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thesis entitled

Suboptimal Foraging Strategies

for a Patchy Environment

presented by

James Edward Breck

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Poneld Chart Major professor

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SUBOPTIMAL FORAGING STRANDOLES CAN

PATCHY SNVIRMENNY

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James Boward Bayer

A DISSERTATION

Submitted to Michigan State University in partial fulfilment of the requirements for the decree of

DOCTOR OF PRILOSOPHY

Department of Zoelogy

SUBOPTIMAL FORAGING STRATEGIES FOR A

PATCHY ENVIRONMENT

By SUBOPTIMAL FORAGING STRATEGIES FOR A

James Edward Breck

Strategies for allocating the search time of a predator in a patchy environment are analyzed. Prev of a single type are assumed to occur only in discrete patches, which are uniform except for the number of prey they contain. Two economic goals are considered: maximization of capture rate and minimization of the risk of finding no prey would usually require very complex computations on the part of a predator, three suboptimal strategies are explored: a Constant Giving-Up TimA DISSERTATIONTY, & Time Expectation

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the addition of le Department of Zoology shaving to forage

James Edward Breck

Capture rate, and optimal leaving times are evaluated analytically of by computer optimization techniques for predetors using the GOT, TE ABSTRACT metrategies, for the Cases of PosuBOPTIMAL FORAGING STRATEGIES FOR A loss of PATCHY ENVIRONMENT Proy among patches. For the two economic goals, maximization

By James Edward Breck

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strategies; optimizing leaving time to maximize capture Strategies for allocating the search time of a rate provides nearly the same degree of risk minimization predator in a patchy environment are analyzed. Prey of a when the risk is greatest -- at low pray densities. The TE single type are assumed to occur only in discrete patches, gy is the best possible strategy for this foraging which are uniform except for the number of prey they conproblem when there is a Poisson distribution of prey among tain. Two economic goals are considered: maximization of The expected capture rate for the Random strategy capture rate and minimization of the risk of finding no prey ies that for the TE strategy as mean prey number per during a foraging period. Since optimal decision-making patch increases and as handling time per prey increases. would usually require very complex computations on the part As the coefficient of variation of the distribution of prey of a predator, three suboptimal strategies are explored: a Constant Giving-Up Time (GUT) strategy, a Time Expectation r maximizing capture rate) (TE) strategy, and a neutral model for comparison purposes, ence of intercapture times. a Random strategy. These models assume that environmental nomes superior to the TE stratecy when conditions, including mean prey density, have been constant of variation is large, when the distribution long enough so that no further learning by the predator ates greatly from the Poisson. Selection pressure is taking place. An important area for further research is te and precise methods of estimating elapsed the addition of learning and monitoring behaviors to foragrch time should be stronger for animals using the GUT ing theory. strategy than for those using the TE strategy; this selection

Formulae are obtained analytically for the expected capture rate, and optimal leaving times are evaluated analytically or by computer optimization techniques for predators using the GUT, TE, and Random strategies, for the cases of Poisson and negative binomial distributions of prey among patches. For the two economic goals, maximization of capture rate and minimization of risk, the optimal leaving times converge at low prey density for both the TE and GUT strategies; optimizing leaving time to maximize capture rate provides nearly the same degree of risk minimization when the risk is greatest -- at low prey densities. The TE strategy is the best possible strategy for this foraging problem when there is a Poisson distribution of prey among patches. The expected capture rate for the Random strategy approaches that for the TE strategy as mean prey number per patch increases and as handling time per prey increases. As the coefficient of variation of the distribution of prey among patches increases, it becomes more and more important (for maximizing capture rate) to utilize the information in the sequence of intercapture times. Thus, the GUT strategy becomes superior to the TE strategy when the coefficient of variation is large, when the distribution of prey deviates greatly from the Poisson. Selection pressure for accurate and precise methods of estimating elapsed search time should be stronger for animals using the GUT strategy than for those using the TE strategy; this selection pressure will increase as mean prey number per patch increases, as searching effectiveness increases, and as transit time decreases, and will be reduced as accuracy and precision improve.

Future foraging experimenters should present frequency distributions of observed giving-up time, total search time per patch, and search time between prey sightings. Mean values alone are unlikely to allow discrimination between search strategies.

tributed to this work. Phil Crowley and members of the ecology group at Michigan State University provided a stimulating intellectual environment.

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	the pase of incurat royarreins
	exponent of the negative binomial distribution (dimensionless)
	a possible value for the number of prey captured in a patch
	a random variable for the number of prey remaining in a patch
	a possible value for the number of prey remaining in a patch
	mean transit time between patches (seconds)
	random variable for the number of prey initially present in a patch
	a possible value for the number of prey initially present in a patch
	a parameter of the negative binomial distribution, P=x/h
	searching-affectiveness parameter (second ⁻¹); the expected capture rate when one prey is in a patch; 1/pk is the expected search time to find

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a parameter of the negative binomial distribution, 0=1+P the random variable for capture rate mean total search time per patch for the Random bability that LIST OF SYMBOLS leave the patch Following standard notation, E[] denotes expected value, P[] denotes probability, and Var[] denotes the variance of a random variable. total search time per patch mean handling time per prey (seconds) b random variable for the number of prey captured C in a patch the two parameters of the gamma distribution c,d the base of natural logarithms е exponent of the negative binomial distribution h (dimensionless) cumulative search time at which the ith prey is ×(1) i a possible value for the number of prey captured in a patch K a random variable for the number of prey remaining in a patch kbbrev a possible value for the number of prey remaining in a patch mean transit time between patches (seconds) m random variable for the number of prey initially N present in a patch a possible value for the number of prey initially n present in a patch a parameter of the negative binomial distribution, P P=x/hsearching-effectiveness parameter (second⁻¹); P the expected capture rate when one prey is in a patch; 1/pk is the expected search time to find

the next prey when k prey are in the patch

- Q a parameter of the negative binomial distribution, Q=1+P
- R the random variable for capture rate
- r mean total search time per patch for the Random strategy (sec.); 1/r is the instantaneous probability that the predator will leave the patch (while searching)
- T duration of the foraging period (seconds)
- t the leaving time (seconds), e.g., the giving-up time or the search time per patch
- Ts random variable for total search time per patch (seconds)
- ts a possible value for the search time per patch (seconds)
- ts the search time to the next prey capture given that r prey have been captured so far (seconds)
- x_i cumulative search time at which prey individual i is found (not the search time to the ith capture).
- x(i) cumulative search time at which the ith prey is found
- x mean number of prey per patch (no. of prey)

and the spatial patters of numbers of prey per patch. The

Abbreviations: campling the environment to estimate prey

ICT intercapture time, the search time (but not pursuit or handling time) between captures

GUT giving-up time

TE time expectation

requirements in foraging theory will be a difficult but

siting challenge for further research.

To analyze optimal foraging strategies for a entry environment it is wise to begin with a simple version of the complex problem. First, assume that there is no patch. That is, to avoid complications involving spatial patterns, movement patterns between patches, etc., assume that the numbers of preINTRODUCTION patches are determined independently. Assuming a surplus of patches and that no

How should a predator allocate time among patches when foraging in a patchy environment? The optimal strategy depends on the economic goal of foraging: the optimal behavior for a predator maximizing prey capture rate can be different than for a predator minimizing the risk of starvation, or for a predator requiring a minimum amount of some essential nutrient. The optimal solution also depends on the details of the foraging problem, such as whether the predator searches randomly or systematically within each patch. Other important aspects of the foraging problem are the statistical distribution of numbers of prey among patches and the spatial pattern of numbers of prey per patch. The requirements of sampling the environment to estimate prey numbers and monitoring for changes in mean prey density adds considerable complexity to the optimal foraging strategy. Inclusion of learning, sampling, and monitoring requirements in foraging theory will be a difficult but exciting challenge for further research.

To analyze optimal foraging strategies for a patchy environment it is wise to begin with a simple version of the complex problem. First, assume that there is no

significant spatial correlation in numbers of prey per patch. That is, to avoid complications involving spatial patterns, movement patterns between patches, etc., assume that the numbers of prey in adjacent patches are determined independently. Assuming a surplus of patches and that no patch is visited more than once, then the expected number of prey in the next patch to be visited will be completely determined by the statistical distribution of prey among patches. The second major simplifying assumption is that the predator has learned this statistical distribution and the foraging parameters of the environment. Thus, the predator's behavior patterns are assumed to be stable, no longer changing due to learning about means, variances, conditional expectations, or the consequences in changed capture rate due to changes in its behavior. Further, assume that the environment is constant, and that the predator does no sampling or monitoring for possible changes in prey density. redictions from the suboptimal strategies

Even though these assumptions make the problem much simpler, optimal time-allocation decisions are still quite complex. Oaten (1977a) has given a general solution for this type of problem, specifying when to leave any given patch in order to attain the goal of maximizing the capture rate of prey. He suggests that this optimal strategy for leaving a patch, involving higher mathematics, is too complex for any animal to actually use. It is very

likely, then, that animals use some much simpler, suboptimal strategies for time allocation. In this dissertation I analyze some simple strategies that have been proposed in the literature, to see what the optimal behavior would be for each suboptimal strategy, and to see how these strategies could be distinguished. Two economic goals are considered: maximization of capture rate and minimization of the risk of doing badly during a foraging period.

In comparing foraging strategies with one another and with laboratory and field observations, reference points are needed. If behavior is suboptimal, how bad is it? What is a relatively good performance? To help answer these questions and provide a bench mark for judging performance I have developed a neutral model, a Random strategy for foraging in a patchy environment.

After some short remarks on hierarchies of foraging decisions, some predictions from the suboptimal strategies and the Random strategy are compared with observations from lab and field. It is clear that detailed comparisons must be made to distinguish between strategies and determine the way time allocation decisions are made by predators. I make some suggestions about what variables are important to measure in future foraging experiments. Frequency distributions of important variables, rather than only means and variances, allow more detailed comparisons with

theoretical predictions and shed more light on the real strategies used. Finally, the questions and problems raised along the way suggest some promising lines of future research on the complex problem of foraging in a patchy environment.

COMPLEXITIES OF FORAGING OPTIMALLY IN

A PATCHY ENVIRONMENT

The Definition of Optimum: Related to a Specific Goal, Predator, and Environment

Predators which hunt for prey that occur in patches are faced with the very complex problem of allocating foraging time among patches. The study of this foraging problem combines two topics of much interest in ecology: optimal foraging theory and spatial heterogeneity. The ecological implications of a spatially heterogeneous enviin two recent reviews (Wiens 1976, Levin 1976). Schooner (1971) gives an excellent review of that rapidly growing body of literature known as optimal formains theory. Pyke, of the theory and tests of the theory. Other useful reviews discuss the applicability of economic models (Rapport and Turner 1977), the behavioral aspects of foraging (Krebs 1973) and recent work on foraging stratagles of birds (Krebs and Cowie 1976). My discussion and analysis of the literature on foraging in a patchy

environment occur in this chapter is connection with some complexities of the problem; other foraging theory and experiments are discussed in Chapter 7, in relation to the results developed here. CHAPTER 1

The foraging strategy which is optimal for a pre-

COMPLEXITIES OF FORAGING OPTIMALLY IN A PATCHY ENVIRONMENT the structure of the

the capabilities of the predator. It depends on the The Definition of Optimum: Related to details of the tuding the a Specific Goal, Predator, and Environment

Predators which hunt for prey that occur in patches are faced with the very complex problem of allocating foraging time among patches. The study of this foraging problem combines two topics of much interest in ecology: optimal foraging theory and spatial heterogeneity. The ecological implications of a spatially heterogeneous environment for population phenomena are thoroughly discussed in two recent reviews (Wiens 1976, Levin 1976). Schoener (1971) gives an excellent review of that rapidly growing body of literature known as optimal foraging theory. Pyke, Pulliam and Charnov (1977) present a more selective review of the theory and tests of the theory. Other useful reviews discuss the applicability of economic models (Rapport and Turner 1977), the behavioral aspects of foraging (Krebs 1973) and recent work on foraging strategies of birds (Krebs and Cowie 1976). My discussion and analysis of the literature on foraging in a patchy

environment occur in this chapter in connection with some complexities of the problem; other foraging theory and experiments are discussed in Chapter 7, in relation to the results developed here.

The foraging strategy which is optimal for a predator depends on at least three factors (MacArthur 1972): the structure of the environment, the economic goals, and the capabilities of the predator. It depends on the details of the structure of the environment, including the numbers, sizes, and spatial patterns of prey and patches. For example, if prey occur only within recognizable patch boundaries, the optimal behavior will include a search within the patch followed by direct movement to the next patch. If there are no distinct patch boundaries, the optimal strategy must include a provision for finding prey aggregations and staying within them once found.

Which foraging strategy is optimal depends on the economic goal: evolutionary theory says that the ultimate goal of an individual should be to maximize its inclusive fitness, so the requirement here is to specify a more proximate goal while foraging. The optimal behavior for a predator with a goal of maximizing prey capture rate while foraging can be different than for a predator minimizing the risk of finding no prey while foraging. There would be yet a different optimal behavior for a predator

stationary prey and those that search systematically.

minimizing the risk of predation while obtaining a quota of energy.

Other important determinants of the optimal strategy are the capabilities of the predator, both functional morphology and the behavioral capabilities, such as learning ability. A word of caution is appropriate here. Some constraints are appropriate for any real searcher: there are limits to velocity, turning rate, etc .-instantaneous jumps in location are not permitted. Such constraints due to physical and morphological limitations seem appropriate when studying optimal time allocation, but constraints and specifications of mental abilities need to be applied with caution. Some of the discrepancies between the predictions of optimal foraging theory and the results of experiments or field tests of that theory are due to a simplifying assumption made in the theory: predators are assumed to know with certainty the profitabilities of patch types and prey types. But predators are not capable of this certain knowledge. Thus, the foraging problem analyzed by the theory is different from that encountered by predators; predators must sample, both to assess profitabilities and prey densities and to monitor for changes through time.

In the following analysis I distinguish between predators that search randomly within each patch for stationary prey and those that search systematically.

Other things being equal, of course, a systematic searcher, which avoids or minimizes re-searching any patch area should always be more efficient at finding prey than a predator that searches randomly and may cross its own search path several times. If the search method is not specified, then systematic search and the consequent time allocations would be part of the optimal foraging strategy. Alternatively, one may specify that the predator uses a random search, in which case the optimal strategy would be different.

It should be possible to specify the capabilities discussing foraging behavior. Pielou (1969) strongly sugand limitations of a predator to such an extent that the that, to avoid ambiguity, the term "distribution" be resulting optimal behavior is exactly what is observed. "For a predator that can only remember the past n events, listribution of a random variable, e.g., the distribution can only judge time intervals to within x percent of the a number of prey per patch true duration, . . . the optimal foraging strategy is . . . " Such a complete specification is an important such as "spat goal of research on foraging behavior. In this case, however, the label "optimal" would be less interesting than the defining set of constraints, environmental structure, and economic goal.

In summary, a foraging strategy by itself cannot be "optimal," it is only optimal in relation to a particular environmental structure, economic goal, and set of predator capabilities. The next section discusses an important distinction for describing the structure of the

soly any specific pattern or arrangement of the items in

environment. One must distinguish the spatial pattern of prey from the statistical distribution of numbers of prey among patches in order to determine the optimal foraging strategy.

Distinguishing Statistical Distribution of Prey Among Patches From Spatial Pattern of Prey Among Patches

A predator's success at foraging can depend upon the spatial pattern of prey as well as the statistical distribution of numbers of prey per patch. It is important, therefore, to distinguish between these two factors when discussing foraging behavior. Pielou (1969) strongly suggests that, to avoid ambiguity, the term "distribution" be used in its statistical sense only: one may speak of the distribution of a random variable, e.g., the distribution of the number of prey per patch. In referring to the behavior or location of organisms in space she recommends terms such as "spatial pattern" or "spatial arrangement," e.g., a clumped pattern of insects in a field.

Another important point is that the statistical distribution of number of items per sample is not sufficient to determine the mechanism underlying that distribution: a particular distribution can often arise by several mechanisms (see, for example, Patil and Stiteler 1974, Boswell and Patil 1970, 1971, Pielou 1969, Skellam 1952, Feller 1943). Furthermore, the distribution does not imply any specific pattern or arrangement of the items in space. Fitting a statistical distribution to data on the number of eggs per patch, for example, provides a convenient way to describe or summarize the data, but information about the spatial relationships of the organisms is lost. Various techniques and indices have been proposed to make use of some of the information contained in the spatial pattern of samples. For a recent review see Patil and Stiteler (1974).

As an example, consider the negative binomial distribution, commonly used by biologists to describe the distribution of numbers of organisms per sample (cf. Bliss 1971, Gurland and Hinz 1971, Bliss and Fisher 1953, Skellam 1952). A review of its properties is given by Bartko (1961). As Pielou (1969) shows, this distribution can be generated by two guite different mechanisms. Suppose the numbers of insect eggs laid per clutch has a logarithmic distribution. Suppose, also, that each female insect chooses patches for oviposition at random; that is, patches are equally attractive to the females and equally likely to be selected for oviposition. Then the number of clutches per patch will have a Poisson distribution. The resulting distribution of total number of eggs per patch will have a negative binomial distribution. Kobayashi (1966) has studied the common cabbage butterfly, Pieris rapae crucivora. He found that a logarithmic distribution fit the number of eggs per clutch, a Poisson

distribution fit the number of oviposition visits by females per cabbage, and a negative binomial fit the distribution of eggs per plant.

Alternatively, suppose that females lay a single egg per clutch, as do most butterflies (Labine 1968). And let them select patches randomly so that the number of visits to patches of equal attractiveness will have a Poisson distribution, with the mean number proportional to the attractiveness. Suppose, however, that the attractiveness of the patches varies with a gamma distribution. The probability density function of the gamma distribution is given by

$$f(x) = (x^{c-1}d^{c}e^{-xd})/\Gamma(c)$$
 (1.1)

where c and d are two parameters, and $\Gamma(c)$ is the gamma function with parameter c. Then this mechanism will also give rise to a negative binomial distribution of eggs per patch. A possible example of this type of mechanism was given by Walker (1942). She analyzed the distribution of numbers of eggs of the American bollworm, <u>Heliothis armigera</u> Hb. (<u>obsoleta</u> F.) among maize plants. This moth lays eggs singly. The attractiveness of the plants to ovipositing females becomes very great during a relatively limited phase of plant growth, during development of the tassels. Walker believed that there is a continuous change through time in the attractiveness of individual plants. She considered the possibility that at a particular point in time there might be a gamma distribution of attractiveness, and she fit the negative binomial to the resulting distribution of eggs among plants. (She felt, however, that it was more likely that there would be only a small number of discrete categories of attractiveness. So she preferred the fit given by the distribution she created by summing three to nine Poisson distributions. It's not surprising that distributions with three to nine parameters would fit the data better than a distribution with only two.) Consult Waters and Henson (1959) for another possible example of this mechanism, here underlying the distribution of numbers of the Nantucket pine tip moth, <u>Rhyacionia frustrata</u> (Comst.), among loblolly pines, Pinus taeda L.

