Adaptive Flexibility in the Foraging Behavior of Fishes

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Flexibility is an important adaptive feature of the foraging behavior of fishes, because most natural environments vary both spatially and temporally. Fish should respond to low levels of food availability by altering their behavior in ways which ensure higher feeding rates, larger feeding territories, and broader diets. It is shown that the gastric sensation of hunger and its rate of change may act as appropriate cues to food availability, and observed hunger-motivated changes in feeding behavior can produce all of these predicted effects. Data are presented to show that juvenile coho salmon (Oncorhynchus kisutch) alter their behavior in an adaptive manner when faced with variable degrees of threat of competition from territorial intruders, and of risk of predation. A review of similar studies on other species supports the generalizability of these results. Learning is an important mechanism providing behavioral flexibility, and changes in fish feeding behavior with experience are summarized. A graphical model is developed to show that these changes can result in training biases and food specialization. Learning also results in increased feeding rates. The consequences of these observations for the development of refined models of foraging are discussed.


Chez les poissons, la flexibilité du comportement alimentaire est un trait adaptatif important car la plupart des environnements naturels varient de façon spatiale et temporelle. Les poissons devraient réagir à de bas niveaux de nourriture disponible en altérant leur comportement de façon à s'assurer un taux plus élevé d'alimentation, des territoires d'alimentation plus grands et une diète plus diverse. Il est démontré que la sensation gastrique de la faim et son taux de changement peuvent agir comme indices de la disponibilité de nourriture, et que les changements du comportement alimentaire motivé par la faim peuvent produire ces effets comme prévu. Des données démontrent que de jeunes saumons argentés (Oncorhynchus kisutch) modifient leur comportement de façon adaptative lorsqu'ils font face à des degrés variables de menace de compétition dus à des intrus de leur territoires, et des risques de predation. Une revue d'études similaires sur d'autres espèces supporte la généralité de ces résultats. Un mécanisme important qui produit une flexibilité comportementale est l'apprentissage, et des changements dans le comportement alimentaire reliés à l'expérience des poissons sont résumés. Un modèle graphique est développé pour montrer que ces changements peuvent aboutir à des biais d'entraînement et à une spécialisation alimentaire. L'apprentissage résulte également en une augmentation du taux d'alimentation. Les conséquences de ces observations pour le développement de modèles raffinés du comportement alimentaire sont discutées.

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Fish, like other animals, must make numerous decisions while foraging. At a macro-level, they must decide where to feed and what types of prey to feed upon. At a micro-level, decisions are required concerning such things as how fast to approach a particular prey item, or how aggressive to be towards a particular territorial intruder. That individual which makes the more correct decisions will feed more efficiently and have higher fitness (expected lifetime reproductive output) relative to other members of the population.

A major problem faced by a foraging fish is that its environment is characterized by heterogeneity in both space and time, and a decision appropriate in one set of circumstances may be inappropriate in others. Some of this variability will be patterned (e.g. diet changes in food availability) and therefore predictable to the fish, but other types of variation will be stochastic and unpredictable. Relevant examples of this latter type of variation include local food availability, the type of territorial intruder encountered, and risk of predation in a particular locality.

Given this variability, it is reasonable to expect that for-
aging fishes will have developed mechanisms which allow them to adjust their foraging behavior to extant environmental circumstances. This implies two things: first, the ability to collect relevant information and thus be sensitive to variation in key environmental parameters; and second, foraging behaviors sufficiently plastic to respond to such information.

Recently, a considerable number of studies have investigated these aspects of fish foraging behavior. The primary purpose of this paper is to review such studies, especially those carried out in my laboratory on juvenile coho salmon (*Oncorhynchus kisutch*), and show that fish foraging behavior is characterized by adaptive flexibility.

Much of my own research has concerned “distance-contingent” behavior, behavior shown only when a particular distance separates the fish and a relevant stimulus object (e.g., food item, competitor, predator). Such behavior implies response thresholds, and because thresholds may be altered both by the internal motivational state of the animal and by features of the external environment, they are potentially very important in allowing flexibility.

The last 15 yr have seen the extensive application of optimization techniques to the study of foraging behavior. These hypothesize an optimality criterion (some quantity the forager is attempting to maximize) and then predict an optimal set of behaviors, or optimal foraging strategy. The approach has been extremely successful as a means of organizing knowledge of foraging behavior, and of directing research. However, applications of the technique to date can be criticized on several grounds (Krebs et al. 1981). Firstly, most optimality techniques presently used by ecologists deal with static rather than dynamic situations; they do not include changes in the animal’s motivational state (and consequent behavior) resulting from feeding. Secondly, they assume perfect knowledge of the part of the forager; for example, the animal is assumed to know the availability of various food types and their relative profitability, and little attention has been paid to how an animal acquires such information. Thirdly, the optimality criterion (usually assumed to be net rate of energy intake) is probably overly simplistic in many circumstances; many foragers will need to trade this off against other demands, e.g., the need to avoid predators. Partly for these reasons, successful tests of optimality predictions have been almost entirely laboratory based. Field tests have been much less successful (Schluter 1981), probably because real environments vary both spatially and temporally as discussed above.

