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Search Strategies of Foraging Animals

W. John O'Brien
Howard I. Browman
Barbara I. Evans

Of all the activities in which animals engage, perhaps the most important are finding and consuming food. In addition to its urgency at the individual level, foraging—in the broad sense of predator-prey interactions—is crucial to ecosystem processes at many levels. In a very real sense, the biosphere runs on the consumption of one organism by another. Fabre has succinctly noted (1913) that “from the least to the greatest in the zoological progression, the stomach sways the world; the data supplied by food are chief among all the documents of life.” The when, where, how, how often, and how many

*Saltatory patterns of movement
in a wide range of animals indicate
that most foragers fall somewhere
between cruisers and ambushers*

of prey capture and consumption are central to studies of individual survival, population dynamics, community structure, nutrient cycling, and energy flow through ecosystems.

It is not surprising, then, that foraging has been studied extensively in virtually all animal groups by physiologists, ethologists, ecologists, and theoreticians (Kamil et al. 1987; Kerfoot and Sih 1987). A recent approach to the study of feeding ecology is optimal foraging theory, which focuses on aspects of foraging behavior presumed to have been honed by evolution (Schoener 1971; Pyke 1984). Theorists of optimal foraging have produced a series of models that make quantitative predictions concerning such aspects of predator-prey interactions as optimizing prey choice, adopting the best prey patch as prey are depleted, and search strategy (see, for example, Hanson and Green 1989; Marshall et al. 1989; O'Brien et al. 1989). These models vary widely in their accuracy when tested against field data, but serve a valuable function in clarifying what is known and what is not known about foraging among particular species in particular environments.

Optimality models are perhaps least useful when they seek to address the question of whether animals are “optimal.” Because natural selection has left only those species and individuals that are efficient feeders, animals do not exhibit a gradient ranging from efficient to ineffi-

cient feeding. Thus models that instead pose the question of *how* animals forage effectively may contribute to an understanding of behavioral factors that are not genetically fixed but vary according to local environmental conditions.

Historically, much of what is known about animal foraging has been obtained from the analysis of stomach contents. A more recent approach, and one that can yield detailed information on the specific mechanisms of foraging behavior, breaks down the act of predation into components (Holling 1959; O'Brien 1979, 1987). The components of the predation cycle are similar for almost all animals: predators must first search for and locate prey, then pursue and attack them, and finally handle and ingest them.

If the prey are larger than the predator (as in the case of a lion preying on gazelles), the pursuit, attack, and



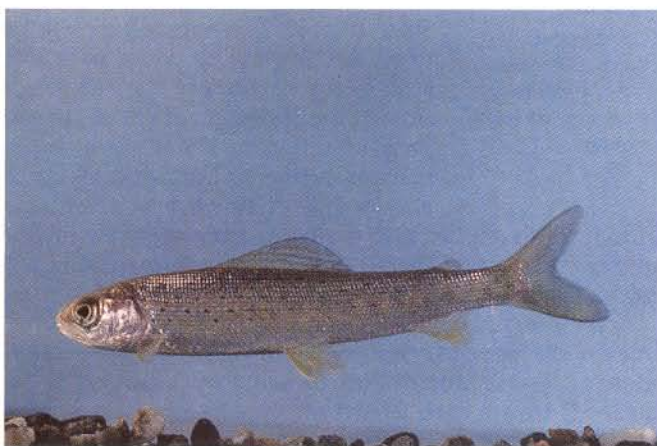
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handling components of the cycle are of paramount importance. In this situation, large size is an advantage for the prey. If the prey are smaller than the predator (as in the case of a bird feeding on small insects), the search component of the cycle is the most important. In this situation, small size may be an advantage for the prey. Many predators prey on animals considerably smaller than themselves, thereby avoiding the severe constraints raised by the time required for handling. When prey are smaller than their predators, they must be consumed often and in large numbers. In this case, search time is the factor that limits all subsequent components of the predation cycle.

The search strategy employed by a given organism has commonly been thought of as a trait dictated by evolution and not open to modification under changing environmental circumstances. Animals are typically divided into two categories, based on their overall search behavior: "cruise" searchers and "ambush" searchers (Greene 1983). These two categories of behavior have also been called "widely ranging" and "sit and wait" (Huey and Pianka 1981). In cruise or widely ranging

search, the forager moves continuously through the environment, searching constantly for its prey at the outer boundary of the volume being searched. Cruise searchers include large fish that swim continuously, such as tuna, and soaring hawks. In ambush or sit-and-wait search, a forager remains stationary for long periods of time, waiting for prey to cross the boundary of its strike space. Herons and rattlesnakes fit the category of ambush searchers.