Notice that the negative binomial can arise both in situations where attractiveness is uniform among patches and where it varies from patch to patch. These two cases are not the only ways to obtain this distribution. Boswell and Patil (1970) provide fourteen different mechanisms which may give rise to the negative binomial! Additional tests would be necessary to determine which mechanism is responsible in a particular case (cf. Bliss 1971, Gurland and Hinz 1971).

The main point of this discussion is that knowledge of the statistical distribution of prey among patches is not sufficient to determine optimal predator search

behavior. One also needs to know the mechanism giving rise to that distribution and the spatial pattern of prey among the patches. For example, is there a significant spatial correlation between patches containing above average numbers of prey? If a predator has just found a patch with low numbers of prey, what is the probability that adjacent patches will also have small numbers of prey?

With the second mechanism described above, heterogeneous attractiveness among patches, it could easily be the case that adjacent patches would have similar attractiveness; e.g., if adjacent corn plants (adjacent patches) were in the same low, moist area of a field they might all be more attractive to some insect (prey) than those plants in high, dry areas. In this situation a predator which visited neighboring patches (plants) whenever an above average patch was discovered would not be exposed to a negative binomial distribution of prey among patches, and could sequentially visit plants with above average numbers of insects. In effect, there could be a hierarchy of patch types, with groups of adjacent plants forming a "higher level patch." In this case, then, the predator would need a hierarchy of strategies to organize his This will be further discussed in foraging behavior. ies and limitations of the predator must be Chapter 4. One of the most significant constraints

Note that within each group of patches which had equal attractiveness to prey the prey distribution could

be Poisson. So even though some prey species may have an overall distribution among patches such that the variance greatly exceeds the mean, the predator may need a strategy for moving among patches where there is a Poisson distribution of prey. Furthermore, as long as the predator stays within a group and moves without revisiting any patch, the strategy for timing the movements can be more important than the spatial pattern of search: <u>when</u> to move to the next patch can be more important than where to move.

With the first mechanism discussed, however, there would be no spatial correlation between locations of above average patches. The predator visiting a sequence of patches would be exposed to a negative binomial distribution of prey among patches, and would need an appropriate strategy for moving among them. Note that with this mechanism of prey behavior there are no useful groups of patches formed, and no hierarchy of strategies needed by the predator. Since the expected number of prey in all unvisited patches is the same, when to move to the next patch can be more important than where to go next.

Sampling: A Necessity of Foraging

To determine the optimal foraging strategy the capabilities and limitations of the predator must be specified. One of the most significant constraints on real (as opposed to hypothetical) predators is the lack of complete information about the environment, about

prey and patch types. Many workers studying optimal diet selection and optimal patch use have correctly pointed out that predators need to sample their environment (e.g., Royama 1970, Smith and Dawkins 1971, Smith and Sweatman 1974, Krebs, Ryan and Charnov 1974, Krebs and Cowie 1976, Krebs, Erichsen, Webber and Charnov 1977, Oster and Heinrich 1976, Oaten 1977a, Zach and Falls 1976a, b, c, and others). They need to estimate, for example, the mean and variance of numbers of prey per patch, for each prey type and each patch type. If a predator knew the mean capture rate in each patch type and the mean travel time between various types, then the optimal range of patch types to be utilized could be determined by the ranking method described by MacArthur and Pianka (1966). However, a real predator needs to estimate these values, and therefore, can never be statistically certain that the ranking or the range of patches utilized is correct--optimal. Even when all parts of the environment, all patch types, all prey types have been sampled and appropriate estimates made, however, there are two continuing problems: monitoring the environment for changes and attempting to discover patterns in the availability, etc. of prey. Developing foraging strategies for predators that must sample the environment for these purposes will be an exciting and challenging task for further research. Several disciplines

is subject to two sources of loss (Holland 1975, p. 77).
have much to contribute to developments in this promising area of foraging theory.

If there are N different patch types, determining the patch types to be visited is a generalized version of the N-armed bandit problem. A much-studied version is the 2-armed bandit, where the problem, given two different slot machines, is to maximize expected winnings (or minimize expected losses) by optimally allocating a fixed number of trials between them.

One version of the problem that is especially relevant to this discussion is analyzed by Holland (1975). Let me outline his problem, describing it in foraging terms. Let the travel time between patches be zero, or a constant, independent of patch types visited. Suppose the predator knows the mean and variance of the capture rate for each of two patch types. To maximize the expected capture rate (or minimize the expected losses) the optimal solution is trivial: visit only the type with the higher mean. With only a little more uncertainty, however, the problem becomes quite complex. Suppose the predator knows the two means and variances, but does not know to which patch type each belongs. Unless the two distributions of capture rate are non-overlapping, no finite number of trials will establish with certainty which patch type has the higher mean. Once foraging begins the predator is subject to two sources of loss (Holland 1975, p. 77).

First, the patch type with the observed higher capture rate may in fact be the second-best type, so that continued foraging in this patch type will realize a smaller overall mean capture rate. Second, the observed best may truly be the best patch type, so any trials allocated to the other type of patch results in a smaller average capture rate. Holland proves that to minimize these sources of loss over some finite number of trials, the number of trials allocated to the observed best type should grow slightly faster than exponential function of the number devoted to the observed second-best patch type.

This allocation plan assumes that the predator knows in advance which patch type will appear best at the end of that finite number of trials. Since this foreknowledge is impossible, Holland suggests a practical plan for this problem which quickly approaches the above minimal loss plan. First, allocate a selected number of trials to each type of patch, where this number is based on the known means and variances and the total number of trials to be allocated. Then, at the end of these initial trials allocate the remaining trials to the patch type with the observed higher capture rate. (Eventually concentrating on a single type is also Oster and Heinrich's (1976) result for a constant environment.) Other plans with different or arbitrary numbers of initial trials to each would result in a larger expected loss, though I am not

sure how sensitive the expected loss is to small deviations from the number selected by Holland's plan. To obtain his result Holland uses some approximations which are poor for small numbers of trials and for small differences between the means. These are cases where the losses due to the approximations would be small. Unfortunately, these are cases that are needed if graphs such as Figure 1 are to be constructed using his plan.

As Holland's (1975) analysis makes clear, the fraction of trials to be allocated to the poorer patch type decreases as the difference between the known means increases, or as the mean of the poorer type divided by the sum of the means departs from one half. Thus, for a given total number of trials, a graph of the fraction of trials devoted to patch type A versus the mean capture rate in type A divided by the sum of the means should be a sigmoid shaped curve, as in Figure 1. For the more general case, discussed below, where the means and variances are not known initially I would also expect a sigmoid curve; but the curve should be more flat, departing even farther from a step function. In either case it should be easiest to distinguish large mean differences and impossible to distinguish two equal means. Because of the need to sample, it will not be a step function. This is the same curve shape suggested by Krebs, Erichsen, Webber and Charnov (1977, their Figure 4) to explain their experimental data



Figure 1. Allocation of search effort between two patch types when sampling is necessary.

for a similar problem: estimating when it is nore pro-

As a further result Holland's (1975) optimal plan allocates a smaller and smaller percentage of trisis to the observed poorer patch type as the sections number of



Relative Capture Rate in Patch Type A, $R_A/(R_A + R_B)$

Figure 1. devote an increasing fraction of the trials to the observed better type. But never completely stop visiting the poorer type (a) because the first assessment may have been incorrect, and (b) because changes in the mean values may occur with time (cf. Oster and Heinrich 1976). Thus, the predator's selection curve should remain signoid and never reach the step function shape. It is most important to monitor patch types that are closest in value to the best type since these types are most likely to for a similar problem: estimating when it is more profitable to include a lower-valued prey in the diet.

As a further result Holland's (1975) optimal plan allocates a smaller and smaller percentage of trials to the observed poorer patch type as the maximum number of trials to be optimally allocated increases. So this analysis predicts that the sigmoid shape should approach a step function as the number of trials approaches infinity.

Holland's problem and allocation plan assume that the means and variances are known to the predator. For a real world predator these values will have to be estimated. Worse than that, the values will certainly change through time. It seems likely that a roughly similar allocation plan will be effective for this more general problem: after an initial estimation period where both patch types are tried, devote an increasing fraction of the trials to the observed better type. But never completely stop visiting the poorer type (a) because the first assessment may have been incorrect, and (b) because changes in the mean values may occur with time (cf. Oster and Heinrich 1976). Thus, the predator's selection curve should remain sigmoid and never reach the step function shape. It is most important to monitor patch types that are closest in value to the best type since these types are most likely to

Psychologists generally analyze the terminal or asymptotic

become the best type; also, the loss from monitoring these types will be least.

This type of foraging situation is very similar to the concurrent variable ratio schedule of reinforcement studied by psychologists (cf. Ferster and Skinner 1957, Reynolds 1968). When the fraction of total responses that are made to one key is plotted against the relative probability of reinforcement on that key, a sigmoid curve is obtained (e.g., Herrnstein and Loveland 1975). The shape is still sigmoid even after lengthy exposure to the schedule, amounting to several hundred trials, often over testing periods of several weeks. Herrnstein and Loveland (1975) have noted that, according to the psychological theory assuming that animals maximize reinforcements per unit time, there is no reason why preference (for the better key and schedule) should not become exclusive. But this psychological theory, as current foraging theory, does not explicitly take into account the estimation or sampling problem that animals have, and the possibility that changes may occur with time. If these problems are considered there are very good reasons why the step function graph would not result, reasons that would explain the sigmoid shape.

The 2-armed bandit problem is very similar to the concurrent variable ratio schedule analyzed in psychology. Psychologists generally analyze the terminal or asymptotic

behavior of animals under these schedules, e.g., the last few days of results after several weeks exposure to a schedule. Statisticians are often interested in the transient behavior as well, in order to maximize the cumulative payoff or minimize cumulative loss (e.g., Holland 1975, Jones 1975). A foraging analysis must be more like the latter (cf. Katz 1974, Katz and Bartnik 1974).

Thus the foraging model which predicts a step function change in trial allocation (or prey type selection) is optimal only for the predator with certain information about the environment--it cannot be the optimal model for real predators. All predators have uncertain information and must sample, and, therefore, the optimal trial allocation model must predict graphs more like Figure 1. The foraging experiments of Smith and Sweatman (1974) provide an example of titmice (Paridae) sampling to assess profitabilities of patches. While the birds generally learned to concentrate their search in the patches with the higher prey densities, there was not a perfect correlation between the number of trials allocated to a patch and the mean number of prey initially present. In fact, one bird of the six seemed to prefer the patch with the third-highest prey density. This is the type of result expected if animals must sample. This sampling explanation would be supported if the data showed a strong correlation between the trial

allocations and the perceived or encountered prey densities--as opposed to the nominal prey densities.

Additional experiments of Smith and Sweatman (1974) provide data consistent with the hypothesis that predators monitor the environment for changes in prey availability. When the experimenters reduced the number of prey in the best patch and increased the number in the poorest patch, the birds switched their preference to that patch which had been second-best. The experiments were not continued long enough for the birds to discover that the formerly poorest patch had become the best. Oster and Heinrich (1976) have suggested that majoring and minoring in the foraging of bumble bees plays a monitoring role. Bumble bees concentrate their major efforts on a particular flower type found to be most rewarding, but continue to make occasional visits to a minor, apparently the second most profitable flower type (cf. Heinrich 1976, Heinrich, Mudge, and Deringis 1977). Many predators respond to strong seasonal shifts in resource availability, and understanding this phenomenon is another reason for including sampling and monitoring in foraging models. Such models may help us understand the dynamics of the switch that many birds make from insects in spring and summer to seeds in fall and winter, or the resource tracking done by fish in following the strong seasonal dynamics of their prey.

Based on the experiments of Smith and Sweatman (1974), Bobisud and Voxman (1978) propose a simple stochastic model for the learning behavior of predators foraging among a finite number of patches, where they assume no depletion within a patch. They suggest that a predator should alternate one visit to the observed best patch with one samplingmonitoring visit. While this may be an acceptable strategy in some situations, it is not the best general solution to allocating visits (cf. Oster and Heinrich 1976). Unless the means are quite close or are changing very rapidly, this results in too few visits to the observed best patch.

Krebs and Cowie (1976) mention that experiments are underway to study how birds assess their environment, specifically, to determine the length of the "learning window." This is the time over which prey density or encounter rate is averaged. If this "window" is too short then the predator is too sensitive to chance variations in the encounter rate. If the "window" is too long, then the animal becomes less and less able to track small changes in encounter rate, but it will be getting a more reliable estimate of the average encounter rate.

In addition to estimating foraging parameters and monitoring for changes, sampling also gives predators the Possibility of recognizing patterns of prey availability. Davies and Green (1976) studying reed warblers show that different types of prey are available at different times of

the day. As the temperature increases flies become more active and, to be most effective in capturing prev, the birds need to change their foraging tactics throughout the day (see also Davies 1977). For another example, more tightly controlled by the experimenter, consider the "Golden Tapes" mentioned by the psychologists, Catania and Reynolds (1968). Loops of punched paper tapes are generally used to control the delivery of reinforcement in Skinner boxes. Each tape specifies a complete variable ratio or variable interval schedule. These particular "Golden Tapes" produce very stable, very regular rates of responding by pigeons subjected to them. When different tapes are used the pigeons are eventually able to detect the subtle patterns, learning, for example, that a long interval (or ratio) is consistently followed by two short intervals. Thus, the responding by the animals is not regular on these other tapes, showing that birds can learn to become sensitive to quite subtle patterns of reinforcement.

Krebs, Erichsen, Webber and Charnov (1977) remark that the difference between the step function prediction and the sigmoid prediction (cf. their Figure 4a vs. 4b) "can be viewed as the price the predator is willing to pay in sampling" (Krebs et al. 1977, p. 36). Real predators have no choice in this matter. This cost of sampling is unavoidable to all but omniscient predators. In fact,

there is a cost for not sampling, too. Holland's (1975) analysis shows one way to find the best trade-off between these opposing costs. (Holland goes on to describe a very general adaptive process, which is based on an analogy with genetic mechanisms and natural selection. This type of general adaptive process could certainly be effective for the difficult foraging problems predators must face, though interpretation of his theory in terms of mental processes and neural mechanisms would be quite speculative in our present state of knowledge.) Another type of cost involved in sampling is the time and effort required to learn how best to utilize new patch or prey types. Bees, for example, often require several visits to a new flower type before becoming efficient at finding and extracting nectar or pollen (Heinrich 1976).

This sampling problem, estimation of profitabilities, monitoring for changes, and recognizing patterns of prey availability, is an area of foraging theory ripe for further development. In this specific area the experimental base is ready for additional advances in theory, to analyze present results and design additional experiments (cf. Smith and Dawkins 1971, Smith and Sweatman 1974, Krebs, Ryan and Charnov 1974, Krebs, Erichsen, Webber and Charnov L974, Heinrich 1976, Heinrich, Mudge, and Deringis 1977). Some significant steps in this direction have been made by Oster and Heinrich (1976) and Bobisud and Voxman (1978),

as mentioned above. Additional simple learning models may prove quite helpful for this next stage of theory development. For a discussion and introduction to stochastic models of learning see Bush and Mosteller (1955) and Atkinson, Bower and Crothers (1965).

The necessity of sampling makes the predator's foraging problem very complex. As discussed in the next section, one way to begin to understand foraging strategies for a patchy environment is to start with a simpler foraging problem.

Simplifying the Problem

As described in the preceding sections the foraging problem faced by predators hunting in a patchy environment is very complex. A simpler foraging situation will be analyzed in this paper, in order to explore more easily the foraging implications of several strategies proposed in the literature for allocating search time in a patchy environment.

As a first simplification, an environment will be considered where prey occur only within discrete patches; patches have recognizable boundaries (to the predator), so that a predator can clearly distinguish when it is inside a Patch, where prey can occur, or when it is in the area between patches, where no prey occur. The prey are considered to be identical and located (uniform) randomly within a patch. All patches are considered to be of the

same type, uniform size, and have an equal degree of search difficulty for the predator. The problems analyzed here assume that there is a surplus of unvisited patches, and that predators do not re-visit patches. One example which is close to this situation is the foraging of coal tits (<u>Parus ater</u>) and blue tits (<u>Parus caeruleus</u>) for moth larvae (<u>Ernarmonia conicolana</u>) hidden in pine cones (Gibb 1958, 1962, 1966). Another similar example is the winter foraging of meadowlarks (<u>Sturnella neglecta</u>) for barley seeds hidden in cattle dung pads (Anderson and Merritt 1977).

It will be assumed that the spatial correlation among neighboring patches in numbers of prey per patch is zero, so that analysis of search paths between patches can be excluded from the present study; this assumption is partly relaxed in Chapter 4. The predator could proceed to the nearest, unvisited patch; but however the paths are chosen, the average time spent traveling between patches, the transit time m, is assumed to be constant, and independent of events occurring within a patch. (See Lewis and Papadimitriou (1978) for a discussion of a similar, shortest-path problem, the traveling salesman's tour.)

It is assumed that conditions in the environment are stable, i.e., that the physical characteristics of the Patches are constant, and that the statistical distribution

of the prey among patches not yet visited is constant; depletion of prey within a patch is permitted.

The important, but complex areas of estimating, monitoring and recognizing patterns in prey availability will not be treated further here. These additions will be fruitful areas for research. Even the analysis of the simpler case where the predator knows the means, variances, conditional expectations, etc., is very complicated, as discussed below. Predators very likely use foraging strategies that approximate optimal time allocation plans.

Suboptimal Foraging

The previous discussion shows some of the complexity of the foraging problem that predators face due to their need to assess profitabilities. Even with one patch type and one prey type in the environment, however, the foraging problem is nontrivial (cf. Oaten 1977a), even though no comparisons of patch and prey profitabilities are necessary.

