side through which currents of water are forced in and out, the species would fall in group 2 of Pipping's (1927) classification and represent a group of fish which do not react to the smell of food. Nevertheless, if a cheese-cloth bag of chopped worms is introduced into a tank, together with another one of exactly the same size filled with sand, the jewel fish will continue to snap only at the bag of worms. Hence, when visual cues are not available, olfactory or gustatory ones may help the jewel fish in the identification of food.

Dykgraaf (1933) found that a pair of *Macropodus* courted for a time after one of the pair was blinded. He attributed this continuation of courtship in the blinded fish to stimulations it was receiving through its lateral line organs. Some species of fish are endowed with an extremely fine sense of touch in their skin (Reinhardt, 1935). It would seem that during normal courtship in the jewel fish both lateral line organs and the tactile organs would be stimulated.

As stated above we have found that blind jewel fish could recognize sex and enter into a few courtship movements with other blind fish. With normal fish of the opposite sex fertile spawnings would result but there was failure to produce normal nests and to synchronize with the partner both in fertilization and brooding. It may be noted, however, that a jewel fish equipped with blinders is unable to enter into courtship at once with another fish, apparently because the caps to the eyes reduce all movements. At least we may conclude that touch or other sensory modalities cannot function during courtship vicariously for vision in the way olfaction may function during food seeking.

Numerous fish have been shown to be able to learn differences in form or size when given adequate training (Schaller, 1926; Herter, 1929; Maes, 1930). They can also learn to distinguish between similar objects which have been differently colored. Whether this indicates that fish have a true color vision or are merely responding to differences in brightness is a subject which has been frequently debated (Warner, 1931). Our work makes no attempt to settle this question. We have, however, showed that males with their erythrophores and melanophores expanded are selected in preference to equally ripe males with these pigment cells more contracted. Further, males artificially stained with neutral red hold the attention of a female more than does an unstained male. In brief, females will select males which have the most developed nuptial dress. This is not, however, sexual selection in fish as Darwin conceived it, for, as shown above, these females are merely responding to the movements of the male which are rendered more conspicuous by the expansion of the pigment cells.

The jewel fish inherits patterns of response toward both moving and motionless objects. Slight differences in motion identify sex and species. The inherited response to motionless objects is more generalized. Courting fish will spawn on a variety of red surfaces. Parent fish will adopt eggs of many other cichlids. Learning may, however, make this response to motionless objects very specific. Parent jewel fish learn the details of their territories and the color pattern of their anaesthetized young. The experiments with the colored disks showed that learning may begin much earlier in the life of fish than previous investigators, such as Goldsmith (1914), have assumed. Further learning is indispensable to some phases of social behavior: as, for example, the recognition of mates. Nevertheless, the basic social responses, namely, species recognition, sex recognition and the formation of nuptial bonds, are dependent on particular movements. In fish such as *Lebistes reticulatus*, which show a marked sex dimorphism, learning may play an important rôle in sex recognition (Noble and Curtis, 1935). In the jewel fish, however, where the sexes are nearly alike, sex recognition is accomplished by an identification of differences in movement. It is remarkable that these differences are so slight that they cannot be seen with the unaided eye.

The courtship of the jewel fish resembles that of many birds in that the male secures territory and courts the female when she arrives with movements "symbolic" of nest building. In many birds as in the jewel fish there are mutual ceremonies which serve to establish a bond between the mated pair. A fundamental difference between fish and birds is that sex recognition is more difficult in the latter and not dependent on slight movement not visible to the unaided eye. In fact a male bird (heron) which is forced into another male's territory and assumes there a subservient attitude may be treated as a female (Noble, Wurm and Schmidt, 1938). This is essentially the same behavior as that found in such sexually dimorphic fish as *Eupomotis gibbosus*. There the male guarding a territory will court a non-aggressive male introduced into his territory (Noble, 1934). Hence, it is highly probable that in some fish, as in birds in general, sex recognition depends on the grosser movements of response to the gesturing of the territory-guarding male. In these fish and birds sexual ripeness, however, in a female is indicated by her willingness to enter a territory-guarding male's area and to remain there in spite of threats of intimidation. The display, therefore, serves primarily to reveal sexual ripeness in both fish and birds.

Much has been written on the functional significance of the display in vertebrate animals. A critical review of the literature dealing with fish has appeared elsewhere (Noble, 1938). Many authors, such as Von Bechterev (1911), find theoretical reasons why the display can be neither an attraction nor a repellent. Unfortunately no one has previously presented sufficient data to settle the question for any one species of fish. We have had the opportunity of observing only one cichlid in the field. This species, *Cichlasoma tetracanthus*, inhabits streams which are sufficiently opaque to obscure objects more than a few feet distant. Under these circumstances the nuptial colors of a territory-guarding fish would obviously have a selective value.

The nuptial colors, however, would render all movement more conspicuous. Territory-guarding cichlids, as stated above, are continuously keeping other fish at a distance by charging them. We have frequently observed that two members of a mated pair are more successful in keeping other fish away from their territories than are single fish. Most fish when charged flee and only rarely does a territory holder inflict a bite on these trespassers. Hence, the gestures and dashes of intimidation have a real function in both a fish's retaining its territory and in rearing its eggs and young.

