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Flexible search tactics and efficient foraging in saltatory searching animals

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Summary. Foraging is one of the most important endeavors undertaken by animals, and it has been studied intensively from both mechanistic-empirical and optimal foraging perspectives. Planktivorous fish make excellent study organisms for foraging studies because they feed frequently and in a relatively simple environment. Most optimal foraging studies of planktivorous fish have focused either on diet choice or habitat selection and have assumed that these animals used a cruise search foraging strategy. We have recently recognized that white crappie do not use a cruise search strategy (swimming continuously and searching constantly) while foraging on zooplankton but move in a stop and go pattern, searching only while paused. We have termed this *saltatory search.* Many other animals move in a stop and go pattern while foraging, but none have been shown to search only while paused. Not only do white crappie search in a saltatory manner but the components of the search cycle change when feeding on prey of different size. When feeding on large prey these fish move further and faster after an unsuccessful search than when feeding on small prey. The fish also pause for a shorter period to search when feeding on large prey. To evaluate the efficiency of these alterations in the search cycle, a net energy gain simulation model was developed. The model computes the likelihood of locating 1 or 2 different size classes of zooplankton prey as a function of the volume of water scanned. The volume of new water searched is dependent upon the dimensions of the search volume and the length of the run. Energy costs for each component of the search cycle, and energy gained from the different sized prey, were assessed. The model predicts that short runs produce maximum net energy gains when crappie feed on small prey but predicts net energy gains will be maximized with longer runs when crappie feed on large prey or a mixed assemblage of large and small prey. There is an optimal run length due to high energy costs of unsuccessful search when runs are short and reveal little new water, and high energy costs of long runs when runs are lengthy. The model predicts that if the greater search times observed when crappie feed on small prey are assessed when they feed on a mixed diet of small and large prey, net energy gained is less than if small prey are deleted from the diet. We believe the model has considerable generality. Many animals are observed to move in a saltatory manner while foraging and some are thought to search only while stationary. Some birds and lizards are known to modify the search cycle in a manner similar to white crappie.

Key words: Optimal foraging behavior – Predation cycle – Behavioral ecology – Saltatory search

The development of optimal foraging theory (MacArthur and Pianka 1966; Emlen 1966) has stimulated considerable research on the feeding ecology of various organisms (Kamil et al. 1987; Stephens and Krebs 1986). Pyke (1984) has recently shown that papers dealing with the subject have been increasing at a nearly exponential rate. The appeal of the approach is that by focusing on aspects of behavior presumed to have been honed by evolution (those most critical to the organism's survival) models that predict the feeding of animals can be generated quickly (Schoener 1971). This view has not been accepted with unanimity (Pierce and Ollason 1987).

Many of the mechanisms suggested for optimal foraging have been difficult to test rigorously because animals do not exhibit an efficient to inefficient feeding gradient. Rather, natural selection has left only those species and individuals that are efficient (Levins 1975; Stearns and Schmid-Hempel 1987) and thus, it is perhaps more appropriate to ask "how do animals manage to forage efficiently?" rather than "are animals optimal?"

The study of feeding behavior in many predators has been hampered somewhat by difficulties in observing their behavior under controlled, yet near natural conditions. Planktivorous fish, however, are excellent study species because their natural environment can be reasonably well simulated in the laboratory. In nature, they feed in an environment which has little or no visible structure and their zooplankton prey are generally randomly distributed over the scale of their vision and feeding (Curio 1976; Greene 1983). Because zooplankton are small relative to their own size, the fish must feed frequently, depending primarily upon vision to locate their prey. Thus, experiments on the foraging behavior of planktivorous fish, and insights and models resulting from them, may be useful to a more general understanding of foraging in animals more difficult to study.

Visually mediated foraging has been well studied in freshwater fish, particularly planktivores (Ivlev 1961; Laz-

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zaro 1987; O'Brien 1987). The fish's ability to locate prey has commonly been assessed by measuring their reaction distance to particular prey in a particular environment (e.g. Werner and Hall 1974; Confer and Blades 1975; Vinyard and O'Brien 1976). Such work has shown that planktivorous fish can locate larger prey at greater distance and that prey pigmentation and motion (Wright and O'Brien 1984) can greatly increase location distance. Visually mediated prey choice behavior of planktivorous fish has also been examined (O'Brien et al. 1976, 1985; Wetterer and Bishop 1985), though there remains uncertainty about precise mechanisms.

To date, most work on optimal foraging in zooplanktivorous fish has focused either on diet choice (Werner and Hall 1974; Gardner 1981; O'Brien et al. 1976) or habitat choice (Werner and Hall 1977; Werner et al. 1981; Mittelbach 1981; Werner et al. 1983a, b; Mittelbach 1983). Ware (1975a) suggested that, by altering swimming speed (and presumably search rate), fish can optimize foraging. However, Gendron and Staddon (1983) pointed out that visual search ability may decrease at high speeds. There has been little theoretical work on animal foraging movement patterns or speed of movement (but see Norberg 1977, 1981; Anderson 1981; Pyke 1984; Speakman 1986; Pierce 1987); what little there is generally involves area-restricted search. The movement patterns of bees have been analyzed (Pyke 1978), but their foraging paths are largely mediated by the choice of which inflorescences to visit next. The effects of alterations in foraging movements on foraging efficiency in planktivorous fish have not been explored.

In recent work (Evans 1986; O'Brien et al. 1986; Evans and O'Brien 1986; Evans and O'Brien 1988), we have called into question the long held view that planktivorous fish are cruise searchers (Ivlev 1961; Ware 1975a; Confer and Blades 1975), and the belief that pauses in the search-pursuit-attack cycle are required for prey "handling" (Werner and Hall 1974). Rather, we have found that the two freshwater planktivorous fish we have studied intensively, white crappie and arctic grayling, search briefly while stationary and, if they do not locate a prey, swim a short distance before stopping to search again (O'Brien et al. 1986; Evans and O'Brien 1988). The crappie search briefly during the pause immediately following an attack and ingestion of a prey, while arctic grayling go directly into a run. In neither case is time taken from the predation cycle to handle prey for ingestion. We have introduced the term *saltatory search* to describe this alternation between swimming and stopping to search. Saltatory movement patterns associated with foraging have been observed in other fish species (Kleerekoper et al. 1970; Janssen 1982; Ehlinger 1986).

