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DIURNAL ACTIVITY RHYTHMS IN FRESH-WATER FISHES

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INTRODUCTION

Rhythmic phenomena involving the orderly recurrence of events are characteristic of inanimate nature. Many of the activities of plants and animals are also marked by physiological rhythms. Their tempo may be extremely rapid as in volleys of nerve impulses passing along a nerve fiber, the heart-beat, or ciliary activity. In such cases the rhythm seems to be determined by a discharge-recovery mechanism associated with the physico-chemical nature of the process. Other activity rhythms have a longer cycle, sometimes of days or even months duration. The physiological rhythm may coincide in time with a rhythmic phenomenon in the physical environment in such a way as to leave little doubt that there is a relationship between the two. Among the commonest of these are activities of plants and animals correlated with the 24-hour cycle and known as diurnal rhythms.

The diurnal-nocturnal fluctuation in light intensity and temperature would be expected to affect certain physiological processes directly and others indirectly. But in some cases when these factors are held constant the physiological rhythm persists over long periods of time. These are then referred to as "innate" rhythms. However, little is known as to whether such phenomena are acquired or racial characters. It is not our intention here to review the literature on diurnal rhythms. The reader is referred to a recent review of the subject by Welsh (1938).

General activity, the sum total of the gross body movements of an animal, is a rough measure of the metabolic rate and can in turn be measured over longer or shorter time intervals

by the use of appropriate apparatus. Szymanski, a pioneer in this field, (1914, 1919) has studied activity in many species of animals by the use of ingenious devices which he designates "actographs." Under conditions as nearly normal as the experimental method would allow he has shown that the activity rhythms of different organisms tend to fall into two general classes. The first class includes those forms which in a 24-hour cycle show a single sustained period of activity followed by one of absolute or relative rest. Such a cycle he designates as "monophasic." In a second type more than one period of activity alternate with a corresponding number of rest periods in a 24-hour cycle. From a consideration of the data Szymanski concludes that the monophasic organisms have their behavior pattern largely influenced by visual stimuli, while in "polyphasic" forms vision plays a role secondary to gustatory, olfactory, or other stimuli.

The most complete study of nocturnal-diurnal rhythm which has come to our attention is that of Johnson (1926) on the forest deer-mouse. By prolonged observations, using a quantitative recording device, he has demonstrated an innate rhythm in this animal with a period of increased activity at night. This was shown to persist even in total darkness. Other experiments have demonstrated the persistence over considerable periods of time, even under constant light and temperature, of activity rhythms of the monophasic type in various species of animals. The data in this field indicate that there is present a rather deeply established 24-hour rhythm in certain animals, but that this may sometimes be altered by external stimuli. This alteration does not, of course, answer the question as to whether the rhythm is an acquired or an inherited one.

We shall here report a series of preliminary experiments dealing with total activity over periods of from one to several days duration in ten species of fresh-water fish. In all 32 specimens were used and quantitative records totaling 267 days and 8 hours were secured.

APPARATUS AND METHODS

Some years ago in the course of studies on the lateral line nerve of the goldfish in the laboratory of animal behavior at the Ohio State University it became apparent that a method of securing quantitative data on total activity would be of

advantage. The apparatus shown in Figure 1 and described under the name of "ichthyometer" (Spencer, 1929) was designed to meet this need. It consists of an extremely light lever, with an adjustable counter-weight on the short recording arm. To the end of the long arm a thread is attached which runs through a rigid screw-eye, fixed about half an inch above the water at one end of the experimental tank. This thread is attached to the dorsum of the fish near the tail by a loop of thread or light aluminum wire. The counter-weight is so adjusted that the short arm is slightly heavier than the long arm, but a pull of approximately one gram will move the lever

