

Some factors influencing short-term food intake of the goldfish¹

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ROZIN, PAUL N., AND JEAN MAYER. *Some factors influencing short-term food intake of the goldfish*. Am. J. Physiol. 206(6): 1430-1436. 1964.—Goldfish press a lever in order to receive a food pellet during 1-hr sessions at the same time each day. They eat much less in 1 hr than when allowed to press the lever for a full day. The day-to-day 1-hr intake is stable. The intake in 1 hr is about the same when the fish have been deprived from 4 to 47 hr. This constancy cannot be accounted for by assuming a steady state in the gut. Four hours postfeeding virtually all undigested food from the previous feeding session remains in the gut; by 47 hr most or all has been excreted.

regulation of food intake fish behavioral techniques
intestinal peristalsis in fish operant conditioning feeding
behavior

PREVIOUS RESEARCH HAS INDICATED that the food intake of the goldfish is regulated (4). Evidence was presented indicating that when goldfish are permitted to feed continuously, the physiological need for nutrient is an important determinant of the amount of food ingested. In particular, it was shown that goldfish increase their food intake significantly in response to dilution of the normal diet and thus seem to eat for calories rather than for bulk. Goldfish, respectively, increase and decrease their intake as ambient temperatures (and hence, intensity of metabolic processes) increase or decrease. The present study was designed to further analyze the characteristics of the regulation of food intake in the goldfish, using short, restricted feeding periods instead of the continuous feeding previously employed. The short (1 hr/day) feeding period also eliminates some of the difficulties encountered with continuous feeding situations. When goldfish are given a pellet each time they press a lever, and the lever is made continuously avail-

able, many (but not all) fish press the lever and do not always consume the pellet delivered. In this manner, a significant number of pellets often accumulate on the aquarium bottom and the water becomes fouled. This tendency can be discouraged, but not eliminated, by requiring the fish to press a number of times to receive each pellet. If the lever is made available for 1 hr each day, this problem rarely arises. Furthermore, with the 1-hr scheduling, it is possible to obtain data from a much larger number of animals with the same amount of equipment.

This present report describes some of the characteristics of food intake in 1-hr feeding sessions, and attempts a preliminary analysis of the factors involved in determining the feeding behavior. It is possible that some factors which might be of little importance in controlling continuous feeding, such as bulk of food ingested, may be critical in a more restricted feeding situation.

GENERAL METHODS

Comet or common goldfish, *Carassius auratus*, served as subjects in these experiments. Both males and females weighing from 15 to 100 g were used.

The apparatus employed is similar to that described in a previous article (4). A Gerbrands pellet dispenser, fish lever (3), and two 6-w bulbs are mounted on a board, forming an experimental unit (Fig. 1). The experimental unit is designed to fit on top of a 5½-gal aquarium. In order to prevent operation of the lever by random movements of the fish, the lever shaft and target are surrounded by a square plastic tube; the tube is cut away on one side so that only the front of the lever target is exposed (Fig. 1). Three experimental units were employed.

Pellets delivered from the dispenser often floated on the water surface. A plastic feeding ring located in each aquarium below the chute from the dispenser assured that floating pellets did not leave the general area below the chute. The fish were kept individually in 5½-gal aquaria, arranged on a rack. Black paper placed between the aquaria prevented the fish from seeing into the neighboring tanks. Demineralized water was used in all

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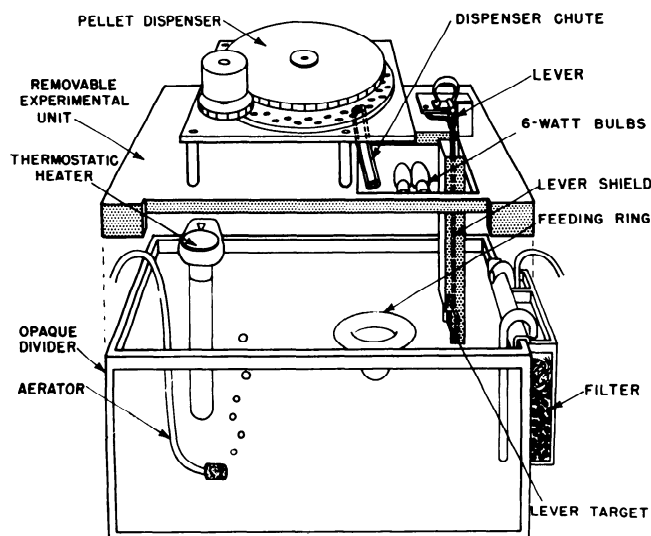


FIG. 1. Diagram of the experimental apparatus.

the tanks and the water was continuously aerated and filtered. Temperature in the aquaria was maintained at 24–25 C by individual thermostatic heaters. The experimental room was continuously illuminated. Fish were removed from their aquaria only for occasional weighings or the complete cleaning of their tanks. The experimental units were moved from one tank to another.

