THE MECHANISM OF SELECTIVE PREDATION IN DRIFT-FEEDING BROWN TROUT (SALMO TRUTTA)

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INTRODUCTION

Abundant evidence has shown that a variety of vertebrate and invertebrate predators consume prey in numbers disproportionate to their density in the environment. In fact, selective feeding probably characterizes the majority of animal species (Ivlev, 1961; de Ruiter, 1967). A simplifying assumption of early predation models, notably those of Lotka (1925) and Volterra (1926), was that predation was in direct proportion to prey abundances. The limited usefulness of these models seems, in part, related to this unrealistic assumption. Selective feeding may affect not only the prey population, but also the fitness of the predator in both a proximate and an evolutionary sense. In the development of useful predation models, a need exists for elucidating the mechanism by which predators select their prey, and for determining the significance of such a selection process.

Consideration of the mechanism and significance of selective feeding is a relatively recent endeavor that has involved two quite different approaches. The first approach has been to examine in considerable detail specific kinds of predators, especially birds, in an attempt to understand the basis of selective feeding. This work is exemplified by Tinbergen's (1960) study of the food (cryptic forest insects) brought to nestling tits by adults. Large, palatable insects were selected by the birds, but at low and high densities fewer than expected on the basis of a "risk index" were taken. A plot of risk against prey density produced an essentially sigmoid curve. To explain this relationship, Tinbergen proposed that the birds initially had difficulty detecting the cryptic prey; as the prey density increased with time, the birds' chance encounters increased, and they learned to recognize the prey against the background. Thus, the rate of predation greatly increased, while that on other species decreased. This phenomenon was primarily viewed as a process of visual filtering, which Tinbergen termed the formation of a "specific searching image." Perhaps somewhat unsatisfactorily, he explained the reduced predation rate at very high densities in terms of the birds' presumed need for a varied diet. Holling (1965) obtained a similar sigmoid curve when the numbers of prey (cocooned sawflies) eaten by deermice in laboratory and field experiments were plotted against prey density. He explained the results on the basis of learning and the hunger level of the predator. The initial accelerated phase of the curve was attributed largely to learning, whereas its deceleration and leveling off were thought to result from prey handling and satiation effects. Rather than viewing the learning as a threshold phenomenon, as Tinbergen did ("breaking the crypsis"), Holling suggested a cumulative learning process.

In another contribution to this approach, Royama (1970) studied the food brought to nestling tits. While his results were similar to Tinbergen's, Royama proposed an alternative explanation that fit both sets of data. His hypothesis was that different prey species occur in different (physical) niches; the birds fed mainly in areas of maximum "profitability" in terms of prey density, but continued to sample other niches periodically. Thus the initial lag in response to new prey results from the bird sampling the niche but finding it unprofitable. At higher densities the birds spend most of their time in the niche, and at very high densities the response is limited by the time required to handle the prey as well as to sample other niches.

Although the profitability hypothesis may provide the best explanation of the diet of nestling tits, careful field and laboratory work by Croze (1970), Dawkins (1971), and Murton (1971) has shown that several species of birds can and do form specific searching images. Krebs (1973) has pointed out that the evidence that other vertebrates, particularly fish, adopt searching images is as yet equivocal. One could envision circumstances where these two hypotheses would not necessarily be mutually exclusive.

Many investigators have used the term "searching image," but not always with the same meaning. Dawkins (1971) has argued that the term should be applied in a very specific manner if it is to be of any value. For example, Krebs (1973) makes a distinction between formation of a searching image and development of preference for a familiar prey. My interpretation of this distinction is that searching image involves a change in the ability to detect prey, whereas a preference for familiar prey suggests an active selection of a prey species. Because the mechanism involved in the selection differs in these two cases, the distinction is a meaningful one.

The second approach to the study of selective feeding has aimed at establishing general principles that apply to a wide variety of predators. An underlying concept of this approach has been the idea that predators feed optimally, so that they "should" select a diet that provides maximum energetic benefit. The models do not incorporate the concepts of searching image or development of a preference for familiar prey, and no consideration is given to prey palatability. A considerable literature has developed around this approach. Although a comprehensive review is not intended here, several representative papers will be considered. Schoener (1969; 1971) has developed broad models of feeding strategy using an optimization procedure in which either energy obtained from the food is assumed to be maximized, or time spent feeding is minimized. These models were not intended to provide explicit predictions of the outcome of selective feeding, but they do emphasize the existence of at least two kinds of feeding strategy. Thus, depending on their behavior and ability, some predators are "energy maximizers," whereas others are better viewed as "time minimizers."

Emlen (1966) tried to relate caloric values and consumption times of different foods to their roles in a predator's diet. He demonstrated mathematically that feeding should be most efficient if the animal accepts all prey encountered when food is scarce, but shows increasing selectivity as food becomes common. Applying this model to previously published carp data, and to his own work with marine gastropods, Emlen concluded that the extent of selectivity could be predicted on the basis of prey density.

