ESSAYS ON OPTIMAL FORAGING THEORY: I. THE FIRST TWO PAPERS (1966)

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The first two papers on optimal foraging theory, one by Robert MacArthur and Eric Pianka and the other by John Merritt Emlen, were published back-to-back in the November-December 1966 issue of the *American Naturalist*. Both papers are among the most frequently cited papers on foraging theory (having been cited 1079 and 504 times, respectively as of 8-5-05). The circumstances of authorship were discussed as Citation Classic commentaries by Emlen (1980) and Pianka (1988). While the basic idea of using optimization to understand behavior has been very influential, it is possible that these papers have been cited more often than read.

The papers by MacArthur and Pianka and by Emlen are the only two papers in common cited by the three best-known reviews of optimal foraging theory, Schoener (1971, cited 1600 times), Pyke, Pulliam and Charnov (1977, cited 1345 times) and Stephens and Krebs (1986, cited 2064 times). Stephens and Krebs do little more than mention these papers. They first point out that MacArthur and Pianka treat both the problem of prey choice and patch choice and then suggest that these two problems correspond to the basic prey and patch models treated by Stephens and Krebs. Second, they mention that these early papers emphasized ecological problems. In fact, Stephens and Krebs join the two choice problems (prey choice and patch choice), which MacArthur and Pianka treat separately, into one problem, which they refer to as the "prey" problem. That is, the distinction between prey and patch problems made by MacArthur and Pianka is completely different from the distinction made by Stephens and Krebs. Stephens and Krebs are right in saying that the goal of the original 1966 papers was to use foraging theory to understand population and community ecology, but in 1986 they believed that the theory of individual behavior needed more testing before being applied to more complex problems.

THE AUTHORS

The three authors of the first papers were all young ecologists. At 36, Robert MacArthur was the oldest of the three. Eric Pianka was a young post-doctoral student working with MacArthur while John Merritt Emlen was a graduate student just about to finish his degree at the University of Washington. All three men went on to write important books (MacArthur 1972, Emlen 1973, Pianka 1974) that were among the new generation of ecology books that appeared in the early 1970s.

John Merritt Emlen

John Merritt Emlen was one of a family of eminent biologists. His father, John Thompson Emlen was for many years a professor in the Zoology Department at the University of Wisconsin in Madison (Lanyon, Emlen and Orians 2000). One brother, Stephen T. Emlen, followed his father into a career studying bird behavior, while another, James W. Emlen became a medical doctor and studied immunology. Despite his family biological background, John M. Emlen began his academic career studying mathematics and moved into biology relatively late (Emlen 1980). Emlen reported that Robert MacArthur was his hero, but that they had not yet met when he wrote his 1966 paper. John M. Emlen's interest in optimal foraging theory was prompted by reading some of MacArthur's earlier work and listening to Gordon Orians discussing natural selection as an "efficiency expert" (Emlen 1980). Emlen was studying intertidal ecology and was puzzling over the prey choice of snails. Gordon Orians, who a professor in Seattle when young John Emlen was a graduate student there, had himself been an undergraduate in Madison when the senior John Emlen was a professor there.

Eric Pianka

Like John Merritt Emlen, Eric Pianka had been a graduate student at the University of Washington in the early 1960s studying lizard ecology (Pianka "obituary"). Pianka took a postdoctoral fellowship with Robert MacArthur, who had just moved to Princeton from the University of Pennsylvania. Pianka (1988) describes his stimulating conversations with MacArthur, who had plenty of time to talk. Pianka describes himself as a sounding board for MacArthur's ideas. Pianka says that the only part of the 1966 paper that was truly his was the table listing factors increased specialization in diet. I think that making lists is something that Pianka likes to do. His list of factors characteristics of r- and K-selected species (Pianka 1970) helped popularize the distinction between r and K selection.

Robert H. MacArthur (1930-1972)

Robert H. MacArthur was the central figure in the early work on optimal foraging theory. If one goes by the commentaries provided later by Emlen (1980) and Pianka (1988), MacArthur provided some of the inspiration for one of the original papers and most of the ideas for the other. MacArthur's (1972) last book, "Geographical Ecology," had a chapter on foraging titled, "The economics of consumer choice." [It is interesting that the book by Stephens and Krebs (1986), which has a section titled, "Economics of Consumer Choice," does not refer to MacArthur's book.]