Dobbie (1968), reviewing the search theory of operations research, mentions that problems realistic enough to include constraints on the searcher's movements usually require approximate solutions. In a fascinating book, Simon (1969) noted that for many complex problems the optimal solution cannot be determined in a reasonable amount of time; for many problems the choice cannot be made between a good solution and the best one--the optimal is not available (cf. Lewis and Papadimitriou 1978).

The problem-solver must then search for the most satisfactory solution. Simon has coined the term "satisficing" to describe this process, in contrast to the "optimizing" procedures possible with simpler problems. Natural selection must work in this way, favoring the most satisfactory among the available solutions to biological problems, and approaching the optimal solution where possible.

A possible example of a "satisfactory" foraging strategy may be that of the spiders described by Turnbull (1964). The spiders keep their webs in the same location if a sufficient number of prey are captured; otherwise, the web location is changed. This may not be an optimal strategy, but it may be quite satisfactory.

Pearson (1976) uses the phrase "suboptimal strategy" to describe a simple decision policy that a predator could use in choosing which prey types to include in its diet. While diet selection is not part of the simplified problem at hand, this example is notable for being "suboptimal" and for its use of a clock or timer. Call the preferred prey Type 1 and the less preferred Type 2. If the density of the Type 1 prey is known with certainty, then the optimal rule is to accept only Type 1 prey if the density of Type 1 is above some critical threshold; the predator should accept both types if the density of Type 1 is below the threshold density (Pearson 1976, Pulliam 1974, Schoener 1971). Real predators are unlikely to know the true prey

density with certainty however, so Pearson suggests a "suboptimal strategy" based on a biological timer or clock. The timer is started whenever searching begins and is reset to zero whenever a Type 1 prey is caught. Prey Type 1 individuals are always accepted when encountered; if the timer ever exceeds some critical value, then prey Type 2 individuals become acceptable as well. Thus, when the density of Type 1 is high, the diet will consist almost entirely of Type 1; when the density of Type 1 is low the acceptance threshold on the timer will almost always be exceeded and both prey types will occur in the diet; a mixture of types will occur in the diet at intermediate densities of Type 1. While not an optimal strategy, it may be quite satisfactory, and it is certainly very simple.

Oaten (1977a) has given a general solution for the optimal foraging strategy for allocating time among patches to maximize the capture rate. The optimal strategy specified, however, he admits is quite complex. He says (Oaten 1977a, p. 283):

Obviously a true optimal procedure would require remarkable feats of computing by the predator. In fact, our criterion for optimality is too narrow; it would not be "optimal" for a predator to develop the memory and computing ability needed to carry out the optimal foraging procedure if other abilities are thereby neglected. A simpler, suboptimal procedure may be preferable, one that requires only minimal memory and computation.

It is of interest, then, to analyze some suboptimal strategies that have been proposed in the literature and

to discuss the situations under which each may be most advantageous. In comparing strategies, Oaten's (1977a) optimal strategy sets the upper limit for a predator's performance in the problem considered here. One reasonable lower limit is the neutral model for foraging presented in Chapter 4. This Random strategy is "neutral" with respect to optimization of time allocation among patches: predators leave a patch at randomly chosen times-no information from previous captures is used in the decision and no "expectations" guide the predator's behavior.

CHAPTER 2

SUBOPTIMAL FORAGING STRATEGIES: THE GIVING-UP TIME AND TIME EXPECTATION STRATEGIES

The Giving-Up Time Strategy

The Giving-up Time (GUT) strategy was proposed for situations in which predators must search for prey hidden in discrete patches (Charnov 1973, Krebs, Ryan, and Charnov 1974, Murdoch and Oaten 1975, Hassell and May 1974). An example of this situation might be blue tits (Parus caeruleus) and coal tits (Parus ater) feeding on moth larvae (Ernarmonia conicolana Heyl.) hidden in pine cones (cf. Gibb 1958, 1962, 1966). A variant of this strategy might apply to cases where prey are generally aggregated but are not restricted to discrete patches (Tinbergen, Impekoven, and Franck 1967, Croze 1970). Tinbergen et al. (1967) were the first to use the phrase "giving-up time." The GUT model provides a basis for the predator's decision to leave one patch and begin searching in another one. The GUT is here defined as the maximum duration of unsuccessful search time a predator will allow before it leaves its current patch. You can consider the predator

to have a timer which is started whenever searching begins. If the timer goes off before any prey is found, then the predator leaves and moves to the next patch. If a prey is found the timer is restarted at zero.

There are several pieces of evidence that animals could have such a timer or clock. Annual and circadian biological clocks are currently under intense investigation; a GUT clock, however, must operate on a much shorter time scale. The first piece of evidence is from psychological research, where much work has been done on fixed-interval schedules of reinforcement (cf. Ferster and Skinner 1957, Reynolds 1968). Here, animals are reinforced for the first response (e.q., key-peck or bar-press) that occurs after a fixed interval of time since the last reinforcement. After sufficient experience with this type of reinforcement schedule, animals stop responding immediately after a reinforcement, and then begin responding at an accelerating rate as the fixed time interval approaches. When cumulative number of responses is plotted against time, the "fixed interval scallop" is apparent (cf. Reynolds 1968, Figure 6.4, p. 73). The animals are effectively responding to the interval of time so as to obtain reinforcement as soon as it becomes available. Church, Getty, and Lerner (1976) mention several other examples of experimental designs used by psychologists in which the performance of an animal is related to the expected time of the next

reinforcing (or punishing) event. "Examples of this sort are numerous," say Church, Getty, and Lerner (1976, p. 303), "and they suggest that animals are capable of estimating the time of occurrence of an event and adjusting their performance in an appropriate manner." Church and Roberts (1975) reported on a set of experiments which "suggests that animals maintain accurate internal representations of time which they can read." Rats "were successfully trained to vary the relationship between real time and its internal representation: to run, stop, or reset an internal clock."

Evidence from neurophysiology also demonstrates a kind of timer related to prey capture. Studying vision and behavior of frogs, Ingle (1975) has found neurons in the optic tectum which could be responsible for selective attention. Frogs seldom strike immediately at a potential prey item that only moves discontinuously--e.g., worms or some insects. One type of these special neurons turns "on" 1 to 2 seconds after the first detected movement, and begins a slow steady discharge for 3 to 6 seconds. If the prey item moves while these cells are "on" the frog will strike; if not, these cells turn "off" and no strike occurs. It seems plausible that a similar neural timing circuit could act as a GUT timer.

(Even if such a GUT clock does not exist, the results here may approximate those implied by other mechanisms.)

Optimal Giving-Up Time to Maximize Capture Rate

Appendix A presents a derivation for the expected capture rate for any given distribution of prey among patches for a predator using the fixed GUT strategy. The derivation is based on the following assumptions:

- The predator searches randomly within a patch (cf. Rogers 1972).
- (2) The prey are uniform--same size, coloration, etc.
- (3) The patches are uniform: the searching effectiveness parameter is constant for all prey in all patches. This parameter is the inverse of the mean search time required to find a specific prey item in a patch.
- (4) Each sighting of a prey results in a capture.This simplifies the algebra, eliminating the need to include terms for conditional probability of capture given a sighting.

(5) The GUT is of fixed duration, and does not depend on how many prey have been found so far in a patch. The parameter b is the mean handling time per prey item. Handling time as defined here includes time required to pursue, attack, and eat the prey, as well as time for any digestive pause that occurs before searching resumes. The parameter m is the average transit time between patches. Similar assumptions were made by Murdoch and Oaten (1975) as they considered the implications of a GUT foraging model

for the stability of a predator prey link. They presented formulae equivalent to (A.10), (A.17), and (A.18), but they did not give their derivation. Oaten (1977b) discusses the derivation of (A.18).

Poisson Distribution of Prey Among Patches

Let us assume that the distribution of prey among patches is Poisson. This could occur if prey selected patches completely randomly. (At very low densities it is often difficult to statistically reject the hypothesis of a Poisson distribution of items among samples. The above assumption might be quite reasonable under these circumstances.) As mentioned in Chapter 1, even though the overall distribution of prey among patches in a region is nonrandom, there may be groups of nearly identical patches where there is a Poisson distribution of prey within each group, and the above assumption would apply. (As discussed above, this is one mechanism that can give rise to the negative binomial distribution.)

Appendix B describes the approximation procedure used to calculate the expected capture rate for a Poisson distribution of prey among patches.

The expected capture rate E[R], equation (A.18), is plotted in Figure 2 as a function of the constant GUT, t, for various values of mean prey number per patch, x.

Figure 2. Expected capture rate as a function of GUT for several levels of mean number of prey per patch, x. p=0.1 sec.⁻¹, m=3.0 sec., and b=1.0 sec.





The optimal GUT to maximize expected capture rate decreases as average number of prey per patch increases.

Figure 3 shows the expected capture rate E[R] for several values of the searching effectiveness parameter, p, with m, x, and b held constant. As the predator becomes a more effective searcher, i.e., as p increases, E[R] increases, and the optimal GUT decreases. The peak of the E[R] curve also becomes sharper as p increases. Therefore, the relative advantage of the optimal GIT over nearby values of GUT becomes greater, and there should be stronger selection for using the optimal GUT as p increases.

One can see from Figure 4 that the expected capture rate increases as the transit time, m, decreases. Here, too, the peak of the E[R] curve becomes sharper as the optimal GUT decreases with decreasing m.

Figures 5 and 6 show the results of a computer simulation of a predator using the GUT strategy. In Figure 5 there is a Poisson distribution of prey among patches. Each vertical line represents one standard error on either side of the mean capture rate, R. These results are as predicted; compare Figure 2. A predator testing trial values of the GUT to find the optimal GUT would have difficulty; for the conditions represented here, even 15 or so replicates of 1 hour of foraging would not be enough to determine the optimal GUT with much confidence. This problem is discussed further in Chapter 6.

Figure 3. Expected capture rate as a function of the GUT for several levels of the searching-effectiveness parameter, p. x=1.0 prey per patch, m=3.0 sec., and b=1.0 sec.



Figure 3.

Figure 4. Expected capture rate as a function of the GUT for several levels of the transit time, m. x=1.0 prey per patch, p=0.1 sec.⁻¹, and b=1.0 sec.



Figure 4.

Figure 5. Mean capture rate as a function of the GUT for a Poisson distribution of prey among patches. Mean capture rate ±11 SE is plotted (10 replicates), p=0.1 sec.⁻¹, m=3.0 sec., b=1.0 sec., T=3600 sec.

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Figure 5.

Figure 6. Mean capture rate as a function of the GUT for a negative binomial distribution of prey among patches. Mean capture rate ± 1 SE is plotted (10 replicated), p=0.1 sec.⁻¹, m=3.0 sec., b= 1.0 sec., T=3600 sec.



Figure 6.

Figure 6 presents simulation results for a negative binomial distribution of prey among patches; other parameter values are the same as in Figure 5. The optimal GUT decreases as x increases and as h, the clumping parameter, decreases. As h decreases, the intercapture time is an increasingly reliable indicator of the number of prey remaining in the patch, and this GUT strategy can exploit this information. (To anticipate some later results, compare this with the conclusions of Appendix D; as h approaches infinity--as the negative binomial approaches the Poisson--only the total search time in the patch, not the intercapture time, is a reliable indicator of the number of prey remaining.) The mean capture rate curve has a sharp peak when the variation in number of prey per patch is large, i.e., at low values of h. So, as h decreases it would be more advantageous to possess an accurate and precise GUT clock. More discussion on this point appears below.

Optimal Giving-Up Time to Minimize Risk of Finding No Prey

Minimization of Risk for a Poisson Distribution of Prey Among Patches

For the goal of minimizing the risk of doing badly One can ask: what is the probability of finding zero prey in the next patch visited? To compute the answer, multiply
the probability of finding zero prey in a patch that contains n prey (A.4), by the probability that the next patch contains n prey, summed over all possible values of n. For a Poisson distribution of prey among patches (B.6), this is:

$$P[C=0 \text{ in next patch}] = \sum_{n=0}^{\infty} P[C=0|n] P[N=n]$$

$$= \sum_{n=0}^{\infty} (e^{-npt}) \frac{(x^n e^{-x})}{n!}$$
(2.1)

where C is the number of prey found in the patch, p is the searching effectiveness parameter, t is the GUT, and x = E[N] is the average number of prey per patch. Remembering that

$$\sum_{n=0}^{\infty} \frac{w^n}{n!} = e^w$$
(2.2)

and letting $xe^{-pt} = w$, equation (2.1) can be reduced to

$$P[C=0 in next patch] = e^{x(e^{-pt}-1)}$$
(2.3)

Now, what should a predator's GUT be to minimize the risk of starvation? The predator may need to minimize the probability of finding zero prey during some relatively long period of time--for example, several hours for a small bird or mammal in winter. When the environment is just a single patch, the way to minimize the probability of not finding any prey is to search for as long as possible in that patch, i.e., let $t \rightarrow \infty$. When there are many patches there will be some search time after which it will be more profitable to try another patch. Let t be the GUT, and m be the transit time, the average time spent moving to the next patch. Let T be the total foraging time; choose T so that T/(t + m) is an integer, or else T > (t + m), so that any fraction of the last patch searched in this time will be a negligible portion of the total time. Then T/(t + m)is a number which represents the maximum number of patches that can be visited during the time interval [0,T]. So then, the probability of finding zero prey during the interval [0,T] is the probability of finding zero prey in the first patch, multiplied by the probability of finding zero prey in the second patch, . . ., multiplied by the probability of finding zero prey in the T/(t + m) patch. That is, the risk is

$$P[C=0 \text{ during } [0,T]] = e^{xT(e^{-pt}-1)/(t + m)}$$
(2.4)

Equation (2.4) is graphed against t, the GUT, in Figures 7, 8, and 9. In Figure 7 the mean number of prey per patch x and the searching effectiveness parameter p are held constant. It shows that as the transit time m increases, the risk (probability of finding no prey during [0,T] increases. The optimal GUT is that GUT which



Figure 7. Probability of finding zero prey in one hour as a function of the GUT for several levels of the transit time, m, and a Poisson distribution of prey among patches. x=0.005 prey per patch, p=0.1 sec.⁻¹, and T=3600 sec.



Figure 7

L

Figure 8. Probability of finding zero prey in one hour as a function of the GUT for several levels of the searching-effectiveness parameter, p, and a Poisson distribution of prey among patches. x=0.005 prey per patch, m=3.0 sec., and T=3600 sec.



Figure 8

L

Figure 9. Probability of finding zero prey in one hour as a function of the GUT for several levels of the mean number of prey per patch, x, and a Poisson distribution of prey among patches. p=0.1 sec.⁻¹, m=3.0 sec., and T=3600 sec.



Figure 9

I.

minimizes this risk; this optimal GUT increases as the transit time m increases.

In Figure 8 the mean number of prey per patch x and the transit time m are constant. Notice that as the searching effectiveness p increases, the risk decreases and the optimal GUT decreases.

The next figure, 9, shows how risk varies with GUT and mean number of prey per patch x; the searching effectiveness parameter p and transit time m are constant. As one might expect, the risk of finding no prey during [0,T] decreases as x increases; but the optimal GUT to minimize risk is independent of mean prey abundance.

From equation (2.4) one can calculate the optimal GUT for minimizing risk--the GUT which minimizes the probability of finding zero prey during the foraging time [0,T]. Take the derivative of (2.4) with respect to t, The GUT.

$$\frac{d P[C=0 \ during [0,T]]}{dt} = (2.5)$$

$$\left(\frac{-xT}{t+m}\right) \left[pe^{-pt} + \frac{(e^{-pt} - 1)}{t+m} \right] e^{xT(e^{-pt} - 1)/(t+m)}$$

A minimum (or a maximum) can occur where the derivative is zero, i.e., where the term in brackets in (2.5) is zero, where

$$e^{-pt}(1 + p(t + m)) = 1.$$
 (2.6)

Appendix C shows that the value of t which satisfies the above (2.6) equation yields a minimum risk, and not a maximum, for 0 < t < T. An examination of the curves in Figures 7, 8, and 9 may help make this analytical result more intuitive.

Assuming p and m are known, equation (2.6) can only be solved iteratively for t. For example, for $p = 0.1 \text{ sec.}^{-1}$ and m = 3.0 sec., the optimal GUT = 6.86 sec. (see Figure 9). Notice that for this case of a Poisson distribution of prey among patches the optimal GUT for minimizing risk is independent of both the mean number of prey per patch x, and the total foraging time T; the optimal GUT depends only on p and m. See Figure 10. The risk itself, however, does depend on x and T, and it decreases as x and T increase: the probability of finding zero prey decreases the longer the foraging bout and the higher the mean number of prey per patch.

Why is this optimal GUT to minimize risk independent of the mean in this case? This optimal leaving time depends on the relative values of the expected number remaining in the current patch to the expected number in the next patch, taking into account the cost of moving between patches. Upon arrival at a patch the expected number of prey present is the mean number, x. For a Poisson distribution of prey among patches the number of Figure 10. The GUT that minimizes the risk of finding zero prey as a function of the transit time, m, for several levels of the searching-effectiveness parameter, p, for a Poisson distribution of prey among patches.



Figure 10

- C P
- f

prey expected to remain in a patch decreases exponentially with search time (see Appendix D).

 $E[K|t, Poisson] = xe^{-pt}$

where K is the number of prey remaining in the patch,

t is the total time spent searching in the patch (sec.),

x is the mean number of prey per patch, and

p is the searching effectiveness parameter (sec.⁻¹). Relative to the mean, x, this is

$$E[K|t, Poisson]/x = e^{-pt}$$
.

Thus, the fraction of the mean (i.e., of the expected number of prey in the next patch) that is expected to remain in the current patch after a given amount of search time is independent of the mean. Therefore, for a riskminimizing predator in an environment with a Poisson distribution of prey among patches, the optimal time to move on to another patch is independent of the mean.

Minimizing the Risk of Finding Zero Prey for a Negative Binomial Distribution of Prey Among Patches

As described before (2.1), the probability of finding zero prey in the next patch is:

$$P[C=0 \text{ in next patch}] = \sum_{n=0}^{\infty} e^{-npt} P[N=n] \qquad (2.1)$$

where C is the number captured in the next patch,

- n is the number of prey initially in the patch,
- p is the searching effectiveness parameter,
- t is the GUT, and
- P[N=n] is the probability function for the distribution of prey among patches.