Clearly, the patterns of motion associated with these two search strategies are profoundly different. It is impossible to conceive of a cruise searcher switching strategies to ambush a particularly appealing prey item. In fact, the kind of search behavior displayed by an organ-



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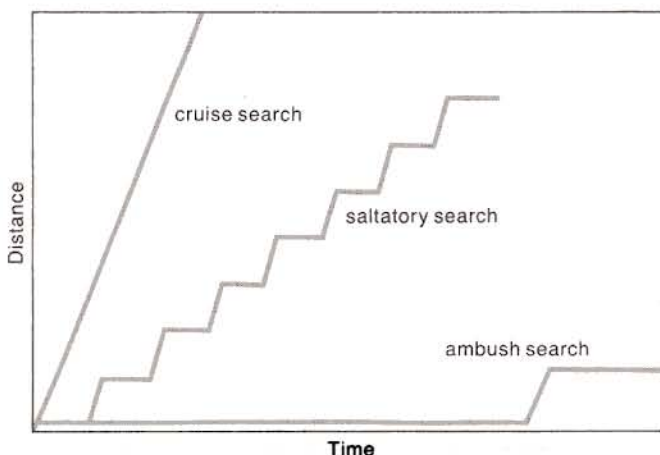


Figure 1. The strategies by which animals search for prey range from the constant motion of cruising foragers such as the red-tailed hawk shown at the far left to the tactics of ambushers such as the crouching lion at the right. Most taxa, however, occupy an intermediate position along this continuum, displaying a distinctive pattern of stops and starts in which pauses to search for prey alternate with moves that reposition the predator to scan new territory. Arctic grayling and white crappie (center, top and bottom respectively) are among the many species of fish, birds, and lizards that have been found to use a saltatory strategy. The graph above shows the characteristic patterns traced by the three strategies in time and space; the velocity of the movement is indicated by the slope of the line.

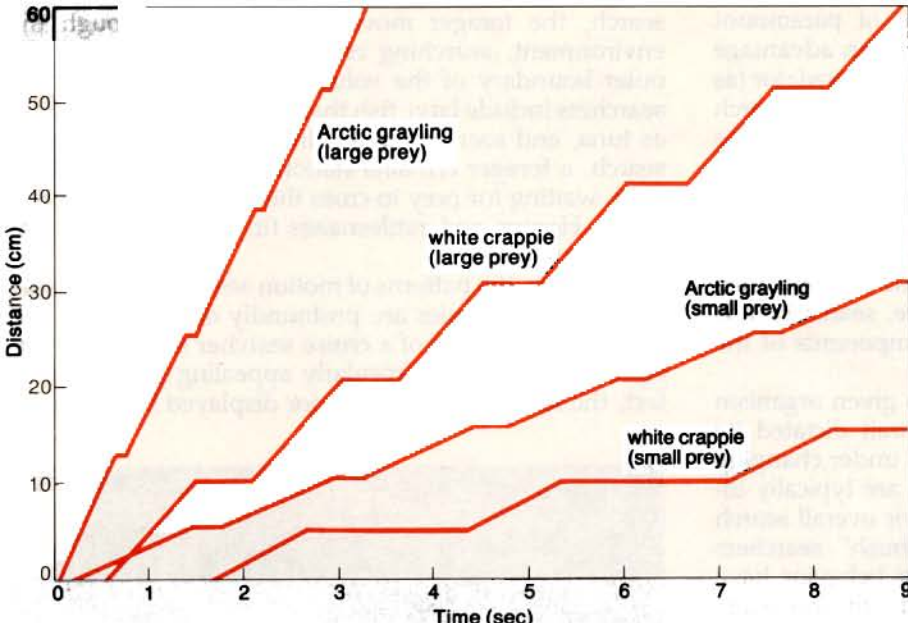


Figure 2. Arctic grayling and white crappie adjust both the duration of pauses and the speed and length of repositioning moves according to the size of their prey. Arctic grayling feeding on large prey (2–3 mm) employ very brief pauses interspersed with fast, long moves, approaching the norm for cruise predators shown in the graph in Figure 1. At the other extreme, white crappie feeding on small prey (0.5–1.2 mm) use very long pauses and slow, short moves, coming close to the behavior of ambush predators. In dealing with small prey, Arctic grayling shifts its strategy to one of longer pauses and slower, shorter moves, whereas white crappie foraging on large prey use shorter pauses and faster, longer moves.

ism has been viewed as in part determining the ecological niche of the species, defined through evolutionary time. Although some investigators have implied that there may be intermediate strategies of search, to date no such strategy has been explicitly described.

In detailed studies of foraging behavior in planktivorous fish, we have found that the search strategies they employ cannot be classified as either cruise or ambush. Rather than swimming continuously while foraging or stopping to wait for extended periods, these fish move in a relatively rapid stop-and-go pattern. We have called this behavior "saltatory search" (Evans and O'Brien 1988). Since identifying this pattern of foraging in fish, we have noted other instances of saltatory movements in foraging birds, lizards, and insects. It seems likely, in fact, that all search behavior can be placed on a "stop-and-go" continuum (Fig. 1). At one extreme are the cruise searchers, which appear to be in constant motion,

and at the other the ambush searchers, which may lie in wait for prey for as long as several days. The vast majority of foraging species fall in the middle of the continuum, pausing for brief or extended periods and moving in discrete units of time and space.

Unlike cruise and ambush search, saltatory search is a strategy that can potentially be varied to suit local environmental conditions. In our observations of planktivorous fish, we have found variations within species in the duration of pauses and the speed and distance of repositioning moves that appear to be related to particular environmental conditions (O'Brien et al. 1989). Both Arctic grayling (*Thymallus arcticus*) and white crappie (*Pomoxis annularis*) pause more briefly and swim faster and farther during repositioning moves when feeding on large prey than on small (Fig. 2). When feeding on large prey, Arctic grayling pause so briefly and swim so rapidly that they approach the condition of cruise search. When feeding on small prey, white crappie pause so long and swim so slowly that they approach ambush

search. Both species also moderate their search behavior under certain conditions, tending to move toward the midpoint of the search continuum.