MacArthur and Pianka (1966) developed a general model of an optimal diet in terms of time spent searching and time spent pursuing the prey. In their model, the predator ranks prey in order of increasing handling time. When a new prey species is added to the diet, search time decreases (greater effective density of prey) and pursuit time increases (inclusion of prey of lower rank). New prey are added to the diet as long as the decrease in search time exceeds the increase in mean pursuit time. MacArthur (1972) also derived a similar model based on energy gain rather than handling time. As long as pursuit time/gram for a new prey is $\leq$ pursuit time/gram plus mean search time/gram of items already in the diet, the new prey should be added to the diet. This kind of model, in a form that allowed quantitative predictions, was tested by Werner and Hall (1974). The experimental subjects were bluegill sunfish fed four sizes of plankton, in several overall densities. They found that at low abundance, prey of different size (and presumably energy content) were eaten as encountered. As prey abundance increased, size classes beginning with the smallest dropped out sequentially from the diet as predicted from the model. Estimates of search and handling times demonstrated that changes in the diet tend to maximize return with respect to time spent foraging.

Another model based on optimization techniques was proposed by Rapport (1971). This is a graphic representation of food selection that attempts to demonstrate the range of possible responses to changes in prey availabilities. The physical capability of the predator to consume two prey species is presented as a "consumption frontier," whereas preference is described by an ordinal ranking of all prey combinations (including those that are not obtainable) in the form of "indifference curves." The optimal combination of selected prey is the intersection of the consumption frontier with the highest obtainable indifference curve. The model is of theoretical interest, but it is not clear how or whether the required data for its testing can be obtained, and more than two prey species cannot be analyzed graphically.

Although the literature cited is only a sample, it represents the recent emphasis by ecologists on a general framework in which to view predation. In general, the testing of these models has not kept pace with their formulation. Surprisingly few studies provide detailed knowledge of how various kinds of predators actually perform. Despite a voluminous natural history literature on feeding, the kinds of data needed to test the simplifying assumptions are scarce.

Some confusion evidently exists between the concept of optimization and the predator's means to approaching an optimum diet. For example, in a recent paper (Marten, 1973) concern was expressed that a complicated optimization function "could prove confusing to a real predator." Food is probably selected on a relatively simple basis. The predator may respond, for example, to prey size or abundance, and the outcome of this response may tend to optimize energy intake. Caution is required if we are to avoid confusing this outcome with the means, or mechanism, by which prey are selected.

Another point of caution concerning the optimization principle is the validity of our assumption as to what is being optimized. Energetic intake is an obvious choice, but we could find that feeding behavior which was optimal in the long run could involve seemingly suboptimal short-term food selection. Optimal feeding must also ultimately be balanced against other activities such as reproduction and avoidance of predators.

The approach taken in this paper involves investigating the mechanism of selective feeding by brown trout in a laboratory stream, followed by the question of the extent to which that selection optimizes energy intake. The study is developed principally from an ecological point of view. Thus, selective feeding is examined in terms of prey size, distribution, and abundance. Patterns of response to these factors are used to infer the mechanism of selective feeding. Implicit in the design and analysis is that capture of a prey item is reinforced by some set of prey attributes, which probably include palatability and texture, but these are not specified. It may be appropriate to add here that, while optimization is probably a valid ecological generalization, determining how the predator obtains an optimum diet is a basic and interesting question deserving considerable attention.

One of the major problems in investigations of feeding selectivity, especially in field studies, is that the abundance of prey species is difficult to determine, and is confounded by interspecific differences in conspicuousness or catchability. Laboratory experiments are often required to permit rigorous control over these factors. In the laboratory, however, experiments must often be contrived to prevent the predator itself from altering prey availability. Thus, the investigator may replace prey as they are eaten (e.g., Beukema, 1968; Chizar and Windell, 1973) or limit the feeding period to very short intervals (e.g., Werner and Hall, 1974). Both of these solutions represent a significant departure from natural feeding conditions. This difficulty can be eliminated when considering a predator such as a trout feeding on drifting prey. The animal is briefly exposed to a prey item, and whether or not the prey is consumed, it is no longer available. This convenient feature has not previously been exploited in the laboratory.

By comparing the contents of fish stomachs with benthos composition, as was done by Leonard (1941) with brook trout, Nilsson (1957) with brown trout, and Atmar and Stewart (1972) with topminnows, investigators have shown that fish feed selectively in natural streams. Additional examples of selective feeding in natural fish populations are reported by Allen (1941; 1951), Popham (1943; 1944), Frost and Smyly (1952), Gerald (1966), White (1967), and Frost and Brown (1967). These studies are important in demonstrating the range of diet in fishes, but because prey species differ in life history and behavior, their availability to fish is not adequately reflected by estimates of benthos composition. A few field investigators have compared the fish's diet to prey abundances in the drift, where availability was presumably similar. Reimers (1957) showed that rainbow and brown trout captured two times more dipterans than would be expected on the basis of proportions of prey in drift samples. A paper by Jenkins, Feldmeth, and Elliot (1970) contains data suggesting strong selectivity for simuliids over baetids by rainbow trout in a short-term field experiment. Reisen's (1972) work on a shiner states that invertebrates were consumed in quantities (weights) proportional to their composition in the drift. Yet his data seem to show selectivity for Ephemerella, Rhyacophila, and ants. My observations with binoculars in Michigan streams suggest that when several prey are available simultaneously, feeding is predominantly on one species, at least for individual fish.