For a negative binomial distribution of prey among patches, the probability that a patch will initially have n prey is:

$$P[N=n] = \begin{pmatrix} h + n - 1 \\ n \end{pmatrix} \frac{P^{n}}{Q^{h+n}}$$
(2.7)

where hP = x is the mean number of prey per patch, E[N],

h is the clumping parameter, h > 0,

Q = 1 + P, and

the variance of N is $Var[N] = x + x^2/h = hPQ$. Substituting (2.7) into (2.1) and rearranging yields:

$$P[C=0 \text{ in next patch}] = Q^{-h} \sum_{n=0}^{\infty} \left(\frac{Pe^{-pt}}{Q}\right)^n \begin{pmatrix} h + n - 1 \\ n \end{pmatrix}$$
(2.8)

Feller (1968, p. 63) notes that:

$$\begin{pmatrix} h + n - 1 \\ n \end{pmatrix} (-1)^{n} = \begin{pmatrix} -h \\ n \end{pmatrix}$$
(2.9)

Thus, (2.8) can be put into the following form:

$$P[C=0 \text{ in next patch}] = Q^{-h} \sum_{n=0}^{\infty} \left(\frac{-Pe^{-Pt}}{Q}\right)^n {\binom{-h}{n}} (2.10)$$

This is now in a form where the binomial theorem (e.g., Feller 1968, p. 165) can be used to obtain a closed form expression.

$$P[C=0 \text{ in next patch}] = (Q - Pe^{-pt})^{-h}$$
(2.11)

As before, (2.4), let T/(t + m) be the maximum number of patches that could be visited in total foraging time T, where T/(t + m) is assumed to be an integer (or T>>t + m so that incomplete searching of final cone is insignificant). Then the probability of finding zero prey in the time interval [0,T] is:

$$P[C=0 \text{ during } [0,T]] = (Q - Pe^{-pt})^{-hT/(t + m)}$$
 (2.12)

In terms of the mean x and clumping parameter h, this is:

$$P[C=0 \text{ during } [0,T]] = (2.13)$$

$$\left(1 + \frac{x(1 - e^{-pt})}{h}\right)^{-hT/(t + m)}$$

where x/h = P and 1 + x/h = Q.

To find the GUT providing the minimum risk of finding zero prey during the interval [0,T], equation (2.13) is differentiated with respect to t, the GUT.

$$\frac{d[P \ C=0 \ during \ [0,T]]}{dt} = \left(\frac{hT}{t+m}\right) \left(1 + \frac{x(1-e^{-pt})}{h}\right)^{-hT/(t+m)}$$

$$\left[\frac{-pxe^{-pt}}{h} \left(1 + x(1-e^{-pt})\right)^{-1} + \left(\frac{1}{t+m}\right)\log_{e}\left(1 + \frac{x(1-e^{-pt})}{h}\right)\right]$$
(2.14)

This risk-minimizing optimal GUT can now be found be solving for the value of t which makes the expression within the brackets in (2.14) equal to zero, subject to the constraint $0 < t < \infty$. That is, the following equation can be solved for a nonzero, noninfinite t:

$$(1/h)(t + m) pxe^{-pt} = G(t) log_{Q} G(t)$$
 (2.15)

where $G(t) = 1 + (1 - e^{-pt})x/h$

Unfortunately, no simple analytical solution is possible, but a numerical answer can easily be found by an iterative process.

Though the probability of finding no prey declines as T increases, the GUT which minimizes this risk is independent of T. Notice that the optimal GUT to minimize risk is dependent on the mean number of prey per patch x, in contrast to the case for a Poisson distribution of prey, and is also dependent on the clumping parameter h. More accurately, the dependence is on the ratio x/h; i.e., on the relative values of x and h, not on the absolute values. As an example, using the values m = 3.0 sec. and p = 0.1sec.⁻¹ as in the computer simulation, x/h = 5.0 yields an optimal GUT = 3.58 sec.; x/h = 1.0 gives $GUT_{opt} = 5.33$ sec.; x/h = 0.01 gives $GUT_{opt} = 6.84$ sec.; as x/h approaches 0.0, GUT_{opt} approaches 6.36 sec.

The Poisson distribution is a limiting form of the negative binomial, obtained as the clumping parameter h approaches infinity. The results above can be partially checked by noting whether the same optimal GUT is found when h approaches infinity as was found in (2.6) for a Poisson distribution of prey among patches. Equation (2.14) can be rearranged as follows:

$$\frac{d P[C=0 \ during [0,T]]}{dt} = (2.16)$$

$$\left(1 + A(t)/h\right)^{-hT/(t + m)} \left[\frac{-Tpxe^{-pt}}{(t + m)(1 + A(t)/h)} + \frac{\log_{e} (1 + A(t)/h)^{hT/(t + m)}}{t + m}\right]$$

where $A(t) = x(1 - e^{-pt})$ Then, using the relationship

$$\lim_{h \to \infty} (1 + a/h)^{bh} = e^{ab}$$
(2.17)

and simplifying, the following limit is obtained as the negative binomial approaches the Poisson distribution:

$$\lim_{h \to \infty} \frac{d P[C=0 \text{ during } [0,T]]}{dt} =$$

$$\frac{Txe^{-x}(1 - e^{-pt})T/(t + m)}{t + m} \left[-pe^{-pt} + \frac{(1 - e^{-pt})}{t + m} \right]$$
(2.18)

Comparing the term in brackets in (2.18) with (2.6), it is obvious that the optimal GUTs are the same in the limit.

Comparing Foraging Goals: Maximization of Capture Rate vs. Minimization of Risk

For a Poisson distribution of prey among patches and a predator using the GUT strategy, the above results show that the two goals of foraging result in different optimal GUTs, one which maximizes the expected capture rate, and a different optimal GUT which minimizes the risk of finding no prey. What are the differences in capture rate and longest intercapture time when these two different goals require different GUTs? Figure 11 shows the results of a stochastic simulation which bear on this question. The left group of histograms shows the mean and one standard error of the longest intercapture time occurring during one hour or five hours of simulated foraging, for 20 The difference in optimal GUTs increases as m replicates. increases; results are compared for transit times of m = 3and 22 seconds. Note that after only one hour (20 reps.) the results happened to come out the opposite of expected: the GUTs which were to minimize the risk of finding no

Figure 11. Comparison of simulation results for optimal GUT to maximize capture rate versus optimal GUT to minimize risk, for a GUT strategy and a Poisson distribution of prey among patches. Mean ± 1 SE (20 replicates), longest inter-Α. capture time during T=1 and T=5 hours of simulated foraging, for transit times of m=3 and m=22 seconds. B. Mean ± 1 SE (20 replicates), capture rate during T=1 and T=5 hours of simulated foraging, for transit times of m=3 and m=22 seconds. X=10.0 prey per patch, p=0.1 sec.⁻¹, and b=1.0 sec. "MAX RATE" indicates results for optimal GUT to maximize capture rate, and "MIN RISK" indicates results for optimal GUT to minimize risk of finding no prey.



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prey resulted in longer maximum intercapture times than the GUTs which were to maximize capture rate. However, after 20 replicates of five hours of foraging the results were as expected: the GUTs which were to minimize the risk resulted in shorter maximum intercapture times. Notice that in all cases the GUTs which were to maximize the capture rate did so; they consistently minimized the average time between prey captures.

If the results shown in Figure 11 generalize to other situations then the advantage of using the riskminimizing GUT may be relatively small. It should be noted that the difference between the two optimal GUTs is smaller at lower values of mean prey number x (in the simulation x = 10.), but these low values of x are where the risk is greatest and the risk-minimizing goal should be most important. Also, the difference in capture rate between the two optimal GUTs appears relatively large compared to the difference in maximum intercapture time: the risk-minimizing predator appears to pay a relatively large cost in reduced capture rate for only a small reduction in maximum intercapture time (which should be closely related to the risk of finding no prey). Further remarks on this comparison are contained in the Discussion.

The Time Expectation Strategy

One possible strategy that a predator could use is the Time Expectation (TE) strategy. Krebs (1973) and

Krebs, Ryan and Charnov (1974) proposed one form of this strategy: the predator spends a constant total amount of time per patch. This was suggested as an alternative to Gibb's (1962) Number Expectation strategy.

Results from Appendix D suggest another form of this strategy. Appendix D shows, for a Poisson distribution of prey among patches and a Poisson search process within patches, that the expected number of prey remaining in a patch depends on the cumulative search time that has elapsed in the patch, and does not depend on the number of prey found up to that time. An intuitive argument may clarify the point. If the distribution of prey among patches is Poisson, then one can consider that each prey in the environment independently and randomly selected a patch to inhabit. Thus, the finding of one or several prey in a patch gives no information about how many others selected that same patch. Upon first arriving at a patch the expected number of prey present is the average number for all patches. Additional time spent searching, however, makes it less and less likely that (more) prey remain to be found: there is an exponential decay with search time in the expected number of prey remaining in the patch. If the predator's foraging strategy was to leave a patch when the expected number remaining reached some threshold (or, alternately, when the expected additional time to

next capture reached a threshold), then the predator could leave each patch after a fixed amount of search time.

This, then, suggests another form of the TE strategy of Krebs (1973) and Krebs, Ryan, and Charnov (1974): the predator spends a constant total amount of search time in each patch (rather than a constant total of search plus handling time). With this TE strategy there will be no extension of search time if additional prey are found. One could imagine the "giving-up time clock" of the GUT strategy pausing as each prey is found and handled, but not being reset; the clock's "alarm" would then indicate when some fixed total search time had elapsed in the current patch.

Expected Capture Rate and Optimal Total Search Time per Patch

Appendix D presents the derivation for the expected number of prey captured per patch, E[C], and Appendix E the expected capture rate, E[R], for a predator using the TE strategy. For a given total search time, t, the expected number captured, E[C], will be

$$E[C] = x(1 - e^{-pt})$$
 (E.7)

where x is the average number of prey per patch, and

p is the searching effectiveness parameter.

This is the stochastic equivalent of the deterministic "Random Predator Equation" of Rogers (1972). As in Rogers' analysis, it assumes the predator searches randomly within a patch.

The expected capture rate, E[R], will be the expected number caught per patch, E[C], divided by the expected total time per patch: search time, t, plus transit time, m, plus total handling time, bE[C]:

$$E[R] = \frac{x (1 - e^{-pt})}{t + m + bx(1 - e^{-pt})}$$
(E.8)

For a given total search time, t, the expected capture rate depends on the average number of prey per patch, x, but not on the form of the distribution for prey among patches. Likewise, the optimal total search time per patch, t_{opt} , which maximizes the mean capture rate, does not depend on either the distribution of prey among patches or the mean of that distribution. Appendix F shows that t_{opt} is a function of p and m, the searching effectiveness parameter and the transit time between patches. The value of t for which the following equation holds is t_{opt} :

$$e^{-pt}(1 + p(t + m)) = 1$$
 (F.2)

Note that this expression for t_{opt} is the same as equation (2.6) above. For the TE strategy the total search time which maximizes the mean capture rate is the same as that

which minimizes the risk of finding no prey for a Poisson distribution of prey among patches, but these two optimal times are different for a negative binomial distribution. In addition, this capture rate-maximizing total search time for the TE strategy is the same as the GUT which minimizes the risk of finding no prey for a Poisson distribution (see equation (2.6)).

Suppose that the predator has no cues or sources of information about the number of prey in a patch other than its own experience in each patch. If the distribution of prey has a large variance/mean ratio, the TE strategy would likely be inferior to a GUT-type strategy. For example, if most patches had a small number or zero prey, and most prey were concentrated in a small proportion of the patches, then a GUT-type strategy would allow the predator to avoid spending a full "total search time" in a poor patch, and would tend to allocate more search time in rich patches. If, however, there is a Poisson distribution of prey among patches, it appears that the TE strategy with total search time t opt is the best possible strategy for either maximizing the mean capture rate or minimizing the risk of finding no prey, or both. For example, in experimental situations where the prey has been distributed randomly among patches (and other assumptions of this model are met-see Chapter 1), the optimal forager should eventually learn not to vary the total search time because of prey

captures or the mean density of prey. Its search time (but not total time) per patch should be a constant, dependent only upon p and m. Figure 5 above is a graph of optimal search time (equivalent to the optimal GUT to minimize risk) versus p and m.

There is another situation where the TE strategy would apparently be the best way to allocate time among a group of patches. If the overall distribution of prey among patches in the environment arises from the compounding of many Poisson distributions, each with a different mean (e.g., the negative binomial), then the predator may choose to forage in a particular group of patches with a high mean. Within this group the distribution of prey would be Poisson and the TE strategy would be best. For deciding how to allocate time among the groups of patches, however, a higher level strategy would be useful (see Chapter 4).

Observed "GUT" Inversely Related to Prey Density

Because the total search time for the TE strategy is independent of the mean prey number per patch, a higher mean will decrease the average time between prey captures; notice, also, that the average time between the last prey capture and emigration from the patch will decrease. Thus, the observed "giving-up time" will decrease as mean prey density increases, but it will not be due to an active

response or changed behavior on the part of the predator. Observing changes in "GUT" with mean prey density, then, does not by itself mean that a GUT foraging strategy is being used by the predator.

The frequency distribution of observed GUT for this strategy is evaluated in Appendix G and discussed in Chapter 5.

Computer Stochastic Simulation: Results and Discussion

Figures 12 and 13 show the results of a computer stochastic simulation of the TE strategy for a Poisson (Figure 12) and a negative binomial (Figure 13) distribution of prey among patches. Comparing these graphs with those for the GUT strategy (Figures 6 and 7) one can see that the peaks of the capture rate are much broader for the TE strategy than for the GUT strategy. A deviation from the optimal search time per patch will thus have less effect on the capture rate for the TE strategy than an equal deviation from the optimal GUT. Stated another way, to maintain a nearly maximal capture rate the animal with the GUT strategy requires a much more accurate clock than the predator using the TE strategy. The TE strategy would appear to be more robust to deviations from the optimal search time. Also, the GUT strategy is more sensitive to noise in the system--chance variations in

Figure 12. Mean capture rate as a function of search time per patch for a Poisson distribution of prey among patches. Mean capture rate ± 1 SE (10 replicates) is plotted. p=0.1 sec. , m=3.0 sec., b=1.0 sec., T=3600 sec.



Figure 12

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Figure 13. Mean capture rate as a function of search time per patch, for a negative binomial distribution of prey among patches. Mean capture rate ± 1 SE (10 replicates) is plotted. x=5.0 prey per patch, h=1.0, p=0.1 sec.⁻¹, m=3.0 sec., b=1.0 sec. and T=3600 sec.



Figure 13

search time between captures, whereas the TE strategy tends to average out stochastic fluctuations in intercapture time.

Optimal Total Search Time per Patch to Minimize the Risk Of Finding No Prey

Equation (E.4) gives the probability of capturing i prey, given n prey are present initially, for a predator using the TE strategy. The probability of finding i = 0 prey, given n prey in a patch, would be:

$$P[C=0|n] = e^{-npt}$$
 (2.19)

where t is the total search time in the patch. The probability of finding zero prey in the next patch visited would take into account the distribution of prey among patches:

$$P[C=0 \text{ in next patch}] = \sum_{n=0}^{\infty} P[N=n] e^{-npt}$$
(2.20)

where P[N=n] is the probability function for the distribution of prey among patches.

Notice that this equation (2.20) is the same as (2.1) above. Thus, whatever the distribution of prey among patches, the optimal search time per patch which minimizes the risk of finding no prey will be the same for both the GUT and TE strategies. Equation (2.6), shows how to find this optimal total search time for the case of a Poisson distribution of prey among patches, and equation (2.15), does the same for a negative binomial distribution.
CHAPTER 3

THE RANDOM STRATEGY: A REFERENCE POINT FOR EVALUATING SUBOPTIMAL STRATEGIES

Expected Capture Rate for a Neutral Model

In evaluating suboptimal foraging strategies reference points are needed. The optimal strategy is one obvious benchmark for comparison, setting an upper limit on performance (cf. Oaten 1977a). What is a reasonable lower limit to performance in a patchy environment? One way to estimate a lower bound on a predator's performance is to construct a neutral model (Caswell 1976, Crowder 1978, Gould 1978) for a foraging strategy. Such a model is designed to be "neutral" with respect to the factor or influence under investigation. For example, make the reasonable assumption that natural selection is acting to optimize (in some way) the amount of search time a predator spends in each patch. Then one neutral model for a search time allocation plan would be a strategy in which search time per patch was determined randomly, and not in a manner optimized by natural selection. Other strategies should be able to do at least this well, and this "Random"

strategy should set a reasonable lower bound on performance in allocating time among patches.

In addition, this Random strategy can help determine how sensitive the expected capture rate is to variations in the leaving time, and, consequently, how great the selective pressure is for an accurate and precise foraging clock.

In this Random strategy the predator's total search time in a patch is determined randomly, perhaps by chance events completely unrelated to foraging. Assume that the predator does not leave a patch while pursuing or handling prey, but only while searching. Suppose that, while searching, the instantaneous probability that the predator will leave is constant and equal to r^{-1} , with $0 < r^{-1} < 1$. This yields a negative exponential distribution of T_s , total search time in a patch, with a mean total search time of r seconds, and a variance of r^2 seconds. The probability density function for total search time will be

 $f(t) = (1/r)e^{-t/r}$ (3.1)

An analytical solution can be found for the expected number of prey found in a patch that initially contains n prey.

$$E[C|n, Random] = \int_{0}^{\infty} E[C|n,t] f(t) dt$$
$$= \int_{0}^{\infty} n(1 - e^{-pt}) (1/r) e^{-t/r} dt \quad (3.2)$$
$$= \frac{nrp}{rp + 1}$$

where r is the mean total search time per patch.

The expected number of prey captured in a patch is found by taking into account the distribution of prey among patches.

$$E[C|Random] = \sum_{n=0}^{\infty} E[C|n, Random] P[N=n]$$
$$= \frac{xrp}{rp+1}$$
(3.3)

where $x = \sum_{n=0}^{\infty} n P[N=n]$ is the mean number of prey per patch. Notice that the average number of prey captured per patch depends on x, but not on the form of the distribution of prey among patches.

The corresponding expected number for the Time Expectation (TE) strategy is (cf. Appendix E):

$$E[C|TE] = x(1 - e^{-pt})$$
 (E.7)

where t is the fixed total search time per patch.