Saltatory movement patterns are not unique to fishes. They are commonly observed in ground-foraging birds (Heppner 1965; Cody 1968, 1971; Baker 1974; Smith 1974a, b; Brownsmith 1977; Myers et al. 1980; Pienkowski 1983). In addition, boreal foraging birds, which glean small insects from leaves and branches, move in a saltatory manner (Eckhardt 1979; Landres and MacMahon 1980; Robinson and Holmes 1982; Moreno 1984). The perch-to-perch movements of birds foraging on flying insects is also a saltatory movement pattern (Davies 1977; Fitzpatrick 1981; Robinson and Holmes 1982). Even head-bobbing in pigeons can be interpreted as a form of saltatory movement; the head remains motionless for a brief period while the body moves continuously forward, and then the head rapidly follows (Frost 1978). Lizards, while generally categorized as sit-and-wait predators (Huey and Pianka 1981), clearly show saltatory movement patterns while foraging (Moermond 1979, 1986; Huey and Pianka 1981; Anderson and Karasov 1981; Pietruszka 1986). Some mammals (Kenagy 1974) and insects (Miller 1979) also use a stop-and-go movement pattern while foraging.

Several investigators were convinced that the birds (Smith 1974a, b; Fitzpatrick 1981; Pienkowski 1983), lizards (Moermond 1979) or fish (Janssen 1982) they studied searched only while paused. However, none present data that addresses the issue of whether search does or does not occur during the movement phase of the search cycle, as has been determined for two species of planktivorous fish (O'Brien et al. 1986; Evans and O'Brien 1988; O'Brien et al. 1989).

White crappie not only move in a saltatory manner while foraging, and search only while paused, they also alter various components of the saltatory search cycle when feeding on prey of different sizes (Evans 1986; Evans and O'Brien 1986; O'Brien et al. 1986). To evaluate the efficiency of these alterations, the foraging behavior of white crappie was closely examined, and a simulation model was developed to analyze the advantages of different repositioning distances, speeds, and search times when feeding on large and small prey. The tradeoffs are fairly clear; the further the fish swims, the more new water it will be able to search when it stops, up to the maximum location distance of the largest prey likely to be encountered. However, during a run, the fish expends energy in swimming and loses time from search because it is not searching while moving. Given these tradeoffs, there should be an optimal run distance and speed which is dependent upon the types and sizes of prey available.

Laboratory observations

Methods

Search behavior of white crappie was quantified by videotaping four fish (9–15 cm TL), feeding two at any given time, in a 90 × 90 cm glass aquarium filled to a depth of 30 cm. Having two fish in the aquarium seems to relax them, although crappie do not school, and we rarely observe any interference behavior. These methods and results have been reported in detail by Evans and O'Brien (1986), O'Brien et al. (1986), and Evans (1986). The variable that affected search behavior and the geometry of the location space most was prey size. Small prey consisted of lake zooplankton, mostly small daphnids, *D. galeata* and *D. ambigua,* which varied in size from 0.6 to 1.5 mm. Large prey consisted of the lab cultured daphnids, *D. magna* and *D. pulex*. The *D. magna* varied in size from 3–4 mm while *D. pulex* varied from 2–3 mm. Experiments were performed with large or small prey exclusively and combined, generally with small prey at densities of 5–15 l^{-1} and large prey at 0.1–1.0 l^{-1}.

Videotapes were analyzed by assigning actions to one of the components of the fish feeding cycle: search (successful and unsuccessful), run, or pursuit (which included attack) (Fig. 1). A run is operationally defined as a repositioning movement that does not end in a pursuit. As discussed by O'Brien et al. (1986), crappie search following pursuit of prey and take no time from the search cycle to handle

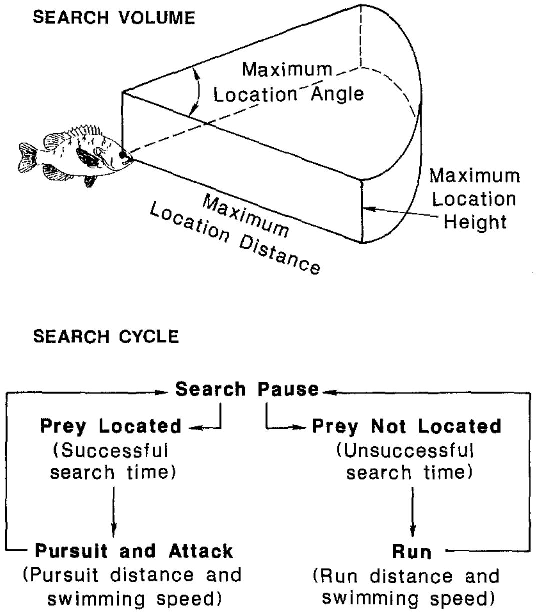

Fig. 1. The search volume and search cycle of white crappie. The dimensions of the search volume are given in the top portion of the Fig. The components of the search cycle (*bold letters*), as well as the parameters measured, are given in the bottom portion of the Fig.

prey. The duration of each component – successful search time (SST), unsuccessful search time (USST), pursuit time (PT) and run time (RT) – was timed from the videotapes using a Cronus digital stop watch. The distances measured on the monitor, run length (RL) and pursuit length (PL), were converted to absolute distances by multiplying the ratio of actual fish length to monitor fish length (Table 1).

Since the fish stop to search and then swim out to pursue a located prey, the shape and dimensions of the location space may be determined from observations of many pursuits. The angles and distances of pursuits were plotted on polar coordinate maps. The location angle was determined by taking the area of this map within which 95% of the pursuits occurred. The location space is shaped much like a pie wedge with the location angle being the angle of the pie wedge; thus, half a pie would have a location angle of 180°. The location distance (LD) is the average of the longest 10% of observed pursuits in the horizontal plane, excluding obvious outliers (Evans 1986; Evans and O'Brien 1986). The location height (LH) is the height of a plane, parallel to the horizontal plane of the fish, which encompassed 95% of the pursuits in the vertical plane.