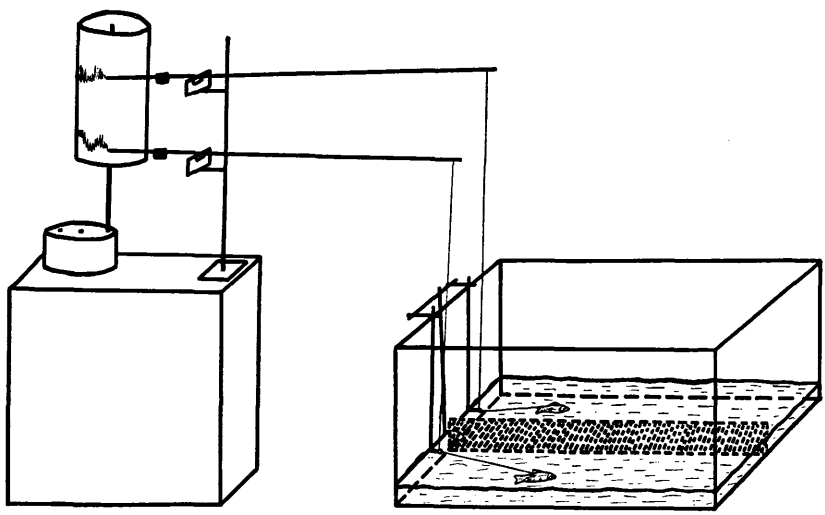


FIGURE 1

as the fish swims away from the end of the tank. Slack in the thread is quickly taken up as the fish swims toward the apparatus. The recording arm writes the record on a slow-kymograph. Time intervals of one hour were marked on the records taken. This was done in the early experiments by marking off the total time interval into parts of one hour when the record was removed, on the assumption that the drum revolved at constant speed. In later experiments an automatic timing device marking one hour intervals was used.

This apparatus not only records the total activity, but also the activity pattern, for in a long tank such as used the graphic record indicates the position of the fish in the tank at all times.

With fishes three inches or more in length direct observation shows that the fish swim about normally, feed and react to stimuli as do other fish in the aquarium. The "actograph" for fish devised by Szymanski consisted of a pulley-wheel suspended from a spring lever. Over the pulley-wheel ran a thread with a fish attached at one end and a weight at the other. This device gave only a rough measure of activity through the agitation of the lever caused by the thread running over the pulley-wheel, and did not record the activity pattern.

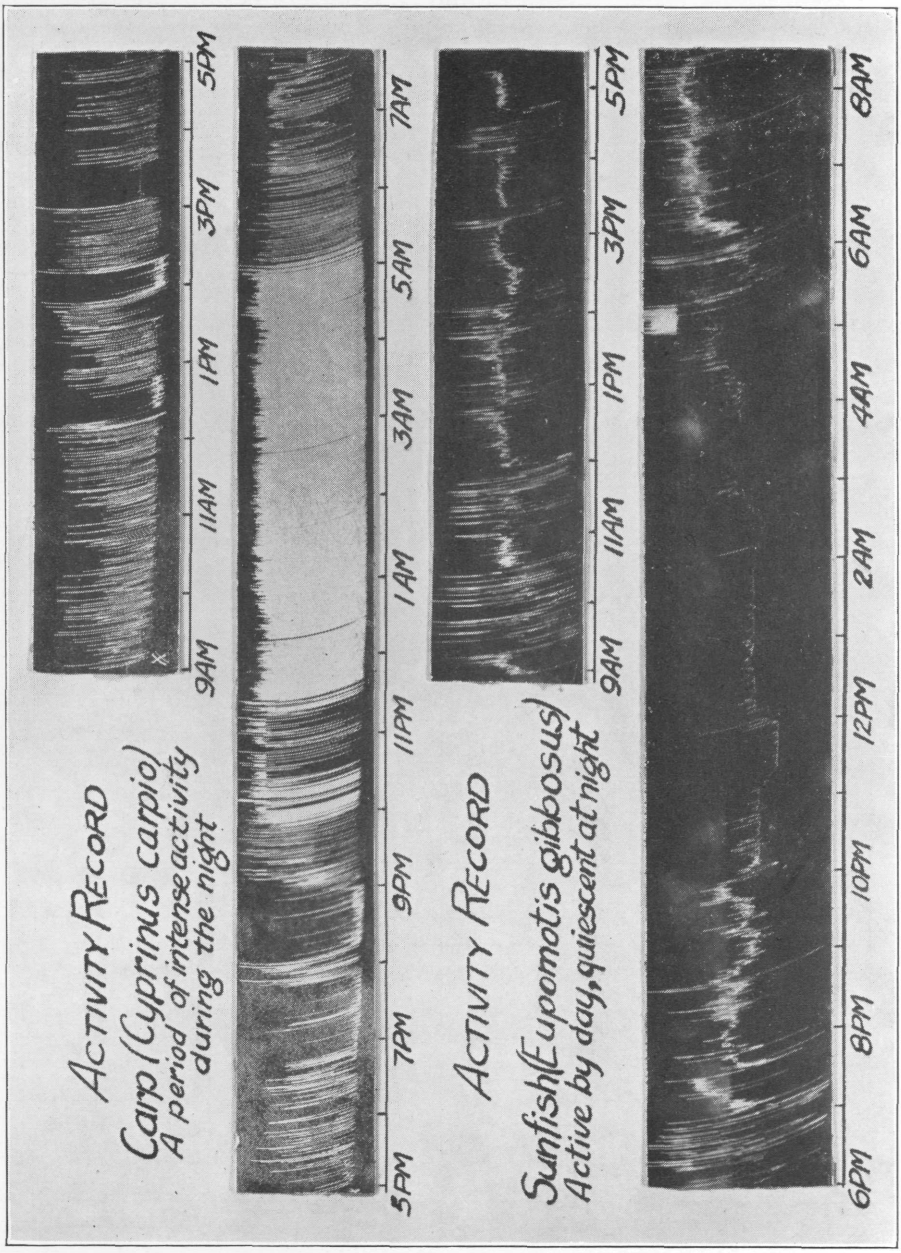
Polimanti (1911) made extensive observations on many of the marine fishes at the Zoological Station at Naples. His method, that of direct observation, is valuable in contributing to the knowledge of the habits and reactions of fish. Obviously it is not entirely satisfactory, particularly at night, where the use of light might conceivably disturb the normal behavior pattern.

