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# OPTIMAL FORAGING THEORY APPLIED TO A FRUGIVOROUS FISH

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*Abstract*. We tested optimal foraging theory by offering frugivorous fish (*Brycon*) prey at different rates. If this theory is correct, giving up time (GUT) for all levels of prey input should be equal. We found GUT was significantly shorter for five pieces of food offered separately over time than for five pieces offered together. This does not support optimal foraging theory. We also found a decrease in GUT for two of three treatments over the course of the day, possibly due to enrichment of the environment. This supports optimal foraging theory. The fish appear to be foraging under two different sets of rules, one for clusters of food and one for food offered in an even distribution through time. We also saw strong evidence of schooling effects. Further studies should (i) determine if the fish do recognize two different situations and are foraging optimally within each situation, and (ii) separate schooling effects from individual fish behavior. (ALG)

## INTRODUCTION (JJS)

While it is probable that individuals forage in such a way as to maximize net energy gain, optimality models often fail to describe accurately actual feeding behavior. One theory, detailed by Schoener (1972), proposes that the optimal diet maximizes the ratio of net energy gained per prey item (e) to expected time required to find, catch and handle the item (t). According to the theory, an item should be consumed if it exceeds the average energy (for items in the area) per unit time gained by leaving and consuming other items. Patches, as well as prey items, can be selected in such a way as to maximize e/t. Foragers should remain in a given patch only as long as e/t for that patch is greater than the e/t of an average patch in the environment. Thus, the forager leaves each patch type at the same final harvesting rate (marginal value). The giving up time (GUT) then would not vary among patches within the same environment (Krebs, et al. 1974).

Feeding behavior of various fish was shown to maximize e/t ratios (Irlev 1961). With this in mind, we set out to test the marginal value theory on frugivorous fish of the genus *Brycon*. The majority (60-70%) of the diet of this genus consists of fruits falling from riparian vegetation, while the remainder is primarily made up of terrestrial insects on the water surface (Burcham 1985, Angermeier and Karr 1983). We hypothesized, in accordance with the theory outlined above, that the time between final capture and patch abandonment (GUT) would remain constant for all rates of prey input.

## METHODS (ALG, JJS)

The individuals used in this study were located at La Selva Research Station, Costa Rica near the south bank of the Rio Puerta Viejo under the suspension bridge. Trials were conducted on 8-9 February 1992 in sets of three with 10min between trials and 30min between sets. A trial consisted of tossing five 1cm thick