The pellets used in most of the experiments were the standard rat lab food pellets (weight approx. 20 mg) (manufactured by the P. J. Noyes Co., Lancaster, N. H.) All pellets used in these experiments were coated with a thin layer of collodion. The coating solution consisted of 50% flexible collodion, 25% ether, and 25% ethanol. The Noyes pellets were dipped into such a solution a few hundred at a time for about 2 sec. After removal from the solution the pellets were rolled down an inclined plane covered with paper towels, to facilitate drying. The pellets were left exposed to air for at least 2 days before use, to insure complete evaporation of the solvent. The coated pellets are accepted by the fish in the same amounts as uncoated pellets after the fish have been allowed a few days to get accustomed to them. The coated pellets dissolve in water less readily than the standard Noyes pellets, so that it is almost always possible to collect and accurately count the number of uneaten pellets, if any, at the end of a 1-hr feeding session.

Ordinarily the pellets were available on a "continuous reinforcement" schedule. Each time the fish pressed the lever, one pellet was discharged into the water. For 3 sec after each lever press, the lever was inoperative, and two 6-w bulbs near the feeder were operated. Fish were trained initially to approach the feeding ring in order to obtain a food pellet when the lights and dispenser were operated. About half of the fish subsequently learned to press the lever for a food pellet when the lever was made available over a period of about 12 hr. Pellets were glued on the lever target for 1 day for the fish that did not learn quickly.

During subsequent experiments the experimental unit was placed on the aquarium for 1 hr. At the end of the hour the number of pellets eaten was recorded. On a few occasions uneaten pellets appeared on the bottom of the aquaria after a session. These were removed and the record of the number of pellets eaten was adjusted accordingly. Maintenance adjustments for the aquaria, such as adding water and cleaning, were performed daily and never within 1 hr before a feeding session.

A different apparatus and procedure was employed in *experiment 1*. The apparatus was identical to that described in a previous communication (4). It consists of essentially the same elements described above, but mounted permanently in a 5½-ft³ refrigerator shell. The apparatus is designed for the study of continuous food intake in a single fish. The subject fish are kept in the 5½-gal tanks in the refrigerator for a period of months, with the lever ordinarily continuously available. An opaque plastic barrier can be slid in front of the lever to prevent the fish from seeing or pressing it. Temperature and maintenance procedure was similar to that for the 1-hr intake sessions described above. The same pellets were employed. Differences in procedure will be discussed under *Method* in *experiment 1*.

Experiment 1: 24-Hr Intake Versus 1-Hr Intake

Previous work (4) has shown that within the limits of the imposed lighting cycle, goldfish distribute their feeding responses fairly uniformly over time when food is continuously available. Restricting the availability of food to 1 hr/day might place significant limitations on the intake of the fish and might therefore serve to emphasize bulk and distension factors in limiting food intake. In a first experiment, daily consumption of food when it was available all 24 hr was compared to the daily intake when food was available only 1 hr/day.

Method. Four goldfish, each in one refrigerator unit as described above, served as subjects for this experiment. The refrigerators were continuously illuminated. After the fish had learned to press the lever, the lever was made available continuously. A single 20-mg coated pellet was delivered following every 12 lever presses (fixed ratio 12, or FR 12 schedule). The FR 12 was employed because on an FR 1 schedule (1 pellet for each lever press) with the lever continuously available, there is usually a fair number of uneaten pellets in the tank each day. The number of uneaten pellets is markedly reduced by using the FR 12 schedule. Food intake (number of pellets eaten) was recorded at the same time each day. Ten consecutive days of 24-hr food intake were followed by 18 days of 1-hr intake, followed again by 10 days of continuous (24-hr) intake. During the 18 days on 1-hr intake, the lever was exposed by removing a piece of opaque plastic mounted in front of it for 1 hr each day (11 AM to 12 noon). During the 1-hr sessions, as well as the 24-hr sessions, food was available on an FR 12 schedule.