Robert H. MacArthur was a brilliant and inspirational leader in the new ecology that emerged in the 1960s. Unfortunately he died in 1972, at the age of 42. Sharon Kingsland (1985) has provided an excellent history of the emergence of theoretical ecology in the middle of the twentieth century, from the mathematical biology of 1920s and 1930s, kept alive by G. Evelyn Hutchinson until it blossomed in the work of his students including

Robert MacArthur. Steven Fretwell (1975) provided some appreciative comments about MacArthur's work. E. O. Wilson (1994) described what it was like to work with MacArthur and includes comments about what MacArthur was working on around the time that they began their collaboration. The book edited by Cody and Diamond (1975) contains papers presented at a memorial conference held in MacArthur's honor at Princeton in 1974.

Fretwell (1975) made one comment of particular interest to those interested in foraging theory. MacArthur had, or might have had, difficulty publishing his work, which was far from the ordinary. MacArthur took advantage of the fact that Hutchinson was a member of the National Academy of Science and, at that time, papers recommended by members could be published in the Proceedings of the National Academy of Sciences without being refereed. MacArthur also started the Princeton Monographs in Population Biology series to publish work such as his. His book with E. O. Wilson (1967), "The theory of island biogeography," was the first of this series, and the book, "Evolution in Changing Environments," by his collaborator Richard Levins was the second. Fretwell, whose 1972 book, "Populations in a Seasonal Environment," was also published in the Princeton monograph series, mentions that MacArthur was involved in the founding of the journal, Theoretical Population Biology, which published some work of the type that MacArthur supported.

In his history of the early years of optimal foraging theory, Schoener (1987) mentions several cases in which authors could not get theoretical papers on foraging published in the standard biological journals, particularly the *American Naturalist*, and had to publish elsewhere. For example, Charnov (1976) could not get his paper on the "marginal value theorem" published in the *American Naturalist*, so he submitted it to *Theoretical Population Biology*, where it was published. In 1977 Oaten published a paper criticizing Charnov, also in *Theoretical Population Biology*, and some of Oaten's followers, including myself (Green 1980) and John McNamara (1982) also published in *Theoretical Population Biology*. The *American Naturalist* might have published some of these later papers, I don't know. They did publish what I think is the most useful paper in the Oaten spirit, that by Iwasa et al. (1981), but that paper was more biological than the others.

A number of people have commented about MacArthur and his ideas an influence. John Lawton (1991) described reading MacArthur's (1958) famous "five warblers" paper with some students. Lawton wanted to make the point that it is good to read old papers. Lawton asserted that scholarship (knowing the literature) is important. This view is in sharp contrast with what Fretwell says when discussing MacArthur, who was notably sparing in his use of citations: "Few scientists realize how antithetic are scholarship and science," Fretwell (1975, p. 5)]

TWO MEN WHO INFLUENCED MacARHUR

G. Evelyn Hutchinson (1903-1991)

G. Evelyn Hutchinson, who has been called the "father of American ecology," was a British-born limnologist who attended Gresham School, which, incidentally, David Lack attended a few years later, and then Cambridge. Hutchinson had an early interest in natural history, stimulated by an uncle who was a zoologist, and by his father, a well-known mineralogist who was master of Pembroke College, Cambridge (Edmondson 1971). Hutchinson spent the year after graduation working at the Zoological Station in Naples, and after two years of teaching and doing research in South Africa, he moved to Yale University, where he spent a long and distinguished career. Hutchinson was a well-educated man with exceptionally wide interests. He wrote about his life (Hutchinson, 1979) and a collection of papers in his honor and some comments about the man were published in a special issue of *Limnology and Oceanography* in 1971. I am not so much interested in his nature, his life or his work as in his influence, particularly his influence in the development of modern ecological theory.

There are four points that I want to make about Hutchinson's influence. First, he was the major professor of many of the outstanding ecologists of his time and these men's students and their students included many outstanding ecologists. A "Phylogenetic Tree of Intellectual Descendants of G. E. Hutchinson" (1971) is given in the special issue of *Limnology and Oceanography* honoring Hutchinson. Second, Hutchinson's manner of encouraging his students is interesting. He would make some suggestions, but for the most part he expressed enthusiasm for whatever his students were doing. Third, he kept the ideas about mathematical biology alive in his mind from its origin in the 1920s and early 1930s through the political and economic turmoil and war of the 1930s and 1940s until it reemerged in the 1950s (Kingsland 1985). Fourth, Hutchinson angered some who felt that there was "no place in science for imaginative hypotheses which have not yet been tested thoroughly" (Riley 1971). Perhaps Robert MacArthur angered some of the same people by advancing ecological models with some, but not much, supporting data.