If the average total search time in the Random strategy is the same as the fixed total search time in the TE strategy, then the expected number of prey found per patch is always less for this Random strategy, for $0 < r = t < \infty$; the two expected numbers converge as r and t both approach either zero or infinity. Letting r = t,

$$E[C|Random] = x\left(\frac{pt}{pt+1}\right)$$
(3.4)

$$E[C|TE] = x(1 - e^{-pt}) = x\left(\frac{e^{pt} - 1}{e^{pt}}\right)$$

$$= x\left(\frac{pt + D}{pt + 1 + D}\right)$$
(3.5)

where $D = \sum_{i=2}^{\infty} \frac{(pt)^{i}}{i!} = e^{pt} - (1 + pt)$

From these two expressions it is easy to show the stated inequality. Let a = pt, then divide each expression by n.

$$\frac{a}{a+1} < \frac{a+D}{a+1+D}$$
(3.6)

$$\Rightarrow a(a+1+D) = a^{2} + a + aD <$$
(a + 1) (a + D) = a² + a + aD + D

$$\Rightarrow 0 < D \quad Q.E.D.$$

In a given environment, then, the animal using the TE strategy is expected to find more prey per patch than the animal with the Random strategy.

The expression for expected capture rate E[R] is given by (3.7), and takes account of the variable search time.

$$E[R] = \left(\frac{(r + m)(rp + 1)}{rpx} + b\right)^{-1}$$
(3.7)

As the mean prey abundance per patch x approaches infinity, the capture rate is limited by the handling time b, as expected.

$$\lim_{x \to \infty} E[R] = 1/b \tag{3.8}$$

Maximizing the Mean Capture Rate

It seems a little strange to consider optimizing a Random strategy, but it is possible to determine the instantaneous probability of leaving, l/r, which maximizes the mean capture rate for this strategy. First, find the derivative of the expected capture rate with respect to r.

$$\frac{d E[R]}{dr} = \frac{1}{x} \left(\frac{m}{pr^2} - 1 \right) \left(\frac{(r + m)(rp + 1)}{rpx} + b \right)^{-2}$$
(3.9)

This derivative will be zero and E[R] will be a maximum when

$$r = r_{opt} = (m/p)^{1/2}$$
 (3.10)

The expected capture rate is a maximum for this value of r since the second derivative evaluated at this point is negative. Notice that this optimal value of r, which maximizes the capture rate for this strategy, depends only upon m and p, the transit time between patches and the searching effectiveness parameter; it does not depend on mean prey number per patch x, or the form of the distribution of prey among patches. Substituting the optimal r into equation (3.7), the maximum expected capture rate is

$$E[R|r = r_{opt}] = \left[\frac{(1 + (mp)^{1/2})^2}{xp} + b\right]^{-1}$$
(3.11)

This maximum expected capture rate for the Random strategy can be compared to the maximum for the TE strategy (the optimal strategy for a Poisson distribution of prey among patches), equation (F.4). The following ratio results:

$$\frac{E[R|Random, r=r_{opt}]}{E[R|TE, t = t_{opt}]} = \frac{1 + p(m + bx + t_{opt})}{1 + p(m + bx + 2(m/p)^{1/2})}$$
(3.12)

Notice that as mean prey number per patch, x, gets very large this ratio approaches 1; this is because both capture rates approach 1/b. As handling time increases toward infinity this ratio also approaches 1; in this case both capture rates are approaching zero. Additional comparisons of these two strategies are made in the next section using results of computer simulations, and in Chapter 5 using experimental data from the literature.

Computer Stochastic Simulation: Results and Discussion

Figure 14 shows the results of a computer simulation of this Random strategy, where mean total search time, $t_s = r$ is on the abscissa. This is compared in the same figure with results from another stochastic simulation Figure 14. Comparison of TE and Random strategies: Mean capture rate as a function of mean search time per patch, r, for a Poisson distribution of prey among patches. Mean capture rate ±11 SE (10 replicates) is plotted. p=0.1 sec. , m=3.0 sec., b=1.0 sec. and T=3600 sec.



Figure 14.

using the Time Expectation (TE) strategy, where the total search time T_s is fixed during a particular simulation run. The Random strategy does quite well, but the capture rate is lower than if a constant T_s had been used. Notice, however, that a predator using this Random strategy with a mean near the optimal total search time would still have a capture rate that is a large fraction of the maximum possible with the TE strategy. For the parameters chosen for these simulation runs (x = 5 prey per patch, m = 3sec., $p = 0.1 \text{ sec.}^{-1}$), the Random strategy with $r_{opt} = 5.48$ seconds results in an expected capture rate of 0.173 prey per second. For the TE strategy with a fixed T of t = 6.86 seconds, the mean capture rate is 0.201 prey per second. So the TE strategy yields a maximum capture rate that is 16% greater than the maximum of the Random strategy under these conditions.

Evaluated at t = 15 seconds for the TE strategy and r = 15 seconds for the Random strategy, the difference between the mean capture rates for the two strategies appears to be increasing. Fairly quickly, however, further increases in leaving times cause the mean capture rates to converge; at very large values of t and r both capture rates approach zero.

These simulation results, shown in Figure 15, are expected from the analytical results given in equations (3.7), (E.8), and (3.12)--expected capture rate for the

Random strategy, expected capture rate for the TE strategy, and the ratio of the maximum capture rates, respectively. These equations show the type of results depicted in Figure 14 to be quite general, i.e., the mean capture rate for the Random strategy is always less than the mean capture rate for the TE strategy, and the mean capture rates converge and approach zero as t and 4 approach zero and as t and r approach infinity. Thus, the parameter values chosen for this simulation run can be quite arbitrary; similar results are expected.

It appears, therefore, that a predator using the Random strategy can do quite well regarding capture rate compared to the TE strategy as long as the mean of the total search time is somewhere near the optimal value, and even this requirement appears to be weak. Conversely, under these circumstances the TE strategy, optimal for a Poisson distribution of prey among patches, does only 16% better than the neutral model, this Random strategy. This 16% advantage could increase fitness very significantly, however. Suppose that the capture rate obtained with the Random strategy is just sufficient to cover a predator's maintenance costs. The higher capture rate of the TE strategy might allow growth and reproduction when neither was possible under the Random strategy. The advantage of leaving some as opposed to no offspring could thus be due to a relatively small increase in capture rate, and the

selective advantage of the better strategy could be quite large.

Remember that this neutral model of foraging in a patchy environment is not intended to provide a realistic description of any predator's behavior. Rather it is merely a reference point for judging performance, for comparing strategies.

CHAPTER 4

A HIERARCHY OF FORAGING STRATEGIES

What is a Patch?

A hierarchy of patch types is generally present in the environment. Small prey-containing units with distinct boundaries, patches, often occur in distinct groups, and these groups occur in larger distinct units. As an example, the pine cones studied by Gibb (1958, 1962, 1966) are distinct prey-containing units--"patches." Gibb (1966) showed that trees differed significantly in the average number of moth larvae found per cone; the pine cones are naturally grouped into distinct units--trees. The trees occur in woodlots or forests, etc. Predators need some strategy for allocating search time among pine cones, and they also need some strategy for allocating time among trees and among groups of trees. A hierarchy of strategies is required. In this context the question "what is a patch?" is largely semantic; the answer depends on which strategy in the hierarchy is being studied. The capture rate may be much more sensitive to changes in strategy or foraging variables (e.g., GUT or total search time) at one level in this hierarchy than at other levels. The

comparison of several levels regarding this sensitivity may be what is implied by the question (cf. Gill and Wolf 1977).

Effectiveness of Strategies

While the TE strategy can sometimes be the optimal time allocation strategy at some levels of the foraging hierarchy, it is unlikely to be useful at all levels in the hierarchy. For example, if prey occur randomly among pine cones according to a Poisson distribution, then a bird seeking to allocate time among cones should use the TE strategy. If, however, as Gibb found with his moth larvae, there happen to be large differences in "intensity" of prey from tree to tree, then a predator should not use this TE strategy at the tree level. The finding of several "good cones" would be a good indication that a specific tree had an above average intensity of infestation. The strategy used should allow the bird to make use of this information in its foraging. But using the TE strategy at this level would not use that information and the animal would make a response based on the overall average intensity. A GUT strategy, however, could be used to exploit cones on "good" trees.

Figure 15 shows how the GUT strategy can be generalized for use at any level in this hierarchy. A timer is used for each level, and the appropriate timer is reset after each "good" event: cone-timer is reset after each Figure 15. The GUT strategy generalized for use at any level in the hierarchy of foraging strategies. Strategies are shown for moving among trees and among cones on a single tree.

TREES







("good") prey capture, tree-timer is reset after each "good" cone, woodlot-timer is reset after each "good" tree, etc. The predator moves to the next unit whenever that timer reaches the appropriate GUT, or when all lower-level units have been searched, e.g., move between trees when either the tree-timer reaches the GUT_{tree} or when all cones on the tree have been searched.

Computer Stochastic Simulation: Results and Discussion

Figure 16 shows the results of a stochastic simulation of a predator foraging among pine cones, with a Poisson distribution of prey among cones on each tree. The mean of the Poisson is different on each tree, and is chosen randomly for each tree from an Erlang distribution. Considering the entire group of trees, then, the distribution of prey among cones has a negative binomial distribution (see Chapter 1). Fifty pine cones are on each tree. The predator is given a TE strategy for moving between cones on a tree--the optimal strategy in this case, because of the Poisson distribution of prey among cones within each tree. The predator is using the GUT strategy at the tree level, as specified in Figure 16. In this example simulation, the overall capture rate is maximized when the GUT_{tree} is 18 seconds; large deviations from this value can make about a 15% difference in overall capture rate.

Figure 16. Mean capture rate as a function of giving-up time for trees. Mean capture rate ± 1 SE (20 replicates) is plotted. There is a Poisson distribution of prey among patches on a tree, with the mean for each tree chosen randomly from an Erlang distribution (mean of 5.0 prey per cone on a tree, variance among trees is 6.250). p=0.1 sec.⁻¹, m=3.0 sec., b=1.0 sec., T=3600 sec., Good-cone-threshold=0.3 prey per sec., total of 50 cones per tree



Figure 16

Notice that at very long values of GUT_{tree} the overall capture rate approaches the average for the environment as a whole (compare with Figure 13). This is because the predator stays so long on each tree in this case that nearly all the cones on each tree are visited; the GUT_{tree} is so long that the predator does not leave poor trees soon enough.

Further exploration of hierarchies of strategies is recommended. In this context, one of the first questions that must be addressed is "How much is enough?" What capture rate will satisfy a predator so that it remains in a particular hunting area or patch group? Comparison of relative sensitivity of overall capture rate to the strategies and variables at each level in the hierarchy should prove illuminating.

CHAPTER 5

COMPARING STRATEGIES WITH OBSERVATIONS FROM LAB AND FIELD

Distinguishing Among Foraging Strategies

How may these foraging strategies, GUT, TE and Random, be compared experimentally? Each strategy assumes that predators have reached stable patterns of behavior, i.e., learning behavior is not complicating the results. The best comparisons between strategies can be made when a complete time-series of foraging events has been recorded. Significant events include arrival at a patch, time of each prey sighting, the time an animal finishes handling a prey item and resumes search, and the time an animal leaves a patch. From this set of data the average handling time and mean transit time can be computed. The giving-up time is defined as the search time from last prey capture until the animal leaves the patch, or, if no prey have been found, the time from arrival in a patch until leaving that patch. The intercapture times are the search times between prey captures in a patch, and total search time is simply the sum of the intercapture times in a patch plus the givingup time.

Each strategy predicts different patterns for the set of intercapture times, giving-up times, and total search times per patch. These differences are summarized in Figure 17. For the constant GUT strategy the giving-up time would be expected to be constant, but due to small variations in measurement by the experimenter and variability in the animal, one would expect a distribution of giving-up times tightly clustered around some mean value. For this strategy all intercapture times must be less than or equal to the giving-up time. If any intercapture time on a single patch exceeds the giving-up time, the predator should leave the patch. An observation that a predator did not leave a patch in this circumstance would constitute evidence that the fixed GUT strategy was not being used. Total search time would be expected to be variable with no total search times being less than the giving-up time.

For the TE strategy the observed giving-up time should be variable, with a unimodal frequency distribution function as described in Appendix G. Some intercapture times will be longer and some shorter than the observed giving-up time. The total search time, however, should be relatively constant; the frequency distribution should be tightly clustered around the mean.

It is expected that predators will have strategies that are more effective than the Random strategy; predictions of this neutral model are presented for

Figure 17. Distinguishing among the constant GUT, TE, and Random strategies. (Search is assumed to be random, continuous.)



Figure 17

comparative purposes. For the Random strategy the observed giving-up time will be variable, with a unimodal frequency distribution function similar to that of the TE strategy, but with a larger range of values. As with the TE strategy some intercapture times will be longer and some shorter than the observed giving-up time. The total search time is variable; the primary assumption of this strategy is that the frequency of total search times is described by a negative exponential equation, or, equivalently, that the instantaneous probability of leaving a patch while searching is constant.

Several pieces of evidence will provide stronger support for establishing which strategy is being used than a single line of evidence. Thus, while comparisons of giving-up time distributions would find two of these strategies with variable giving-up time distributions, these two strategies (TE and Random) can be distinguished by examining the frequency distribution of total search time. The major differences between strategies are apparent in the frequency distributions of these variables. Comparisons of means of these variables would be a much less powerful test. Of course, these three strategies are not the only possible policies for allocating time in a patchy environment. Examination of the means and frequency distributions of intercapture time, observed giving-up time, and total search time per patch can provide much insight into the

actual mechanisms of foraging, the actual strategies used by predators.

Search	Within a	a Pat	cch:	Continu	ous
vs.	Discrete	e Tri	ial	Search,	
and	l Random	vs.	Sys	tematic	
	Se	earch	1		

The formulae for predicted capture rate, etc., given here for these three strategies should not be applied in their present forms to experiments such as those of Krebs, Ryan and Charnov (1974), Smith and Dawkins (1971), or Smith and Sweatman (1974), because two important assumptions are not met. First, these formulae apply only to continuously searching predators, where, until the next prey is found, the probability of finding a prey at any instant of search time is constant (the constant does depend on the number of prey remaining in the patch). This is not the case for the experiments mentioned above; prey were placed in holes or cups within a patch, and the probability of finding a prey changed abruptly as each hole or cup was opened. I would call this latter case a discrete trial search. Second, these equations assume that the predator searches at random, not systematically, within a patch. This random search analysis assumes that there is a depletion effect in the patch, but that when one of k prey is found the subsequent search can be described exactly as before the capture except that k - 1 prey now remain. This would not be the case for a systematic

searcher, since a capture would mean both that k - 1 prey are left and that a smaller patch area remains to be searched.

Foraging strategies can be cross-classified by making these distinctions between discrete trial search and continuous search, and between random and systematic search. As implied above, the predictions of these strategies will vary depending on which pair of search categories applies; the mathematical models for each of the four possible pairs are different, and the best course of action for the predator changes accordingly. The classification of the search depends on both the experimental design and the behavior of the predator. Systematic search requires a predator capable of either recognizing and using external signs of a previous search or of internally generating a patterned movement.

As mentioned above, the discrete trial search experiments of Krebs, Ryan and Charnov (1974), Smith and Dawkins (1971), and Smith and Sweatman (1974) lend themselves to systematic search. Removal of foil caps from cups or gummed tape over holes leaves a clear indication of which parts of the patch have been searched. As noted by Zach and Falls (1976c) and Krebs and Cowie (1976), if no depletion or depression effects occur, and none were reported in the experiments of Krebs, Ryan and Charnov (1974), then the model of Charnov (1973, 1976) does not apply. Recognition of the distinction between random and systematic search would have helped clarify the theory's applicability.

Zach and Falls (1976c) report that the ovenbirds (Seiurus aurocapillus) they observed searched in a fairly systematic manner within a patch; apparently the birds continuously scanned the patch. Zach and Falls concluded that the birds were not hunting by number or time expectation strategies; they suggested that the optimal leaving time may "coincide with complete coverage" of the patch (Zach and Falls 1976c, p. 1894). I can show, however, that for a systematic and continuous searcher using a TE strategy, the optimal behavior to maximize the capture rate is to search the entire patch. Thus, their results agree with this prediction of the TE strategy, rather than conflict with it. Variations in search speed and the complicating effects of area restricted search, not included in the present models, should account for some of the variations in total search time per patch that they observed.

As observed in the next section of this chapter the experiments of Cowie (1977) and some of the foraging tasks of Partridge (1976) can be classified as continuous and random search, and, therefore, best fit the models presented in Chapters 2 and 3. In these cases birds probe in small cups of sawdust or shredded paper for pieces of mealworms. Because the material in the patch (cup) shifts so easily, a systematic search would be difficult, and the rapid, probing beak movements of the birds probably come very close to a continuous search.

I have not found any foraging experiments in the published literature that are unambiguous examples of the random and discrete trial search combination. This general type of search can be illustrated by the urn models of probability theory, where a collection of red and white balls ("prey" and "no prey") are sampled with replacement.

It should be clear from these examples that it is very important to correctly classify foraging experiments, and compare the appropriate version of each strategy with the results.

Formulae to describe discrete trial search and systematic search are under development for these three strategies. As a beginning step, Appendix H presents the probability functions and mean values for the number of trials between captures in a discrete trial search, for both randomly and systematically searching predators.

Cowie's Laboratory Experiments With Birds

In comparing the predictions of strategies with observations from lab and field, it is important to meet the assumptions of the models as closely as possible. Among recent foraging experiments those of Cowie (1977) seem to come closest to meeting the assumptions of the

suboptimal foraging models analyzed above. Cowie performed foraging experiments using six wild-caught great tits (Parus major). Experiments were run in an aviary (4.6 m x 3.7 m) containing five artificial trees. The patches, six to a tree, were made from short sections of plastic pipe, sealed at one end and filled with sawdust. The prey were quarter sections of mealworms. Six prey were hidden in each patch. Each bird was subjected to two types of experiments, identical in every respect, except for the traveling time between patches. Each patch was covered with a cardboard lid. In one experiment these lids could be easily pulled off, and in the other set of experiments the lids were modified so that they just fit inside the rim of the cup and had to be pried out. For each experimental type the lids were all of one kind or the other, and the environments were classified as "hard" or "easy," corresponding to these differences in "Traveling Time" between patches. Six ten minute trials were performed on each bird in each environment.