I will largely avoid the optimality approach in this paper. Rather than predicting fish foraging behavior from some assumed criterion, I will emphasize empirical evidence of what fish actually achieve. It is frequently difficult to argue convincingly that a particular behavior is optimal in any event, as this depends on the function which the investigator assumes the animal is attempting to maximize. However, it is usually possible to argue less rigorously that the observed flexibility is adaptive, in that it will contribute to increased fitness. In the sections that follow, I will apply this approach to examining how fish respond to different levels of three critical ecological variables: food availability, threat of competition, and risk of predation. In the final section I will discuss how fish alter their behavior as a result of experience, as this is an obvious means of adjusting behavior to particular environmental conditions.

### Food Availability

Spatial and temporal variations in food availability are clearly of particular relevance from the viewpoint of a foraging fish. It is of paramount importance for the forager to monitor food availability, and to respond adaptively to variation; I will examine these points in turn.

#### Monitoring Food Availability

It is unlikely that a fish can visually assess the numbers and energetic contents of prey available, or count and weigh prey as eaten, and integrate this information over time to estimate food availability. However, the fish can use stretch receptors to monitor gut fullness, and this gastric sensation of hunger may be a reliable cue to food availability in many instances.

Hunger motivation in fishes undoubtedly has two components — gastric (stomach fullness) and metabolic (levels of circulating metabolites). Accordingly, hunger can be manipulated in two ways — via satiation (short-term) or deprivation (long-term). That stomach fullness is not a complete descriptor of hunger is indicated by experiments such as those by Beukema (1968): variation in length of a preceding deprivation period influenced the amount eaten by threespine sticklebacks in the 1st hour of feeding, even though all of the fishes’ stomachs were equally empty at the start of the trial. However, because fish are unlikely to be entirely deprived of food for long periods of time in nature, the amount of food in the gut is probably the best operational measure of hunger and probably corresponds best to the sensation experienced by a fish. During a feeding session, as the gut fills, satiation increases and perceived hunger declines. The question is whether food availability and hunger defined in this way are correlated, and whether hunger (or its first derivative) can therefore be used by a fish as an estimate of food availability. Charnov (1976) argued that this would be possible once an animal reaches equilibrium with its food supply, i.e. once intake rate equals loss rate and the amount of food in the gut remains constant. This equilibrium requirement may be unnecessarily restrictive, however.

Although feeding is a discontinuous process, Elliot and Persson (1978) have shown that the amount of food in a fish’s stomach at any point in time ($S_t$) after starting with an empty gut (i.e., $S_0 = 0$) can be predicted from the continuous approximation:

$$S_t = \frac{F}{R}(1 - e^{-Rt})$$

where $F$ is the feeding rate (assumed to be constant) and $R$ the evacuation (digestion) rate. The rate of change of hunger is then:

$$\frac{dS}{dt} = Fe^{-Rt}.$$ 

From rearrangement of equation (1)

$$Fe^{-Rt} = F - RS_t.$$
and therefore, substituting (3) into (2):

\[
\frac{dS_t}{dt} = F - RS_t.
\]

If a steady state is reached \(dS_t/dt\) becomes 0 and \(S_{eq}\) the amount of food in the gut at equilibrium equals \(F/R\). Thus, under the assumption that \(F\) is constant over time and directly related to food availability, the amount of food in the gut at equilibrium and equilibrium hunger (gut capacity less \(S_{eq}\)) are also directly related to food availability. This agrees with Charnov’s (1976) conclusion.

Even if a steady state is not reached, at any given time the rate of filling of the gut is also directly related to \(F\) and therefore to food availability (eq. 2). Also of interest is the fact that the rate of filling of the gut is a good indicator of the ultimate steady state level, for substituting \(R \cdot S_{eq} = F\) into eq. (4) and rearranging gives:

\[
\frac{dS_t}{dt} + RS_t = RS_{eq}.
\]

This means that at any time after beginning feeding, a fish can predict its ultimate steady state gut fullness from present fullness and rate of filling. The total amount of food consumed in a period \(t\) \((C_t)\), assuming a constant feeding rate, is simply (Elliott and Persson 1978):

\[
C_t = Ft.
\]