Results

The video observation analysis provided estimates of the seven parameters used in the search cycle model: 3 dimensions of the location space (location distance, LD, location height, LH, and location angle, LA) and the duration of the four components of the search cycle (unsuccessful search time, USST, successful search time, SST, run time, RT, and pursuit time, PT). All abbreviations that appear in the text are listed at the end of the article.

The key element in the white crappie search cycle is that search only occurs while the fish is stationary after a run or pursuit (Fig. 1). However, the actual distances, speeds and time involved in the search cycle, and the dimensions of the location space, change as crappie feed on large or small prey. When feeding on large prey, not only are LD and LH greater than for small prey, but LA is greater as well (Table 1).

Table 1. Search cycle parameters and location volumes for white crappie feeding on large and small daphnids. Values are taken from Evans (1986); O'Brien et al. (1986)

	Small prey	Large prey
Location distance (cm)	8	20
Location height (cm)	4	10
Location angle (°)	40	90
Run length (cm)	5.18 ± 0.73	9.8 ± 2.15
Swim speed (cm/sec)	6.3 ± 0.65	14.3 ± 2.03
Unsuccessful search time (sec)	1.65 ± 0.56	0.55 ± 0.32
Successful search time (sec)	1.36 ± 0.70	0.29 ± 0.20

White crappie also behave differently when feeding on different prey types. When encountering large prey, the fish swim further and faster during a run or pursuit than when feeding on small prey (Table 1). Unsuccessful and successful search times are both briefer when feeding on large prey versus small prey (Table 1). When both large and small prey are present at the same time, the location space and search pattern observed are the same as those exhibited when only large prey are available.

These observations have led us to pose the following questions for white crappie feeding on the different prey sizes and abundances. Are the run distances observed those that maximize net energy gain? Is it advantageous to increase swimming speeds (SS) when feeding on large prey, even at the cost of extra energy expenditure? Is it efficient to ignore small prey when large prey are also available? To answer these questions, we developed a simulation model of the search cycle and energy budget of white crappie.

Model development

Methods

The current foraging model is a modification of traditional net energy gain models (e.g. MacArthur and Pianka 1966; Emlen 1966; Speakman 1986) combined with an iterative stochastic subroutine to compute the likelihood of successful prey location (i.e. a mechanistic model). The model's currency is thus net energy maximization, and the decision variables are run length, run speed and search time.

The net energy gain model is:

$$\mathrm{NEG} = \frac{E_{\mathrm{I}} - E_{\mathrm{E}}}{T_{\mathrm{T}}} \qquad (1)$$

where (E_{I}) equals total energy input, (E_{E}) total energy expenditures, and (T_{T}) the total time taken to acquire the number of prey eaten. Further,

$$E_{\mathrm{I}} = P_{\mathrm{I}} \times e_{\mathrm{p}} \qquad (2)$$

$$E_{\mathrm{E}} = (\sum \mathrm{USST} + \sum \mathrm{SST})\, e_{\mathrm{r}} + (\sum \mathrm{RT} + \sum \mathrm{PT})\, e_{\mathrm{s}} \qquad (3)$$

$$T_{\mathrm{T}} = \sum \mathrm{USST} + \sum \mathrm{SST} + \sum \mathrm{RT} + \sum \mathrm{PT} \qquad (4)$$

where P_{I} is the total number of prey ingested, e_{p} is the energy content of each prey, $\sum$USST is the total unsuccessful search time, $\sum$SST is the total successful search time, e_r is the energy cost of resting (not moving) metabolism, $\sum$RT is the total run time, $\sum$PT is the total pursuit time and e_s is the energy cost of swimming. RT and PT times are calculated by dividing RD and PD by swimming speed (see definitions).

The likelihood of a search being unsuccessful and then followed by a run, or of being successful and then followed by a pursuit and prey ingestion, is dependent upon the location probability (LP), the probability of there being one or more prey in the location space. For a given location space, here a volume, as prey density increases visual density (VD) (i.e. the density of prey within the search volume) increases, and the likelihood of successful search goes up. VD also changes as a function of run length (RL) because RL determines the volume of unsearched water (SV_u). When RL is short relative to LD, little new water is searched and search volume (SV_u) is low relative to the maximum search volume (SV_{MAX}). When RL is $\geqq$LD, $SV_u = SV_{MAX}$.

If a prey is located, a pursuit is initiated. PD is a random variable adjusted to reflect the greater area at the periphery of the search volume than near the apex. If, in a given search bout, a prey is not located, a run is initiated. RL was varied systematically, by 1 cm increments, from 2 cm up to LD. To compute the probability of 1 or more prey being present in the search volume the model first computes the maximum search volume (SV_{MAX}) for the one (or two) sizes of prey that are simulated:

$$SV_{MAX} = (LD \times LD \times LH) \times TH \qquad (5)$$

TH = LA/2 (radians). The location angles and location heights for large and small prey are given in Table 1. The length of the search "wedge" is equal to the LD for the size of prey and light intensity simulated (Fig. 1). For 1.0 and 2.5 mm daphnid prey at high light intensity (300 lx) the location distances used were 8 and 20 cm respectively. Multiplying the search volume (SV_{MAX}) by the absolute density (AD, numbers per liter) yields an estimate of VD for each prey size.

$$VD = AD \times (SV_{MAX}) \qquad (6)$$

The likelihood of a successful search is a stochastic function,

$$LP = (1 - e^{-VD}). \qquad (7)$$

LP is computed as 1 minus the probability that the search volume is empty and compared to a random number, RND. If LP < RND, then no prey were located and the model adds USST to total time and implements a run. If LP > RND, the model adds SST to total time, implements a pursuit, and adds 1 to total prey consumed. LP varies linearly with low values of visual density. However, as VD nears 0.2 the location probability deviates from a linearly increasing visual density and asymptotically approaches 1 as VD increases further.