Results. In order to compare the 24-hr and 1-hr intakes,

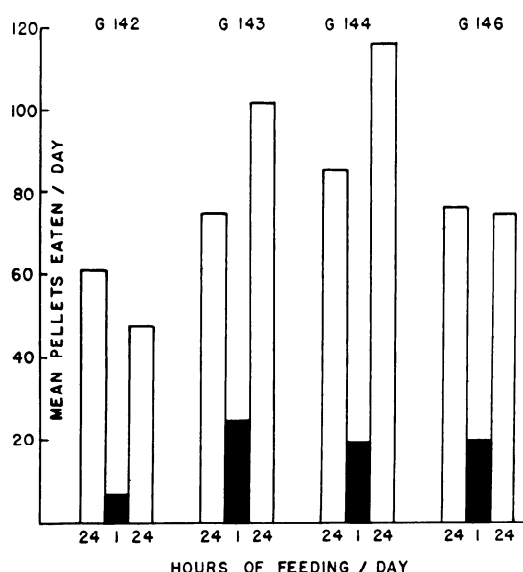


FIG. 2. Comparison of food intakes during 24-hr and 1-hr feeding sessions.

it is necessary to be sure that the fish are adapted to the 1-hr schedule. The data from the last 10 days of the 18-day period on 1 hr/day feeding were used for comparison. The first 8 days were considered an adaptation period. By the end of the first 8 days, the fish responded readily when the lever was exposed for the 1-hr sessions, and hourly food intake had stabilized. Mean intakes in pellets per day for each fish on 10 days of continuous feeding, 10 days of 1-hr feeding (following 8 days of adaptation) and 10 days of continuous feeding again are presented in Fig. 2. There was a significant drop in the intake of each fish when food availability was restricted to 1 hr/day. None of the fish ate more than one-third of their 24-hr intake in 1 hr. The results of fish *G 142* are misleading, in that the 1-hr intake was extremely low (less than seven pellets per day) during part of the 10-day period. This fish showed much higher variability in 1-hr intake than the others, and ate as many as 15 pellets on a number of 1-hr sessions.

Discussion. It is clear that the goldfish cannot consume a normal 24-hr food intake when duration of feeding is restricted to 1 hr. On the other hand, the fish eat much more than they would normally eat in 1 hr on a 24-hr feeding schedule. The period of anorexia experienced by *G 142* during the 1-hr feeding sessions tends to exaggerate the limitation produced by the 1-hr feeding sessions. It is also possible that the FR 12 had a slightly limiting effect on the intake in the 1-hr session (see experiment 3). One-hour intake records of fish on FR 1 from other experiments described later in this paper show a higher intake for fish of weights equivalent to the weights of the fish used in this experiment.

Experiment 2: Characteristics of Food Intake on a 23-Hr Deprivation Schedule

This experiment was designed to investigate the constancy of intake in 1 hr/day feeding sessions. Later experi-

ments, incidentally, are built upon the "base line" established in this experiment.

Method. After the fish had learned to press the lever, each fish was "run" at a specific time for 1 hr each day on a 23-hr deprivation, 1-hr feeding schedule. The fish were run in this manner for a week or more before further experiments were performed. Additional periods for the determination of base line occurred in between some of the experiments reported later in this paper.

Results. The 1-hr intake of the fish over a number of days was less variable than the daily intake of goldfish fed 24 hr/day (4). However, the variability was well above that normally encountered in the laboratory rat. Figure 3 shows 14 consecutive days of food intake on the 23-hr deprivation schedule for four fish. The daily intake usually varied within 10–20% of the mean over periods of about 10 days. The occasional wider departures were followed by a return to the normal intake within a few days at most (e.g., *G 133*, day 4, in Fig. 3). Occasionally, significant drifts or relatively abrupt changes in level of intake occur, as can be seen in the first 8 as opposed to the last 6 days of intakes for *G 133* (Fig. 3). In general, we observed a tendency for the intake to rise slowly over a period of weeks or months, although this is not obvious from Fig. 3. There is a positive correlation between food intake and weight of the fish. All the fish used for a month or more showed a weight increase in the course of the experiments. This may, of course, explain the slow rise in intake.