If an organism's search strategy can change depending on the species, density, and visibility of the prey, then a precise description of saltatory behavior is required if we are to construct accurate foraging models for species in which search is the primary factor of the cycle. Clearly, differences in the duration of pauses and the speed and length of movement will affect net energy gain, and how well an organism can maximize energy gain by selecting a particular saltatory search strategy becomes crucial to relative reproductive success. Further, the recognition of a continuum of search strategies and the establishment of criteria for positioning a given forager on that continuum have obvious importance for an understanding of the overall ecology, morphology, and behavior of a predator.

Animals for which a component of the predation cycle other than search is most important or those that search for prey distributed in patches cannot be classified on a search-behavior continuum. However, it is possible that other continuums, analogous to this one, can be applied to other components of the predation cycle—for instance, the factor of handling time. The relationship between prey size and the costs of search, pursuit, and handling or subduing have been discussed by Griffiths (1980), who suggests that the relative importance of these components can be classified along a prey-size continuum. For example, animals that search for prey larger than themselves are often sit-and-wait searchers with high subduing costs.

Table 1. Changes in saltatory search with size of prey

	White crappie		Arctic grayling	
	small prey	large prey	small prey	large prey
Pause (sec)	1.65	0.55	0.3	0.07
Distance moved (cm)	5.2	9.8	6.5	12.0
Angle turned	22°	44°	25°	65°

SOURCES: O'Brien et al. 1986; Evans and O'Brien 1988; O'Brien et al. 1989

Saltatory search behavior

Although we first identified saltatory search through observations of planktivorous fish, this strategy appears to be used by a broad range of animals, all of whom feed often and search for widely-distributed prey that are much smaller than themselves. This general description fits many species of fish, birds, lizards, and insects. Many of the reports on behavior that fits this pattern depend on qualitative or categorical descriptions, but some quantitative data are available.

Among the most intriguing data of this sort are those on birds. Quantitative results gathered by Cody (1968, 1971) indicate that many birds, especially ground-foraging species feeding on insects or seeds, move in a saltatory manner; some species pause briefly and move a short distance, whereas others pause for longer periods and move short distances (Fig. 3). Descriptive reports are equally suggestive in the case of thrushes and starlings, which pause longer and move a shorter distance when searching for hidden prey or in a more complex environment (Smith 1974a, 1974b; Brownsmith 1977). Birds that glean insects from branches, twigs, and leaves also exhibit a pattern of pauses and repositioning movements, as do fly-catching insectivorous birds as they fly from perch to perch, waiting briefly before either moving to another perch or pursuing and capturing a located prey (Davies 1977; Fitzpatrick 1981; Robinson and Holmes 1982; Moreno 1984). Some birds that forage on beaches or mudflats, feeding on small benthic invertebrates, typically move in a saltatory manner (Meyers et al. 1980; Pienkowski 1983). Even the head bobbing of pigeons can be interpreted as presenting a saltatory pattern; in each cycle, the head and eye remain motionless for about one tenth of a second while the body moves continuously forward, with the head rapidly following (Frost 1978).

Quantitative data on lizards show that they, too, move in a saltatory manner while foraging (Fig. 3). Huey and Pianka (1981) classified the lizards in their study in relative terms as widely ranging or sit-and-wait predators. The four species classified as widely foraging were frequently stationary for up to 10 seconds between forward movements. By contrast, the two species classified as sit-and-wait foragers moved approximately twice a minute and were stationary for only about 30 seconds. Clearly, these behaviors can be classified as saltatory movement patterns.

Several fish species other than those we studied, such as large goldfish (Kleerekoper et al. 1970), have also been described in terms that suggest the use of saltatory movements. Indeed, the stop-and-go foraging of bluegill sunfish (*Lepomis macrochirus*) has been labeled "hover-search" (Janssen 1982; Ehlinger and Wilson 1988). Some insects, such as wingless phorid flies searching a surface, also exhibit stop-and-start foraging movements (Miller 1979).

For that matter, humans foraging on the written word exhibit a type of saltatory eye movement as the eye shifts focus from point to point along a line of type (Huey 1968). At each point of focus there is a brief pause, during which the actual reading occurs. Humans searching for a specific letter sequence in a vertical list four letters wide