These studies demonstrate that fish make a selection among drifting prey. They do not, however, provide a means of evaluating the pattern or the mechanism of that selection. For example, the data do not show how the diet changes over time, how relative prey abundance, size, and distribution affect the selected diet, or the extent to which the fish's prior experience affects the outcome. Laboratory experiments encompassing some of these objectives have been performed, but these have invariably simulated lentic conditions. Ivlev (1961) studied carp, bream, roach, and bleak in aquaria. He found that feeding preference was related to predator satiation, total and relative prey abundance, and spatial distribution of the prey. Although the work has been criticized because unnaturally high prey densities were used, perhaps the most serious criticism of the study is his emphasis on the effects of satiation on diet selection, with little regard for experience with the prey. Ware (1971; 1972) using rainbow trout, and Beukema (1968) with sticklebacks, have studied the influence of hunger, experience, and prey density on feeding behavior in aquaria. Their major emphasis was not in evaluating the mechanism of selective feeding, but their work bears directly on that problem. Their results will be considered later.

The objectives of the present study were threefold:

1. To describe selective feeding of brown trout in a laboratory stream environment where prey availability and distribution were controlled.
2. To examine the mechanism by which drifting prey are selected. Specifically, to evaluate the effect of prey size, relative and total abundance, and spatial distribution on the fish's response. This objective involved two alternative hypotheses:
   - A. The selected diet results from a differential response to stimuli (e.g., size) characteristic of the prey. Changes in the diet are brought about by a learning process involving either 1) the formation of a "specific searching image" (Tinbergen, 1960), so that in effect the predator "learns to see" a prey species and concentrates its attacks on it, or 2) the development of a preference for specific kinds of prey (Krebs, 1973), so that the predator makes an active "choice" among available species.
   - B. The selected diet results from variation in prey distribution. Changes in the diet are brought about by altering the area searched (e.g., Beukema, 1968; Krebs et al., 1972), so that the predator tends to move into areas of maximum "profitability" in terms of biomass consumed/time (Royama, 1970).

3. To determine the extent to which the diet corresponds to an optimal selection. The underlying hypothesis was that the observed prey selections should optimize energy intake relative to a random diet (MacArthur and Pianka, 1966; MacArthur, 1972).

DISCUSSION

This study has shown how the diet selected by brown trout in a laboratory stream is affected by the size, distribution, and abundance of prey. Trout moved into areas of high prey density, but prey selection was not explicable solely on the basis of this movement. The fish actively selected certain prey species, and this selection was influenced by previous experience with the prey. A surprisingly large number of encounters was required before the responses stabilized among species. Prey size and total abundance (drift rate) had a marked and continuing effect on the observed diet; relative abundance (ratio) had a more limited and largely temporary effect. Selective feeding ultimately increased more than threefold the caloric content of the diet relative to a random diet, but a hypothetical optimum diet was never attained.

These findings are of value only to the extent that they reflect natural feeding behavior. While emphasizing the value of laboratory streams as a research tool, Warren and Davis (1971) have also cautioned against our being led astray by the visual resemblance of such systems to nature. Major differences exist between the laboratory system employed here and a natural stream, but these differences are precisely the reason for turning to the laboratory in the first place. Thus, while the influence, for example, of social facilitation of feeding, fluctuating prey abundances, and differences in prey behavior have not been dealt with at all, their elimination from the experiments permits us to at least characterize the capability of trout under specified conditions. With this knowledge we may be able to hypothesize the consequences of a variety of natural circumstances, and these hypotheses can eventually be tested in the laboratory, in nature, or both.

In the discussion to follow, I will interpret my results in relation to those of other investigators, and consider the implications of this study for certain predation models. A tentative synthesis of our current knowledge of selective feeding will then be formulated that may prove useful in future research. Finally, selective predation as an optimum strategy will be considered.

Interpretation and Implications of Selective Predation by Brown Trout

My investigation revolved around two alternative hypotheses, as explained in the Introduction. The first hypothesis was that the selected diet results from a differential response to prey stimuli. Two kinds of learning processes were considered to explain changes in the response: 1) Formation of a searching image ("learning to see" - Tinbergen, 1960), and 2) Development of a preference for specific kinds of prey (active "choice" among species - e.g., Krebs, 1973). The trout did ultimately search more intensely for the alternate prey, but the evidence did not support the idea that changes in response resulted from a sudden change in the ability to detect the prey. The experimental conditions, however, probably minimized detection as a requirement in the feeding situation. The three prey species were readily visible (at least to the investigator), and most necessarily passed through the fish's visual field. All drifting items were also edible; no twigs or other bits of debris could have been mistaken for prey. In natural streams, where cryptic prey, turbid water, and constantly changing light conditions present a more demanding feeding situation, prey detection might become a significant, or even dominant, factor. Thus, my results do not refute the search image idea; they simply show that prey selection in trout can also result from an active, differential response to the characteristics of the prey.