Experiment 3: Variation of Work Required to Obtain Food

It is hoped that the 1-hr intake measured truly represents the feeding motivation of the fish, and is not directly influenced to a significant extent by factors such as the

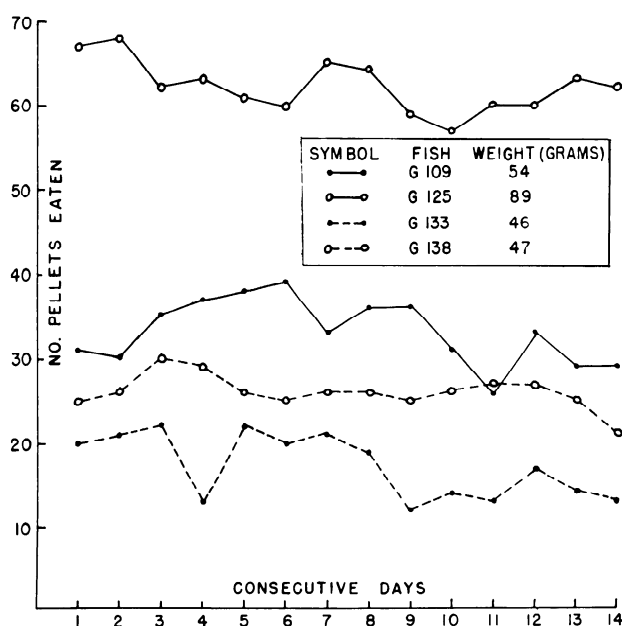


FIG. 3. Representative day-to-day food intakes on a 23-hr deprivation schedule.

general activity level or pattern of the fish. The shield around the lever makes it unlikely that random activity would significantly affect the number of lever presses, but this was further investigated by varying the number of lever presses required for each food pellet. If the lever pressing response reflects primarily feeding motivation, the number of responses should be adjusted to maintain the pellet intake approximately constant over a range of lever press-to-food pellet ratios. *Experiment 3* was designed to provide information on the characteristics and modifiability of the lever-pressing behavior employed.

Method. Seven goldfish were employed. All had some previous experience in lever pressing on continuous reinforcement (one press per pellet). The fish were run as in *experiment 2*, for 1 hr each day on a 23-hr deprivation schedule. They were run for 3 consecutive days on each ratio of presses-to-pellets, and then moved to the next highest ratios. The fixed ratios (FR) employed were FR 1, FR 3, FR 10, FR 20, FR 30, FR 50, and FR 100. Thus, the entire sequence lasted 21 days. Following the third day on FR 100, the fish were gradually brought down to FR 1 again over a 3-day period, running on FR 30 for the day following FR 100, FR 10 on the next day, and FR 1 on the third. Number of presses and number of pellets received were recorded for each 1-hr session.

Results. The data were analyzed in terms of mean pellets received in a 1-hr session for the last 2 days of the 3 days on each ratio. The data for the first day on each

ratio were not employed in plotting the curves in Fig. 4. In order to present the data from all the fish on the same graph, percentages of food intake on the FR 1 schedule (continuous reinforcement) were plotted, so that values of 100% indicate a constant food intake or perfectly compensated response output. The dashed curve in the figure represents the value of food intake at each ratio if the number of presses remained constant throughout the sessions. It is clear from Fig. 4 that fish increase the number of presses as the ratio of presses-to-pellets rises. For example, at FR 3, the median value of 92% indicates that considerable compensation in number of responses has occurred, as constancy in response rate would have yielded 33% of the total intake on continuous reinforcement. Median values were 84% for FR 10 and 79% for FR 20, all the way to 33% (in contrast to 1% predicted on the basis of constant number of responses) for FR 100. Clearly, a considerable amount of compensation occurs. Yet, it is also clear that there is a significant reduction in food intake, particularly at ratios greater than 20. The low intakes on FR 100 could be attributed to cumulative effects of chronic underfeeding, as the fish had been eating much less than normal for a number of days before the FR 100 sessions. However, when the fish were placed on FR 30 following the last day on FR 100, and on FR 10 the next day, their intake increased markedly, indicating that it was the high ratio or high amount of work per se that caused the reduced intake.