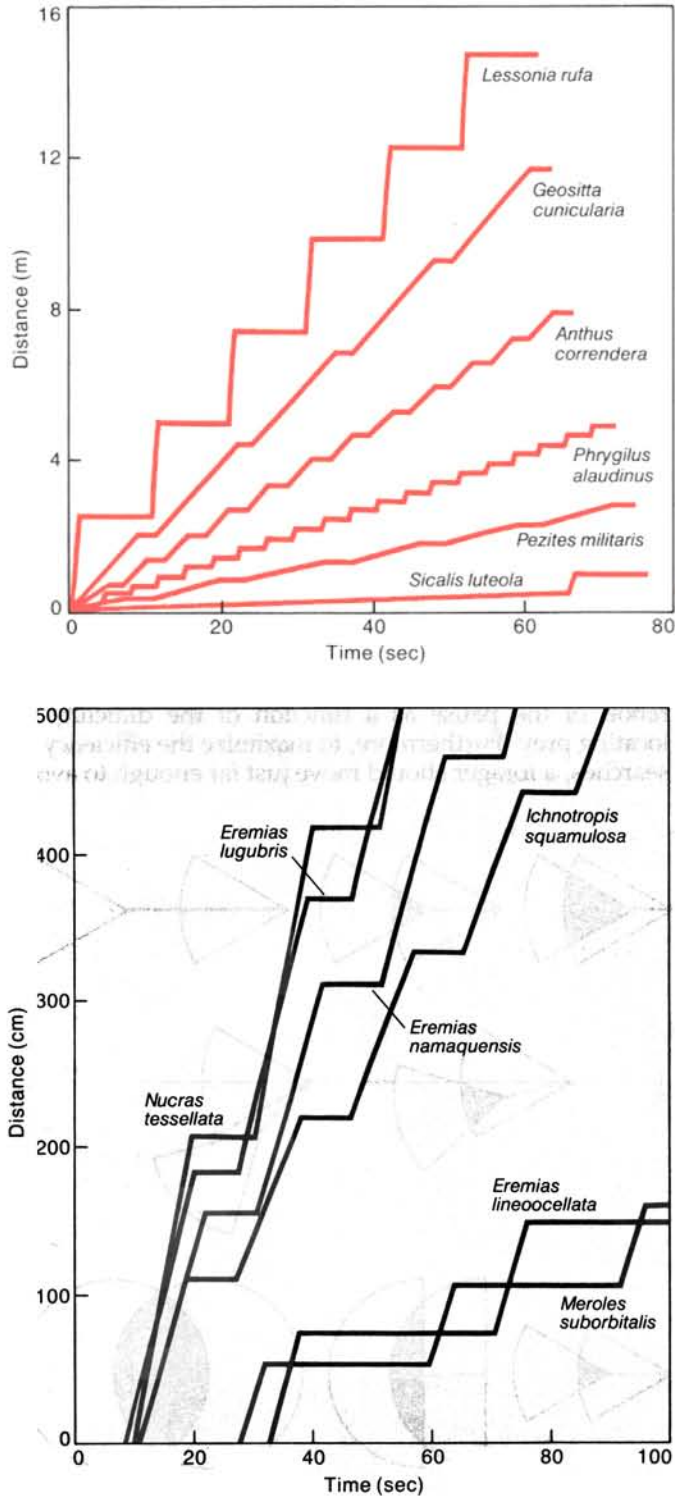


Figure 3. Grassland birds foraging for insects or seeds (top) show varied patterns of stops and starts resembling those of the planktivorous fish studied. Foraging movements range from the near-cruise behavior of *Geositta cunicularia*, which displays very brief pauses and fast, long moves, to the near-ambush pattern of *Sicalis luteola*, which is characterized by very long pauses and infrequent, short moves. The classic saltatory rhythm of stops and starts is visible in *Lessonia rufa*, which combines fairly long pauses with fairly fast, long moves. A similar spectrum of saltatory patterns has been observed in various species of sand lizards, as shown in the graph at the bottom. (Data from Cody 1968 and Huey and Pianka 1981.)

Pausing and searching

To reach a better understanding of the saltatory search strategy, it is necessary to examine both the "stop" and the "go" phases of the pattern—that is, both the pauses and the repositioning movements that alternate with them. Our studies of feeding behavior in Arctic grayling and white crappie have demonstrated that neither of these fish search for prey while moving. Instead, they search only during the stationary pauses between repositioning moves (O'Brien et al. 1986; Evans and O'Brien 1988). Janssen (1982) believes that bluegill, too, search only during such pauses. The repositioning moves between pauses, then, serve only to move the fish into previously unscanned space.

Studies of other predators showing stop-and-go patterns of movement while foraging have not been carried out in sufficient detail to determine whether they search only during pauses. In general, however, a predator moving in this pattern and searching only while pausing should pause frequently and moderate the duration of the pause as a function of the difficulty of locating prey. Furthermore, to maximize the efficiency of searches, a forager should move just far enough to avoid

rescanning a previously searched area without skipping over any area. Finally, a saltatory searcher should pursue prey throughout the volume being searched, while cruising or ambushing predators should pursue prey near the outer boundary of this volume.

There is the possibility that pauses may serve a purpose other than search—for example, they might help the predator to orient toward prey or to organize the attack phase of the predation cycle. If either of these were the case, all or most pauses would be followed by a pursuit. However, it is clear that white crappie frequently pause without subsequently pursuing prey (O'Brien et al. 1986). In fact, as prey abundance decreased, fewer pauses were followed by pursuit and attack of prey. Neither of these observations support the alternate explanations for the function of stationary pauses, but they are consistent with the hypothesis that predators search during pauses. In addition, the duration of pauses in both white crappie and Arctic grayling decreased when the fish were searching for large, more easily located prey (Table 1)—a behavior also consistent with stationary search. This phenomenon has been noted in other species as well. Janssen (1982) found that the duration of "hover-search" in bluegill sunfish decreased as apparent prey size increased. Ehlinger and Wilson (1988) have reported that bluegill foraging among vegetation exhibit longer pauses than those foraging in open water, suggesting that as the difficulty of the search increases, the pauses become more lengthy.