Most Cichlidae develop conspicuous colors in both sexes during the breeding season. In these species the courtship is very similar to that of the jewel fish and both sexes take care of the eggs and young. In those cichlids where the female after a courtship essentially like that of the jewel fish takes full charge of the eggs and drives the male away she alone retains brilliant nuptial colors after egg laying. Such a procedure is characteristic of the genera *Apistogramma*, *Heterogramma* and *Nannacara* and lends support to the view expressed above that the colors serve to emphasize the threat of an egg-guarding fish. In most species of these three genera which have found their way into the aquarium trade the females are much smaller than the males and yet the vigor of their defense is so great that the males soon flee after fertilization (Dörschel, 1934; Stoye, 1935; Ludwig, 1935; Waldmann, 1936).

Conversely, those cichlids which have no occasion to defend either eggs or young in the manner of the jewel fish fail to develop conspicuous nuptial colors in the female. This group includes the "mouth-breeders," *Haplochromis*, *Tilapia* and some *Pelmatochromis*. In some species the female carries the eggs and young in the mouth, in others the male has this habit, and yet it is always the male that develops the chief if not the only conspicuous nuptial colors. Since their courtship resembles that of the jewel fish closely we may assume that these adornments have the same function as in that species, namely, making the male's movements more conspicuous.

One might expect that in those species

where the female has no guard duty, sexual selection would have ample opportunity of bringing about an extreme sexual dimorphism. Nevertheless, in some forms, such as in *Tilapia macrocephala*, the most conspicuous change is restricted to the gill covers. This species under laboratory conditions shows a much greater tendency to school than does the jewel fish. Hence it is possible that there are other factors, such as proximity of females, which have a regulatory influence on the degree of sexual dimorphism attainable in any one group.

The mouth-brooding habit evolved within the Cichlidae and several intermediate steps are found within the genus *Geophagus*. *G. jurupari* approaches the mouth-breeders closely in habit and yet exhibits very little heightening of color during the breeding season. This may be correlated with the gentle disposition of the species as described by Härtel (1936). In the gentle Scalare (*Pterophyllum*), an egg-brooding species, there appears to be less rivalry than in the jewel fish, for two females may deposit spawn together (Armbruster, 1934) and in this species the color change of the breeding season is restricted to a darkening of the vertical striping. In brief, there are many factors to consider in accounting for the degree of sexual adornment in the Cichlidae. Wherever movement has social significance the rendering of these movements conspicuous by nuptial colors would presumably lend advantage to the owner.

CONCLUSIONS

Young cichlid fishes are attracted by moving objects from the time they become free swimming until approximately 24 days old. Young *Hemichromis bimaculatus* hatch with a greater interest in moving red disks than in black, blue, green or yellow ones. Young *Cichlasoma bimaculatum* and *C. cutteri* of the same age are attracted more by black than by red disks. This inherited preference may be modified by training but it is never completely lost. The degree of attraction varies with the size of the object. Parent cichlids make abrupt movements of the fins which serve to attract their young. Adults of species which are attracted more by red early in life develop red breeding colors, those which are attracted more by black develop black or very dark tones. Young fish reared by foster parents of little attractive color lose their ability to respond quickly to disks of the attractive color. Since young reared in isolation are also slow to respond, the association with the parents tends to strengthen an inherited tendency to swim toward moving disks of a particular color.

The schooling of older cichlids is primarily a visual response to specific movements. Fish reared alone or with other species school with their own kind upon first encounter. Strange surroundings and a variety of external irritations will induce schooling.

Sex recognition is accomplished by the identification of particular movements in the partners. Gravid *H. bimaculatus* can distinguish the sex of other fish of this species when they are in separate aquaria. Slowing down the movements of fish by blindfolding them prevents the identification of their sex. A mated fish may, however, identify its partner under these circumstances provided there is some motion.

Sexual selection has been demonstrated in *H. bimaculatus* by inducing the female to select between males with pigment cells artificially expanded with yohimbine and others with these cells contracted with adrenalin. The female has also been found to show greater preference for males stained with neutral red than for unstained ones. But a pale, active male is preferred to a red, sluggish one. The nuptial colors serve to render both the sex identifying and the sex stimulating movements of the male more conspicuous to the female. Nuptial colors *per se* are not attractive to the female, although the greater interest of *H. bimaculatus* in red is expressed in its selection of red nesting sites.

Cichlids of either sex may claim territory but in *H. bimaculatus* the male usually secures it first. *H. bimaculatus* possesses a native tendency to select red objects for a nesting site. Fish with no previous spawning experience, if forced to spawn twice on black objects, will show a change of behavior on the next spawning, the female selecting a black, and the male, a red object. The nesting site is identified either in or out of the territory by details of size, form or pattern. A female reveals her gravidity by entering a male's territory and failing to flee before his display. A female trained to select a black nesting site will follow the male to a red one when egg laying is imminent. A territory-holding fish is dominant to those without territory but until nuptial bonds have been formed between members of a pair the male usually attacks only males, and the female only females. After the bonds are formed each fish recognizes its mate by details of its color pattern, especially those on the head, and then the driving of other fish occurs regardless of sex.