For straight-ahead movement (Case 1 in Appendix A), the volume of water previously searched, (SV_R), is given by

$$\begin{aligned} SV_R = {} & [RL^2 \operatorname{Cos}(TH) \operatorname{Sin}(TH) + LD^2(TH) \\ & - (RL)\operatorname{Sin}(TH)[LD^2 - RL^2 \operatorname{Sin}^2(TH)]^{\frac{1}{2}} \\ & - LD \operatorname{Arc\,Sin}(RL \operatorname{Sin}(TH)/LD)] \times LH. \end{aligned} \qquad (8)$$

Table 2. Energy inputs and expenditures used in model simulation of white crappie feeding

	Small prey	Large prey
Prey energy content (cal)	0.0144	0.378
Cost of search (cal/sec)	0.0007	0.0007
Cost of run and pursuit (cal/sec)	0.003	0.006

The volume of new, unsearched water (SV_u) for a given RL was computed by subtracting that portion of the search volume previously searched (SV_R), from the full search volume (SV_{MAX}):

$$SV_u = SV_{MAX} - (SV_R) \qquad (9)$$

SV_u is then substituted into equation 6 and the probability of the two possible outcomes are determined as described above.

Because we were unable to obtain estimates of energy expenditures associated with turns, they were not modelled. However, the mathematical solutions for overlapping search volumes that would result from turns are presented in Appendix A.

With respect to choice, we dealt only with the efficiency of choosing to pursue or not to pursue small prey when large prey were available, but not located on a given search. If the large prey was located it was always pursued and ingested. However, if a large prey was not located then the chance of locating the small prey was assessed. The time involved in locating small prey was handled in two ways. In one simulation, no extra search time was assessed in searching for small prey over that already assessed for searching for large prey. In the other case, extra time was assessed in searching for small prey. The extra time assessed were the SSTs and USSTs for small prey as observed and measured in the laboratory (Table 1), less the USST for large prey (already assessed).

The caloric content of daphnid prey was taken from Cummins and Wuycheck (1971). Other important model inputs are energy expenditures for stationary searches, runs and pursuits (Table 2). Search time and swimming speeds varied depending upon prey type (Table 1). Resting metabolism values used in the model to estimate cost of search are (0.0007 cal/sec) Evans and O'Brien (personal communication). The energy values for the cost of swimming were estimated by increasing the resting metabolism by a factor of 4.2 to 0.003 cal/sec for swimming while feeding on small prey (7 cm/sec) and doubling that value to 0.006 cal/sec to account for the faster swimming speed while feeding on large prey (15 cm/sec) (Brett and Sutherland 1965).

At the end of a specified number of successful searches (generally 10,000) the program sums all energy intakes and expenditures. It then computes net energy gain per unit time by subtracting energy expenditure from energy intake and dividing by the total time (Eqn 1).

The efficiencies of various run lengths were determined by running the model, using RLs from 2 cm to LD, and calculating the NEG for each specific RL. The NEG of various run speeds, with different energy costs associated with each speed, were also computed across various RLs. The NEG for different small prey search times, when large prey are also present, were also computed across various RLs.

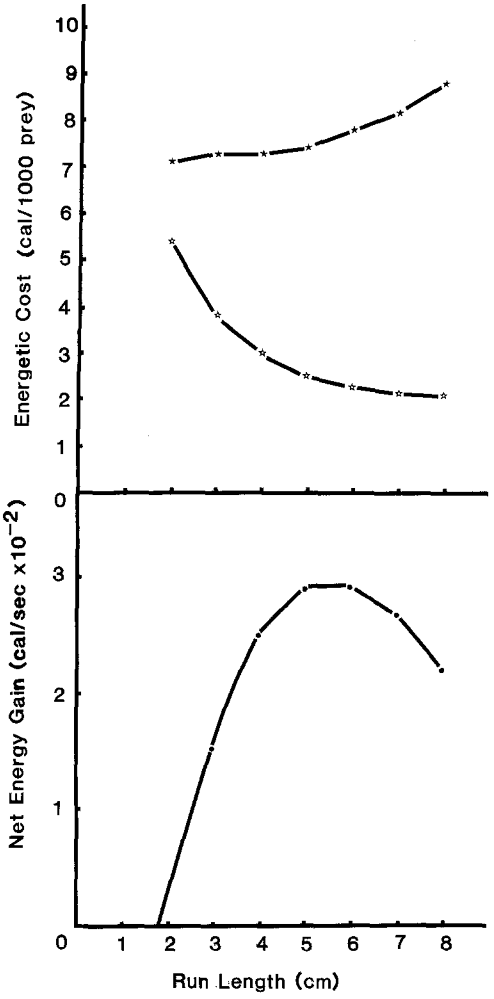

Fig. 2. Predicted net energy gain under varied run lengths when small prey were simulated (*bottom panel*). The predicted energy costs of unsuccessful search time (USST; *open stars*) and run time (RT; *closed stars*) under varied run lengths when small prey were simulated (*top panel*)

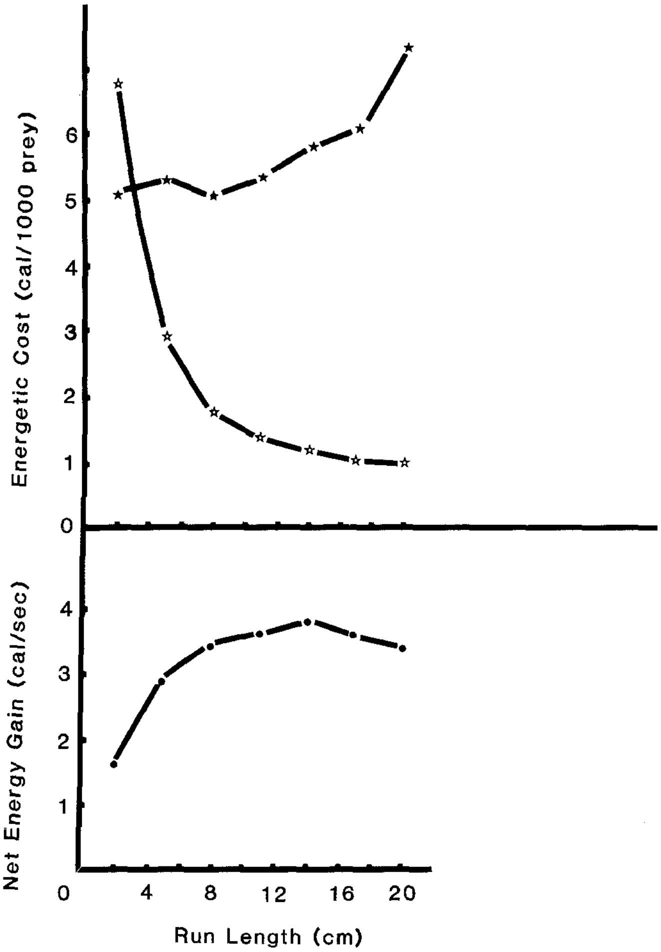

Fig. 3. The predicted net energy gain under varied run lengths when large prey were simulated (*bottom panel*). The predicted energy costs of unsuccessful search time (USST; *open stars*) and run time (RT; *closed stars*), under varied run lengths when large prey were simulated (*top panel*)