Several species of birds also vary the duration of foraging pauses as a function of the difficulty of scanning a given space or locating a particular type of prey. For example, plovers spend less time in scanning when searching for larger prey than for small (Pienkowski 1983). Starlings pause for a mean of 1.7 seconds when foraging in tall grass as opposed to 1.2 seconds in short grass (Brownsmith 1977). Robinson and Holmes (1982) found that red-eyed vireos paused for shorter times when they fed in the subcanopy of a deciduous forest than when they searched the more dense canopy. Tyrant flycatchers also alter their search time in response to local conditions, assessing each perch independently and moving after varying periods that depend on the visual characteristics of the environment (Fitzpatrick 1981).

Movement and search space

If foragers indeed move only to enter previously unscanned space, there should be a relationship between the distance traveled in repositioning moves and the size and geometry of the space previously scanned. If after an unsuccessful search an animal were to move only a short distance relative to the maximum distance at which it can locate prey, much of the volume just searched would be scanned again (Fig. 4). On the other hand, if the animal were to move completely through and beyond the previous search space, it would be wasting time and energy.

In both white crappie and Arctic grayling, the dimensions of the search space change with the size of prey (Table 1). Moreover, the length of the repositioning moves is directly related to these changes. For white crappie, the maximum distance at which small prey can be located is 8 cm. When these fish make a repositioning

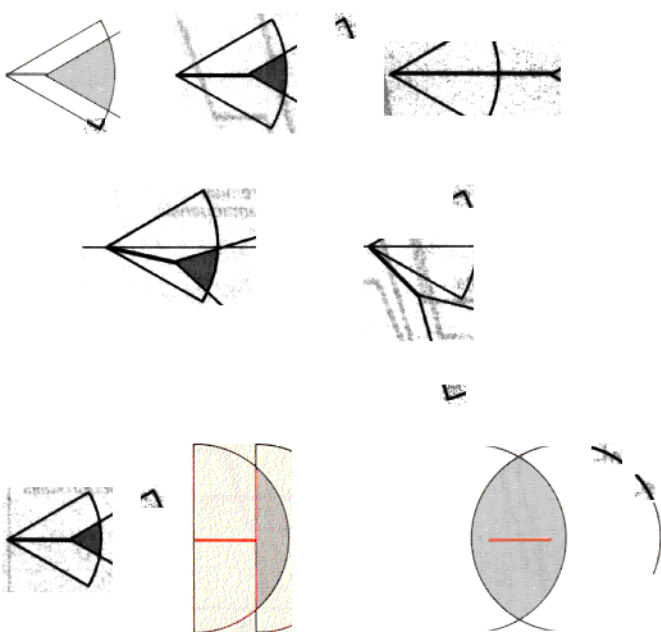


Figure 4. The most efficient length for repositioning moves is related to both the direction of the move and the shape of the volume being searched. In the case of a pie-shaped search space (top), a short, straight move results in the rescanning of a considerable area, indicated by shading, while a long move leaves a large area unscanned. By contrast, a move of intermediate length (color) results in a relatively small overlap with space already scanned. When a move of this same length is made at an angle rather than straight ahead (middle), a small angle still yields some overlap, while a large angle results in the maximum gain of unscanned area. As the geometry of the search space shifts from pie-shaped to semicircular to circular (bottom), a move of identical length creates an ever-greater overlap with space already scanned.

move after an unsuccessful search for small prey, the length of the move averages 5.2 cm. White crappie can locate large daphnid prey at about 20 cm, and moves made after an unsuccessful search for prey of this size average 9.8 cm. A simple model of net energy gain described in more detail below has shown that these distances are optimal.

Other taxa behave in a similar manner. Blackbirds, for example, move an average of 60 cm when searching for brown-colored prey on a green lawn but only an average of 40 cm when searching for less obvious green-colored prey of the same size on the same lawn (Smith 1974a). Plovers move just far enough to scan a totally new area after an unsuccessful search for beach-dwelling invertebrates (Pienkowski 1983). In the lizards studied by Moermond (1979), movements to new search sites were directly related to the average distance traveled in capturing prey. Thus a number of animals appear to modify the length of repositioning moves after an unsuccessful search in such a way as to minimize redundant search efforts.

Not only the maximum distance at which a given prey can be located but the geometry of the search space is important in determining the most efficient distance to move. When the horizontal dimension of the search space is less than 180° (90° on each side, looking forward), fairly short moves yield a high proportion of unsearched space (Fig. 5). White crappie search a pie-shaped space, and on average move only 60% of the maximum distance at which the prey in question can be located. Because of the geometry of the space, repositioning movements of this length provide a high proportion of new, unsearched territory.

As the geometry of the space being searched approaches a circle, the length of the repositioning moves must increase to a distance greater than the maximum distance at which prey can be located in order to obtain a high proportion of unsearched space. Plovers search a space of 240° (Pienkowski 1983), and consequently must move about 90% of the maximum prey location distance to obtain a high proportion of unsearched space. Tyrant flycatchers and other birds that feed on flying insects scan a nearly spherical space and move slightly more than twice the average pursuit distance to new perches (Fitzpatrick 1981; Robinson and Holmes 1982). This is necessary for foragers searching a circular space.