David Lack (1910-1973)

An excellent summary of David Lack's life and work is provided in an obituary by W. H. Thorpe (1974). David Lack was the son of a prominent London surgeon. Neither his father nor his mother had much to do with Lack as a boy. At an early age he developed a keen interest in birds which he maintained all his life. After getting a degree from Cambridge he became a school teacher, using his vacations to study birds and to travel. During the war he worked on radar. One of his fellow workers was George Varley, whose later work on insect populations, and particularly on population regulation, influenced Lack greatly. After the war Lack moved to Oxford and became the director of the Edward Grey Institute of Field Ornithology, where he decided to emphasize population studies of birds, in particular, studies of Great Tits, whose nests are easy to find because they are hole-nesters who are happy to nest in boxes if they are provided.

Lack was interested in behavior as well as ecology, and he thought that evolution was relevant to the studies of behavior and ecology. Lack's studies on clutch size had an important influence on behavioral ecology, a new discipline that was to arise in large part from his work. Lack believed that populations were limited by density-dependent factors such as food limitation, not by density-independent factors such as weather. In the appendix of his 1966 book, "Population Studies of Birds," Lack argues against both the Wynne-Edwards (1962) view that population is regulated behaviorally and the Andrewartha and Birch (1954) view that population regulation is largely density independent. Here, Lack provides an excellent argument for individual selection as opposed to group selection. Lack was quite convincing, and he won the argument about the nature of selection, at least for a while, but I think that it would be a mistake to believe that the arguments in favor of density-dependent population regulation and individual selection discredit everything that Wynne-Edwards and Andrewartha and Birch had to say. Further, the debate on what is the level (or the levels) at which selection operates is still not settled. [If, for example, one were interesting in resolving the way that selection operates on territorial birds, after admitting that Lack's view of selection is more sophisticated than that of Wynne-Edwards, a still more sophisticated view might be necessary to understand the facts.]

Thorpe (1974, pp. 279-280, 281)) points out that while Lack restricted himself to field observations, his ideas did stimulate many others to do experimental work. Crawley and Krebs (1992) mention the importance of Lack's use of "selectionist thinking" was in the development of behavioral ecology. Thorpe (1974, p. 279) added, however, that Lack rejected most examples of experimental work because it was done under artificial conditions. Thorpe concludes that both field observations and experimental studies are necessary. Unaware of these comments, I made some similar warnings about experimental studies of foraging theory during a talk given at Oxford in 1983. Based on the reading of some recent literature, I suggested that experimenters should ask whether the problems are setting their animals are realistic, whether the problem that their experimental animals are solving are the same that the experimenters are asking, and whether it makes any difference to the animals what they do. Ten years later I wrote a paper (Green 1993) that repeated these three points, and was able to illustrate each with a paper (published after 1983) that violated that suggestion.

THE PAPERS

1. MacArthur and Pianka (1966)

The paper by MacArthur and Pianka (1966) treats two problems, (a) which kinds of prey an efficient predator should include in its diet, and (b) which kinds of food patches should be included in a predator's itinerary. The optimal strategies for the two problems are found by minimizing time; time spent searching and pursuing prey for the prey choice problem or the time spent traveling between patches and hunting in each patch for the patch choice problem. Time is measured per prey item. [This properly should be time per unit energy obtained from prey.]

(a) The problem of prey choice.