Because \(F = R \cdot S_{eq}\) can be estimated from gut volume and its first derivative (eq. 5), a fish can in theory predict the total value of a patch which it has entered and use this information in deciding whether to leave or stay. This is a potentially powerful sampling rule, providing that food availability is relatively constant during the sampling period. Among other things this implies that a patch is not depleted by the fish; if that occurs, perceived hunger will lag too far behind current conditions to be of much use (Ebersole during a single feeding trial, and several such effects are listed in Table 1. A word of caution is in order, however, as other aspects of motivation may change during a feeding sequence. For example, Thomas (1977) found that the probability of a

<table>
<thead>
<tr>
<th>Table 1: Effects of satiation on fish foraging behavior.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Behavior affected</strong></td>
</tr>
<tr>
<td>Response to prey odor</td>
</tr>
<tr>
<td>Swimming speed</td>
</tr>
<tr>
<td>Reactive distance</td>
</tr>
<tr>
<td><strong>Grasp/discovery</strong></td>
</tr>
<tr>
<td>Eat/grasp</td>
</tr>
<tr>
<td>Eat/encounter</td>
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<tr>
<td>Attack/approach</td>
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<tr>
<td>Attack/response</td>
</tr>
<tr>
<td>Eat/attack</td>
</tr>
<tr>
<td><strong>Handling time increases</strong></td>
</tr>
<tr>
<td>Bluegill sunfish</td>
</tr>
<tr>
<td>Threespine stickleback</td>
</tr>
<tr>
<td>Fifteenspine stickleback</td>
</tr>
<tr>
<td><strong>Species</strong></td>
</tr>
<tr>
<td>Yellowfin tuna ((Thunnus albacares))</td>
</tr>
<tr>
<td>Threespine stickleback ((Gasterosteus aculeatus))</td>
</tr>
<tr>
<td>Lake trout ((Salvelinus namaycush))</td>
</tr>
<tr>
<td>Threespine stickleback</td>
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<tr>
<td>Threespine stickleback</td>
</tr>
<tr>
<td>Pumpkinseed sunfish ((Lepomis gibbosus)</td>
</tr>
<tr>
<td>Bluegill sunfish ((Lepomis macrochirus)</td>
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<tr>
<td>Skipjack tuna ((Katsuwonus pelamis)</td>
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<td>Threespine stickleback</td>
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<td>Bluegill sunfish</td>
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<td>Threespine stickleback</td>
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<tr>
<td>Fifteenspine stickleback</td>
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<tr>
<td><strong>Source</strong></td>
</tr>
<tr>
<td>Atema et al. (1980)</td>
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<tr>
<td>Beukema (1963)</td>
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<tr>
<td>Confer et al. (1978)</td>
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<td>Beukema (1968)</td>
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<td>Beukema (1968)</td>
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<td>Colgan (1973)</td>
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<td>Chiszar and Windell (1973)</td>
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<td>Magnuson (1969)</td>
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<td>Tugendhat (1960)</td>
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<td>Werner (1974)</td>
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<td>Beukema (1968)</td>
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<tr>
<td>Kislalioglu and Gibson (1976)</td>
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</tbody>
</table>
Eggers (1978) and the experimental studies of Ivlev to include less preferred prey as the availability of the preferred prey declines (and hunger consequently increases). Diet broadening will be an adaptive response if it increases the for prey not already included in the diet of well fed fish, and the counter rate with the preferred prey were small relative to changes in profitability, even if these were proportional for all prey types. It is therefore of interest that several authors have been unable to document changes in reactive distance (an important determinant of encounter rate) with hunger: Ware (1971a) for rainbow trout; Dunbrack and Dill (1983) for juvenile coho salmon; and Beukema (1968) for threespine sticklebacks over most hunger levels. The data of Confer et al. (1978) are based on a single lake trout — a second individual showed no such effect.

Optimal foraging models allow predictions to be made concerning which sorts of behavioral changes should lead to diet broadening, i.e. when this response will increase net energetic intake rate. However, most current optimality models ignore the metabolic cost of searching and therefore are not useful when searching rate (and consequently cost) increases with hunger (R. L. Dunbrack unpublished data).

Aggressive behavior and territorial defense can also be considered part of a fish’s foraging strategy, to the extent that food is the resource contested or defended. For example, the optimal territory size will be that which maximizes energy intake rate, and energetic models predict that an increase in food availability should decrease this optimal size (Dill 1978a). Although various experimental protocols and feeding regimes have produced conflicting data on the response of salmonid aggression and territory size to manipulations of the food supply (reviewed in Dill et al. 1981), we have demonstrated that the territories of juvenile coho are smaller in habitats rich in benthic foods (Dill et al. 1981). Similar results have been reported for rainbow trout Salmo gairdneri (Slaney and Northcote 1974), surf-perch Embiotoca jacksoni (Hixon 1981), and male damselfish Eupomacentrus leucostictus (Ebersole 1980) based on experimental manipulation of food supply. In coho salmon the distance from which an intruder is attacked is an increasing function of short-term hunger (Dill et al. 1981), a phenomenon which would produce the observed inverse relationship between food availability and territory size, and maximize the fish's net rate of energy intake.