Repositioning moves are not always necessarily in the same direction. Turning after pausing is another way saltatory searchers can quickly move into unsearched areas. By contrast, cruise searchers, which continuously scan the outer boundary of the volume searched, would obtain little or no benefit from turning; it would be no more effective than simply moving straight ahead.

Both species of fish we studied turned after each unsuccessful search. As with the length of forward-

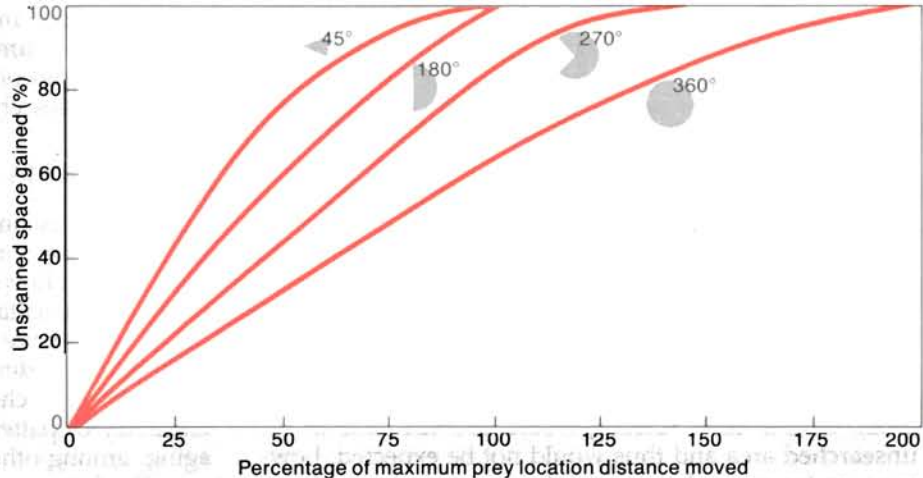


Figure 5. The percentage of previously unscanned space gained by straight moves of varying lengths is strongly influenced by the geometry of the search space. For search spaces of 180° or less, fairly short moves will produce a high proportion of previously unsearched space. Search spaces of more than 180° require the predator to move an increasingly greater percentage of the maximum distance at which prey can be located in order to obtain a high percentage of new search space. A predator searching a circular space must move 200% of the maximum location distance to achieve the smallest possible overlap.

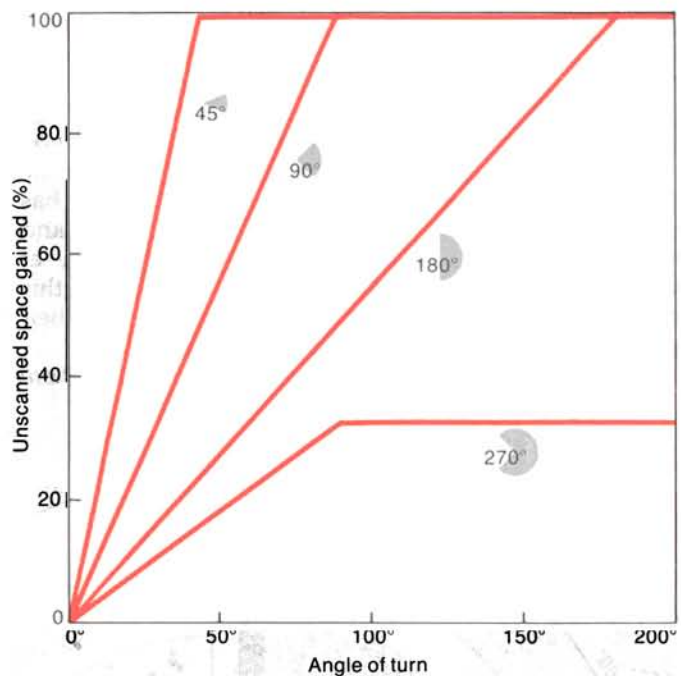


Figure 6. The effect of turns of varying angles on the percentage of previously unscanned space gained is shown for search spaces of different geometries. When the search area is less than 180° , an increase in the angle turned results in a high percentage of new space. If the search area is greater than a hemisphere, however, turns of greater angle will yield progressively less and less previously unsearched space.

directed repositioning movements, the angle turned increased with prey size (Table 1). Both white crappie and Arctic grayling scan a volume of greater angle for large prey than for small. Thus, to benefit from turning in terms of yield of unsearched space, the fish must make greater turns when feeding on large prey than when feeding on small prey.

Similar data are available for other taxa. Blackbirds make alternating left and right turns, with 67% of the turns lying within 43° of the forward path (Smith 1974b). Phorid flies, which search in a stop-and-go manner, make sharp turns after each pause (Miller 1979). Plovers also turn after search pauses (Pienkowski 1983).

Whereas the expected length of the repositioning move is directly related to the maximum distance at which a given prey can be located, the opposite is expected for turns. Once the geometry of the space searched exceeds a hemisphere, less and less unsearched area can be obtained through greater turns (Fig. 6). Birds foraging in forests, for example, seem to search a nearly spherical space (Eckhardt 1979; Robinson and Holmes 1982). In this case, turning would provide little or no unsearched area and thus would not be expected; however, as far as we know no information is available on turning in these birds.