Our data with experimental procedure involved can best be presented separately for each species or group of species studied: the Centrarchidae, the carp, the mud-minnow, the goldfish, and a few other fishes.

THE CENTRARCHIDAE

All records on the Centrarchidae were secured at the Stone Laboratory of the Ohio State University, Put-in-Bay, Ohio, during the summers of 1929 and 1932. The apparatus was set up in a dark basement room, with a little light filtering in during the day and temperature of about 21° C. The aquarium used was approximately 24 inches long, and divided by an opaque partition down the center into two tanks each about 7 inches wide. Water pumped from the lake circulated slowly through the tanks. The fish were fed on earthworms, crustacea and small fish and readily took food while attached to the apparatus.

Records were taken simultaneously on a rock-bass, *Amblo-plitus rupestris*, and a sunfish, *Eupomotis gibbosus*, from 6:00 P. M. July 20th to 8:30 A. M. July 23rd. A sample record of the sunfish is shown in Plate I. Throughout the experiment the sunfish was active by day. At night from about 8:00 or 9:00 P. M. until about 5:00 A. M. there ensued a period of almost total quiescence. The records of the rock-bass showed no such periodic fluctuation. This fish swam more than the sunfish at night and less by day. These data are of particular


ACTIVITY RECORD
Carp (Cyprinus carpio)
A period of intense activity during the night
9AM
11AM
1PM
3PM
5PM
5PM
7PM
9PM
11PM
1AM
3AM
5AM
7AM
ACTIVITY RECORD
Sunfish (Eupomotis gibbosus)
Active by day, quiescent at night
9AM
11AM
1PM
3PM
5PM
6PM
8PM
10PM
12PM
2AM
4AM
6AM
8AM

interest in connection with what is known of the feeding habits of the two. Rock-bass may be caught at almost any hour of day or night, while it is not the usual thing to catch sunfish at night.

Two blue gills, *Lepomis pallidus*, approximately 6 inches long, were studied in July, 1932. Continuous records of two days duration were taken for each. These showed that both specimens swam day and night with no apparent diurnal variation, and that they were somewhat more active than the rock-bass.