Results

When simulating feeding on small prey the model predicted maximum net energy intake at a run length of 5.5 cm (Fig. 2), while mean run lengths of 5.2 cm were observed. For large prey, the model predicted maximum net energy gain at a run length of 13.5 cm (Fig. 3), while mean run lengths of 9.8 cm were observed. The net energy gain curve is flatter with a rich resource such as large daphnids.

The property of the model that results in a maximum net energy value is the changing relationship between the cost of USST and the cost of increasingly longer runs. At short RLs, little unsearched water is revealed after each run; thus, the likelihood of successful search is low. As a result, most searches are unsuccessful and search costs are high (Figs. 2 and 3). However, because these runs are short, their energetic cost is relatively low. With increasingly longer runs, more unsearched water is revealed and more searches are successful, although run cost increases. Run cost changes only slightly at the shorter RLs because, while they are short and thus not energy costly there are many of them due to numerous unsuccessful searches (Figs. 2 and 3). The higher energy costs of long runs results in increased overall energy expenditure.

If the swimming speed and the cost of swimming are increased by the same percentage, (i.e. both doubled) the model predicts that it is always more efficient to swim faster even with the additional energy cost. This is because the energy cost for swimming a given distance remains constant, but the distance is traversed in less time. Therefore, if the fish could swim at twice the speed (and twice the cost), this should be adaptive in terms of cost per unit time. Of course, there are other constraints that restrict such a strategy. If a more reasonable assumption of doubling the swimming speed and quadrupling the cost of swimming this fast is applied, the model predicts reduced efficiency for the small prey diet. The small prey diet is close to a break even point and can not support increased energetic costs.

Interestingly, for the larger prey diet the cost of swimming for runs and pursuits can be quadrupled, the swimming speed doubled, and yet more net energy is gained than at the lower speeds and costs. While such a strategy does increase the energy expended somewhat, it halves the

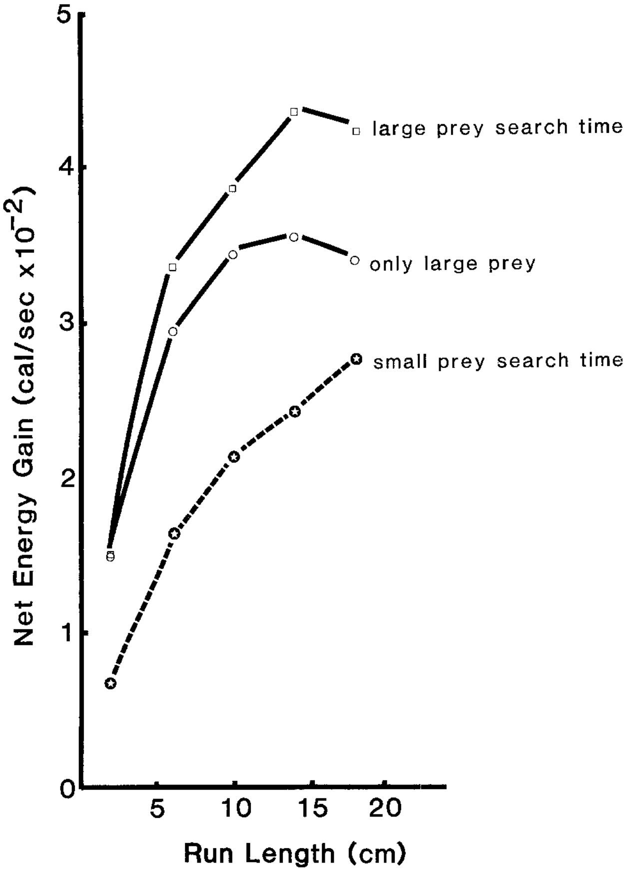

Fig. 4. The net energy gain under different assumptions of small prey inclusion in the diet. The simulation illustrated with open circles represents the net energy gain when only large prey are considered. The two other curves demonstrate whether net energy gain is increased or decreased when small prey are included in the diet but search times vary. The open squares illustrate the net energy gain when small prey are searched for and pursued if located, when large prey are not located. In this case no time, in addition to that already used to search for large prey, is assessed for search of small prey. The stars show the net energy gain when small prey are searched for and pursued if located, when large prey are not located. However, in this case the extra search time observed when white crappie feed on small prey is assessed

time spent in run or pursuit. This is in part due to the brief and generally successful search times with large prey as well as longer run and pursuit distances with large prey compared to small prey.

We have not dealt with choice among several simultaneously located prey because this may be uncommon in natural circumstances (O'Brien et al. 1986). Furthermore, even after much research and discussion it is still not clear what mechanism(s) planktivorous fish employ in choosing among several simultaneously located prey (Wetterer and Bishop 1985; O'Brien et al. 1985). We did, however, investigate the efficiency of ignoring small prey when large prey are available. First, net energy gain when feeding on large prey with no small prey present was simulated (Fig. 4). The next scenario simulated was that in which large prey were present, but if not located, small prey (if located) were pursued. If we assess no extra time to find the small prey, other than that already assessed for searching for large prey, the model predicts greater net energy gain from pursuing small prey if located (Fig. 4). However, we have observed that white crappie take considerably longer to search for small prey than for large prey (Table 1). If this extra time is assessed, the model predicts a reduction in net energy gain compared to a diet of exclusively large prey (Fig. 4). Our preliminary laboratory observations of white crappie feeding with both large and small prey present are consistent with model prediction. When large and small prey are present the fish pause for the same brief period as when only large prey are present, and small prey are rarely pursued. Either the fish do not locate the small prey during brief stationary search or, if located, they are ignored.