These experiments seem to fit the assumptions of my model strategies quite closely, except perhaps for the assumption of experience. With a total of only one hour experience in each environment it is not clear that the animals' behavior patterns had stabilized, or that the animals had learned enough about the environment in that short interval to optimize their behavior. Other

assumptions are met by the discrete patches used and by the continuous search within a patch. (This is to be distinguished from experiments such as those of Krebs, Ryan and Charnov (1974) or Smith and Sweatman (1974) in which searching within a patch occurred as discrete trials, e.g., where a patch was composed of an array of cups, opened one by one.) It also appears likely that the birds searched randomly within a patch rather than searching systematically.

Parameterization of the GUT, TE, and Random strategies is accomplished in the following way. The transit time, m, was measured by Cowie for each environment. Handling times, b, were not significantly different in each environment, so a mean value of 8.21 seconds is used. Multiplying total time per patch (Cowie's Time in Patch plus Traveling Time) by the average capture rate, the average number of prey captured per patch in each environment is obtained. In both environments this is about 2 prey captured per patch. Assuming that search is a Poisson process, the expected intercapture interval measured when exactly two prey are taken from each patch will be equal to 1/2(1/6p + 1/5p), where p is the searching effectiveness parameter. Using an average value of the measured intercapture time of 14.89 seconds, the value for p is found to be 0.01231 second⁻¹. Since all patches contained n=6 prey, and knowing p, m, and b, the optimal total search

time for the TE strategy can be computed (cf. equation (F.2)), as well as the optimal GUT for the GUT strategy (using a search technique on equation (A.18)). By subtracting handling time from the time spent in the patch given by Cowie, the total search time in each patch can be obtained. Averaging this value for both environments provides one estimate for r, the parameter of the Random strategy. An optimal value of r can be obtained from equation (4.10), $r_{opt} = (m/p)^{1/2}$.

Two questions can be asked about the birds in Cowie's (1977) foraging experiments. First, what strategy are the birds actually using? Second, how good is their mean capture rate (a) relative to the optimum, the best possible for this search problem, and (b) relative to a neutral model, the Random strategy? Please refer to Table 1 as these questions are discussed.

First, it should be noted that the fit of these three strategies (TE, GUT, and Random) to Cowie's (1977) data could be made even closer. The leaving times for these strategies were not chosen to provide the best fit to the data in Table 1, but were computed using the minimum information necessary from that published by Cowie. A better fit to all the data in Table 1 could be obtained by varying p and the TE or GUT or r values. For example, if a slightly shorter total search time were used for the TE strategy, then all three variables for that

Table l. Comparison of su Cowie (1977).	boptimal strat	tegies with d	ata on great ti	ts (<u>Parus ma</u>	j <u>or</u>) from
	Cowie's	TE	GUT	Random St	crategy
variable	Data	Strategy	Strategy	Estimated r	r=r _{opt}
"Hard" Environment: Mean	Transit Time	Between Patc	hes is 21.03 se	c. (S.E. = 3.	.65 sec.) ^b
Time in Patch (sec.) (search + handling time)	73.67 (8.06) ^b	75.52	72.19	58.18	57.94
Mean Capture Rate (prey per sec.)	0.0264 (0.00277) ^b	0.0294	0.0272	0.0256	0.0256
Mean No. Captured per patch	2.50	2.84	2.53	2.03	2.02
Leaving Time Parameters ^a	-	TE _{opt} =52.2	GUT _{opt} =26.2	r=41.52	r _{opt} =41.33
"Easy" Environment: Mean	Transit Time	Between Patc	hes is 4.76 sec	. (S.E. = 0.8	30 sec.) ^b
Time in Patch (sec.) (search + handling time)	45.80 (6.77) b	39.93	33.66	58.18	29.26
Mean Capture Rate (prey per sec.)	0.0366 (0.00541) ^b	0.0372	0.0350	0.0322	0.0344
Mean No. Captured per patch	1.85	1.66	1.34	2.03	1.17
Leaving Time Parameters ^a	1	TEopt=26.3	GUT _{opt} =14.4	r=41.52	r _{opt} =19.66
^a For all strategie	s b = 8.21 se	c., p = 0.012	31 per sec., an	d n = 6.	

 $^{\rm b}$ Standard error of the mean; N is not given by Cowie (1977).

strategy in Table 1 would be reduced and come even closer to Cowie's results.

The information available is not sufficient to determine what strategy the birds are actually using. The predictions of all three suboptimal strategies fit the data fairly well, but the predictions of the TE and GUT strategies are more in agreement with the data than those of the Random strategy. The time in the patch predicted by the TE and GUT strategies comes quite close to the observed values; the corresponding values for the Random strategy are low. All expected capture rates except one are within one standard error of the observed mean value, and all expected capture rates are within two standard errors of the observed. Thus, capture rate alone is not sufficient to distinguish these three strategies. The pattern in mean number captured per patch is not clear, but the predictions of the Random strategy with $r = r_{opt}$ are farthest from the observed mean The GUT strategy value is very close for the "hard" number. environment, but predictions of the TE and Random strategies are closer for the "easy" environment. More pieces of evidence than that presented here will be required to distinguish among these strategies or to reject them all. Frequency distributions of variables such as the total search time in the patch, the GUT, and the intercapture times would be very helpful. Also, the numbers predicted by these strategies should be based on values obtained

from independent estimation of all parameters. It would also be helpful to further reduce the standard errors by additional replication.

How well did these birds perform? That is, how good was their time allocation strategy? To make a comparison with the best possible strategy for this foraging problem the reader is invited to consult Oaten (1977a) for determination of the maximum expected capture rate. His analysis in that paper assumes that the birds know the values of all parameters as well as the necessary conditional expectations; if this assumption is not met the predicted maximum expected capture rate will be an overestimate.

How good is the observed average capture rate of the birds relative to the capture rate predicted by the neutral model of time allocation? In the "hard" environment the birds' mean capture rate is only 3.1% higher than that predicted by the Random strategy (with an estimated r of 41.52 seconds). The Random strategy's capture rate is within 1 standard error of the observed capture rate; for the "hard" environment the standard error is 10.5% of the mean. In the "easy" environment the birds' mean capture rate is 13.7% higher than that of the Random strategy (whose r is 41.52 seconds). In this environment the standard error is 14.8% of the observed mean capture

rate, so, again, the capture rate from the Random strategy is within 1 standard error of the observed.

While the other data, time in a patch and mean number of prey found per patch, suggest that the Random strategy is probably not the one used by the birds, it is noteworthy that the capture rates are so relatively close. Of course, if these differences are real, even this relatively small improvement over the Random strategy could make an important difference over a long foraging time, especially in times of stress--bottlenecks (Wiens 1977).

Notice that the mean capture rates predicted by the TE strategy are higher than those observed as well as higher than those predicted by the constant GUT strategy. Based on expected capture rates the TE strategy is superior to the GUT strategy for this experimental situation, and results in 6.3% and 8.1% larger capture rates in the "hard" and "easy" environments, respectively. Though the TE strategy capture rates are larger than those actually observed, they are within two standard errors of the observed mean; it would be helpful to confirm this result with additional experiments.

What conclusions can be drawn from this experiment about the selective pressure for accurate and precise clocks or timers? Notice that the curve of expected capture rate versus leaving time is quite flat for all three strategies. Examine Figures 18, 19, and 20. (Because Cowie used a
Figure 18. Expected capture rate as a function of search time per patch (TE strategy), for the conditions in the experiments of $Cowie_1(1977)$. N=6 prey per patch, p=0.01231 sec.⁻¹, m=4.76 and 21.03 sec., b=8.21 sec.; optimal search time per patch = 26.3 sec. for m=4.76 sec., and optimal T_s=52.2 sec. for m=21.03 sec. Expected capture rate is computed by substituting E[C|N=6], equation (E.5), for E[C] in equation (E.8).





Figure 19. Expected capture rate as a function of the GUT (GUT strategy), for the conditions in the experiments of Cowie (1977). N=6 prey per patch, p=0.01231 sec.⁻¹, m=4.76 and 21.03 sec., b=8.21 sec., optimal GUT = 14.4 sec. for m=4.76 sec. and optimal GUT=26.2 sec. for m=21.03 sec. Expected capture rate is computed by substituting E[C|N=6], equation (A.9), for E[C], and $E[T_{s}|N=6]$, equation (A.16), for $E[T_{s}]$ in equation (A.18).



Figure 19

Figure 20. Expected capture rate as a function of mean search time per patch (Random strategy) for the conditions in the experiments of Cowie (1977). N=6 prey per patch, p=0.01231 sec.⁻¹, m=4.76 and 21.03 sec., b=8.21 sec. r estimated to be 41.52 sec., and r_{opt} =19.66 sec. for m=4.76 sec. and r_{opt} =41.33 sec. for m=21.03 sec. Expected capture rate is computed by substituting E[C|N=6], equation (4.2), for E[C], and r for $E[T_c]$ in equation (A.18).





constant number of prey in each patch, corresponding adjustments were made in the equations for expected capture rate; e.g., for Figure 18, expected capture rate was computed by substituting E[C|N=6], equation (E.5), for E[C]in equation (E.8).) From these graphs it can be seen that fairly large changes in search time, or GUT, or mean total search time (for Figures 18, 19, and 20, respectively) will produce only slight differences in mean capture rate. Thus, under these conditions, selective pressure for an accurate timer appears weak. If the animals use any of these strategies I would expect great variability in the observed leaving times for the same reason. I would expect that it would take much experience with these conditions for an animal to find the optimal leaving time, but these capture rate curves are so flat that any leaving time somewhat close to the optimum may be quite sufficient, especially if the environment can change slightly.

If the birds had a goal of minimizing the risk of finding zero prey while foraging, then their predicted behavior would be quite different. If a predator knows that all patches contain the same number of prey initially, then the risk of finding zero prey is minimized by spending all foraging time in one patch: do not waste time moving between patches since no patch is better than the one currently occupied. This result may be different if there is a

nonzero quota of prey that must be met, e.g., the optimal behavior may be to change patches after 1 prey is found.

The analysis of foraging experiments such as this one should be more fruitful if it were done on individual birds, rather than on results averaged across birds, but such data were not published for this experiment. Other workers have found significant individual differences in the patterns of behavior used to obtain reinforcements (e.g., Will 1974) and in time required to obtain prey in a variety of foraging tasks (Partridge 1976).

A Prey Distribution From Published Field Data: Simulation Results

Here is an example of how these suboptimal foraging strategies compare using a prey distribution based on published field data. These data come from Gibb's (1966) study of titmice foraging on pine cones for larvae of the eucosmid moth <u>Ernarmonia conicolana</u>. Gibb examined 13,045 pine cones collected in three different years, and was able to tell the number of moth larvae that were available to titmice, and also how many the birds had found. Gibb found that the two-parameter Neyman Type A distribution (Neyman 1939) fit these combined data quite closely, while data were significantly different from the one-parameter Poisson distribution. From the data presented by Gibb (1966, his Table 5) I computed a mean of 0.4289 prey per pine cone, and a variance about the mean of 0.6174. Fitting the data to the Neyman Type A distribution, I obrained $m_1 = 0.4395$ and $m_2 = 0.9759$ for the two parameters. These values were used for the computer simulation whose results are shown in Figure 21 for the TE strategy and Figure 22 for the GUT strategy.

Even for this significantly non-Poisson distribution of prey the TE strategy results in a slightly greater maximum capture rate than the GUT strategy. It appears that the flexibility of the GUT strategy in permitting the predator to search longer on an especially good pine cone is more than offset by the sensitivity of this strategy to chance variations in intercapture time. That is, mean capture rate is reduced on those occasions when a predator leaves "too soon" due to long intercapture intervals that occur on patches with several prey still remaining. This sensitivity is not as great for the TE strategy, and for this prey distribution this offsets the TE strategy's lack of flexibility in search time.

For this set of parameter values (see below), the Capture rate curves for both strategies are quite flat. Mean capture rate is not very sensitive to small changes in GUT or total search time per patch, and a broad range of those leaving times gives nearly the same capture rate. If this prey distribution is typical of natural prey distributions (see below), then there may be little selective pressure to have an accurate foraging clock.

Two caveats must be made about these simulations. First, though the prey distribution is based on Gibb's data, the values for searching effectiveness, p, transit time, m, and handling time, b, are only guesses. Gibb did not record such data while observing birds directly. Rather he inferred the birds' behavior from examination of their foraging marks on the cones. These capture rate curves would vary if my guesses are incorrect. The capture rate curves would be more sharply peaked if searching effectiveness is increased, or if transit time is decreased (see Figures 3 and 4), or if mean number of prey per patch is increased; notice the sharper peak when the mean number of prey per cone is increased about twelve-fold (to 5.0 prey per cone) from the observed mean number per cone.

Second, this prey distribution is based on pooling pine cone data from three separate years. While the fitted Neyman Type A distribution summarizes the combined data succinctly, no bird would be exposed to that exact distribution on a single foraging occasion in a single year. This may be a fair approximation, however. A better foraging analysis could be made if simulations were done using information on the distribution of prey among cones on a single tree, and information on the distribution of prey among trees in the forest.

Nonetheless, this provides some idea of a prey distribution to which predators may be exposed in a natural situation.

Figure 21. Mean capture rate as a function of search time per patch (TE strategy), for a Neyman Type-A distribution of prey among patches. Mean capture rate ± 1 SE is plotted (10 replicates). x=5.000 prey_per patch (s²=7.197) or 0.429 prey per patch (s²=0.6174), m=3.0 sec., p=0.1 sec.⁻¹, b=1.0 sec., and T=3600 sec.



Figure 21.

Figure 22. Mean capture rate as a function of giving-up time (GUT strategy) for a Neyman Type-A distribution of prey among patches. Mean capture rate ± 1 SE is plotted (10 replicates). x=5.000 prey per_patch (s²=7.197) or 0.429 prey per patch (s²=0.6174), m=3.0 sec., p=0.1 sec.⁻¹, b=1.0 sec., T=3600 sec.





Some Observed Parameter Values for the Negative Binomial

What are some realistic parameter values for the negative binomial distribution of prey among patches? Table 2 presents some of the parameter values of the negative binomial distribution that have been measured for animals in several natural habitat units--single leaves, tip of pine shoot, branch whorl, and trees. These units might be considered patches or patch groups in a hierarchy of patch levels. While the negative binomial is commonly used to describe the numbers of organisms per guadrat or other artificial sampling unit (e.g., Ryan 1974), the results of such an application would need careful scrutiny to determine their relevance to foraging theory. This is because (a) such quadrats are not discrete patches observable by a predator, and (b) guadrat size is chosen by the researcher, and, as Patil and Stiteler (1974) and others (cf. Southwood 1966) have pointed out, the values of the parameters of the negative binomial are known to change with quadrat size.

Some of the entries in Table 2 require explanation. Tamaki et al. (1973) marked 500 peach tree leaves per year in 1970 and 1971 and counted the number of green peach aphids (<u>Myzus persicae</u>) on these leaves several times per week during September and October. For each year the three sets of values for x and h given in the table represent (1) the smallest mean number per leaf observed that fall,

Table 2. Som C [CpOrt (among nature	2d parameter values for al habitat units.	the negative bin	omial distribution of	organisms
Organism	Sampling Unit	Mean Number, x	Exponent, h	Reference
Nantucket pine	Tip of shoot	0.49 (0.03)	0.449 (0.021)	Waters and
Rhyacionia frustrana,	Branch whorl	2.36 (0.36)	0.214 (0.035)	(CCCT) HOSHAU
Pinus taeda	Tree	13.13 (4.21)	0.253 (0.074)	
European red mite on McIntosh apple	Single leaf	1.15 (SE=0.12)	1.02 (SE=0.28,N=150)	Bliss and Fisher (1953)
Green peach aphid, <u>Myzus persicae</u> , on Elberta or	Single leaf, 1970 27 counts of 500 peach leaves			Tamaki, McGuire, and Onsager
HALE PEACH LIEES	min. obs. mean	0.004	(volsson, n+∞)	(C/AT)
	min. non-Pois.	1.74	0.98 (95%CL=0.65-1.32)	
	max. non-Pois.	11.81	1.11 (95%CL=0.80-1.43)	
	Single leaf, 1971 41 counts of 500			Tamaki, McGuire, and Onsager
	min. obs. mean	0.12	(Poisson, h→∞)	(1973)
	min. non-Pois.	0.46	0.34 (95%CL=0.18-0.51)	
	max. non-Pois.	11.31	0.67 (95%CL=0.54-0.80)	

(2) the smallest mean where the distribution of numbers per leaf was significantly different than a Poisson distribution, and (3) the largest mean among those for which the distribution was significantly non-Poisson. Thus, these values in Table 5.2 give an indication for a natural population of the variation in the distribution of numbers of animals per natural sampling unit, i.e., per patch.

The listed values for h, the exponent of the negative binomial, are near 1 or smaller. Theoretically the negative binomial distribution converges to the Poisson as h approaches infinity; practically speaking, Southwood (1966) says that a value of h greater than about 8 suggests that the negative binomial is approaching the Poisson, implying that when h is this large it becomes very difficult to show that an observed distribution is significantly different than the Poisson.

Values of h = 0.1 and h = 1.0, then, appear to be reasonable values to use in computer simulations of foraging.

A discussion of the implications of the statistical distribution of prey among patches on choice of foraging strategy appears below.

CHAPTER 6

DISCUSSION

Foraging Theory for a Patchy Environment

Theory for foraging in a patchy environment has been developed for several different aspects of the foraging Among the topics considered are the foraging path problem. when patches are not discrete units (Cody 1971, Smith 1977, 1974a, b, Thomas 1974, 1977, Croze 1970, and references therein); the patch types to be included in an optimal itinerary (MacArthur and Pianka 1966, Charnov 1973); optimal flock size for foraging (Thompson, Vertinsky and Krebs 1974, Thompson and Vertinsky 1975); assessing and monitoring patch profitability (Oster and Heinrich 1976, Bobisud and Voxman 1978); the stability of the predatorprey system in a patchy environment (Oaten 1977b, Murdoch and Oaten 1975, Hassell and May 1974); the aggregative response of predators (Readshaw 1973, Hassell and May 1973, 1974, Bobisud and Voxman 1978, Royama 1970, 1971); the proportion of prey in a patch that are consumed (Gibb 1962, Emlen 1973); and strategies for determining when to leave a patch (Oaten 1977a, Parker and Stuart 1976, Cook and Hubbard 1977, Charnov 1973, 1976, Krebs 1973,

Krebs, Ryan and Charnov 1974, Krebs and Cowie 1976, Charnov, Orians and Hyatt 1976, Emlen 1973, Tullock 1971, Gibb 1962).