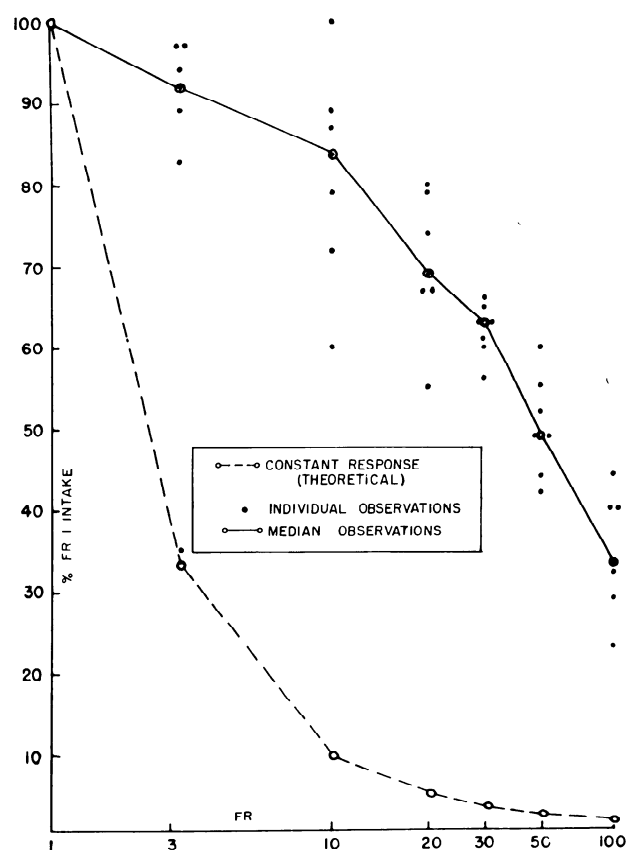


FIG. 4. Relation between number of presses required per pellet and food intake in 1-hr sessions.

Experiment 4: Effect of Food Deprivation on 1-Hr Intake

Experiment 2 showed that there is a fair constancy in the day-to-day food intake on a 23-hr food deprivation schedule. The 1-hr intake on this schedule might represent a maximum food intake for the fish. Alternatively, it is possible that the 1-hr food intake could be increased by lengthening the time between sessions. It is conceivable that the goldfish will always eat the same amount in a 1-hr session independent of the time between sessions. In order to elucidate the factors affecting 1-hr food intake, the intersession interval or deprivation time was varied in this experiment.

Method. Eight goldfish were employed in this experiment. Following training, base lines were obtained for about 10 days on the 23-hr deprivation schedule, and then the present experiment was begun. Deprivation levels of 0, 1, 2, 3, 4, 5, 6, 23, 47, and 95 hr were investigated. Deprivations were timed from the end of one session to the beginning of the next. The deprivations were presented in a mixed order to each fish, and each fish was tested two times at each level of deprivation. Each deprivation test began with a 1-hr session called the standard session, preceded by 16–23 hr of deprivation. Preliminary work indicated clearly that the same amount was eaten in 1 hr after deprivations of 16–23 hr. A certain number of hours after the completion of the standard session (e.g., 0, 1, 2, 3, 4, 5, 6, 23, 47, 95) a 1-hr deprivation session was run. A paradigm illustrating a single deprivation test and a table of the day-to-day scheduling for a few tests is presented in Table 1.

TABLE 1. *Paradigm of single deprivation test*

(16–23 hr of deprivation)
 1-hr session (standard session)
 (0, 1, 2, 3, 4, 5, 6, 23, 47, or 95 hr of deprivation)
 1-hr session (deprivation session)

Scheduling of a few deprivation tests

Day	Feeding Time	Session
1	9–10 AM	Standard
2	None	
3	9–10 AM	47 hr deprivation
4	9–10 AM	Standard
	4–5 PM	6 hr deprivation
5	9–10 AM	Standard
	10–11 AM	0 hr deprivation
6	9–10 AM	Standard

At the conclusion of the complete deprivation series, the median intake on the standard sessions for each fish was computed. Intakes on individual standard sessions for any fish that departed by more than 20% from the median for that fish were discarded, and the deprivation test associated with this value was repeated.

Results. The effects of deprivation are expressed by computing the percentage:

$$\frac{\text{intake in a single deprivation session} \times 100}{\text{intake in corresponding (preceding) standard session}}$$

Values of greater than 100% indicate that the fish ate more in the deprivation than in the standard session and, conversely, values of less than 100% indicate that less was eaten in the deprivation session. The 16 observations at each deprivation level and the median values are indicated in Fig. 5. There is a clear tendency toward increased food intake as deprivation is increased from 0 to 4 hr. There is not a large difference in intake for deprivation values of 4, 5, 6, 23, and 47 hr, and a decrease in intake relative to that in the standard session at 95 hr of deprivation. The data indicate that goldfish will eat about the same amount in 1 hr after deprivations ranging from 4 to 47 hr.