Although increased feeding rate, diet breadth, and territory size with increasing hunger are evidently adaptive, the question can just as easily be framed in reverse; i.e. is it adaptive for feeding rate and aggressive behavior to decrease as satiation nears? Because it is likely that high activity levels increase vulnerability to predation, decreased foraging activity may be viewed as an adaptive response to predation risk. This question is considered in a later section. Assimilation efficiency, and thus net energy value of prey, may also decrease as satiation nears (Elliott 1976), and this could also make a decreasing feeding rate adaptive.

**Threat of Competition**

If, as argued in the last section, defense of a feeding territory can be viewed as a part of some fishes’ foraging strategy, then there should be an optimal amount of aggressive behavior, one which ensures that the cost of defense does not outweigh the benefits gained thereby. All intruders on a territory do not represent equivalent degrees of threat to the food resource of the territorial resident. The benefits gained by their expulsion are therefore not equal; nor will be the optimal expenditure on defense. It would therefore be adaptive if the aggressiveness of a resident were in some way “scaled” to the degree of threat posed by a particular intruder, and there is considerable evidence suggesting that this is indeed the case.

Damselfishes (Pomacentridae) have been especially well studied in this regard. Although their territories are undoubtedly multifunctional, providing food, shelter, and nesting sites, most of a pomacentrid’s food is produced within its territory. Using what he calls the “model bottle” technique (an intruder is placed in a glass jar and moved in steps successively closer to the center of a territory), Thresher (1976) has shown that the threespot damselfish (Eupomacentrus planifrons) defends the largest territories against those species which feed on the same benthic algae as itself, and that
territory size correlates significantly with the amount of algae in the diet of each intruder species. Such "serial territoriality" (different defense radii for different species of intruder) has also been documented in the laboratory (Patterson 1975; Thresher 1978).

Ebersole (1977) has shown in a related species, the Beau Gregory (E. leucostictus), that the degree of aggression shown towards an intruder is highly correlated with its potential competitive impact (diet overlap multiplied by relative metabolic demand). Because metabolic rate is a power function of body size, one would expect there to be a relationship between aggressiveness and intruder size for conspecific intruders as well; I will return to this point later.

A number of other aspects of the territorial defense system of Pomacentrids appear to be adaptive in energetic terms. Eupomacentrus planifrons distinguish between neighbors and strange conspecifics in model bottle tests, attacking the latter at greater distances (Thresher 1979), and have the greatest threat distance when on their preferred staghorn coral substrate (Izukowitz 1979). Neighboring territory holders presumably represent less threat to the food supply, and preferred substrate is more worth defending. Finally, E. fasciolatus learn to attack novel intruders (tilapia) after seeing them grazing just outside the territory (Losse 1981).

As noted above the size of a conspecific should be an indication of the degree of threat it poses to a territory resident's resources, not only because of increased metabolic demand with increasing size, but also because of shifts in diet with growth. Thus both interspecific and intraspecific territoriality might be expected to be "serial" with intruder size, the largest territories being defended against that size posing the greatest threat. Pomacentrids have been examined in this regard but the evidence is equivocal. Patterson (1975) concludes that territory size in juvenile E. planifrons depends on the size of the intruder, but her data are very limited. Using the same species Myrberg and Thresher (1974) showed that small Holacanthus tricolor were attacked at a significantly shorter distance than larger ones, but there was no such effect in a second intruder species. The anemonefish Amphiprion melanopus does attack small juveniles at shorter distances and with less intensity than larger adults, but Ross (1978) does not consider these fish to be defending feeding territories.

We have attempted to examine this question in juvenile coho salmon. This species defends feeding territories in streams and, owing to variable emergence times and growth rates, and to the presence of two year-classes in the stream at certain times, residents are faced with the possibility of intrusions by individuals of a wide range of sizes. As the diet (characterized by prey size) of coho changes with body size (R. L. Dunbrack unpublished data), threat of competition will not be constant. In fact, competitive impact will be potentially most severe when the intruder is slightly larger than the resident (Wilson 1975), because large intruders still eat many of the prey sizes consumed by the smaller resident and, moreover, eat more of them. Attack distance should therefore also be greatest to intruders slightly larger than the territory holder itself.