In this study a dominant characteristic affecting the selection was prey size, although considerable time was required before the fish stabilized their response to this factor. Ware (1972) found that the distance from which rainbow trout attacked prey was closely correlated with prey size, and suggested that this property of foraging behavior contributes to, and may explain, size selective predation. I was unable to record the reaction distances to the three prey species, but some of the brown trout did appear to move further to attack large mealworms that small crickets. However, size-selective predation may involve more than simply reactive distance. I observed instances in which the smallest drifting prey, brine shrimp, actually touched the snout of a fish that was feeding on crickets and mealworms, yet no attack occurred. These instances suggest an active refusal of brine shrimp even though the distance to the prey approached zero.

Considerable interest has focused recently around prey size selection by planktivores and its effect on the community composition of zooplankton (e.g., Brooks and Dodsen, 1965; Galbraith, 1967; Hall et al., 1970; Warshaw, 1972). However, Zaret (1972) found that feeding by an atherinid was more closely correlated with eye pigmentation area than with body size of the prey (Ceriodaphnia cornuta). He suggested that since plankton are virtually transparent, the eye pigment area may be a more relevant measure than body size. Zaret and Kerfoot (1975) measured eye pigment area and body size of the cladoceran Bosmina longirostris in a Panama lake. Comparisons before and after (morning and afternoon) predation by an atherinid revealed a dramatic reduction in mean eye-pigment diameter, but no significant change in mean body size. They concluded that the fish fed according to "visibility selection" and that body-size selection was of negligible importance. Their results are important in demonstrating that measurements of prey size must be appropriate to the physical properties of the prey, and to the visual capability of the predator. In the present study the prey used were opaque; they were visible in their entirety to the investigator, and presumably to the experimental animals as well. The observed prey selection was probably not the result of differences in response to specific portions (e.g., eyes) of the prey. In natural streams, the bodies of most invertebrates are opaque, or at least translucent. Therefore, body size appears to be a suitable criterion of the effective size of drifting prey.

The second hypothesis in this study was that the selected diet is related to heterogeneous prey distribution. Changes in the diet are brought about by altering the area searched, so that the predator moves into regions of maximum "profitability" (Royama, 1970) in terms of prey consumed/time. Although this hypothesis was originally considered here as an alternative to that of searching images or other responses to specific prey stimuli, it is evident from the data that these two kinds of mechanisms need not be considered mutually exclusive. Brown trout did move into the upper water column, and several lines of evidence supported the idea that this movement was in response to prey density. Their continued capture of at least a few brine shrimp at all depths supported Royama's prediction of periodic sampling of all "niches". Ware

(1972) found that a minimum rate of prey captures (3.5/minute) was required by rainbow trout to maintain substrate-oriented search behavior. He offers the conjecture that rate of capture serves as an internal signal to control foraging behavior, and that this provides a sufficient condition for Royama's "profitability" hypothesis to operate. My data do not provide a test of this conjecture in the context of drift feeding, but one could envision such a test with a series of concentrations of brine shrimp provided at several levels in the water column. If Ware's idea is correct, then we should find discrete rates of capture above which movement would be largely restricted to specific depths (prey concentrations).

Despite the movement by brown trout into areas of high prey density, analysis of the response to the three ratios of small:large prey did not generally support the idea of selective predation on the more abundant prey. Murdoch (1969) has considered the stabilizing effect on animal community structure of predator "switching", which was defined as disproportionate predation on the most abundant prey species. He found that, in most circumstances, no switch occurred when marine snails were provided mussels and barnacles in ratios ranging from 5:1 to 5:9. Murdoch suggested the possibility that the predator-prey system used was not typical. He also suggested that the simplification inherent in his laboratory experiments eliminated some necessary condition for switching, and that this condition may have been prey heterogeneity. The results of the present study seem to provide an additional example of the absence of switching as defined by Murdoch. An exception was the initial (Day 2) disproportionate response to small crickets when these were five times as abundant as large mealworms. The large size discrepancy between prey may have minimized the effect of prey abundance. Thus, the available data do not rule out the concept of switching, but they do suggest that within a given area prey size may be more important than abundance in determining the outcome of a feeding situation. If trout predation does lead to stabilization of prey communities, such stabilization probably results mainly from movement into areas containing disproportionately large numbers of a given prey species.

In all experiments discussed in the present paper, the hunger state of the fish was maintained at a similar level by allowing 24 hours between trials. Detailed analysis of gastric evacuation rates in brown trout by Elliot (1972) showed that about 95 percent of the digestible organic matter in a meal of Tenebrio molitor was evacuated in 24 hours at 17° C. Although my meal sizes were considerably larger than Elliot's, he found that evacuation rates were not significantly different for 1) different sized meals, 2) different sized prey of the same taxon, 3) different sized fish, and 4) meals of mixed prey. Since crickets and brine shrimp contain less fat than mealworms, they may have been evacuated at a faster rate. The important point, however, is that based on Elliot's data, it is unlikely that significant amounts of food remained in the fish stomachs at the beginning of each feeding period. Examination of the gut contents of 4 fish fed 25 large mealworms, and 4 fish fed 50 small crickets, suggested that Elliot's results were applicable to the present study. Therefore, the changes in prey selection that I observed on a daily basis were not simply the result of an accumulation of prey in the stomach. Assuming that stomach fullness is at least a close correlate of hunger, daily changes in hunger state did not adequately explain the results.