Charnov (1973, 1976) was apparently the first to mathematically describe a procedure for choosing an optimal leaving time for a patchy environment, for a goal of maximizing capture rate of prey. His treatment is quite general. He does not analyze any specific search processes or prey distributions; this is apparently the reason only qualitative predictions are made between his theory and the experimental data of Krebs, Ryan and Charnov (1974). In what Charnov (1973, 1976) terms the "marginal value theorem," from an analogy with economic theory, he determines that the predator should leave a patch when the expected capture rate (the "marginal" capture rate) declines to the average capture rate for the set of patches visited. Charnov (1973) and co-workers (Krebs, Ryan and Charnov 1974, Charnov, Orians and Hyatt 1976) give a simplified version of the movement rule based on the GUT concept. He states that when handling time is small the rate of prey capture is approximately proportional to the inverse of the average time between prey captures. Thus, he suggests that a predator might use the time between Captures as a measure of the food intake rate. Translating the theorem's predictions into the GUT measurement, a predator is predicted to leave a rich (poor) environment

when the time between captures is small (large). Charnov predicts that the GUT should be longer in a poor environment than in a rich environment, and that the GUT should be constant for all patches within an environment. Both of these predictions were generally supported by the data of Krebs, Ryan and Charnov (1974) (but see below).

Charnov (1973, 1976) does not explicitly mention the distinction between random and systematic search within a patch. He refers to one case where the expected capture rate remains constant: when prey abundance does not change during the foraging time. Charnov points out that the best strategy in that case is to find a patch of the best type and to remain in it. A predator searching systematically within a patch might not experience a decrease in capture rate until the entire patch has been searched, and Charnov's theory would not apply unqualified to such a Some kind of behavioral "depression" (Charnov, case. Orians and Hyatt 1976) could occur, however, where the remaining prey become increasingly difficult to find, so that assumption of his model would be met. It is not clear that Charnov's model applies to the experiments of Krebs, Ryan and Charnov; the birds probably searched systematically, and behavioral "depression" appears impossible.

Oaten (1977a) argues convincingly that stochastic models are necessary for formulating optimal foraging

strategies. He gives a general solution for the problem of optimizing time spent in a patch for the goal of maximizing the capture rate. His optimal strategy uses all the information in the sequences of successive search times in a patch, combined with the previously "known" distribution of prey among patches, to compute the best time to leave that patch. Oaten gives a thorough critique of Charnov's analysis, and shows that Charnov's strategy (of leaving when the expected capture rate drops to the average for the patches visited) is not the optimal time-allocation strategy. The optimum is a dynamic GUT strategy; the optimal GUT is not a constant, but depends at each foraging instant on the expected capture rate and, unlike Charnov's movement rule, also depends on "the future success an optimal predator could expect to have if another prey were captured in the next instant, together with the instantaneous likelihood of such a capture" (Oaten 1977a, p. 276). Noting the mathematical complexity of computing the optimal behavior, Oaten suggests the analysis of stochastic models of simpler, suboptimal foraging strategies -- "stochastic optimization under clearly specified constraints," such as the predator being able to remember only a limited number of events and times (Oaten 1977a, p. 283). Oaten criticizes other applicable models (Charnov 1973, 1976, Parker and Stuart 1976, Cook and Hubbard 1977) for being

deterministic, and shows that Charnov's strategy can do arbitrarily poorly compared to Oaten's optimal strategy.

Parker and Stuart (1976) examine the problem of optimally allocating investments in patches that contain resources. Their general analysis is done using the "currency" (Schoener 1971) of fitness or fitness-gain rate. They arrive at a theorem equivalent to Charnov's (1973, 1976) "marginal value theorem." Oaten (1977a) says that Parker and Stuart's paper can be criticized for somewhat the same reasons he criticized Charnov. The case where resources in patches decay exponentially is considered; fitness-gain is assumed to vary with investment in the same manner that capture rate varies with total search time in my equation (E.7). They derive an equation for optimal investment in a patch that is equivalent to my equations (2.6) and (F.2). By starting from a given form for resource decay, attention is diverted from the underlying mechanisms and some of the assumptions giving rise to equations of that form. They do not explicitly distinguish between randomly and systematically searching predators, even though their particular result will not generally apply to systematic searchers.

As an example application of their theory they predicted the optimal time that a male dung fly should invest in copulation to maximize its fitness-gain rate, i.e., to maximize the percentage of all females' eggs

fertilized by that male. Parker and Stuart do not suggest a mechanism by which male flies could decide on the optimal time, the optimal duration of copulation. It seems very unlikely that male flies could observe the percentage or total number of all females' eggs that they are fertilizing as a function of copulation duration. It also seems that a genetic feedback is precluded by the possibility of changes in the proportion of virgins or the density of females requiring a different leaving time. A neutral model analysis would be very helpful here. It seems that their model needs to include other information the flies can use; e.g., Parker and Stuart mention that there is some evidence that males can assess the egg content of females.

Parker and Stuart take a further step in the foraging analysis and consider the influences of competing predators on leaving time. They use a game theory approach and determine the evolutionarily stable strategy (cf. Maynard Smith 1974) for several specified conditions.

Cook and Hubbard (1977) study the time allocation of parasites among a finite number of patches containing hosts. In this analysis the parasites' goal is to maximize the number of hosts parasitized in some fixed time. Cook and Hubbard argue that when both the number of patches and the total hunting time available are fixed, the optimal solution is to reduce the encounter rate

with healthy hosts to the same level in all patches. For a given density of hosts in each patch, a given total foraging time, and a fixed amount of time spent in transit between patches, they compute the amount of time that should be spent in each patch. They predict that the threshold encounter rate with healthy hosts should decline as the time available for foraging increases. This solution would not apply, e.g., to situations where the total foraging time was unpredictable or unknown to the parasite. In such cases the parasite should switch more frequently between patches so that at any potential stopping time all patches have been reduced to approximately the same rate of encounter with healthy hosts; this would involve much more time spent traveling between patches, however, so less time would be available for searching within each patch. This would also mean that the total transit time would vary, contrary to the assumption of their model. Cook and Hubbard feel that the similarity between the predictions of their model and the experimental data of Hassell (1971) suggests that "the parasites are able to get quite close to the optimal solution" (Cook and Hubbard 1977, p. 120). A neutral model would be helpful in assessing to what extent this similarity is due to effective time allocation decisions or other factors. Oaten (1977a) offers some criticisms of this paper, noting that this solution does not give the optimal time allocation because

some information is neglected (as above). He also points out some other weaknesses in their assumptions, logic, and mathematical technique.

Emlen (1973) analyzes a strategy which might be called the threshold food capture rate strategy. Here he assumes that an animal leaves a patch whenever the food capture rate within a patch drops to some constant threshold rate. He does not suggest how an animal might measure food capture rate. If prey items are of equal food value and an animal estimates capture rate by the inverse of the search time since the last capture (or arrival) in the current patch, then this strategy is equivalent to the constant GUT strategy. Emlen uses this strategy to predict the proportion of prey taken as a function of the number available prey initially in the patch. Applied to Gibb's (1966) pine cone data, "the fit is far from perfect, but is an approximate description of the behavior of the birds" (Emlen, 1973, p. 185). Emlen suggests, as Charnov does, that predators might lower the threshold capture rate in poor hunting areas and raise it in good areas. Emlen does not attempt to determine the optimal threshold food capture rate for the general case.

Murdoch and Oaten (1975) develop capture rate equations for the constant GUT strategy, for a Poisson and a negative binomial distribution of prey among patches, and random search within a patch. They did not determine optimal GUT, however; they applied the equations to an analysis of stability of the predator-prey system.

The "Number Expectation" strategy was proposed by Gibb (1962, see also Krebs, Ryan, and Charnov 1974) to explain why pine cones with above-average numbers of moth larvae had a lower percentage of larvae taken by foraging birds than cones with an intermediate number of prey. If a bird came to expect a certain number of larvae on each cone, he reasoned, it might leave above-average cones when this "expected number" of prey had been found, as evidenced either by its own success or by the marks on the cone indicating the success of other birds. Gibb (1962) suggested that in small plots with very low numbers of prey on each cone the birds sampled these cones and rejected them as uneconomical. He did not, however, suggest the strategy used in these cases of rejection.

As others have implied (Simons and Alcock 1971) this Number Expectation strategy is an incomplete strategy; that is, it does not specify what to do under all circumstances. ("Strategy" is used here in the game theory sense, meaning a complete specification of what is to be done in every possible situation of the specific problem studied.) If the birds find the "expected number" they are to leave a patch (cone), but how are they to proceed if they cannot find this number of prey in a patch--for example, if the patch contains less than this number of

prey? Simons and Alcock (1971) propose a "test strategy" for deciding on how long to forage in any patch: "test" an area by searching for some short time and leave if no prey are found; otherwise, stay and search the area "carefully." The hypothesis that birds use the Number Expectation strategy has been tested and rejected by Simon and Alcock (1971), Krebs, Ryan and Charnov (1974), and Zach and Falls (1976c), and as Krebs (1973) notes, it is not supported by the original data.

Conditions Where Each Suboptimal Strategy Does Best

Let Gibb's (1962) terminology be reinterpreted so that the "expected number" refers to the expected optimal number of prey to be captured rather than to the expected total number of prey in a patch. In this case, then, there is a certain situation where a type of Number Expectation strategy is optimal, when combined with a GUT strategy (cf. Krebs, Ryan, and Charnov 1974), a type of "test strategy" (Simons and Alcock 1971). Suppose that all patches contain either zero prey or some constant number of prey, n. The optimal strategy (Oaten 1977a) is to search a patch for some fixed amount of time and then leave if no prey have been found. If any prey have been seen, however, it must mean that the patch has n prey. The predator should then remain in the patch until some fixed number j of prey have been found (and n-j remain), and then leave the patch immediately. Note that this strategy is optimal only if it is certain that all prey occur in groups of size n, a very unlikely circumstance in the real world. This situation can easily be constructed in the laboratory, however (e.g., Simons and Alcock, 1971; Krebs, Ryan, and Charnov, 1974). If there is a variation in the number of prey occurring together in a patch, then this strategy is no longer optimal. And if there are any (nonzero) groups of prey smaller than the fixed number j, then this strategy will not work at all: predators would get "stuck" in these patches searching for the "expected number" of prey, j, when there were no more to be found.

The Time Expectation strategy will be optimal when there is a Poisson distribution of prey among patches, and there is no spatial correlation of prey numbers per patch. This would be the case, for example, if each prey individual randomly selected a patch to inhabit. In this case the total time spent searching in the patch contains all the revelant information for optimal time allocation; there is no additional information to be gained from the number of prey items found and the sequence of search times in the current patch. The predator should eventually learn not to be "distracted" by short or long search times, or the number of prey already found, but should spend a constant total search time per patch. If there is any deviation from the random distribution of prey, however,

the sequence of numbers and search times will contain useful information and the Time Expectation strategy will be suboptimal.

The fixed GUT strategy should do better and better compared to the Time Expectation strategy as the distribution of prey among patches becomes more "clumped," i.e., as the coefficient of variation gets larger and larger than one. When the prey distribution is Poisson the TE strategy is superior because the GUT strategy is too sensitive to stochastic variations in the series of search times; predators tend to leave too soon when an early search time is long, and tend to stay too long when a series of short search times occurs. As the coefficient of variation of numbers of prey per patch increases, however, it becomes more and more important to utilize the information contained in the series of search times in order to obtain a high capture rate.

I can think of no realistic situations where the Random strategy would be optimal. As prey density gets very large, however, the capture rate under this Random strategy approaches 1/b (cf. equation (3.8)); the same limit is approached by the TE and fixed GUT strategies, and the optimal one. Let the "minimum cost" of using one strategy compared to another strategy be defined as the difference between the expected maximum capture rates expressed as a percentage of the greater maximum rate.

(This is similar to Bryant's (1973) definition of the "cost of using a tactic.") Then the minimum cost of using the Random strategy compared to the TE, fixed GUT, or an optimal strategy is small at very high prey densities; the minimum cost approaches zero as prey density approaches infinity (See equation (3.12) in Chapter 3). The minimum cost of using the Random strategy relative to these other strategies also decreases as the handling time increases. So, the lower the prey density and the shorter the handling time, the more important it is for predators to use strategies superior to this Random strategy, i.e., the greater the cost of using this Random strategy. Since prey densities fluctuate through time, this provides an analytical confirmation of the arguments made by Wiens (1977) that selective pressure for optimal behavior may be intense or significant only in certain "bottle-neck" situations.

How sensitive are these suboptimal strategies to small deviations away from the optimal leaving time? Compared to the TE strategy the constant GUT strategy is relatively sensitive to small deviations from the optimal GUT. That is, a predator with a GUT strategy needs a more accurate clock than a predator with a TE strategy to maintain a near-optimal capture rate. It becomes more sensitive as transit time decreases, as searching-effectiveness increases, and as mean prey number per patch increases. This is shown in Figures 4, 3, and 2, respectively. It is clear

for both of these strategies that a predator with a more accurate and precise clock would have an advantage: a higher average capture rate. In examining Figures 23 and 24 it can be seen that the capture rate curve is much more flattened near the peak for the TE strategy than for the GUT strategy. If animals have difficulty measuring time very accurately and precisely (cf. Church et al. 1976, and references therein), then the TE strategy may be more advantageous than the fixed GUT strategy. If other possible uses for the clock are ignored, it can be suggested that selective pressure for a more accurate and precise foraging clock will decrease as precision and accuracy increase. It should also be the case that a tradeoff is reached between the gain in average capture rate due to increases in the clock's accuracy and precision and the cost of further improvements in the clock. For the Random strategy variation in leaving time is inherent in the model, but like the TE strategy, the Random strategy is relatively insensitive to small changes in r, the mean total search time per patch.

How sensitive are these three strategies to the Variation in number of prey per patch? For the constant GUT strategy a higher variance leads to a better performance, a higher average capture rate. See Figure 6, which shows results for a negative binomial distribution of prey among patches. This strategy can take advantage of the

information contained in the sequences of intercapture times in a patch. Thus, it is better able to take advantage of patches with above average numbers of prey and avoid patches with less than average numbers of prey. The TE strategy is relatively insensitive to variance. In fact, its expected capture rate is sensitive only to the mean of the distribution of prey. As the variance in the number of prey per patch increases, the performance of this strategy is degraded relative to the fixed GUT strategy, which is more able to capitalize on the extreme values of prey per patch. As with the TE strategy the Random strategy is sensitive to the mean and relatively insensitive to the variance in the distribution of prey among patches. Therefore, for prey distributions close to the Poisson the TE strategy is the best of these three strategies; for prey distributions with a high coefficient of variation the GUT strategy will be the best.

Comparing Foraging Goals

Two goals have been considered here: maximization of the capture rate and minimization of the risk of finding no prey while foraging. The results presented above indicate that for the GUT and TE strategies the optimal leaving times for these goals converge as mean prey density declines; that is, for both strategies, when prey are scarce, the optimal leaving time to maximize the capture rate approaches the optimal leaving time to minimize the

But occasions of low prey density are precisely the risk. occasions where it would be most important to minimize If an animal could switch goals at appropriate risk. times to maximize fitness, one might expect a predator to have a capture rate-maximizing goal at high prey densities and a risk-minimizing goal at low prey densities. Results above, however, suggest that a predator with a capture rate-maximizing goal need not switch goals at low prey densities, since the optimal leaving time will approach that of the risk-minimizing goal on the appropriate occasions--low prey densities. If experiments were designed to test whether a predator used a risk-minimizing or a capture rate-maximizing leaving time, one might mistakenly think that a high risk, low prey density situation would be most appropriate. Such an experiment would not answer the question, since the leaving times for each goal would probably be indistinguishable.

The risk-minimizing goal may be more appropriate for determining other aspects of the foraging process, e.g., flock size in birds. Thompson, Vertinsky and Krebs (1974) analyzed a simulation model of flocks of foraging birds and found that the optimal flock size to maximize capture rate was different from the flock size to minimize the wide fluctuations of capture rate, especially the low values. Animals employ many means of buffering the fluctuations in food intake rate--large crop size or stomach capacity, fat deposits, etc. (cf. Calow and Jennings, 1977); it is clear that such features reduce the risk of starvation. Note that the "risk" analyzed in the earlier chapters is the "risk of finding zero prey during some foraging period"; this should be closely related to the predator's risk of starvation, certainly an important influence on fitness. While the risk-minimizing leaving time reduces the probability of finding no prey, it also reduces the expected capture rate. The reduction in mean capture rate caused by this risk-minimizing leaving time may itself be a factor contributing to the risk of starvation. I suggest, therefore, that the risk of starvation may be more effectively reduced by other adaptations than by a choice of a risk-minimizing leaving time.

Finding the Optimal Leaving Time

The papers of Charnov (1973, 1976), Parker and Stuart (1976), Cook and Hubbard (1977), and Oaten (1977a) are all seeking to determine the optimal strategy for allocating time in a patchy environment. As Oaten (1977a) demonstrates, the optimal strategy would require great information-handling ability of the optimal forager; probability functions, conditional expectations, various means, etc., are used in the mathematical computation of optimal leaving time. Predators that use the suboptimal strategies presented here could also estimate the necessary parameters and compute the optimal leaving time.

However, suboptimal foragers could use much simpler methods of finding the best leaving time for a particular strategy.

One guite simple method of finding the best leaving time would be to try a particular value of leaving time for a short period and then compare the capture rate with that for a different leaving time. Some technique or algorithm could be used to home in on the best leaving time, e.g., an adaptive process like those studied by Holland (1975). Figures 23 and 24 are the results of stochastic simulations, showing the mean capture rate (and one standard error of the mean, for five replicates) after five minutes of simulated foraging. Figure 23 shows results for a Poisson distribution of prey among patches, and Figure 24 for a negative binomial distribution. The optimal leaving time in field situations will vary in time and space, so it is important that the predator be able to find the optimum as quickly as possible. Short (5 minute) "test" periods were compared here.

Two points can be made about these results. First, there is a great deal of noise; a predator would not be wise to place too much confidence in the results of any one five-minute test. Second, the Time Expectation strategy is less sensitive to change in leaving time than is the constant Giving-Up Time strategy.