Discussion

We have demonstrated that a relatively simple mechanistic model predicts the observed behavior of foraging fish to maximize the rate of net energy gain. White crappie obviously change their run lengths when feeding on large vs small prey and this is clearly efficient. The simulation presented here is significant in that it represents a composite net energy gain – mechanistic feeding model. Though generated from observations of planktivorous fish foraging behavior, this model will be easy to modify for other taxa that forage in a similar manner.

Other animals alter components of their search cycles. Several species, representing a wide range of taxonomic groups, move a distance about equal to the average prey pursuit distance after an unsuccessful search. Seven species of lizards studied by Moermond (1979) all moved a distance very close to their respective prey pursuit distances, even though these varied considerably among the species. After an unsuccessful search, the boreal-foraging birds studied by Robinson and Holmes (1982), and the flycatchers studied by Fitzpatrick (1981), made repositioning movements just long enough to take them into a new scanning field. The flycatchers, feeding on flying insects, moved twice the average pursuit distances, while those gleaning insects from leaves and branches moved to about the average pursuit distance (Fitzpatrick 1981). If the birds foraging on flying insects scan a spherical search space, while those gleaning insects from leaves and branches scan a semicircular search space, then these data are consistent with our model predictions for white crappie (O'Brien et al. 1989).

Plovers foraging on different-sized prey behave in a manner similar to that exhibited by white crappie (Pienkowski 1983). After an unsuccessful search, these birds make repositioning moves about twice as long when feeding on large prey as when feeding on small prey. Pienkowski (1983) observed that the pursuit distance for large prey was about twice that of small prey. Thrushes show a similar response when foraging on cryptic versus easy-to-locate prey (Smith 1974b). When feeding on easy-to-locate prey, they move 78 cm after an unsuccessful search, but only 57 cm when feeding on cryptic prey. Their location distance for cryptic prey is about 60 cm. It is noteworthy that, after the grass in which they searched was cut, the thrushes made longer repositioning movements (Smith 1974b). Foraging starlings also make longer repositioning movements in short grass (110 cm) than in long grass (30 cm) (Brownsmith 1977). These data are all consistent with those we have presented for white crappie.

Several species alter the stationary pause preceding a repositioning move when faced with different sized prey, or a more complex environment. Plovers paused for a longer period when foraging primarily on small prey (Pienkowski 1983). Starlings paused for an average of 1.7 s in tall grass but only 1.2 s in short grass (Brownsmith 1977). Two species of flycatchers also increase pause time in a complex environment (Fitzpatrick 1981). Janssen (1982) found that the duration of "hover-search" in bluegill sunfish decreased with increasing prey size. Ehlinger (1986) and Ehlinger and Wilson (1988) have reported that bluegill foraging among vegetation exhibit longer pauses than fish foraging in open water.

The model also predicts that white crappie should increase run and pursuit speeds when feeding on large prey but not when feeding on small prey. Crappie do in fact increase run and pursuit speeds, although the model predicts that they should swim faster, even if the respiration cost is increased four-fold when feeding on large prey. We have not, however, considered the energy and time costs associated with braking; at very rapid swim speeds such costs could be considerable (e.g. Webb 1975, 1984).

White crappie should ignore sufficiently small prey if large items are available, and there is a significant time cost associated with searching for small items. This result is consistent with the predictions of Werner and Hall's (1974) optimal foraging model. Under laboratory conditions, when both large and small prey are available, the crappie spend the same time searching as when feeding on large prey alone. Thus the "choice" not to feed on small prey may simply be the result of insufficient time to locate them during the brief, large prey search interval. Not only is the search shorter when crappie feed on large prey, but they are searching up to 35 times more water compared to the small prey search volume (Fig. 1, Table 1). It should be noted that under field conditions large sized prey are only available to white crappie at dawn when *Chaoborus* are high in the water column. The guts of fish captured just after dawn contain many *Chaoborus,* but few other prey. Guts of fish captured later in the morning contain many smaller zooplankton (Loveless 1985).

Pienkowski (1983) found that Plovers behave in a manner similar to crappie when feeding on large and small prey. When two sizes of prey were available, the birds appeared to select the large prey, at least they did not respond to small prey. Again, this could indicate either that the birds failed to locate small prey during the abbreviated search pause when both sizes were present, or that they ignored small prey when located. Both thrushes (Smith 1974a, b) and starlings (Brownsmith 1977) show shortened search pauses when prey are more conspicuous, but it is not known how this affects their choice behavior.

Model sensitivity and assumptions

The magnitude of net energy gain is sensitive to changes in prey density and any parameter that changes the search volume. At high prey density and/or large search volume, net energy intake is greater than for low prey density and/or small search volume. Concurrently, the curve of net energy intake versus run length becomes flatter with increased prey density and/or increased search volume. The same run lengths still maximize net energy intake, but longer or shorter run lengths are only slightly less efficient.

Different location heights do not change the geometry of SV as a function of run length; however, changing the search angle does change this geometry. Simulations with search angles of 30° or 180° did not shift the maximally efficient run length more than 0.5 cm from that observed with a 90° search angle.

The model is not sensitive to energy inputs or outputs. Increasing or decreasing either the energy expended or acquired shifts the absolute value of net energy gain but does not alter the prediction of the maximally efficient run length. In a manner similar to its response to changes in prey density or location volume, the model's net energy gain curve may become flatter or more peaked with changes in the assumptions of energy acquired or expended; however, the same maximally efficient run lengths are predicted.

Prey choice among different sized prey located simultaneously was not included in the model analysis because, at the visual densities used, the likelihood of more than one prey being located simultaneously was low. However, when visual densities are high, choice, such as choosing the apparently largest or absolutely largest prey (O'Brien et al. 1976; O'Brien et al. 1985), might also increase net energy gain. Evidence for what "rule of thumb" fish may use to accomplish such choices is still ambiguous.

As in many other optimal foraging models (e.g. Cheverton et al. 1985), the adaptive currency assumed in this model is net energy gain. It is often assumed that net energy intake is directly related to fitness (Pyke 1984). Although small white crappie are not yet at reproductive age, increased body size leads to an increased reproductive output (Nikolski 1969; Ware 1975b). Thus, it would seem that net energy gain should be optimized given no other counterselective pressure.