To test this hypothesis we presented juvenile coho resident in small aquaria with model intruders moved at intervals toward them, and recorded their attack (charge) distances. Details of the general experimental procedure are provided in Dill et al. (1981). The residents were either 40 mm (n = 27) or 50 mm (n = 22) fork length. The model intruders ranged from 30 to 70 and 30 to 80 mm, respectively, in increments of 10 mm. They were blowups to various size of a single color photograph of a coho salmon. Each resident was tested with each intruder size, in random order, and fed one brine shrimp between trials. Figure 1 shows the mean charge distances for each size of resident as a function of the intruder-resident size ratio (e.g. the response of a 50-mm resident to a 70-mm intruder is plotted at I:R 1.4). For each resident size, charge distance was maximal when the intruder was 25-30% larger than the resident. The decline above this size is significant for 50-mm residents (one-tailed t-test, P < 0.05 for both 70- and 80-mm intruders), but not for 40-mm residents. Nevertheless, it is apparent that charge distance is a continually increasing function of intruder size only if model intruders (Fig. 1) and live intruders (Dill 1978b) are smaller than the resident. Thus charge distance is adaptively, if imperfectly, scaled to the threat of competition.

We have not determined whether the intensity of aggression in coho is related to threat of competition in the same way, although charge velocity is an increasing function of intruder size for small intruders (Dill 1978b). It would not be surprising to find such scaling in this measure of aggression, although Thresher (1978) has demonstrated that the mechanisms underlying distance of attack and vigor of attack are causally independent in three-spot damselfish.

Wakowski and Thorpe (1979) reported that the greater the difference in length between dominant and subordinate Atlant-
tic salmon (*Salmo salar*), the fewer the bouts of fighting which occur; less fighting is also seen among subordinates when there is greater length variation within the group. The behavioral mechanism is uncertain, but these findings are also explicable as a result of the scaling of aggression to threat of competition (although risk of injury from fighting could be invoked as an alternate explanation). The importance of aggressive scaling in the field is uncertain, as many salmonids have a tendency to move to deeper and faster water as they grow, resulting in a certain amount of habitat segregation by size (Chapman and Bjornn 1969; Smith and Li 1983; Wańkowski and Thorpe 1979). Attack distances of salmonids to other species of about the same size (e.g., coho vs. steelhead) have not been examined, but might repay study given the work on damselfish discussed earlier.

**Risk of Predation**

Foraging has potential costs associated with it other than the expenditure of energy and time; the most obvious of these is risk of predation. Because many predators are simultaneously prey of animals higher on the trophic scale, a foraging behavior would be expected to strike an adaptive balance between energetic return and risk. However, foraging strategy models seldom consider risk of predation, primarily because energy and risk cannot be expressed in the same units, or "currency," and simple models with soluble optima therefore cannot be constructed. Unlike many areas of ecology, this is a field in which theory lags behind data: there have been several empirical demonstrations that animals, including fishes, respond to risk of predation by modifying their foraging behavior in ways which appear to be adaptive.

Some habitat patches may be energetically rewarding but harbor dangerous predators. If fishes are faced with a choice between such a patch and one both less rewarding and less dangerous, their decision should reflect both the degree of risk involved, and the relative energetic advantage (Sih 1980). Foraging behavior in bluegill sunfish (*Lepomis macrochirus*) is consistent with this prediction (Mittelbach 1981). Large bluegill (>100 mm) shift from the vegetated littoral zone to the open water of lakes at a time in nearly complete accordance with predictions for maximizing net energetic intake. Although smaller size-classes should switch at the same time, they do not, but instead continue to use the vegetated habitat. This reduces their energetic return but primarily minimizes their chances of being eaten by largemouth bass (*Micropterus salmoides*) in open water. Large bluegill are less vulnerable to this predator. In a pond without predators, even small bluegill forage in the habitat best from the standpoint of energetic return (Werner and Mittelbach 1981). Although not collected for this purpose, the observation of Kramer et al. (1983) that many species of fish respond to an aerial predator by increasing their mean depth in the water column suggests that surface-feeders might also reduce risk at the cost of foraging efficiency.

Differences in risk between habitats may be more subtle than this. Schools or swarms of prey may provide good feeding opportunities but, because of a "confusion" effect, interfere with a forager's ability to detect the approach of a predator. Milinski and Heller (1978) have shown that the threespine stickleback's choice of *Daphnia* swarm density can be altered by exposure to a model of an avian predator (a kingfisher). Prior to exposure hungry fish choose the high density swarm, where their feeding rate is highest (Heller and Milinski 1979); after exposure to the model, they attack swarm regions of lower density. Although this decreases feeding rate, it may increase ability to detect predators. Partially satiated sticklebacks actually feed at the highest rates in the lowest swarm densities, being either unwilling or unable to feed efficiently at high densities (Heller and Milinski 1979). This observation suggests a trade-off between energetic return and risk which varies as a function of the energetic need (hunger) of the fish.