Nuptial colors make intimidatory gestures conspicuous and hence are of value in guarding territory or young. A single pair of territory-guarding *H. bimaculatus* in tanks up to 50 gallon capacity may prevent other fish of this species from breeding. Since older males breed more frequently than females a surplus of males may be present. It is of advantage for the female to select a well-colored male because his intimidation display will insure greater protection to the young. It is of advantage for the female to be well colored for the same reason and also because her courtship movements are indispensable to the formation of nuptial bonds.

Cichlids are unable to distinguish their own eggs from those of other species. They are attracted to eggs even when scraped off the nesting site and offered in glass dishes in a new territory. Experienced cichlids, on the other hand, readily distinguish young of their own species from those of other species even when the young are rendered motionless. When the young are stained with various dyes they are treated as foreign species. Cichlids which have had no previous brooding experience will adopt and rear young of other species. The features of the young are learned in 2 days or less. Parent *H. bimaculatus* with previous brooding experience will brood with their own species other young of their own species provided there is a difference of not more than 2 days between the ages of their own and the introduced young.

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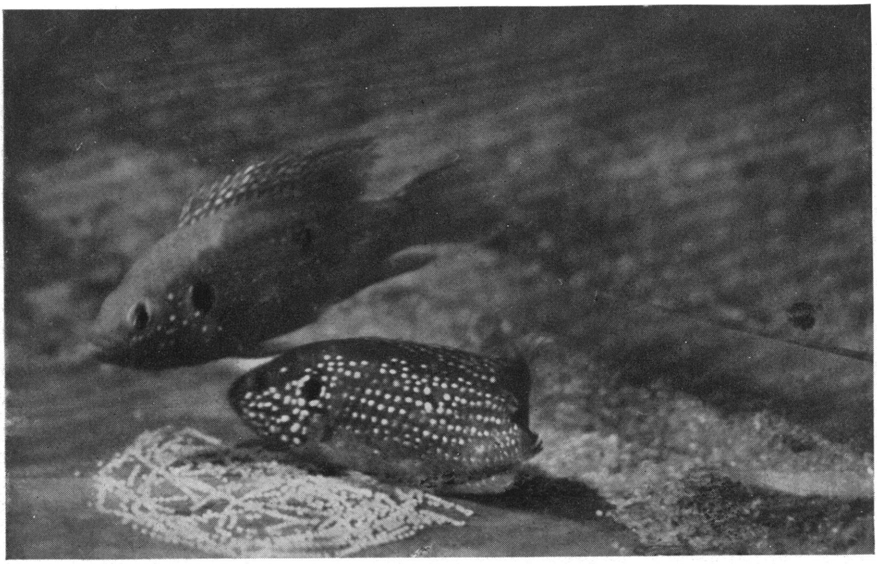

Fig. 1. Spawning jewel fish. The male is fertilizing the eggs while the female is swimming forward to lay an additional row of eggs.

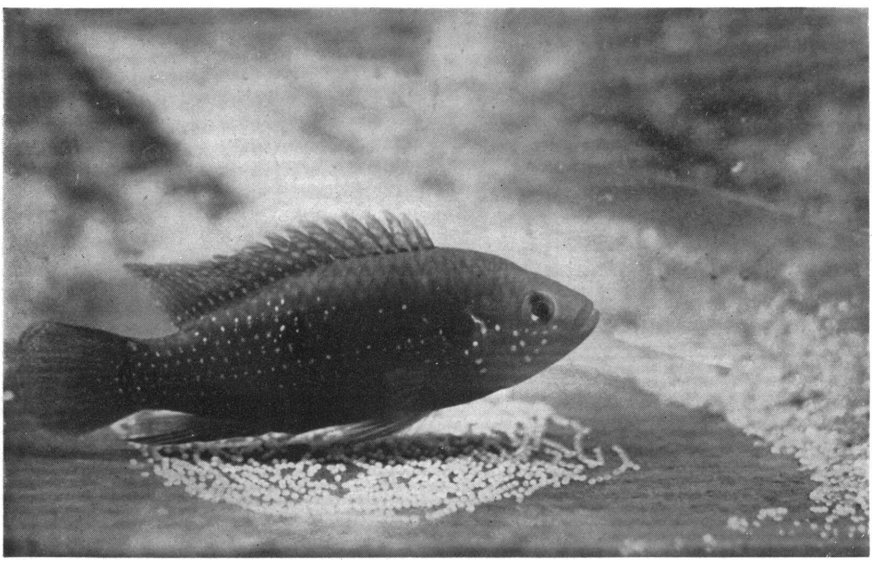

Fig. 2. Female jewel fish brooding. Both parents cleaned the sand from an area in one corner of the tank before the eggs were laid.