Records on two large-mouth black bass, *Micropterus salmoides*, taken in July, one for a little over a day and the other for two days, showed continuous swimming with a period of lessened activity rather poorly defined between 1:00 and 5:00 A. M. The fish used were a little over 6 inches long.

Of the Centrarchids studied it may be concluded that the sunfish showed a very clearly defined 24-hour rhythm, the black bass a poorly defined one, rock-bass and blue-gills none. The sunfish was least active, the rock-bass intermediate, and blue-gills and black bass most active. The data are too fragmentary to be of much value in determining relative amounts of activity, but do give some information on the pattern for the different species.

THE CARP
(*Cyprinus carpio*)

During the summer of 1929 activity records were taken at the Stone Laboratory on three young carp each about 4 inches long. These were individuals from the spring hatch. The fish were kept in a still-water aquarium in a basement room, well lighted by day and with some artificial light entering at night until 10:00 P. M. from lights outside the laboratory. The tank was approximately 24 inches by 7 inches with water 4 inches deep. The temperature remained close to 21° C. with little fluctuation from day to night. The experiments on these fish covered a total period of 7 days and 13 hours during the latter part of July and early August. All records showed a period of intense activity during the night followed by lessened activity in the day. The carp at this age are very active night swimmers with a clearly defined monophasic pattern. A sample activity graph appears in Plate I. Table I gives the approximate times of the beginning and end of each period of hyperactivity.

Two larger carp, each 9½ inches long, were secured in the summer of 1932 and records taken on them over a period of about 4 days. These fish were a year older than the first ones used. In carp No. 4, the larger of the two specimens (greatest depth 3 inches) the record, continued over 43.4 hours, showed a total lack of the diurnal rhythm so apparent in younger specimens. Carp No. 5 (greatest depth 2¾ inches) showed a tendency to swim more by night than by day, but the cycle was not as well defined as in the younger fish. These records were taken in the latter part of July. The records indicate clearly a change in activity pattern with age in the carp. The

TABLE I

NOCTURNAL DRIVE IN YOUNG CARP

Fish No.	Begins	Ends	Duration in Hours
1	10:30 P. M. July 28	4:45 A. M. July 29	6.25
1	10:00 P. M. July 29	5:15 A. M. July 30	7.25
1	11:30 P. M. July 30	4:50 A. M. July 31	5.33
1	10:15 P. M. Aug. 1	4:15 A. M. Aug. 2	6.00
2	10:00 P. M. Aug. 10	4:45 A. M. Aug. 11	6.45
3	8:30 P. M. Aug. 11	8:30 A. M. Aug. 12	12.00
3	7:30 P. M. Aug. 12	6:20 A. M. Aug. 13	10.83
3	5:30 P. M. Aug. 13	6:30 A. M. Aug. 14	13.00

carp, often thought of as lazy and sluggish, when measured in terms of total movements over a long period, is among the most active of the fishes studied. This seems correlated with its foraging and omnivorous habits. Conceivably the shift in activity pattern may have to do with an adaptive mechanism in relation to predators.

THE MUD MINNOW

(Umbra limi)

Records on five adult mud minnows, 4 to 5 inches long, taken the last of July and first of August, 1929, at the Stone Laboratory, covered a period of 12 days, 2½ hours. The aquarium and other experimental conditions were the same as those used for the young carp. All of these fish were extremely sluggish during the day, lying by the hour without swimming the length of the aquarium. At night, however, a period of activity ensued which, while not intense, was well delimited from the rest of the day.

During the months of October and December ichthyograms were taken of mud minnows which had been carried from Put-in-Bay to the laboratory of Biology at Wooster. The experimental tanks were approximately 24 by 7 inches, of stone and with a sand bottom, in a basement room with temperature ranging from 17° C. to 24° C. Activity of three fishes covering 12 days and 20 hours was recorded. It was rather surprising that the fish were much more active than during the summer. Furthermore the pattern had entirely changed. There was no period of increased activity at night. If anything, the fish were more active by day.