Empirical demonstrations to date of predator risk sensitivity have dealt with patch utilization. Little attention has been given to the possibility that risk of predation may alter the choice of diet items by a forager within a given habitat. We are beginning to explore this issue in juvenile coho salmon. The size-distribution of drifting prey in a juvenile coho's diet can be accurately predicted from knowledge of the relative abundance of different prey size-classes and the fish's reactive distance for each prey size (Dunbrack and Dill 1983). Reactive distance is an increasing, but decelerating, function of prey size. Upon detecting a prey item the fish swims upstream from its holding station to intercept it, and the distance swum (attack distance) is less than, but highly correlated with, reactive distance. Although cryptic when stationary, the coho presumably becomes more visible, and hence more vulnerable, to predators during these feeding excursions. Consequently, prey size and predation risk are associated variables, and we hypothesize that the fish will swim shorter distances for a given prey item when it perceives risk to be high.

We tested this hypothesis by measuring the attack distance of twelve 70- to 73-mm fork length coho in response to three sizes of surface-drifting flies in the artificial stream channel.

**Fig. 2.** The effect of the presentation of a model predator (rainbow trout) on the distance swum to attack flies of different size (length \( \times \) width) by juvenile coho salmon. Only the reduction for the largest fly size is significant (\( P < 0.001 \)).
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Fitness is likely to be decreased as a result of the reduced rate of predation. The object is a black rectangle of the same size, is more reducing the rate of energy intake, and consequently the growth rate (this can be thought of as an example of behavioral resource depression, Charnov et al. 1976). Whereas fitness is likely to be decreased as a result of the reduced growth rate (Dill 1978a), this may be compensated for by a reduced rate of predation.

Despite such empirical evidence that fish do trade-off risk of predation and foraging efficiency, it is not yet possible to include such considerations in foraging models because, as mentioned earlier, these factors have not yet been measured in comparable units. Two solutions to this dilemma are possible. First, the animal could be presented with a variety of combinations of risk and energetic reward, and its choices observed. The amount of risk the animal is willing to accept for a given increase in energetic reward (or, conversely, the energy it will forego for a given reduction of risk) should provide us with the weightings of these two factors used by the animal itself. In effect, the fish could tell us how to express the two factors in a common currency. This is the approach we are adopting in our ongoing studies. Alternatively, the effects of both risk and energy intake on some direct measure of fitness can be estimated. An appropriate measure would be expected lifetime reproductive output, which integrates age-specific fecundity (size- and thus growth rate-dependent) and age-specific mortality. This approach is being adopted in further studies of habitat choice in sunfish (E. E. Werner personal communication).

The Role of Experience

Learning, defined most simply as a change in behavior with experience, is an important mechanism of adaptation to environmental unpredictability. By means of it, fish can fine-tune a generalized foraging pattern to the current environmental situation, increasing their foraging efficiency by developing behaviors appropriate to the currently most abundant prey, or by learning to avoid prey difficult to catch or handle (Vinyard 1980; Ohguchi 1981).

Well-documented effects of experience on foraging behavior of fishes are listed in Table 2 (I have not included several effects reported for larval fishes, as these may have resulted from maturational processes). One obvious consequence of these changes will be an increased capture rate with experience of a prey type, as shown by Werner et al. (1981) for bluegill sunfish feeding on Daphnia or Chironomus larvae; in the latter case the increase with experience was about four-fold. Ringler (1979) has similarly documented an increase in attack rate with experience in drift-feeding brown trout (Salmo trutta). Not only will a prey type be captured more rapidly but its profitability value will increase with experience: net energetic value will increase and handling time will decrease as a result of changes in both attack latency and capture efficiency (less time, and thus energy, will be required for each successful attack). The net energy value of a prey type could also be altered in another way as a result of experience with it. If experience results in a physiological change, such as in the relative proportions of various digestive enzymes, the assimilation efficiency for a particular prey type will rise, increasing its net worth. This possibility has been suggested by workers on several animal groups (Milinski and Loewenstein 1988; Ohguchi 1981).

A predator should find it energetically advantageous to specialize on the most profitable prey (type 1) whenever its net energy return will be greater by doing so than by broadening its diet to include the next most profitable prey (type 2). This can be stated in the form of the following inequality (Krebs and Davies 1981): it is energetically advantageous to specialize on prey type 1 if

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**Table 2. Effects of experience on fish foraging behavior.**

<table>
<thead>
<tr>
<th>Behavior affected</th>
<th>Species</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Searching increases</td>
<td>Yellowfin tuna</td>
<td>Atema et al. (1980)</td>
</tr>
<tr>
<td>Response to prey odor</td>
<td>Three-spined stickleback</td>
<td>Beukema (1968)</td>
</tr>
<tr>
<td>Reactive distance</td>
<td>Rainbow trout</td>
<td>Ware (1981b)</td>
</tr>
<tr>
<td>Reactive distance</td>
<td>Carassius melampygus</td>
<td>Potts (1980)</td>
</tr>
<tr>
<td>Path efficiency</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Attack latency decreases</td>
<td>Pink salmon (<em>Oncorhynchus gorbuscha</em>)</td>
<td>Godin (1978)</td>
</tr>
<tr>
<td></td>
<td>Sacramento perch (<em>Archoplites interruptus</em>)</td>
<td>Vinyard (1982)</td>
</tr>
</tbody>
</table>