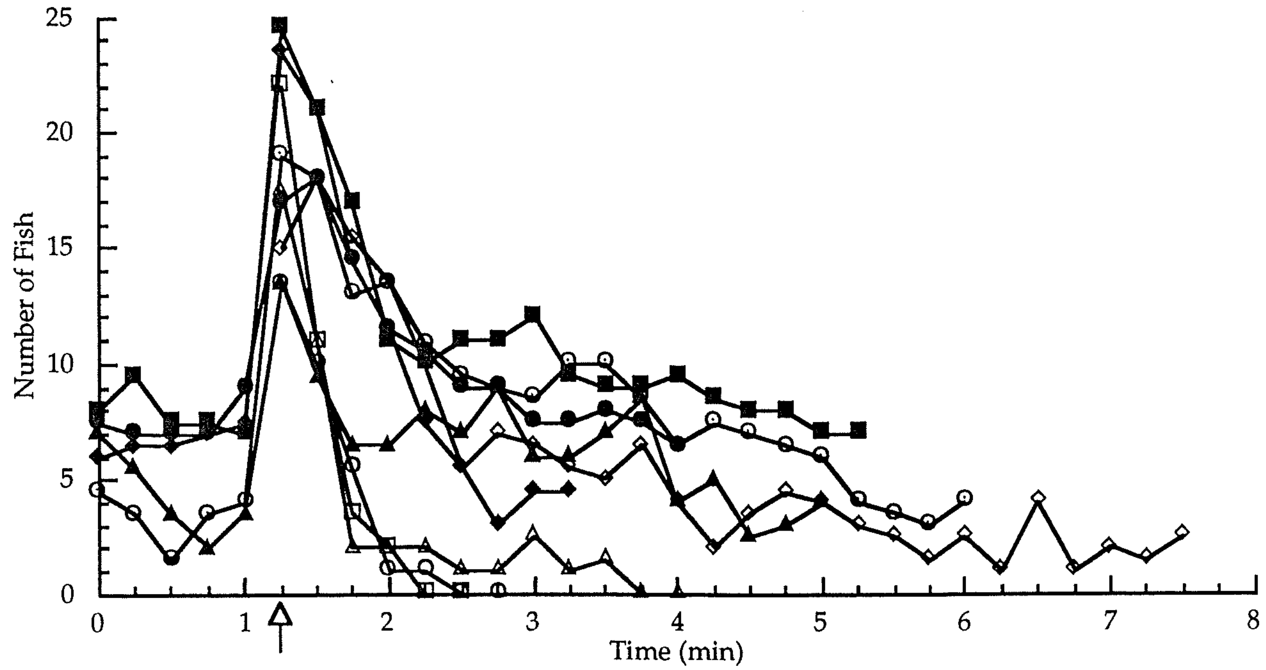


Figure 1. The number of fish observed over time in nine trials of treatment A. The arrow indicates the time at which the banana was offered.

semi-circular pieces of banana (prey) using one of three treatments:

Treatment A: All five pieces thrown in at once at the same spot.
Treatment B: Five pieces thrown to approximately the same spot, one every fifteen seconds.
Treatment C: Five pieces thrown to approximately the same spot, one every 45 seconds.

Every fifteen seconds, beginning one minute before prey input, we counted the number of fish within a circle of roughly $4m^2$, centered at the point of prey input. Two observers recorded the number of fish, and the mean of these two values was used as a measure of fish density.

The $4m^2$ area was obtained by holding a circle of 7cm radius 1m from the eye and looking through it at the water from a height of 14.5m. We continued counting fish until the number present was equal to the average number before the start of the trial, for three consecutive timings.

When throwing the bananas, we targeted an area in the main river current 3m from an eddy where the fish spent most of their time. We estimated the energy costs of maintaining position in both areas by counting the number of tail beats per minute.

In analysis we treated the school of fish as a foraging unit. GUT was measured as the time from final prey input until a return to the level of fish density measured before prey input.

## RESULTS (JMH)

Numbers of fish varied over time for each treatment (Figures 1-3). The general forms of the three patterns are overlain for comparison in Figure 4. The mean giving up times



Table 1. Correlations of GUT with time of day for day 2.

| | Treatment | | |
|---|---|---|---|
| | A | B | C |
| n= | 5 | 6 | 8 |
| r= | -0.8621 | -0.7182 | 0.3737 |
| t= | -2.947 | -2.0643 | 0.9869 |
| | $p<0.05$ | $0.1>p>0.05$ | $0.4>p>0.1$ |

and standard deviations for the treatments were as follows: treatment A, 127±50sec; treatment B, 266±45sec; and treatment C, 260±61sec. GUTs were significantly different between treatments A and B ($t=4.11$, $p<0.01$). We found no significant difference in GUTs of treatments B and C ($t=0.21$, $p<0.5$). The mean rate of tail beats of fish in the current (85.1±24.3 beats/min, n=6) was significantly greater than that of fish in the eddy (17.6±5.6 beats/min, n=7; $U=42$, $p=0.001$). A significant negative correlation was found between GUT and time of day in the A treatment ($p<0.05$), a marginally significant negative correlation was found in the B treatment ($0.1>p>0.5$), and no significant correlation between GUT and time of day was found in the C treatment ($0.4>p>0.1$; Table 1).