Another major assumption of the model is that white crappie are capable of altering run length. Crappie definitely alter run lengths in a laboratory arena. However, in the pelagia of lakes there are few cues to judge distance traveled and thus, the mechanism involved in run length regulation is uncertain.

General considerations

Ecologists generally categorize animal search strategies as either "cruise" or "ambush" (Pianka 1966; Ware 1975a; Gerritsen and Strickler 1977; Gendron and Staddon 1983). While some researchers who have dealt with search strategies add that there must be a gradient bridging the two extremes (e.g. Pianka 1978; Speakman 1986; Formanowicz and Bradley 1987), saltatory search is the first intermediate strategy to be explicitly described. The discovery of saltatory search in planktivorous fish implies a gradient of search behavior from ambush to cruise, rather than the dichotomy previously accepted and modeled for foraging fish. At one extreme is ambush predation, characterized by a long motionless period of scanning and then a repositioning move. The primary difference between this and saltatory search is the frequency of repositioning moves. The other extreme, cruise predation, is thought to be characterized by uninterrupted scanning. If, however, cruise searchers actually scan in a series of very brief "snapshots", then the primary difference between this and saltatory search is the duration of the snapshot or, again, the frequency of moves between scans. Arctic grayling (*Thymalus arcticus*), bluegill sunfish (*Lepomis macrochirus*) and white crappie illustrate this gradient. The white crappie seems an archetype saltatory searcher, stopping to scan for an average of 0.3–1.0 sec, depending upon the size of the prey, while bluegill stop for an average of 0.1–0.4 sec (Evans 1986). Arctic grayling, which were previously thought to be cruise searchers, stop to scan for only 0.05–0.2 sec, depending upon the size of the prey (Evans and O'Brien 1988). Thus, a saltatory searcher that makes briefer and briefer search pauses becomes more like a cruise searcher. An ambush predator that makes frequent repositioning moves becomes more like a saltatory searcher.

We have shown that several of the components of saltatory search are efficient, but what of its overall efficiency? A cruise-search strategy might initially seem to be more efficient. However, for cruise search to be more efficient than saltatory search, all of the search volume (or at least the forward-directed boundary) must be searched all of the time. If the fish were able to search only part of the forward-directed boundary while swimming, and/or if increased swimming speeds erodes the location distance (see Gendron and Staddon 1983), cruise (continuous) search would seemingly be even less advantageous. Further, we propose that there may be a particularly elegant advantage inherent in a saltatory search pattern. Foragers must alot their time to conflicting demands (e.g. Ydenberg and Dill 1986; Stephens and Krebs 1986); for example, predator vigilance and scanning for prey. We suggest that a saltatory search pattern may allow for an effective balance between these demands; vigilance for predators would be highest during repositioning movements and lowest during scanning for prey.

These results represent a demonstration of an animal altering specific components of its foraging behavior in a manner consistent with optimal foraging theory. This substantiates the proposal that it is most likely an ability to alter tactics and strategies in the face of changing conditions that enables animals to approach optimality (see Dill 1983, 1987; Ringler 1983; Marcotte and Browman 1986; Browman and Marcotte 1987).

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Appendix A

There are three possible cases for which the search volume of the current scan can overlap that of the preceding scan (see Fig. 5). The conditions under which each case will occur and the mathematical formulae to calculate the areas of overlap, are given below. These formulae yield the area of two-dimensional (i.e. flat) pie wedges. To obtain the actual location volume, these values must be multiplied by the location height.

The following symbols and terms are used:

SV_I = The initial search volume with no consideration given for overlap (bold pie wedge Fig. 5A).

SV_R = The search volume following a run with no consideration given for overlap (the 3 light pie wedges in Fig. 5A).

SV_{RL} = The part of the SV_R which overlaps SV_I in each of the three possible cases (the shaded areas of Fig. 5B–D).

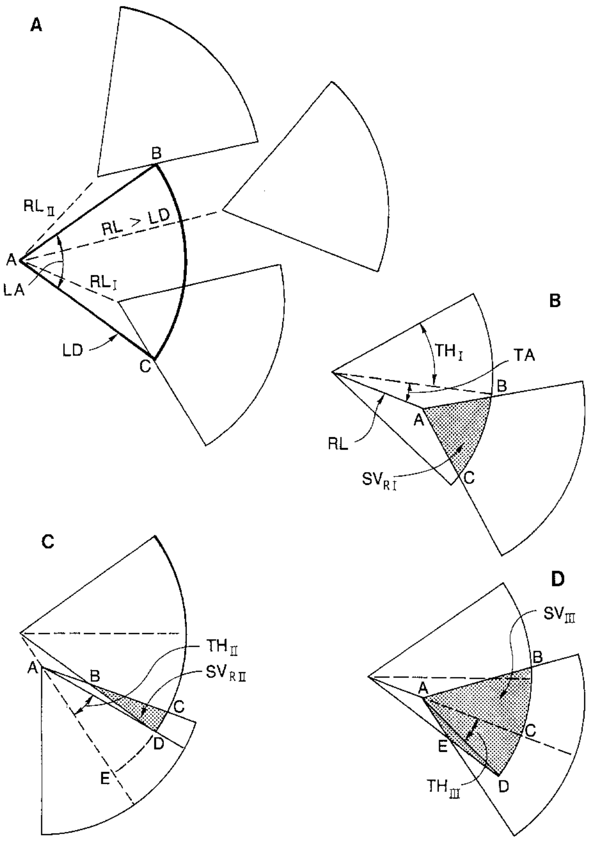

Fig. 5A–D. Diagrams of search volume dimensions and 3 possible scenarios for overlapping visual fields. **A** Diagram showing the dimensions of the search volume (*SV*) and several cases of differing run lengths (*RL*). **B** *Case I*. The simplest case of search volume overlap, for which the new search volume does not intersect the sides of the previous search volume. This is the case simulated in the paper. **C** *Case II*. The situation for which the new search volume projects back into the side of the previous search volume. **D** *Case III*. The situation for which the new search volume projects out of the side of the previous search volume. In all three situations the shading represents the area of overlap between the new search volume and the previous search volume. The symbols used in the figure are defined in the appendix

LD = The location distance, which is the radius of the search volume and is considered the greatest distance at which a given prey (under specified conditions) can be located (Fig. 5A).