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Table 2. Effects of experience on fish foraging behavior.
DILL: FLEXIBILITY IN FORAGING BEHAVIOR OF FISHES

Fig. 3. Graphical analysis of the effect of experience on prey preference. (A) The effect of consecutive encounters with prey type 1 on encounter rates ($\lambda_1$), net energy values ($E_1$), and handling times ($h_1$) for two prey types. Learning is assumed to be antagonistic and although prey 2 is initially the most profitable ($E_2/h_2 > E_1/h_1$), this is reversed after a number of consecutive encounters with prey 1. (B) The effect of these changes on the terms in inequality (12). Once $1/\lambda_1$ falls below the dotted line, specialization on prey 1 is predicted. (C) The equivalent terms for prey 2. Specialization on this prey becomes increasingly unlikely after several consecutive encounters with prey 1. (D) The hypothesized effect of random sampling on the likelihood of diet specialization. The two prey are assumed to be of equal abundance and profitability initially, but at any point in time the proportions of the two types in the diet will deviate from perfect equality. The boundaries represent the proportions of prey 1 in the diet ($p_1$) required to cause $1/\lambda_1$ to fall below $(E_1/E_2)h_2 - h_1$ (upper dotted line) or $1/\lambda_2$ below $(E_2/E_1)h_1 - h_2$ (lower). These changes in parallel, but in antiphase and phase with $p_1$, respectively (compare [B] and [C] above). In this example, chance crossing of the lower boundary results in specialization on prey type 2, but specialization on type 1 is equally likely. Once specialization has occurred a large change in relative availability would be required to cause switching to the alternate prey. The number of individuals likely to specialize on each of two prey types will depend on the initial differences in abundance and profitability of the two prey, and on the fish's sampling procedure.

\begin{equation}
1/\lambda_1 < \frac{E_1}{E_2}h_2 - h_1
\end{equation}

where $E_1$ and $h_1$ are the net energy values and handling times of the two prey types, and $\lambda_1$ is the encounter rate with prey 1 ($1/\lambda_1$ is the average time between encounters with this most preferred prey). Notice that the value of every parameter in this inequality can be modified through experience of a particular prey type.

The fact that prey will be captured at an increasing rate (up to some asymptote determined by the predator's learning capability), while their profitability increases simultaneously,
lends an element of positive feedback to the system; a preferred prey will become even more so. The simultaneous increases in \( \lambda_1 \) and \( E_1 \), and the decrease in \( h_1 \), mean that once a fish has begun feeding on prey type 1, there is an increasing likelihood that the inequality will hold and the animal will find it profitable to continue to specialize on this prey type. If learning is antagonistic in any sense, e.g. if developing an ability to handle one type of prey reduces the ability to handle other types, experience with prey type 1 will reduce the profitability of type 2, and further drive the animal towards specialization. These effects are summarized in Fig. 3A–C with reference to the inequality equation.

This mechanism can produce the phenomenon of "training bias," the tendency for an animal to prefer the food type which it has eaten most recently. Training bias for familiar foods has been reported in rainbow trout (Bryan 1973), chum salmon fry Oncorhynchus keta (LeBrasseur 1969), and threespine sticklebacks (Meesters 1940; Milinski and Loewenstein 1980). This training bias can be an important factor leading to dietary differences between individuals in a population, even when they are exposed to the same prey spectrum in a single habitat. The random element involved in initial sampling of a habitat is of critical importance. A few consecutive encounters with a particular type of prey (a finite possibility even if the prey is rare) can alter the parameters of the inequality that specialization on this prey becomes optimal (Fig. 3D). However, such specialization may not be globally optimal. The fish might have done better by specializing on a different prey type initially, but (to use current jargon) finds itself trapped on a local peak in the adaptive landscape; to reach a higher neighboring peak requires traversing a valley bottom and sacrificing short-term foraging efficiency. It is unlikely, however, that the heights of these adaptive peaks could be vastly different. If they were, the local optimum would probably be unstable, and all fish would tend toward the global optimum over time.