A final point regarding movement concerns the distribution of pursuit within the search space. Both cruise and ambush searchers are expected to pursue prey at the boundary of the search space. However, saltatory searchers are distinguished by the fact that they pursue prey throughout the space being searched, as shown in Figure 7 for white crappie feeding on *Daphnia pulex* (Evans and O'Brien 1986; O'Brien et al. 1986). There are very few data of this sort for other taxa, and those that are available present pursuit distances as mean values, obscuring the distribution throughout the search volume. However, Eckhardt (1979), in mapping what he terms the "foraging space" of insectivorous birds, has shown that most of the attacks of both gleaners and flycatchers are well within the maximum distance at which the prey is typically located. Thus, at least in this case, birds that forage in a saltatory manner pursue their prey throughout the volume being searched.

The characteristics of saltatory search outlined here

and the ways in which it differs from other search strategies are summarized in Table 2, together with the likely attributes of prey most commonly sought through the various search strategies.

Implications of saltatory search

It is usually assumed that animals that move frequently while foraging employ a cruise search strategy. As we have shown, however, many of these animals are doubtless using a saltatory strategy. This distinction is not trivial; it can have important ramifications for measuring and understanding the frequency of predator-prey encounters, prey choice and dietary preferences, and the efficiency of patterns of movement associated with foraging, among other things.

The frequency or likelihood of encounter is a fundamental parameter in predator-prey dynamics. To determine the probability of encounter accurately, it is essential to know the volume a given forager can search and how that volume is scanned. A tool commonly used in estimating search volume is the average distance at which a predator responds to a specific prey type under specific environmental conditions (O'Brien 1979). That is, the predator is allowed to search for prey under experimental conditions, and the distance at which it first reacts to it—for example, by orienting toward it—is recorded. Typically, many such measurements are made and a mean is calculated.

For an animal using a cruise search strategy, and thus scanning the outer boundary of the volume as it moves, measurements of reaction distance will yield accurate estimates of the maximum distance at which the prey is located. However, for an animal using a saltatory strategy, and thus scanning nearly the entire volume being searched during the pause phase, measuring the mean reaction distance is not a good method of estimating the maximum distance for prey location. For the saltatory searcher, only the longest observed pursuit or reaction distances are at or near the outer boundary of the search volume. In birds feeding in forests, most pursuit and reaction distances are well short of the maximum distance for locating the prey (Eckhardt 1979; Robinson and Holmes 1982). Estimates of search volume based on measurements of reaction distance therefore underestimate the maximum distance at which prey may be located in saltatory search.

The opportunity, likelihood, and mechanics of choosing among several prey will also vary with the type of search strategy employed. Prey choice is unlikely for cruise or ambush searchers. Both types of foragers search the outer boundary of the search space, and presumably pursue prey almost as soon as it is detected. Under these conditions, choice among several prey seems un-

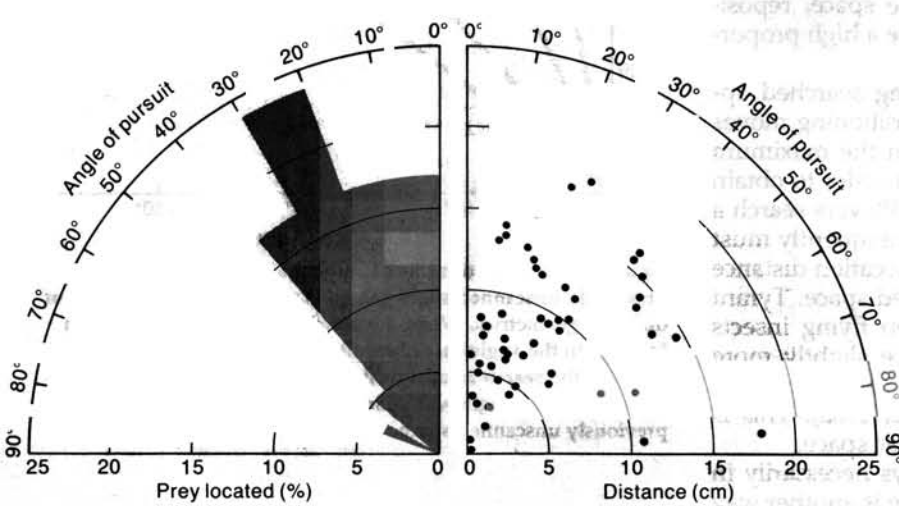


Figure 7. The distribution of prey located and pursued by white crappie feeding on *D. pulex* illustrates both the distinctive saltatory strategy of foraging throughout the volume searched and the influence of the geometry of the search space. When all the events within a 180° space in front of the fish are plotted as dots (right)—here conflated within 90°, with 0° as the forward path of the fish—it is apparent that white crappie rarely located *D. pulex* farther away than 18 cm or at an angle greater than 90° from the forward path. As shown at the left, the highest percentage of prey were located between 20° and 40° of this forward path, with very few prey located at angles greater than 50°.