## DISCUSSION (JLB)

Two different patterns of foraging were observed in this experiment – one for grouped prey items and one for prey spaced over time. One possible explanation relates to the schooling behavior of fish. Fish in the eddy responded to undetermined (probably visual) cues of prey input, or to schooling around the area of food input. The energy cost (tail beats/min) to remain in the current was greater than that to stay in the eddy; therefore the energy gain must be correspondingly greater in order to make foraging in the current energetically profitable. A con-

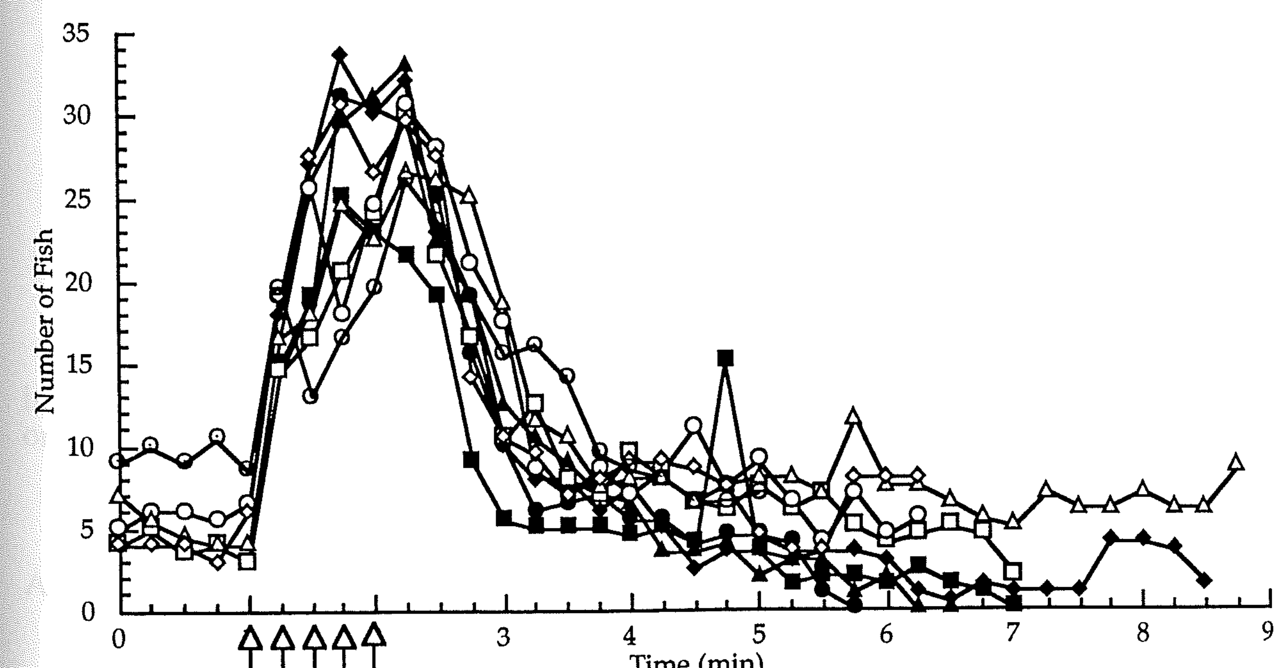


Figure 2. The number of fish observed over time in eight trials of treatment B. The arrows indicate th time at which the bananas were offered.