Individual diet specialization is a fairly common phenomenon in fish, being reported in brook trout Salvelinus fontinalis (Allan 1981), brook, rainbow, and cutthroat trout (Salmo clarki) (Bryan and Larkin 1972), and larval herring Clupea harengus (Rosenthal and Hempel 1970). Werner et al. (1981) observed that individual bluegill sunfish tended to specialize on either benthos or plankton, achieving about the same return rates in the two habitats. Both types of specialist did better (in terms of prey items per stomach) than the generalists. Similarly, Bryan and Larkin (1972) found no effect of degree of specialization on feeding or growth rates. Thus, available evidence suggests that different types of specialist do equally well, i.e. that the adaptive peaks are of nearly equal height. However, the possibility remains that specialization can at times be maladaptive, particularly in situations in which the least profitable prey is also the most abundant.

It is worth pointing out that although several of the effects of experience on foraging (Table 2) are similar to those of hunger (Table 1), diet specialization may result in the former case, and diet generalization in the latter. This is entirely due to the fact that only experience has well documented effects on encounter rate (\( \lambda \)), and that only the \( E \) and \( h \) terms for prey 1 are affected by learning.

The possible role of experience in producing training bias and diet specialization has not escaped the attention of other workers. Hughes (1979) modeled a situation in which handling time (or attack success rate) is a function of encounter rate with a prey type (i.e. dependent on \( \lambda_1 \)). Under this assumption, prey types may be transposed in profitability rank as a result of learning, and it may become optimal to specialize on an abundant prey, even if it is initially the least profitable type. This violates a general conclusion from optimal foraging theory (Pyke et al. 1977), which states that a less-preferred prey cannot become preferred by virtue of becoming more abundant. McNair (1981) reached similar conclusions using a slightly different model (the ability to see, capture, and/or handle prey is dependent upon the relative abundance of prey types; for ability to see, this is true even if some prey are not attacked). McNair (1979) pointed out that any tendency for the type of prey last encountered to influence the type of prey next encountered will have the same effect. This will occur, for instance, if search is concentrated in the vicinity of a capture ("area restricted searching"), as shown in larval herring (Rosenthal and Hempel 1970), larval anchovy Engraulis mordax (Hunter and Thomas 1974), and threespine sticklebacks (Thomas 1974). Conversely, after rejecting a prey, sticklebacks swim faster and along a straighter path than previously, apparently showing "area avoided searching" (Thomas 1974). These behaviors will speed up any learning process and increase the chances of specialization. Werner et al. (1981) discussed the role of learning in a fish's decision as to which habitat to forage in, pointing out that profitability of alternative habitats may be underestimated by naive fish, resulting in lags in switching to the best patch. This will obviously be important in the context of prey choice as well, as a novel prey will initially have low profitability, requiring a substantial increase in abundance before the fish switches its attention to it. In both diet and habitat choice situations, the predator may not behave optimally in the short term.

**Concluding Remarks**

In this brief, and by no means comprehensive, review of their foraging behavior, I hope to have demonstrated that fishes possess the ability to alter their behavior appropriately in response to variations in such factors as food availability, threat of competition, risk of predation, and experience. The main point is that fish foraging behavior is characterized by adaptive flexibility.

Flexibility in response to varying food availability is not surprising; this is one type of environmental change concerning which optimal foraging theory makes a precise prediction. Accordingly, my emphasis was on behavioral mechanisms; hunger was proposed as an appropriate motivational system linking food availability and predatory behavior in a way which ensures that fish alter their behavior in an adaptive fashion. The scaling of aggressive behavior to degree of competitive threat is also predictable from current foraging theory, if the theory is extended to consider aggression and territorial defense as part of an animal's foraging strategy.

In the case of predation risk, the empirical evidence presented begs reassessment of the optimality criterion assumed by most current foraging models. It is clear that at least fishes (and in all likelihood most animals) are optimizing a
function much more complex than energy intake rate alone. Risk of predation will have to be included explicitly in future generations of models, although doing so presents some formidable practical problems. The lack of realism of current models is also emphasized by the failure of most of them to consider dynamic changes in the behavior of animals mediated by learning. Certain important conclusions of present models are no longer valid once learning processes are included.

I am of the opinion that the application of current optimality models of foraging has reached a stage of diminishing returns. Many recent papers either make only minor modifications to the theoretical structure, or test it on yet another species, providing no new insights. Papers titled "Optimal foraging by species X" are not vastly different in terms of their contribution to understanding than those titled "Food of species Y in lake Z."

Although I have criticized the realism and applicability of current foraging models, I remain a believer in the usefulness of optimality models in behavior. I am optimistic that future generations of foraging models will improve considerably on current ones, applying techniques such as dynamic optimization, which allows explicit consideration of feedbacks and trade-offs (Krebs et al. 1981). Hopefully, these modeling efforts will be based upon empirical research on behavioral mechanisms and capabilities, and will be experimentally verified at each step, lest the theory again outstrip the data. In the meantime, it is not unreasonable to claim that fish are more sophisticated than models (and modelers).

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