Predators in a fine-grained environment find kinds of prey at rates proportional to the density of the kinds in the whole environment. The optimization problem for such predators is to decide what kinds of prey to include in their diet. The time a predator spends per prey can be broken into two parts, a search time, S, and a pursuit time, P, (which includes pursuit, capture and eating). Imagine that a predator includes the best N kinds of prey in its diet [best is defined as most prey calories caught per unit time—the authors are not very clear about this]. Now, the question is whether to include another kind of prey in the diet. The average time per prey item is the sum of search and pursuit time: S + P. If one calculates this sum for a diet with N + 1 kinds of prey and subtracts the sum for a diet with N kinds, one gets the change in time resulting from expanding the diet. If the change is negative, that is, if time per prey item decreases, then the diet should be expanded. If ΔS is the decrease in average search time per prey item found, this can be plotted against N, the number or kinds of prey in the diet. [Note: a positive ΔS means a negative change in search time. Changes in search time are always negative because adding a kind of prey to the diet means that there are more prey to find and therefore a lower average search time.] The change in average pursuit time per prey, ΔP, must be positive because the kinds of prey are ordered in terms of pursuit time. These ΔP changes are plotted against N in the same figure as the ΔS changes. As long as ΔS is larger than ΔP the decrease in search time exceeds the increase in pursuit time and it is better to include another kind of prey in the diet.

There are two biological conclusions that can be seen by plotting the ΔS and ΔG changes together against N. First, if overall prey density is lower, then search times will be longer and changes in search time, ΔS, will be greater, and the ΔS and ΔG curves will tend to intersect further to the right (higher N), which means that more kinds of prey should be included in the diet. Second, if a predator is more specialized, that is, if it is relatively better at handling some prey than others, in comparison with a more generalized predator, then the ΔG curve will rise more steeply and intersect the ΔS curve at a lower value of N, implying that the optimal diet should be narrower.

(b) The problem of patch choice.

If they live in a coarse-grained environment and prey are distributed in patches of various kinds, then predators face the problem of which kinds of patches to include in their itinerary. This problem is solved by the same graphical method as the problem of prey choice, but with travel time, per prey caught, T, between patches replacing the search time, S, to find a prey, and with hunting time, per prey, H, within each patch, replacing the pursuit time, P, to pursue, capture and eat a prey.

While the method of solving the patch choice problem is the same as that used to solve the prey choice problem, the biological conclusions are not the same. For example, if prey density is higher in all patches, hunting time there is shorter because the search component of hunting is reduced, but travel time between patches is also effectively reduced because patches are bigger (have more prey). Predators that have a high ratio of

pursuit time to search time ("pursuers") will have their hunting time less affected by changes in prey density and the accompanying change in search time than will "searchers," but both "pursuers" and "searchers" will be equally affected by the effective change in travel time between patches. Therefore, "pursuers" will tend to restrict their patch utilization more than will "searchers" if prey density increases in patches. [This result might be better understood by looking at an illustration, that is, a Fig. 2B analogous to Fig. 1B, but the authors do not provide one.]

Another result is that if patches increase in size, but all else remains the same, including prey density in all the patches, then travel time between patches per prey caught in each patch is effectively smaller and predators should be more selective in their choice of patches.

MacArthur and Pianka (1966) conclude by considering the effect of competition on prey and patch choice. The general conclusion is that in the face of competition a predator should reduce the range of kinds of patches it uses but it should not reduce the number of kinds of prey that it takes. A final example involves the question of species coexistence. Can a jack-of-all-trade predator that competes with two specialists displace the two. A jack-of-all trades spends less time traveling because it uses a wider range of kinds of patches. However, it spends more time harvesting prey because it is less specialized. If the gain in travel time outweighs the loss in harvesting time, then a jack-of-all-trades can out-compete the specialists. This is an interesting idea, but the argument is based on averages. It is not clear what would happen if one looked at the various kinds of patches and not just the average.

2. Emlen (1966)

Emlen (1966) considers a predator that has to decide whether to accept food items of either of two subsets (I will refer to "types of prey."). Prey are rated according to their food value and the time required to handle them. A forager should accept a particular prey if the ratio of its food value to handling time exceeds the ratio of food value obtained to time spent searching and handling, from the time that the present prey is encountered through the time that the next prey is encountered, and if accepted, handled and devoured. Unfortunately, this second ratio is calculated using averages involving the time between finding a prey of one type and another prey of the same type, and the time between finding a prey of one type and another prey of a different type. This is a mistake. If prey are found at random, as Emlen assumes, it will be more likely that the next prey is common than rare, but the search time (or its distribution) will be the same whether the next prey is common or rare.

Emlen's (1966) paper is much more mathematical than that of MacArthur and Pianka (1966), at least in the sense that it has many more equations (MacArthur and Pianka have essentially one equation), and Emlen has many terms which he must define. There are advantages in making explicit mathematical assumptions. For example, it is easier to see what you are doing and you can point to important details to the reader. However, if the terms are not defined clearly then the equations will be confusing. Emlen defines E as

net calories obtained per unit time, but one cannot see exactly what this means until looking at the equations that define E, and then the interpretation is far from clear.