The effects of hunger state were not emphasized in this study, in part because a number of thorough studies have examined the influence of hunger on predation rates in general, and in part because of the difficulty of separating the effects of hunger and experience on selective feeding in particular. The latter consideration apparently did not deter Ivlev (1961), who concluded that satiation was the controlling mechanism behind increased prey selection by carp among chironomids, amphipods, and mollusks. In a very detailed model of vertebrate predation ("Type III"), Holling (1965) proposed that a change in the number of a prey species eaten (the "functional response") involved learning by the predator. When a palatable prey species was eaten the predator "learned a lesson" which gradually was extinguished in the absence of reinforcement. Hunger was considered of critical importance to this learning process, in the sense that capture of palatable food operated to lower the level of hunger required before a subsequent attack would occur. The model predicted that the distance of reaction to a prey item would increase ("improve") with experience. Beukema (1968) found that food deprivation did not alter the reactive distance in sticklebacks. Ware (1971) has shown this same phenomenon in rainbow trout; he therefore suggested that experience can modify reactive distance directly, rather than indirectly through hunger as proposed by Holling. My observation of no major change in selection during the last few days of an experiment suggests that considerable changes in hunger state may not be reflected in changes in the selected diet. On the other hand, during some of the early days of the experiments my results were very much as predicted by Holling's model. His simulated results showed that with increasing satiation predators will become restricted to the most attractive prey, but that the less attractive ones may be accepted in the beginning of a feeding cycle (i.e., when hunger is high). Thus, at very high prey densities representation of foods other than the preferred one should approach zero (as brine shrimp did). It may be that the model proposed by Holling predicts the correct results in certain, or even most, cases, but the predictions could be the result of the correlation between hunger and experience. In any event, his model is of considerable value in providing a testable framework for viewing predation. Thus Holling observes that ". . . although the model might be wrong in detail, its close agreement with observed features provides a reasonable basis for confidence in the insight it provides into the structure and characteristics of vertebrate predation."

It is not implied here that hunger is unimportant in predation, only that it is not likely to be the mechanism of prey selection. Ware (1972), Hanson (1972), Beukema (1968) and others have shown that predation rates can be stimulated by depriving fish of food for varying lengths of time. Chizar and Windell (1973) found that certain behavioral responses of bluegill sunfish to mealworms (e.g., "approach", "stop", "turnaway") became more frequent with increasing satiety. These pre-consummatory acts were more susceptible to the effects of satiation than was the act of eating the prey. The authors hypothesized that satiety produces "more selective responsiveness" to prey rather than simple diminution of feeding behavior. Unfortunately, their results are not directly comparable to those reported here, because only one prey species was used in most of their trials.

A prediction of Holling's (1968) model that does not fit the present data is that the total number of prey eaten remains the same over a wide range of total densities. We saw that at the high drift rate considerably more prey were taken than at the low rate (c.f. Fig. 39 with Holling's

Fig. 6.2). Holling considered this to be a "buffering effect" of the alternate (in this case least palatable) prey, which acted at low densities to maintain the total response to the available prey. My results suggest that this effect need not produce a stable response over a range of densities, perhaps because general feeding activity is stimulated where prey are abundant. The idea of buffering, however, did agree with the observed results when the total number of prey eaten over time was examined. Thus, there were shifts in the amounts of the three prey species in the diet, but for a given density relatively little change occurred in the total number eaten throughout an experiment.

Holling (1965) has suggested that the functional response can be much more rapid where an absence of alternate prey provides for no buffering effect. While this may be true once the response begins, I found in a series of pilot experiments a considerable delay before mealworms were attacked, when these were presented alone. In fact, only 9 of 20 such fish were observed to feed on mealworms after 6 days of exposure. In contrast, all but one of the fish treated in this paper eventually fed on mealworms (or crickets) when these were presented along with brine shrimp.

A Sythesis of the Mechanism of Selective Feeding

From the results presented in this paper, and those particularly of Tinbergen (1960), Royama (1970), Holling (1965), and Ware (1971; 1972), a preliminary synthesis is possible that may serve as a guide to further research on selective feeding. The synthesis takes the form of an explanatory model, which though developed in terms of trout, may prove applicable to a variety of vertebrate predators. The model can be briefly stated as follows:

Trout exhibit area-specific search patterns, but by chance encounters they can shift the area searched and move into regions of maximum prey density. Movement among areas may, in part, be related to the hunger state of the animal. Once in such areas, they tend to remain as long as captures exceed some threshold level. Trout respond to the available prey in a size-selective fashion, but a number of encounters are required to gain familiarity with a novel prey species, and a period of extinction exists for familiar, even though less "desirable", prey. Because detection of prey depends on chance encounters, individual fish may differ temporarily in their diet selection. Even at high densities, the trout continue periodically to sample all palatable prey, so that the idea of sampling different (physical) "niches" may be extended to include sampling of different species within these niches. Thus, predation tends more toward an adjustment in the selected diet than complete elimination of certain prey species.