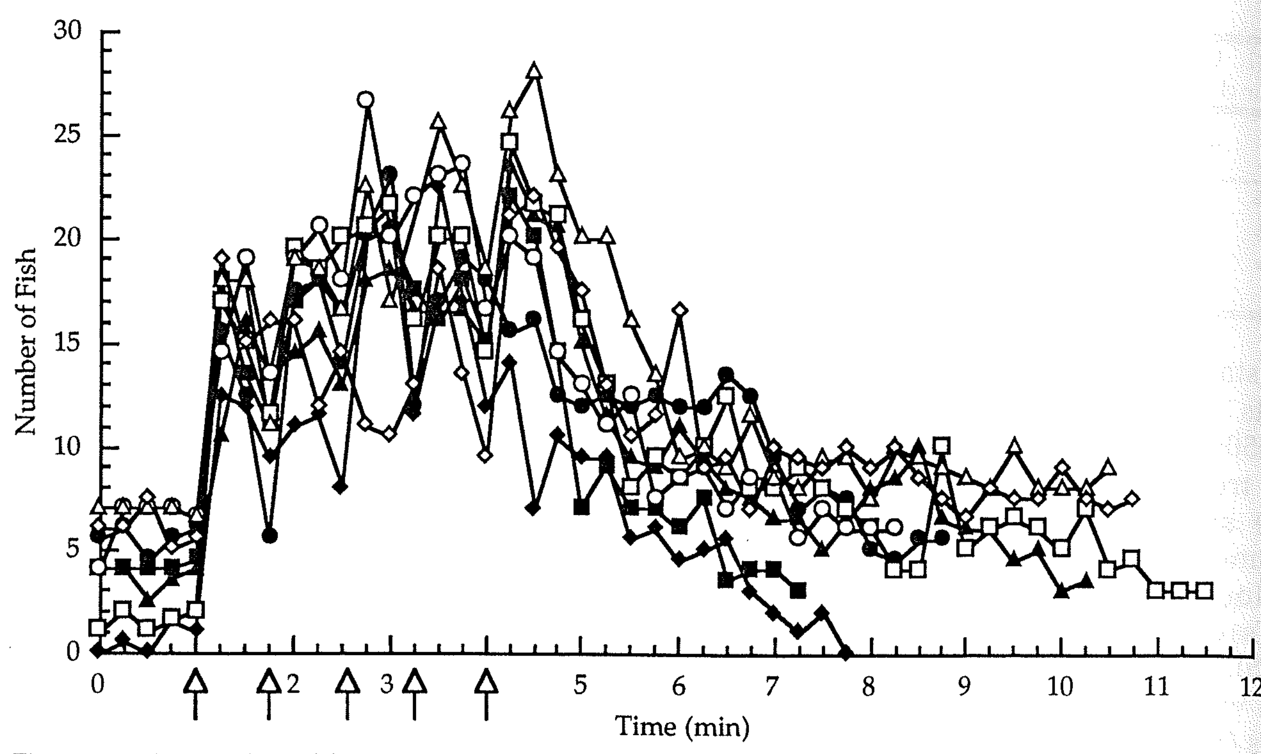


Figure 3. The number of fish observed over time in eight trials of treatment C. The arrows indicate th time at which the banana were offered.

tinued stimulus (steady food input over time) may allow more fish to recognize a potential for energy gain than when food was introduced at one time. Presumably this continued stimulus would differ from the stimulus provided by the behavior of other fish. The trend in fish numbers for treatment C supports this theory, as the total number of fish remaining in the patch increased with the addition of each prey item. These fish, could be responding initially to a schooling stimulus but returning to and remaining in the area because of the stimulus of food input. Perhaps a continuous food input carries a greater potential for continued energy gain even if total number of prey is not greater than a clumped input. Further research could clarify these results. This might include use of marked individuals to compare GUT between fish that actually catch a prey item to GUT for those that respond to a schooling stimulus but do not catch prey.

As the day progressed, GUT decreased for trials A and B. This could be due to the enrichment of the environment caused by the steady addition of food throughout the day (by us). As the average food abundance in the environment increases, GUT for each patch should decrease. However, as GUT for treatment C did not follow this trend, more research into the effects of environmental enrichment over time is needed.