One of the implications of Emlen's (1966) model is that when both types of prey are rare the forager should not be selective. This agrees with a conclusion of later versions of the prey choice model (Stephens and Krebs 1986). If prey are relatively common then predators should be more selective, but the pattern of selectivity depends on the relative quality of prey and not just on their quality. Emlen points out that if neither prey type is scarce, but one is more common than the other, then the forager may prefer prey of the common type, even though they are less nutritious and harder to handle. This conclusion is quite different from that of later models, which predict that better prey should always be taken, no matter how rare they are. I found this result of Emlen's puzzling until I looked at his 1968 paper, which does not have any formulas, but does have graphs illustrating the variability in the quality of prey of a given type. The reason that a predator may prefer prey of a generally inferior type is that some of the inferior type may be better than any of the better type. Thus, the common inferior type is preferred because some individuals of that type are actually best, and if prey are common and time between encounters are short, there is no point in eating any but the best. Emlen (1973) gives a more coherent version of the foraging story, with the graphs from his 1968 paper (and one from the 1966 paper), but omits the formulas that were found in the 1966 paper.

The point of Emlen's (1966) paper is to understand food preference in terms of foraging efficiency. One way to measure food preference is to compare the proportions of different food types in the diet with their proportions in the environment. Emlen is particularly interested in how the proportion of a particular type of food in the diet changes as its proportion in the environment changes. The problem that motivated this theoretical work was a predatory snail that preferred to attack barnacles rather than mussels even though mussels were easier to deal with. The snail switched to mussels only when the mussels had essentially wiped out the barnacles.

SUMMARY

The papers by MacArthur and Pianka (1966) and by Emlen (1966) were the first papers on optimal foraging theory. That is, they were the first papers that tried to understand foraging behavior in terms of efficiency. All three authors were ecologists, interested in ecological ideas, and both papers considered the problem of prey choice. In other ways, the papers were quite different. MacArthur and Pianka also considered the problem of patch choice. The ecological questions asked were quite different. MacArthur and Pianka were interested in diet breadth more than food preference, and one of their conclusions contrasted specialist and generalist foragers. Emlen was interested in food preference, particularly the choice between two types of prey. The methods used were also quite different. MacArthur and Pianka asked whether a predator that was taking some number N of different types of prey could save time by increasing its diet by including an N + 1st type. Energy obtained was not considered explicitly, but it was implicit, because the types were ordered according to the ratio of their nutritional value to handling time. Emlen considered both energy and handling time and compared the ratio

of net energy obtained by eating a particular prey to the time to handle that prey with a longer-term ratio of energy to handling time after deciding what to do with the present prey.

Emlen, MacArthur and Pianka were feeling their way when they invented optimal foraging theory. Neither of the first two papers was very clear in the way its model was formulated. Assumptions were not stated explicitly and terms were not defined carefully. Both papers approached foraging from an ecological point of view, but there was a difference in the spirits of the two papers. MacArthur and Pianka (1966) sought to use a model of foraging behavior to understand an ecological question about how specialized a forager should be. Emlen (1966) used his model to answer a behavioral question about how a forager's diet depends and prey quantity and quality.

The essential idea that the first two papers on optimal foraging theory added to what had gone before was to focus on decisions that animals have to make and to consider those decisions in terms of efficiency. In both papers the strategic problem was imbedded in an ecological context, and the goal was to discover the implications of efficient foraging. For the next few years foraging problems were treated in an ecological context, but eventually a simpler, clearer mathematical theory arose that was used to make behavioral predictions that could be tested experimentally. Some of the simplest, most obvious predictions were confirmed by experiments. Other, less obvious predictions were not confirmed. Sometimes this led to revisions in the theory, which took into account some factors that were not contained in the simplified theory. For example, one prediction of the prey choice model as described by Stephens and Krebs (1986) was the 0-1 rule, that under a particular set of circumstances an optimal forager should take all of a one type of prey or none, but should not take some, but not all prey of one type. This prediction is different from the conclusion reached by Emlen (1966, 1968) that would have a forager taking some, but not all of a less favorable prey when prey density is high. Of course, the later models were different because they assumed that all prey of a particular type were the same. What happened to the theory is interesting. First, a rather vague model, incorporating biological reality, was proposed. This model was supplanted by a simpler, clearer mathematical model. When this later model was found to be unrealistic, modifications were proposed that tended to make the model more realistic, but they also made it less clear. These modifications may have muddied the simple theory that was so attractive in the late 1970s and early 1980s. This may have led to a decline in the interest in optimal foraging theory. At present there is great interest in foraging, but much less interest in optimal foraging theory.