In graphical form (Fig. 48), the model depicts prey selection as the combined outcome of responding to specific prey characteristics (e.g., size) and searching in different areas. These areas could, for example, correspond to the

FIGURE 48. A graphical model of the mechanism of selective feeding.

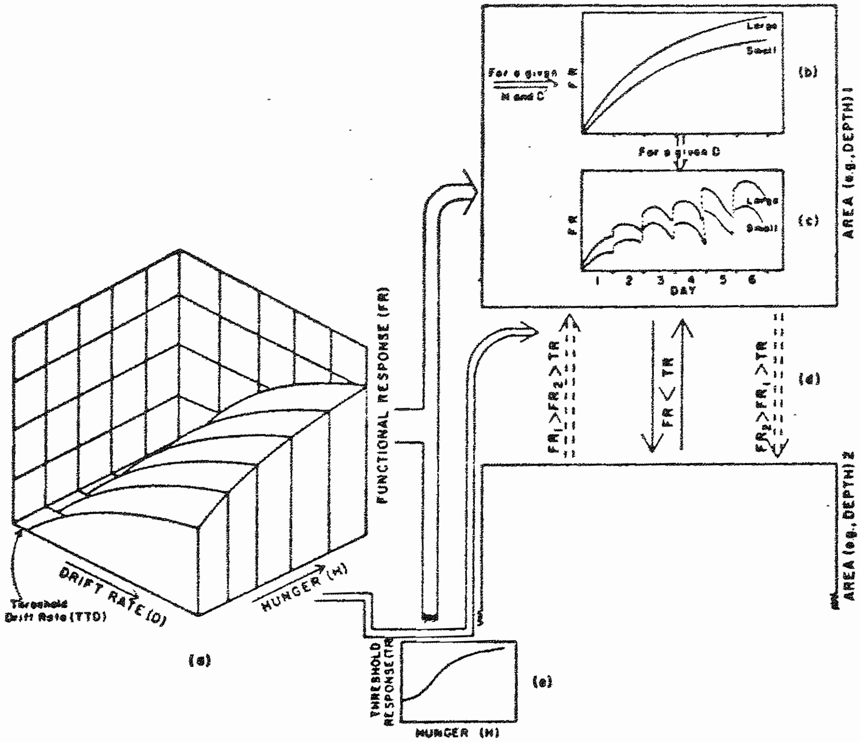
Threshold Drift Rate (TTD)
DRIFT RATE (D)
HUNGER (H)
(a)
FUNCTIONAL RESPONSE (FR)
For a given H and C
FR
Large
Small
(b)
For a given D
FR
Large
Small
(c)
1 2 3 4 5 6
DAY
AREA (e.g., DEPTH) 1
$FR_1 > FR_2 > TR$
$FR < TR$
$FR_2 > FR_1 > TR$
(d)
AREA (eg., DEPTH) 2
THRESHOLD RESPONSE (TR)
HUNGER (H)
(e)

FIGURE 48

surface versus mid-water depth in the water column, or the head versus tail of a pool. Within a given area the response to prey (functional response) is here shown as the number of prey eaten, although other indices could be appropriate. The functional response is related not only to drift rate and hunger (a), but also to exposure time because of the period required to gain familiarity with the prey. Based on the experiments in the present study, large prey are ultimately selected over small prey when available simultaneously in the same area, and the responses are essentially parallel (b). In the model, <u>selection</u> among prey species within a given area is not directly influenced by hunger. However, the hypothetical effect of hunger on prey <u>intake</u> can be seen by contrasting the functional response for a given drift rate and hunger state (b) with that for a given drift rate (c).

A threshold total drift rate (TTD) is hypothesized, below which feeding does not occur. While not essential to the model, such a threshold was suggested by preliminary experiments in which brine shrimp presented at a drift rate of less than about 5/minute were not attacked even though the trout were familiar with them and had not been fed for 24 hours. The fish did attack when the drift rate was raised to 15/minute. Circumstantial field evidence (personal observation) also points to some lower limit to the number of drifting prey that will elicit feeding behavior by trout, even when they are familiar with the prey. The threshold might be dependent on prey size; it seems reasonable that fewer large items would be required to simulate feeding than would small items. One could also hypothesize that feeding by other fish might lower the threshold for a given fish. Social facilitation of feeding (e.g., Turner, 1964; Olla and Samet, 1974) would then enter the model.

Movement between areas (d) is shown to be related to a threshold value (TR) of the functional response. The trout tends to remain in an area as long as the functional response exceeds TR. A threshold can permit fine discrimination, or assessment, between areas of differing prey densities if periodic sampling of different areas occurs. Such sampling was evident in the laboratory, where at least some brine shrimp were taken at all depths throughout the experiments, even though 70 percent of the brine shrimp and all of the alternate prey were found in the upper half of the water column. In natural streams, abundant opportunity exists for periodic sampling of different areas. For example, in feeding at the surface, trout may pass through several depth strata in the course of approaching and attacking prey. Predation on emerging insects may also lead fish to upper strata as a consequence of upward pursuit. In this instance, periodic sampling of different areas becomes the indirect consequence of prey behavior.