Experiment 5: Rate of Passage of Food Through Digestive System

The results of *experiment 4* indicate that food intake is the same after deprivation intervals of about 4–47 hr. A simple explanation of this result would be that the fish eats as much as its gut can hold in a 1-hr session. The “total gut capacity” explanation would have to assume a steady state in the gut contents over the period of 4–47 hr. The simplest means of accounting for this constant intake is that the digestive system is completely emptied about 4 hr after a 1-hr meal at 25°C. In light of these considerations, the rate of passage of food through the digestive system was investigated.

Method. Nine goldfish served as subjects in *experiment 5*. Seven of these had previously served as subjects in

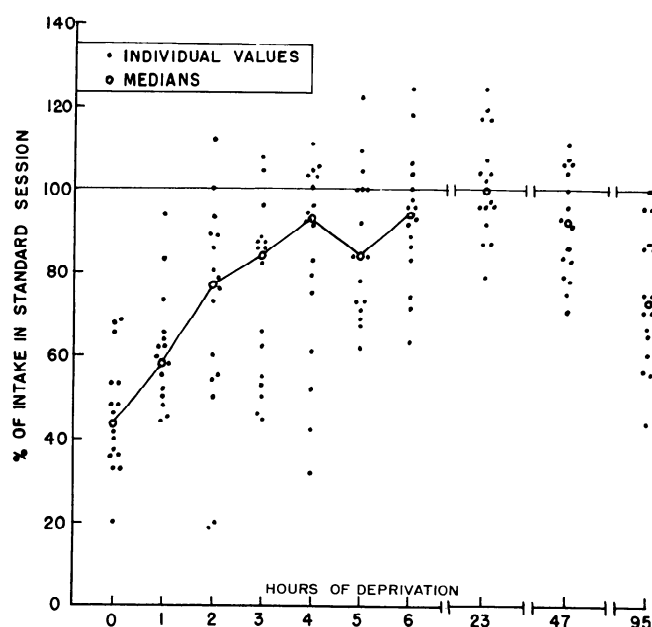


FIG. 5. Relation between food intake and hours of food deprivation.

experiment 4. Carmine pellets were employed in order to provide a visual indication of the rate of passage of food through the gut. The carmine pellets were made from the same mold as the standard laboratory chow pellets, and were coated in the same way. They consisted of 99½% laboratory chow and ½% carmine, a red dye. The fish were run on a 23-hr deprivation schedule with coated Purina pellets for the first 3 days of the experiment. On *day 4*, they received carmine pellets for each lever press instead of Purina pellets. On completion of the carmine pellet session, the tank of each fish was carefully examined for feces, and any feces found were siphoned off. The color of the feces was recorded. Observations of the color of the feces and siphoning was repeated regularly every hour after completion of the session for a total of 8 hr. A similar procedure was followed the following morning preceding the feeding session for each fish. Carmine pellets were offered twice to each fish, each time following 3 days on Purina pellets. The 3 days on Purina pellets insured that all carmine in the fish from a previous session was out of the gut.

In a second part of this experiment, the same basic procedure was followed. In order to more closely approximate the conditions of *experiment 4*, the fish were fed twice on the day carmine was offered. They were offered carmine for the 1st-hr session. Four hours later (4 hr deprivation) they were run again for 1 hr on Purina pellets. Observations on appearance of feces were made every hour for 8 hr after the initial carmine session.

Results. The number of carmine pellets consumed in 1 hr was approximately the same as the number of standard laboratory chow pellets. Typically, a number of hours after the completion of the carmine session, the usually light brown feces would appear slightly pink.

TABLE 2. *Rate of passage of food through digestive system*

23-Hr Deprivation Series, No. of Fish	Hours After Completion of Carmine Session	4-Hr Deprivation Series, No. of Fish
2	4	1
3	5	7
3	6	5
5	7	3
4	8	0
1	>8	0

Usually, within 1–2 hr of the pink feces, the feces would appear bright red. The observation of a piece of bright red feces was employed as an indication that the carmine meal previously ingested is being excreted in significant amounts. As indicated in Table 2, the median time of appearance of red feces was 7 hr after completion of the feeding session, with 4 hr the lowest value and only 1 out of the total of 18 observations above 8 hr. The great majority of the red feces was excreted following 8 hr in all cases, and some was almost always excreted following the next day's session on laboratory chow pellets. As expected, the addition of a 1-hr laboratory chow pellet session 4 hr after the carmine session seemed to speed up the passage of food, yielding a median first appearance of red feces of 5.5 hr, and no observations above 7 hr. Two observations had to be discarded because the fish consumed an abnormally small number of carmine pellets. Again, most of the red feces was excreted more than 8 hr after the carmine session. Entrance of food from the second meal into the gut seemed to stimulate excretion of contents of the first meal. In 7 of the 16 observations, red feces appeared first during the second meal.