REFERENCES

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology 9:129-136.

Crawley, M. J. and Krebs, J. R. 1992. Foraging theory. In: M. J. Crawley, ed. Natural Enemies: The Population Biology of Predators, Parasites and Diseases. Blackwell Scientific Publications, Oxford.

Edmondson, Y. H. 1971. Some components of the Hutchinson legend. Limnology and Oceanography 16:157-161, 476-477.

Emlen, J. M. 1966. The role of time and energy in food preference. American Naturalist 100:611-617.

Emlen, J. M. 1968. Optimal choice in animals. American Naturalist 102:385-389.

Emlen, J. M. 1973. Ecology: An Evolutionary Approach. Addison-Wesley, Reading, Massachusetts.

Emlen, J. M. 1980. This week's citation classic. Current Contents 12(27):196.

Fretwell, S. D. 1972. Populations in a Seasonal Environment. Princeton University Press, Princeton, New Jersey.

Fretwell, S. D. 1975. The impact of Robert MacArthur on ecology. Annual Review of Ecology and Systematics 6:1-13.

Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. Theoretical Population Biology 18:244-256.

Green, R. F. 1993. Can ethology help make optimal foraging theory more realistic and useful? Department of Mathematics and Statistics, University of Minnesota Duluth, Technical Report 93-8.

Hutchinson, G. E. 1979. The Kindly Fruits of the Earth. Recollectons of an Embryo Ecologist. Yale University Press, New Haven, Connecticut.

Iwasa, Y., Higashi, M, and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. American Naturalist 117:710-723.

Kingsland, S. E. 1985. Modeling Nature: Episodes in the History of Population Ecology. University of Chicago Press, Chicago.

Lanyon, W. E., Emlen, S. T. and Orinas, G. H. 2000. In memoriam: John Thompson Emlen, Jr., 1908-1997. Auk 117(1):222-227.

Lawton, J. H. 1991. John Lawton's view from the park 2: Warbling in different ways. Oikos 60:273-4.

Levins, R. 1968. Evolution in Changing Environments. Princton University Press, Princeton, New Jersey.

MacArthur, R. H. 1958. Population ecology of some warblers in northwestern coniferous forests. Ecology 39:598-619.

MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, New York.

MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. American Naturalist 100:603-609.

MacArthur, R. H. and Wilson, E. O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

McNamara, J. M. 1982. Optimal patch use in a stochastic environment. Theoretical Population Biology 21:269-288.

Oaten, A. 1977. Optimal foraging in patches: a case for stochasticity. Theoretical Population Biology 12:263-285.

Pianka, E. R. 1970. On r- and K-selection. American Naturalist 104:592-597.

Pianka, E. R. 1974. Evolutionary Ecology. Harper and Row, New York.

Pianka, E. R. 1988. This week's citation classic. Current Contents (Social and Behavioral Sciences) 20(31):16.

Pianka, E. R. (no date) Obituary (He's not dead yet!) Available online at http://uts.cc.utexas.edu/~varanus/obit.html

[Phylogenetic tree of intellectual descendants of G. E. Hutchinson] 1971. Limnology and Oceanography 16:162-163.

Pyke, G. H., Pulliam, H. R. and Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137-154.

Riley, G. A. 1971. Introduction. Limnology and Oceanography 16:177-179.

Stephens, D. W. and Krebs, J. R. 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369-404.

Thorpe, W. H. 1974. David Lambert Lack, 1910-1973. Biographical Memoirs of Fellows of the Royal Society 20:271-293.

TABLE

Number of references to certain phrases in the Science Citation Index (as of 8-19-05)

Foraging	14308
Optimal foraging	423
Optimal foraging theory	224
Foraging theory	572
Total (OF, OFT, FT)	771
Foraging behavior	2687
Foraging behaviour	1201
Total	3888