THE "FEED:FEED" DECISION: HOW GOLDFISH SOLVE THE PATCH DEPLETION PROBLEM

by

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(With 7 Figures)

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Introduction

The "feed:feed" decision is defined as the action taken by an animal when choosing among a number of activities, each of which results in consumption of food. The so-called optimal predator makes this decision by choosing the activity that maximizes its net rate of energy gain. Such a response might be expected if animals were always well-informed of their feeding opportunities, but in general this will not be so. An example is the case where an animal forages in a patchy environment. In order to assess its feeding opportunities the animal must first visit each patch. Local rates of feeding in each patch will inform the animal of the present state of its external environment and it might respond to this information by exclusively visiting the most profitable patch. In doing so, it maximizes its feeding rate but ceases to sample its environment. Consequently, changes that occur in patches not visited would go undetected and the predator would be ill-informed of its alternative feeding opportunities. In order to remain well-informed, the predator must continue to visit other patches in spite of the fact that they were previously assessed as less profitable.

How, then, should an animal respond? The answer depends on whether the environment is likely to change. In a constant environment the animal has nothing to gain by persisting in sampling once a significant difference in patch profitability has been detected. It maximizes its

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future food intake by fixating on the patch assessed as most profitable. However, in an environment that is subject to change, this response will have certain disadvantages. While it maximizes food intake in the short run, it also prevents an appropriate response to future changes in patch profitabilities. In the long run it would be more efficient to sacrifice some of this short-term gain by responding in a manner that permits an adaptive response in the future. This requires that the animal continues to visit all patches but favours the patch assessed as most profitable. Only in this way can it monitor the environment and still profit from this investment in sampling.

Since the appropriate response depends on whether the environment is likely to change, the problem facing a predator is how does it know when this is the case. The hypothesis entertained here is that a predator need not know this: it might simply employ a decision rule that results in behaviour which is efficient in both types of environment, although optimal in neither. In this paper, I shall first show that a simple rule suggested by the behaviour of animals in a constant environment correctly predicts how an animal forages in a changing environment. Below I discuss this rule and the data that support it. I then state the predictions made by this rule when patches are depleted as a consequence of foraging, and report an experiment that used goldfish (Carassius auratus) to test these predictions. Finally, I discuss certain refinements to this rule.

The dynamic matching rule

The idea that some fixed rule allows animals to do reasonably well in most of the foraging situations they encounter has often been suggested (Oaten, 1977; Krebs et al., 1978; Lea, 1979). More recently, Herrnstein & Vaughan (1980) and Harley (1981) have each proposed a rule that might be used. Herrnstein & Vaughan's model states that an animal compares local reward rates recently obtained in each patch and reallocates time in a relatively continuous manner towards the more profitable alternative. Herrnstein & Vaughan emphasize that the animal's immediate response does not maximize feeding rate, but simply shifts responding in favour of the better alternative. They refer to this process as "melioration", a word meaning the act of bettering. How such a process might work is stated more precisely by a model that Harley (1981) proposed. This model, known as the "relative payoff sum" rule, describes how rewards recently obtained in each patch influence the animal's decision about how to distribute its time between