During the course of a six-day experiment on mud minnow No. 6 a cover was placed on the experimental tank in such a way that the end of the tank farthest from the apparatus was darkened as contrasted to the other end. The graphs show clearly the gradual development of an activity pattern in response to this situation. On the first three days the fish was to be found about as frequently during the day hours in one part of the aquarium as in another. On the fourth day during the morning a rather marked "preference" for the dark end of the tank developed. Still there were frequent trips to the lighter end. During the afternoon the fish went only twice to the lighter end. But at 6:00 P. M. it started swimming the length of the aquarium and made many such excursions during the night. The next morning the fish remained at the dark end of the tank. The cover of the tank was carefully removed at 11:15 A. M. and replaced at 12:30 P. M. During this interval the fish swam the length of the tank 24 times. At 2:30 P. M. the cover was again removed and replaced at 3:45 P. M. In this interval there were 26 excursions the length of the tank. At 5:30 P. M. the fish again started swimming the length of the aquarium and continued intermittently until 7:30 A. M. Experiments on this day with removal of the tank cover were followed by similar results. Again at 5:30 P. M., about dusk, excursions the length of the tank began.

It is quite clear that the position of the fish in the aquarium was regulated by response to light stimuli. In fact one could determine quite well from these records the hours of dusk and dawn. The response of the fish when the cover was removed was in no case immediate, but occurred about two minutes after the change in light took place. During the course of experiments on mud minnows records were taken on three

specimens over periods sufficiently long to indicate that there is a change in total activity from day to day with the suggestion of a cycle of several days duration.

THE GOLDFISH
(*Carassius auratus*)

In the winter of 1932 activity records were secured for 5 goldfish varying in length from 4 to 6 inches. The experimental tanks in the Wooster laboratory were similar to those used for the mud minnow, but were not covered. Temperatures ranged from 17½° C. to 21° C. Water flowed slowly through the tanks during the experiments. The fish were fed once a day on dried entomostraca.

Between January 10th and February 17th a total of 39 days of activity records were taken of these 5 fish. Approximately 10 days' records were taken under continuous light, a 75-watt light bulb suspended 3 feet above the center of the experimental tank. The remainder of the records were taken under the natural light which entered the basement room.

Under natural light conditions the goldfish were, in general, more active during the day, and particularly during the hours from 1:00 A. M. to 6:30 A. M. there was a tendency to slow down. These findings are in accord with those of Szymanski (1914) for the goldfish. Continuous light of the intensity used served to reduce the total activity, and at the same time to distribute it more evenly over the 24 hours. However, the diurnal rhythm was not entirely eliminated after several days exposure to continuous light.

All of the ichthyograms on fishes No. 4 and 5 were taken under natural light conditions and they indicate that activity rises slowly to a peak over a period of several days' duration and then drops off rather suddenly to rise again. This rhythm in No. 4 consisted of a cycle approximately 6 days long and in No. 5 of a cycle 2 to 3 days long. It is clear from our records that activity in individuals cannot be properly compared and contrasted by taking records for one or two days only. Some of the records on Nos. 4 and 5 were taken simultaneously in parallel compartments under identical conditions and for a certain day one fish was more active and for another day the other was the more active. These long cycles of activity in fish are of particular interest in comparison with the findings of Richter (1927) on such cycles in rats.

Our experiments showed individuals differing from one another in total activity over periods covering the entire cycle, so that one goldfish might be described as sluggish and another as hyperactive. More striking than the variation in total activity was the tendency for certain individuals to develop an individual activity pattern. Three of the goldfish, Nos. 1, 3, and 5, swam during the night hours mostly at the end of the tank farthest from the recording apparatus. During the day their preference if any was for the other end of the tank. Fishes 2 and 4 showed no tendency to develop this particular activity pattern. The pattern referred to could be broken up

TABLE II

ACTIVITY CYCLES IN THE GOLDFISH

Fish No.	Dates of Minimum Act.	Dates of Maximum Act.	Duration of Cycle in Days
1	Dec. 10	Dec. 14	4
1	Dec. 14	Dec. 19	5
2	Jan. 16	Jan. 21	5
2	Jan. 21	Jan. 26	5
2	Jan. 26	Jan. 31	5
2	Jan. 31	Feb. 6	6
2	Feb. 6	Feb. 11	5
2	Feb. 11	Feb. 16	5
2	Feb. 16	Feb. 22	6
2	Feb. 22	Feb. 28	6
2	Feb. 28	Mar. 6	7
2	Mar. 6	Mar. 10	4
2	Mar. 10	Mar. 16	6
3	Mar. 16	Mar. 20	4
3	Mar. 20	Mar. 25	5
3	Mar. 25	Mar. 29	4
3	Mar. 29	April 2	4

immediately by the use of continuous light. However, it is not understood why at dusk the far end of the tank was sought and occupied until dawn or a little after.