TR is not regarded as fixed, but as a quantity that can increase within certain limits as a direct effect of hunger. The relationship of TR to hunger shown here (e) is largely hypothetical, but some evidence has shown that distance traversed/time by sticklebacks searching for food decreases with satiation, though even satiated fish performed some searching movements (Beukema, 1968). This relationship is not essential to the model, but it may prove a fruitful consideration in future research.

While the search image concept is not included in the graphical presentation, it does seem likely that prey detection often plays a significant role in the response to a prey species. Variation among individuals in the selected diet may, in part, be explained on the basis of the chance encounters needed to detect a new prey item. Bryan and Larkin (1972) have shown that individual trout in a small stream and in experimental ponds may exhibit small but significant differences in their selected diet, and that these differences persist to result in "food specialization". The results were evidently not attributable solely to heterogeneous distribution of prey. Their explanation for specialization was that individuals differ in the probability of detecting a particular kind of prey, because of differences in searching technique, capturing technique, and feeding rhythm. Taking the search image point of view, these behavioral differences could result from initial learning by individuals of different prey species encountered by chance. Interaction among individuals may also have played a role in bringing about specialization, as the authors did observe frequent agonistic displays among fish. Further investigation into the extent and causation of individual differences in prey selection appears to be a promising area of research.

One outcome of the model proposed here is that we can expect fish temporarily to remain in areas of low prey density if the prey are very familiar there. If the temporal availability of prey differs between areas, we can also expect cases in which a small prey item is temporarily selected even though a large and abundant species is available in another area. Even within a given area small, familiar prey can be expected, initially, to be selected over large, novel items. These expectations are based on the time required to gain experience with the prey. They point to the necessity of relatively long-term studies in investigations of selective feeding. Conclusions drawn from a brief examination of the selected diet will not only be incomplete, but misleading as well. Failure to provide for temporal changes in the diet is one of the major inadequacies of models such as those proposed by MacArthur and Pianka (1966) and Rapport (1971).

A major criticism of Holling's (1965) predation model has been the difficulty of assessing the effects of fluctuating prey densities (Krebs, 1973). Although the same criticism could be made of the present model, it is instructive to hypothesize the consequences of a change in available prey. For example, if the ratio of small:large prey suddenly changed from 1:1 to 5:1, a response pattern such as that shown in Fig. 49 might be expected. Based on knowledge of rates of learning and forgetting in trout, it should eventually be possible to develop a model to predict the response to changing prey abundances. These predictions could then be compared with results of laboratory experiments in which trout are exposed to sudden changes in prey density.

For the present, one can speculate that responses to prey may not keep pace with changes in prey abundance or availability. This suggests a fruitful field of research, for both aquatic entomologists and fish ecologists. A delayed response to suddenly abundant prey would suggest that nearly simultaneous emergences (characteristic of many mayflies and stoneflies) permit large numbers of prey to escape before trout fully respond. On the other hand, very prolonged emergence patterns (e.g., some caddisflies) may function to keep densities below the threshold (TR in the model) required to keep a fish in the area, and/or may inhibit the development of familiarity with the prey. Detailed studies of the behavior of representative aquatic insects at each relevant stage of their life history could reveal other mechanisms that serve to inhibit the response of fishes to changes in prey availability.

Except for the study by Horton (1961) in an English stream, where from 14 percent (Protonemura meyeri) to 37 percent (Amphinemura sulcicollis) of the emerging stoneflies were eaten by brown trout, little is known of

FIGURE 49. Hypothetical pattern of response to a sudden change in relative numbers of large and small prey.