Table 2. Characteristics of the three search strategies and typical prey

<i>Behavioral patterns</i>	<i>Cruise strategy</i>	<i>Saltatory strategy</i>	<i>Ambush strategy</i>
Search			
When	while moving	while pausing	while pausing
Duration of pause	rarely pause	brief	long
Variation in duration of pause	rarely pause	related to prey characteristics and environmental conditions	related to prey characteristics and environmental conditions
Prey encounter			
When	while moving	while pausing	while pausing
Where in volume searched	outer boundary only	throughout	outer boundary only
Forward movement after pause			
Length of move	move continuously	related to size of prey	rarely move
Relationship to volume searched	none	length increases with size of area searched	uncertain
Relationship to prey density	length decreases with density of prey	none	none
Turning movement after pause			
Frequency	rare	after every pause	rare
When	while moving	only after pause	rarely turn
Relationship to volume searched	none	angle increases with size of area searched	none
Characteristics of prey			
Size relative to predator	large	small	large
Movement	variable	little	extensive
Major defense strategy	speed or hiding	hiding	large size

likely, because this could occur only on the rare occasion when two or more prey were simultaneously detected at the boundary of the search space. By contrast, saltatory foragers scan the entire search space while stationary, and it is therefore far more likely that two or more prey could be in the volume searched during any given search episode. Many theoretical studies of prey choice and dietary preference in animals, including many models of optimal foraging, implicitly assume that the forager is searching continuously except when pursuing and handling prey.

As described above, not only white crappie but several species of birds and lizards have been found to vary the distance moved after an unsuccessful search depending on the size of the prey. It seems reasonable to ask if there is a specific length of repositioning movement that would most efficiently balance a high proportion of unscanned space against the cost of moving.

In a model of net energy gain we constructed to investigate this problem in the white crappie, we found that the distances the fish actually moved were in close agreement with those the model identified as most efficient (O'Brien et al. 1989). For small prey, the model predicted that 5 to 6 cm would be the most efficient distance for repositioning moves, while for large prey it predicted that any distance greater than 8 to 9 cm would be most efficient. These predictions are very close to the findings outlined in Table 1. Given the prevalence of saltatory search and the fact that three different taxa are known to alter the length of their repositioning movements, this may prove to be an important component of optimal foraging theory.

Foragers must divide their time between conflicting demands—for example, vigilance for predators and scanning for prey (Ydenberg and Dill 1986). Saltatory search may allow a balance between these demands. In

general, a potential prey is more likely to be detected while it is moving than while it is stationary (Wright and O'Brien 1982; Howick and O'Brien 1983). For saltatory searchers, we would predict that vigilance for predators would be highest during repositioning movements and lowest during the pause to scan for prey. It is also likely that there will be a relationship between the risk of being preyed on and the components of the saltatory search cycle. For example, all else being equal, in the presence of a predator a saltatory searcher should increase its stationary search time and decrease the speed and length of its repositioning moves.

Obviously, some taxa do not employ saltatory search. They may be discouraged from doing so by body size, structure, or other considerations. One might assume that insects, bats, and birds would not exhibit saltatory search, due to the need to remain airborne. However, insects and birds that can hover—dragonflies and hummingbirds, for example—could and perhaps do use saltatory search. Under some conditions, many birds may be able to approach the patterns of saltatory search. Forster's tern appears to use cruise search at low wind velocities (Salt and Willard 1971), but at modest wind speeds the birds have been observed to hover for some

W. John O'Brien is professor of systematics and ecology at the University of Kansas, and completed his Ph.D. at Cornell and Michigan State universities. His research, which focuses primarily on the predator-prey interactions of zooplankton and fish, currently involves the classification of animal search patterns and their ecological implications. Howard I. Browman received his Ph.D. from the University of Kansas in 1989, and is now an E. B. Eastburn Fellow in the Department of Biology at the University of Montreal. Barbara I. Evans received her Ph.D. from the University of Kansas in 1986; she is currently a NSERC Canada postdoctoral fellow at the Institute of Neuroscience at the University of Oregon. Address for Dr. O'Brien: Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045-2106.

over a particular spot of water. This can be interpreted as approaching the condition of ambush search. At even higher wind speeds the birds fly up above the surface of the lake and then dive down directly at one spot. This in effect keeps them briefly over one spot, and might allow saltatory search. Soaring hawks may be able to move their eyes in a saltatory manner. That is, they may visually "lock in" on an area as they soar over it and then skip ahead to lock in on another area.

Constraints on the use of saltatory movements are varied. Large swimming animals, such as tunas and sharks, may not be able to use saltatory search efficiently due to the energy required to start and stop such a large mass. On the other hand, very small aquatic animals such as copepods expend no energy to stop; at low Reynolds numbers they begin to sink as soon as the expenditure of energy for forward motion ceases (Greene 1988). The placement of the fins on the fusiform body of salmonids and other fish makes braking with the pectoral and pelvic fins difficult (Geerlink 1987), and thus hinders pausing. Further, our observations indicate that Arctic grayling can pause only briefly at the end of each swimming stroke, suggesting how advantageous even a brief pause can be in searching for small or hidden prey (Evans and O'Brien 1988).

Animals have evolved not only specific search strategies that are effective in their particular situations but the flexibility to deal efficiently with a changing environment. It is within this ecological and evolutionary framework that we propose saltatory search as a new explanatory and predictive tool.

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