From December 11th, 1935, to March 23rd, 1936, Mr. William Kieffer and the author secured an extensive series of graphs of the activity of 7 goldfish totaling 4,326 hours recorded. These experiments were run in the same tank as those described above with the temperature at about 20° C. and seldom fluctuating more than two degrees from this. These fish were fed regularly once a day about .1 gram of imported oriental fish food. All grew during the course of the experiment and

there was no mortality except one accidental death due to a fish jumping out of the aquarium. This series of experiments corroborated the findings recorded above on individual variability in total activity and pattern of activity. All showed long cycles of activity lasting from 4 to 7 days. Some of the data on this point are given in Table II. Four of the seven fish showed a marked tendency to turn much more frequently to the right than to the left. Most of the fish generally came to rest with the tail under the eyelet of the recording apparatus. One rested with the head under the eyelet.

The data secured by Kieffer show a very definite relationship of activity to feeding. When the fish are well and regularly fed there is an intense activity period lasting from one to three hours after the food is placed in the tank. The fish actually consume the food in 15 minutes or less and the intense activity far exceeds this time. By covering the tank by day and lighting artificially at night and feeding at night the regular diurnal rhythm could be obliterated.

RECORDS ON OTHER SPECIES

Fragmentary records of a day or so were taken on the yellow perch, *Perca flavescens*, showing long periods of 15 minutes to an hour in which the fish remained motionless, interspersed with short excursions seldom more than the length of the tank and back, and often shorter. The record, totally different from that of carp, goldfish or the Centrarchidae, is probably typical of a darter, lying quietly on the bottom of stream or lake for a long time.

Records of the bull-head, *Ameiurus melas*, and the channel-cat, *Ictalurus* sp., also fragmentary, showed the former to be somewhat more active than the latter. Neither showed much difference between day and night swimming, certainly no clearly defined rhythm as in sunfish and young carp.

SUMMARY AND CONCLUSIONS

The author presents these data as a preliminary study of behavior patterns in fresh-water fishes. He is fully aware that the experiments are not complete, and that many factors could be more carefully controlled and studied. However, the data here presented indicate some of the problems which might further be investigated and the possibilities of the ichthyometer as a tool for their study.

Obviously it is impossible to have published all of the graphic records secured, which total over 200 yards of material and represent more than 100 swimming miles. It seems unwise even to include adequate samples of all the points covered. Rather we have chosen to publish one plate to illustrate the nature of these ichthyograms.

The findings reported here may be summarized as follows:

1. By the use of the ichthyometer it is possible to take continuous quantitative records of the total activity of various species of fish over long periods of time and under a variety of conditions planned by the investigator.

2. Fish show either a fairly continuous pattern of activity over a 24-hour period or a monophasic one conditioned apparently by reaction to light. There is no indication of any well defined short-period rhythm such as reported for rats and birds.

3. Certain fish are active by day and quiet at night; other species show the reverse pattern.

4. There appear to be marked seasonal and age differences in the activity pattern of certain species.

5. Individuals of a species show marked variations both in the intensity of their activity and in its pattern, so that it may be stated that the individual pattern is superimposed on the racial one.

6. Long cycles of some days duration leading gradually to a peak of activity followed by a sudden drop to a minimum and subsequent rise have been shown to occur in goldfish and seem to be present in the mud minnow. Records of other species studied do not cover periods long enough to furnish data on this point.

7. Light intensity and time of feeding definitely affect activity. The response to both of these stimuli outlasts by an appreciable length of time the application of the stimulus. In the mud minnow it has been shown that the application of certain light stimuli is followed by a latent period of a minute or more before the swimming reaction occurs.

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