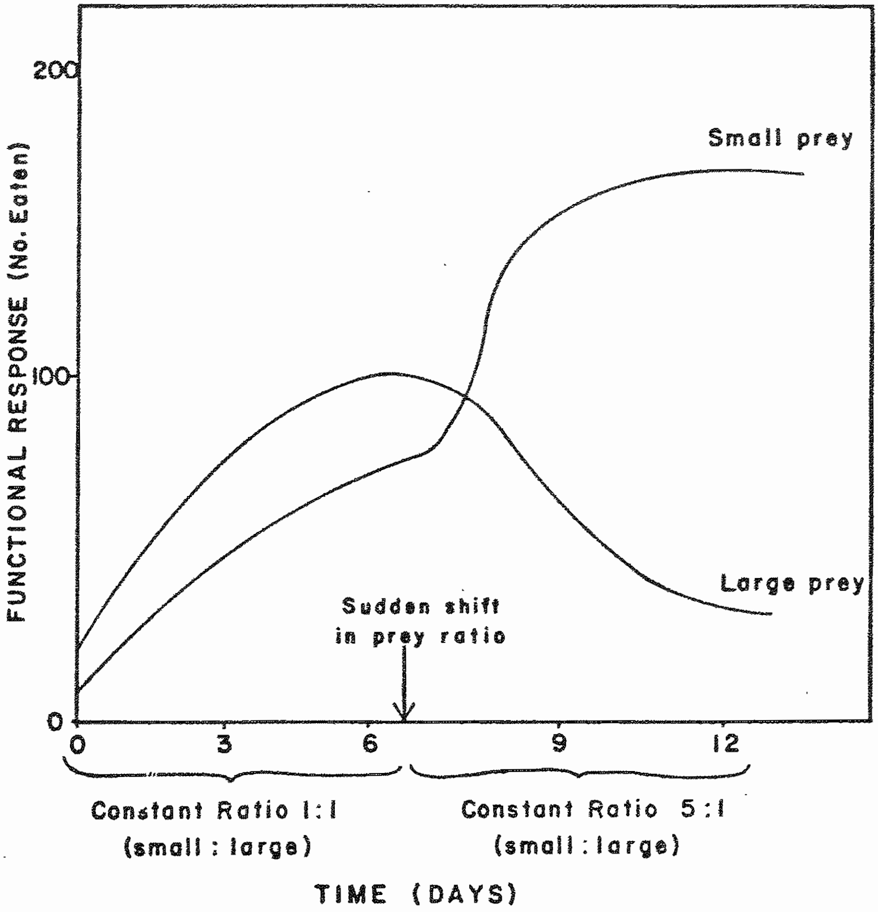
FUNCTIONAL RESPONSE (No. Eaten)
200
100
0
0
3
6
9
12
Small prey
Large prey
Sudden shift in prey ratio
Constant Ratio 1:1 (small : large)
Constant Ratio 5:1 (small : large)
TIME (DAYS)

FIGURE 49

the impact of trout predation on emerging insects. For some aquatic insect larvae predation due to other insects is probably much greater than that due to fish,[3] but this is not likely to be the case for emerging adults. Perhaps environmental factors other than fish predation, particularly predation by birds and adverse weather conditions, are of overriding importance to emerging insects. Whether trout "anticipate" predictable patterns of availability (emergences) has evidently not been investigated. Initially ecologists should probably consider relatively simple functions of the trout's response to prey size, density, and spatial distribution. If our predictions remain inaccurate, then investigations of more subtle learning processes are called for. Even for biologists mainly interested in behavioral capabilities, however, integrated knowledge of the kinds of processes treated in this paper will be a necessary basis for investigation.

Selective Feeding as an Optimum Strategy

That the predator behaves in a manner to maximize fitness in an evolutionary sense is a stimulating point of view in studies of selective feeding. Application of optimization theory, however, usually involves the simplifying assumption that it is the caloric content of the

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[3] W. P. Kovilak. Personal communication. The University of Michigan. August, 1974.

diet that should be optimized. My experimental results showed that brown trout ultimately approached a hypothetical optimum, but this occurred over a relatively long period. This period was probably exaggerated in the laboratory because prey were presented for only 30 minutes per day. While such brief emergence periods do occur in natural streams, this is the lower end of a spectrum extending to at least four or five hours for a single species.

Another factor that probably exaggerated the period required for a maximum response was the prolonged exposure to brine shrimp prior to the introduction of (calorically) more desirable prey. This prior exposure consisted of several weeks in the holding facility plus one or two days in the experimental stream. The new prey were then introduced suddenly at a constant rate. During natural insect emergences a few individuals begin to appear on a given day, and the number increases daily to a peak, followed by a gradual decline. From the model, we expect that some threshold drift rate (TTD) must exist before <u>attacks</u> are initiated. We cannot assume, however, that prey in numbers below the threshold have no effect on the fish. In the laboratory I have observed lateral eye movements that indicated a response by the trout long before any overt feeding occurred. In nature, then, the response to a suddenly abundant prey item may be much more rapid than might be inferred from the available data. Nevertheless, because of the time required to gain familiarity with the prey, we can expect to find some departure from an optimal caloric intake.

Although selective feeding did ultimately lead to 70-90 percent of the hypothetical optimum, the pattern of the response showed little indication that 100 percent would ever be reached. According to the feeding model, trout periodically sample areas of low density, as well as species of low caloric content. Such sampling appears to represent a "cost" to the animal. Yet, in the context of heterogeneous spatial and temporal distribution of prey, this cost is probably essential to an overall optimum feeding strategy. Leaving areas of high density permits sampling of areas where density may have recently become even higher. Within a given area, periodic sampling of even the least desirable prey (e.g., brine shrimp) may function to maintain the ability to respond rapidly to subsequent changes in abundance. Thus, because of constraints imposed by the distribution of the prey and the behavioral capabilities of the predator, an optimal feeding strategy need not be directly reflected in an optimization of caloric intake.

The model proposed here is only a provisional representation of our knowledge of selective feeding. Formulation of the model and consideration of some of its consequences, however, have shown that studies of the mechanism of selective feeding can provide significant insights into predation processes. Combining the concept of an hypothetical optimum with an investigation of the mechanism of attaining that optimum proved to be a meaningful approach. It is hoped that this kind of approach will be useful in future analyses of the evolution of predator-prey relationships, and in developing meaningful models of a variety of predator-prey systems.