Our results indicate that *Brycon* does not forage in strict accordance with the optimal foraging theory. Further research, as suggested earlier, on foraging techniques of schools versus individuals could more thoroughly



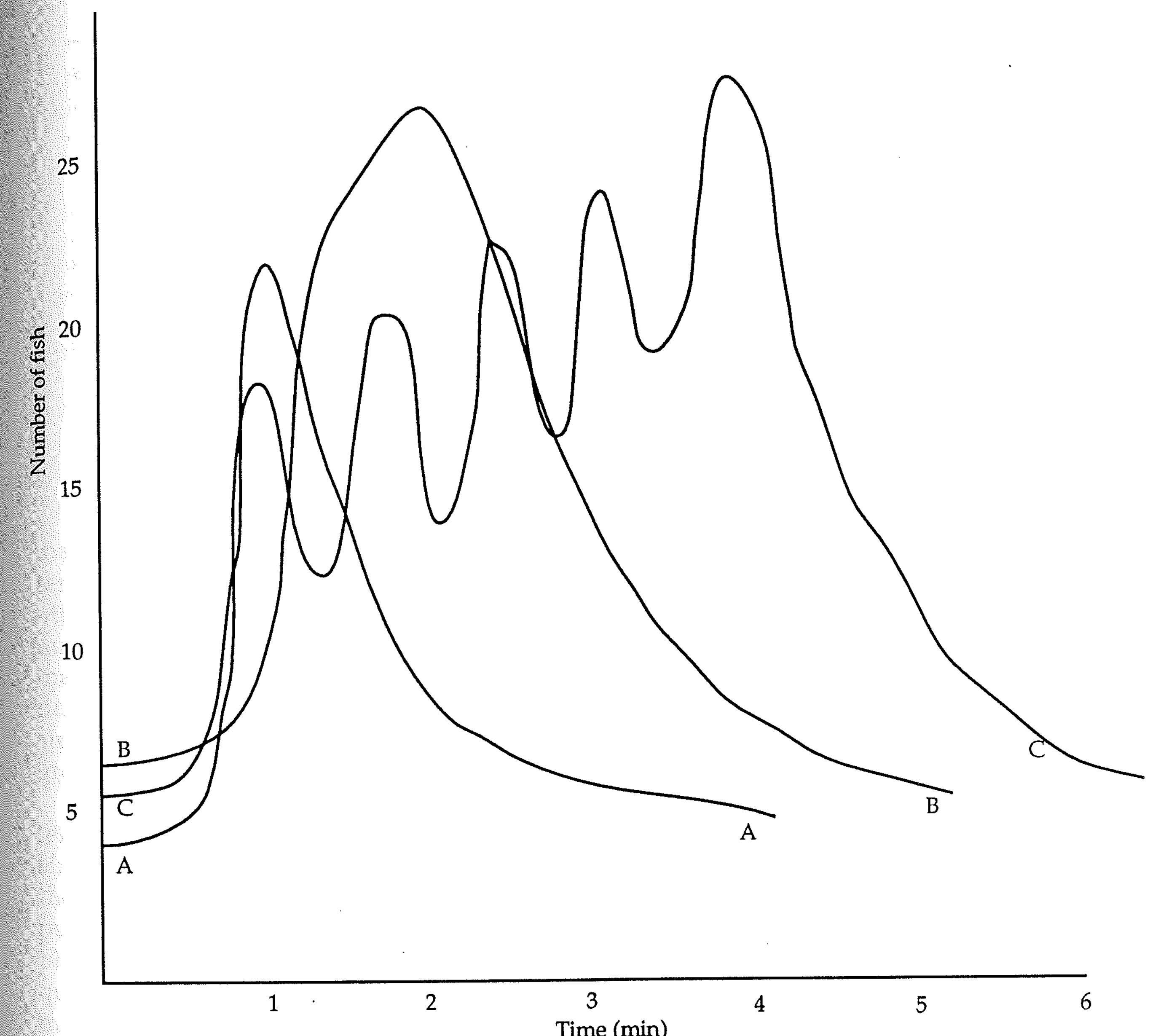


Figure 4. Comparison of trends for the three treatments.

investigate the applicability of the theory to this case.

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