DISCUSSION

The 1-hr food intake on a 23-hr deprivation schedule is regulated, in the sense that a more or less constant amount is eaten each day. Enough food is consumed during that daily period for the fish to show clear weight gains, but this amount is much smaller than when food is constantly available. Since the goldfish is capable of indefinite growth, it is possible that the upper limit on food intake is not of as great physiological importance as it is in the adult mammal. A lower intake, within a certain range, means a slower rate of growth but produces no permanent or crippling effects. In any event, the regularity of the 1-hr intake leads one to examine the factors that contribute to this result. The food storage capacity in the gut of the goldfish is limited due to the absence of a stomach. A reasonable hypothesis might therefore be that the 1-hr intake is less than the 24-hr intake because the volume of the gut limits total intake. Regardless of the factors limiting 24-hr intake, bulk might be critical in the shorter feeding periods. This notion receives support from the work by Brown (2) on trout fry. She found that fry fed to satiation once or twice a week became visibly distorted from ingested food at the conclusion of their feeding periods, whereas

fish fed once or twice a day never appeared distorted. Previous data on goldfish (4) have shown that bulk was not a critical factor in limiting 24-hr intake of Purina pellets. On the other hand, the fish did not appear visibly distorted after the 1-hr feeding sessions.

The deprivation experiment also provides important information which needs to be accounted for by any explanation of factors regulating food intake. The gradual increase in intake with deprivation over the first few hours of deprivation is consistent with the notion that volume of the gut is critical, as food is passing down the gut during this period. However, it is also consistent with the idea that metabolic factors control intake as longer intervals between feeding obviously increase deprivation of nutrients. The leveling of the intake curve between 4 and 47 hr is not consistent with the idea that metabolic factors critically determine intake as increased nutrient need is associated with constant intake. An interpretation based exclusively on limitations of gut capacity would have to assume that the gut was emptied by 4 hr after a meal: *experiment 5* indicated that at this time virtually all of the undigested food from the first meal remained in the gut and that the great part of this intake was passed much later. It is possible that some portion of the gut, presumably the foregut or enlargement of the anterior intestine, is the structure critically involved, and that its state of fullness critically limits the short-term intake. This could be determined by seeing if fish would compensate for bulk or calorie dilution in a 1-hr session, as well as by directly manipulating this area of the gut.

The reduction in intake after 95 hr is puzzling. It does not appear to be due to a weakening from the 3-day fast as these fish show no obvious signs of weakness and can go without food for many weeks without showing any marked signs of deterioration other than moderate weight loss. It is also unlikely that "forgetting" of the response is involved as all the fish responded readily to the lever and did consume substantial amounts of food.

The data of *experiment 4* are not in quantitative agreement with similar experiments on other teleost fish. Both Tugedhat (5) working with sticklebacks *Gasterosteus aculeatus*, and Bitterman, Wodinsky, and Candland (1), working with the African mouthbreeder, *Tilapia macrocephala*, measured food intake as a function of deprivation using short feeding sessions. Both species increased food intake as deprivation time increased, over a range of 1–3 days for the stickleback and 1–7 days for the mouthbreeder. Brown's work (2) on trout fry is also mildly contradictory to the present data. The basic difference between these experiments and those presented here is that food intake increases with intervals of deprivation much longer than the 4-hr maximum for the goldfish. It must be remembered that the trout, stickleback, and mouthbreeder are carnivorous fish, and all have stomachs. The retention of food over considerable periods in the stomachs of these fish could lead to different deprivation functions because of increased storage space, slower digestion, and different diet com-

position. None of these species is closely related to the goldfish.

The experiments described in this paper have indicated that the short-term food intake of the goldfish is regulated in some manner, and that this regulation

cannot be based solely on the limitation of the total capacity of the gut.

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