LA = The location angle, which is the angle at the apex of the search volume and is considered the greatest angle at which a given prey (under specified conditions) can be located (Fig. 1A).

TH_I = LA/2 (in radians)

LH = The location height is the height of the search volume and is considered the greatest height at which a given prey (under specified conditions) can be located (see Fig. 1).

TA = The turn angle is the angle the fish turns on the run after a search pause (Fig. 5B).

RL = The run length is the distance the fish moves after an unsuccessful search pause (Fig. 5B).

There are three general conditions that it is reasonable to assume.

$LA \leq 180°$
$TA \leq LA$
$RL \leq LD$

Case I. The apex of SV_R is inside SV_I and SV_R does not intersect either side of SV_I (Fig. 5B). In this case the following additional conditions apply:

$$TA \leqq LA/2$$
$$RL > RL_I$$

Where: RL_I is that RL for which SV_R intersects SV_I at points B or C (Fig. 5B).

$$RL_I = \frac{LD \text{ Sin } (TA)}{\text{Sin } (TH_I)}$$

SV_{RI} is the area of overlap, wedge ABC in Fig. 5B

$SV_{RI} = RL^2 \text{ Cos } (TH_I) \text{ Sin } (TH_I) + LD^2(TH_I) - (RL) \text{ Sin } (TH_I) [LD^2 - RL^2 \text{Sin}^2 (TH_I)]^{\frac{1}{2}} - LD^2 \text{ Arc Sin } (RL \text{ Sin } (TH_I)/LD)$

This formula is also used in the computation of Cases II and III.

Case II. The apex of SV_R is outside SV_I and SV_R intersects a side of SV_I (Fig. 5C). In this case the following additional conditions apply:

$$TA > LA/2$$
$$RL < RL_{II}$$

Where: RL_{II} is that run length for which SV_{RII} just does not intersect SV_I (Fig. 5A)

$$RL_{II} = \frac{LD \text{ Sin } (2TH_I - TA)}{\text{Sin } (TH_I)}$$

For computation of case II a new angle is computed, TH_{II} (Fig. 5C):

$$TH_{II} = \text{Arctan}\left(\frac{LD \text{ Sin } (TA - TH_I)}{LD \text{ Cos } (TA - TH_I) - RL}\right)$$

The general approach is to compute wedge ACE (Fig. 5C) and subtract wedge ADE and triangle ABD to obtain SV_{RII}, the area of overlap (Fig. 5C).

$$SV_{RII} = \tfrac{1}{2} SV_{RI} \text{ (using } TH_I) - \tfrac{1}{2} SV_{RI} \text{ (using } TH_{II}) - \left(\frac{RL^2}{2}\right)\left(\frac{\text{Sin}^2(TA - TH_I) \text{ Sin}(TH_I - TH_{II})}{\text{Sin}(TH_I + TH_{II} - TA) \text{ Sin}(2\,TH_I - TA)}\right)$$

Case III. The apex of SV_R is within SV_I, but SV_R intersects a side of SV_I (Fig. 5D). In this case the following additional conditions apply:

$$TA \leqq LA/2$$
$$RL < RL_I$$

Where: RL_I is as given in case I (Fig. 5A). For computation of case III a new angle is computed, TH_{III} (Fig. 5D).

$$TH_{III} = \text{Arctan}\left(\frac{LD \text{ Sin}(TH_I - TA)}{LD \text{ Cos } (TH_I - TA) - RL}\right)$$

The general approach is to compute wedge ABC and add wedge ACD and add triangle ADE to determine the area of overlap (Fig. 5D)

$$SV_{RIII} = \tfrac{1}{2} SV_{RI} \text{ (using } TH_I) + \tfrac{1}{2} SV_{RI} \text{ (using } TH_{III}) + \left(\frac{RL^2}{2}\right)\left(\frac{\text{Sin}(TH_I - TH_{III}) \text{ Sin}^2 (TH_I - TA)}{\text{Sin}(TA) \text{ Sin}(TA + TH_{III} - TH_I)}\right)$$

List of Abbreviations

Components of the search cycle and dimensions of the location space

SST (sec)	Successful search time – the average time stationary prior to a pursuit
USST (sec)	Unsuccessful search time – the average time stationary prior to a run
PT (sec)	Pursuit time – PL/SS – the time to pursue prey at a given distance away. It is calculated by dividing the pursuit distance by swim speed
RT (sec)	Run time – RL/SS – the time to complete a run of a given length. It is calculated by dividing the run length by swim speed
PL (cm)	Pursuit length – distance moved to attack prey
RL (cm)	Run length – distance moved between consecutive searches
SS (cm/sec)	Swim speed – the speed of movement during a pursuit or run
LS (l)	Location space – the area or volume within which prey are located. In the case of white crappie the search space is shaped like a pie wedge with the fish positioned at the apex of the wedge
LA (°)	Location angle – the angle of the wedge-shaped search space
LH (cm)	Location height – the height of the wedge-shaped search space
LD (cm)	Location distance – the length of long axis of the wedge-shaped search space.

Components of the location probability model

RND	Random number – random number generated through BASICA
SV (l)	Search volume – the volume of water actually searched after one run of given length
SV_{MAX} (l)	Maximum search volume – the greatest search volume that can be based upon LA, LH, LD and unaffected by the previous search
SV_R (l)	Search volume researched – that volume of SV_{MAX} that is researched where RL < LD (see Appendix A)
SV_u	Search volume unsearched – that volume of SV_{MAX} not previously searched
AD (#/l)	Absolute density – the density of zooplankton prey in numbers per liter
VD (#)	Visual density – the number of zooplankton prey in the search volume
LP (%)	Location probability – the probability that one or more prey are in the search volume

Components of the net energy gain model

NEG (cal/sec)	Net energy gain – total calories ingested, less total calories used, divided by total time.
E_e (cal)	Energy expended on the search cycle
E_i (cal)	Energy intake
e_p (cal)	Energy content of a given individual prey
P_i	Total number of prey ingested
e_r (cal)	Energy expended while searching
e_s (cal)	Energy expended while swimming
T_t (sec)	Total time – time expended to eat a given number of prey

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