The inclusion of learning models in foraging theory will enable more realistic predictions about predators'

Figure 23. Mean capture rate as a function of search time per patch (TE strategy) or giving-up time (GUT strategy), for a Poisson distribution of prey among patches. Mean capture rate + 1 SE is plotted (5 replicates). x = 5.0 prey per patch, m = 3.0 sec., p = 0.1 sec.⁻¹, b = 1.0 sec., and T = 300 sec.


Figure 24. Mean capture rate as a function of search time per patch (TE strategy) or giving-up time (GUT strategy), for a negative binomial distribution of prey among patches. Mean capture rate + 1 SE is plotted (5 replicates). x = 5.0 prey per patch, h = 1.0, m = 3.0 sec., p = 0.1 sec.-1, b = 1.0 sec., T = 300 sec.



behavior, especially for experiments of short duration and for situations where conditions are changing. Timesequences of foraging events from lab and field are needed to test and suggest such models.

CHAPTER 7

SUMMARY AND CONCLUSIONS

In discussions of foraging theory the distinction should be made between the spatial pattern of prey and the statistical distribution of prey among patches. Both types of information are important to the determination of an optimal foraging strategy. As has been noted several times before (e.g., Pielou, 1969; Boswell and Patil, 1970, 1971) it is generally the case that several different mechanisms can give rise to the same statistical distribution. Knowledge of the mechanisms giving rise to the statistical distribution and spatial pattern of prey can be used to further specify the optimal foraging strategy.

When observing predators that must assess profitabilities of patch types and prey types, one should not expect step-function shifts in patch utilization and diet breadth, as predicted by that foraging theory which assumes certain knowledge of profitabilities. The predator's sampling problem is closely related to some problems in the fields of operations research, statistics, and psychology.

Advances in understanding the foraging process can be made by studying the contributions of these other disciplines.

The general problem of optimally searching for prey in a patchy environment is extremely complex. Animals have likely found "suboptimal" strategies which give results that approximate the optimal strategy at a much reduced "cost of computation."

General formulae are given for the expected capture rate for predators using the fixed Giving-Up Time, Time Expectation, and Random strategies, and specific formulae are given for Poisson and negative binomial distributions of prey among patches. Both randomly and systematically searching predators are considered. These formulae can be easily applied to experimental situations for the prediction of capture rates under each of these time allocation strategies.

For the two economic goals maximization of capture rate and minimization of risk, the optimal leaving times of the TE and GUT strategies converge at low prey densities. This low density is precisely the situation where it should be most important to minimize risk, since one can afford to be "risky" when prey density is high and the absolute level of risk is much reduced. Thus, there may be very few situations where the risk minimization goal is a critically important one for the determination of the optimal leaving time; the capture rate-maximization goal provides nearly

the same degree of risk minimization when the risk is greatest--at low prey densities. This goal may be important in maximizing the contribution to fitness of other factors, such as optimal flock size (cf. Thompson, Vertinsky and Krebs, 1974).

The capture rate under the Time Expectation strategy is less sensitive to timing errors than under the Giving-Up Time strategy. Predators which cannot estimate or predict time (durations) very accurately or precisely may generally have a higher capture rate under the TE strategy than under the GUT strategy.

For a Poisson distribution of prey among patches the Time Expectation strategy is the optimal strategy for allocating time among patches for the assumptions made here; it is superior in this case to the fixed GUT strategy because (a) the TE strategy is less sensitive to stochastic variations in intercapture time, and (b) there is no additional information in the sequence of intercapture times.

As the coefficient of variation of the distribution of prey among patches increases, it becomes more and more important (for maximizing the capture rate) to utilize the information in the sequence of intercapture times. Thus, the GUT strategy becomes superior to the TE strategy when the CV is large, when the distribution of prey deviates greatly from the Poisson.

The "cost" (in reduced capture rate) of using the Random strategy decreases as prey density increases; the

"cost" approaches zero as the prey density approaches infinity. For this reason, predators which hunt for prey types that have high mean numbers per patch may not be under as severe selective pressure to forage optimally as predators which hunt for prey types that have small mean numbers per patch; for example, predators may trade off hunting for large numbers of small-sized prey with foraging for small numbers of large-sized prey. The large numbers per patch may allow even a Random strategy to be quite satisfactory.

A hierarchy of "patch types" is generally present in the environment, e.g., pine cones, groups of cones, pine trees, forests. Strategies are needed by predators for allocating foraging time among "patch types" at each level. The GUT strategy can be generalized for use at any level in the hierarchy.

Each suboptimal strategy studied here--GUT, TE, and Random--predicts different patterns for the frequency distributions of intercapture times, giving-up times, and total search times per patch. Comparisons of only the means of these variables would be a much less powerful test for discriminating between strategies.

The predictions of a strategy will vary depending on the type of search done by the predator. It is important, therefore, to distinguish random from systematic search, and continuous from discrete trial search.

The three suboptimal strategies are compared with experimental data of Cowie (1977). The maximum mean capture rates predicted by the TE strategy are higher than those observed as well as higher than those predicted by the constant GUT strategy. The maximum mean capture rate predicted by the constant GUT strategy is higher than the observed rate in the "hard" environment (long transit time), and lower than the observed rate in the "easy" environment (short transit time). In each case the GUT strategy's predicted capture rate is within one standard error of that observed. The observed capture rates are higher than those predicted by the Random strategy, but the predictions are within one standard error of the observed capture rates.

CHAPTER 8

RECOMMENDATIONS

It is important to emphasize again that the definition of optimal behavior depends on the particular goal as well as on the particular constraints of a foraging problem. Charnov (1973) distinguishes the goal from the "game." If we expect to find the optimal behavior predicted by theory we must be sure that the goal and the "game" of the model are the same as those of the animal.

As every researcher knows, it is important to design experiments to fit the assumptions of the model being tested. I would like to state here some important considerations for designing foraging experiments. The animal species chosen should be those likely to have the goals and strategies under consideration. Vertebrates such as mammals or birds would probably be most likely to utilize complex decision-making strategies, while arthropods may have much simpler strategies. Most foregoing theory to date assumes that the animals have much experience with the environment, and that stable patterns of behavior have been reached. It is important, therefore, to allow the animals to become thoroughly familiar with the experimental

conditions. Animals may persist for a long time, however, with sampling or monitoring behavior, so that assumptions that this behavior is not occurring may be incorrect. It is important to specify discrete patches for experiments involving any of the strategies developed here. The theory of area-restricted search would apply if prey do not occur in discrete patches. Predictions will vary depending on whether predators search randomly or systematically within a patch. In situations where a patch consists of many smaller cells (e.g., Krebs, Ryan and Charnov, 1974; Smith and Sweatman, 1974; Smith and Dawkins, 1971), any marks on individual cells which could identify them as having been searched would facilitate systematic foraging, clearly superior to random foraging in such cases. Notice that the theories involving random search generally assume depletion of the prey within a patch (cf. Charnov, 1973). A systematic forager would not experience depletion of the prey in those areas of the patch not yet searched, unless a type of behavioral depression was occurring (Charnov, Orians and Hyatt, 1976). To avoid significant depletion, trials may be of short duration, or better yet, continuous replacement of the prey may occur (e.g., Krebs, Erichsen, Webber and Charnov, 1977).

Experiments should be designed to measure all important variables which are needed by the theories being tested. In some field situations it is very difficult to pinpoint the time of successful captures (Baker, 1973;

Davies, 1977). While other interesting observations on foraging may be made under these conditions, data lacking capture times are not sufficient to allow discrimination between certain foraging strategies. If the number of prey initially present in each patch is known and can be followed through time, then nearly all important foraging variables can be determined from a time-sequence of the following foraging events: time of arrival at a patch, the finding of each prey, time when handling is completed, the finding of the next prey, time when handling is completed, . . . , time of departure from the patch, time of arrival at the next patch, . . . From this data the mean GUT can be computed, as well as the intercapture time, given a known number of prey remaining in the patch. From this sequence the searching effectiveness parameter, p, the transit time, m, the handling time, b, and the total search time per patch, T_c, can also be computed. It is assumed that n or x, the number or mean number of prey per patch is known for all patches.

For a more complete analysis of foraging behavior and comparisons with predictions from strategies, frequency distributions of certain important variables should be presented along with means and variances (e.g., Davies, 1977). Frequency distributions should be compiled for GUT, T_s (analogous to "run length" in a patch, studied by Bobisud and Voxman (1978) for discrete trial search),

total time per patch, and intercapture time given k prey per patch, for all possible k. Because alternative strategies and goals make different predictions about the frequency distributions these presentations are useful for distinguishing strategies and contain much more information than just means and variances.

Another recommendation is that results be compared with a neutral model, a null hypothesis of the foraging sequence.

Further research is needed to explain the large variability in foraging behavior among individuals (cf. Partridge, 1976; Smith and Sweatman, 1974; Cowie, 1977; Krebs, Erichsen, Webber and Charnov, 1977). If natural selection is optimizing animals' behavior why should we expect such variability? Krebs, Ryan and Charnov (1974) suggest that part of the variation in their results is due to using hand-reared as opposed to wild caught birds. They suggest that natural selection may act to remove the lower tail of a distribution, those individuals which perform least well. The variation in performance among Cowie's (1977) birds also appears large, though his birds were wild-caught. It is clear that part of the variation is due to differences in foraging history, in previous learning experience. This implies that it would be useful to record the foraging history of each individual during an experiment to see if this accounts for some of the

variation--for example, that variation caused by each individual making different estimates of the foraging parameters. One version of this type of analysis would be to examine the prey densities per patch experienced by each predator, rather than the nominal patch densities, in relation to subsequent patch utilization by each individual. The stochastic learning model developed by Bobisud and Voxman (1978) predicts that differences in patch ranking by individuals is to be expected due to chance differences in their foraging experiences in each patch. The study of the causes of individual variation, then, can give us insights into the foraging strategies used by predators, and the addition of learning models (including sampling and monitoring the environment) to foraging strategies should be especially rewarding.

Another area under active investigation is the length of the learning "window," the time period over which prey densities and other foraging parameters are estimated (Krebs and Cowie, 1976).

Additional suboptimal strategies need to be developed for problems with other constraints. Several recent experiments have involved systematic search by the predator (Smith & Dawkins, 1971; Smith & Sweatman, 1974; Zach & Falls, 1976c; probably Krebs, Ryan & Charnov, 1974), and appropriate model strategies are needed for predictive and comparative purposes. The risk of predation appears to be an important foraging constraint for some

animals, and minimization of the risk of predation (See the models of Pearson, 1976; Katz, 1974; Schoener, 1971) should be analyzed in the context of a patchy environment. Other constraints include the time required to satisfy other needs and the influence of hunger level and internal energy supply (Sibly and McFarland, 1976; McFarland and Lloyd, 1973; Gill and Wolf, 1975; Wolf and Hainsworth, 1977). Spatial factors are important in the real world and foraging theory for a patchy environment will need to include studies of search path between patches and the influence of the prey's spatial pattern (cf. Gill and Wolf, 1977; Zach and Falls, 1976a; Smith, 1974a, b, and references therein), as well as the predator's spatial memory (Olton and Samuelson, 1976; Barnett and Cowan, 1976). A variety of other neutral models should provide additional insight. The capture rate which will satisfy a predator so that it remains in a particular hunting area or patch group needs to be determined. Comparison of relative sensitivity of overall capture rate to the strategies and variables at each level in the foraging hierarchy should prove illuminating.

These areas of foraging theory provide several interesting problems where workers from several disciplines will be needed--workers from psychology, statistics, and operations research. With these allies the future looks very promising for the continued analysis of foraging strategies for a patchy environment.

APPENDICES

APPENDIX A

EXPECTED CAPTURE RATE FOR A PREDATOR USING A GIVING-UP TIME STRATEGY

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Assume that either prey are located at random within a patch, or the predator searches at random within a patch, or both (cf. Rogers, 1972). Then the predator's search will be a Poisson process (as assumed by Murdoch and Oaten, 1975). Assume for simplicity that each successful search results in a capture. Handling time will include time to pursue, attack, and eat the prey, as well as any "digestive pause" before searching resumes.

Define n as the number of prey initially in a patch,

- t as the giving-up time, GUT, and
- p as the mean capture rate when only one prey is in the patch, or, alternatively, l/p is the expected search time required to find a specific prey individual in a patch.

Arbitrarily number the prey individuals from 1 to n. Let X_1, X_2, \ldots, X_n be the cumulative search times at which prey #1, prey #2, ..., prey #n are found. (Count

only search time now, not handling or transit time.) Notice that these individuals could be caught in any order. Let $X_{(1)}$, $X_{(2)}$, . . . be the order statistics for the search time at which the predator makes its first find, its second find, etc. This problem has a counterpart in queueing theory: Feller (1971, p. 18) examines the same situation when he considers parallel waiting lines. He interprets X_1 , . . ., X_n as the lengths of n service times commencing at time 0 at a post office with n counters. In his case the order statistics $X_{(1)}$, $X_{(2)}$, . . ., $X_{(n)}$ represent the successive times of terminations, or successive discharges.

As Feller notes, the event $[X_{(1)} > t]$ is the simultaneous realization of n independent events $[X_n > t]$, each of which has probability e^{-pt} . So the probabilities multiply and the result is

$$P[X_{(1)} > t] = e^{-npt}$$
 (A.1)

Because this is a Poisson process, where individual events occur independently of one another, the continuation of the process should be independent of $X_{(1)}$, so that the search time between the first and second captures, $X_{(2)}-X_{(1)}$, should have the distribution

$$P[X_{(2)} - X_{(1)} > t] = e^{-(n-1)pt}$$
 (A.2)

Reasoning in an analogous manner, Feller (1971, p. 19) proves that the n variables $X_{(1)}$, $X_{(2)}$ - $X_{(1)}$, \dots , $X_{(n)}$ - $X_{(n-1)}$ are independent and that the density of $X_{(i+1)}$ - $X_{(i)}$ is given by ke^{-kpt}, where i + k = n. (A.3)

What is the expected number of prey captured, given that initially n prey are in the patch? Let C be the random variable for the number of prey captured.

$$E[C|n] = \sum iP[C=i|n]$$

$$i = 0$$
(A.4)

where C is the random variable for number of prey found (captured) in the patch,

To be completely general, one can allow different giving-up times to be specified for successive captures: t_0 is the GUT when 0 prey have been captured, . . . , t_i is the GUT after i prey have been captured in this patch. For example, the giving-up time may change with hunger as successive prey captures are made in a patch.

Following from the above definitions, the probability of finding no prey given n is the probability that the predator left the patch before the "first capture" occurred. That is,

$$P[C=0|n] = P[X_{(1)} > t_0|n] = e^{-npt}0$$
 (A.5)

Likewise, the probability of finding exactly 1 prey given n is the probability that the predator made the first capture but not the second capture.

$$P[C=1|n] = P[X_{(1)} < t_0 \text{ and } X_{(2)} - X_{(1)} > t_1] =$$

$$(1-e^{-npt}0) (e^{-(n-1)pt}1)$$
 (A.6)

In general, the probability that the (i+1)th prey was not found, but all i previous prey were found is

$$P[C=i \leq n|n] = e \qquad \begin{array}{c} -(n-i)pt & i-l & -(n-j)pt \\ I & I & (l-e & j \\ j=0 & \end{array}$$
(A.7)

Notice that P[C=i|n] can be computed from the following recursive formula:

$$P[C=i|n] = P[C=i-1|n]$$
 $(\frac{1}{Q}-1)e^{-(n-1)pt}i$ (A.8)

where $Q = e^{-(n-(i-1))pt}$

$$P[C=0|n] = e^{-npt}$$

Of course the predator cannot find more prey than are there, so

$$P[C=i > n | n] = 0$$

One can now compute the expected number of prey captured, given n

$$E[C|n] = \sum_{i=0}^{n} iP[C=i|n]$$

$$= \sum_{i=0}^{n} ie^{-(n-i)pt}i \prod_{j=0}^{i-1} (1-e^{-(n-j)pt}j)$$

(A.9)

Let P[N=n] describe the probability distribution of prey among patches, with E[N] = x. Then the expected number of prey found per patch, given the mean number of prey per patch is given by

$$E[C] = \sum_{n=0}^{\infty} P[N=n]E[C|n]$$
(A.10)

If all successive giving-up times are the same duration, $t_0 = t_1 = \ldots = t$ a constant, then the expected number found per patch is

$$E[C] = \sum_{n=0}^{\infty} P[N=n] \begin{pmatrix} n \\ \Sigma & ie^{-(n-i)pt} & i-1 \\ \Pi & (1-e^{-(n-j)pt}) \\ i=0 & j=0 \end{pmatrix}$$
(A.11)

Expected Search Time Between Captures, Given a GUT

It was shown above that if search is a Poisson process, then the probability density function for search time to the next capture is

$$f(t_s) = kpe^{-kpt}s$$
 (A.3)

- where k is the number of prey currently in the patch, and
 - t is the search time to the next capture, and

The mean of this negative exponential distribution of search times is 1/kp and the variance is $k^{-2}p^{-2}$. Note that here only search time is measured, and not the total time between captures.

What is the mean search time between captures, conditional on the search time being less than the GUT? That is, the mean search time only of those searches that could result in a prey capture is

$$E[t_{s}|t_{s} \leq t,k] = \frac{0}{t_{s}} = \frac{1}{kp} - \frac{t}{(e^{kpt} - 1)} \quad \text{for } k \geq 1$$

$$\int kpe^{s} dt_{s} \quad (A.12)$$

If n prey are in a patch and r=n-k have been captured so far, then

$$E[t_{s_{r}}|t_{s_{r}} < t_{r}, r, n] = \frac{1}{(n-r)p} - \frac{t}{(e^{(n-r)pt}-1)}$$
(A.13)

Expected Total Search Time Per Patch

First calculate $E[T_{s}|n]$, the expected total search time per patch, given that there are n prey in the patch initially. This is done by multiplying the expected search time given i prey are found and n prey are present initially by the probability that i prey are found (given n) and summing over all possible values of i. The expected search time given that i prey are found includes the mean time spent searching for each of the i prey plus the final giving-up time.

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$$E[T_{s}|n] = P[C=0|n] \cdot t_{0}$$

$$+ P[C=1|n] \cdot \left(E[t_{s_{0}}|t_{s_{0}} \leq t_{0}, 0, n] + t_{1}\right)$$

$$+ P[C=2|n] \cdot \left(E[t_{s_{0}}|t_{s_{0}} \leq t_{0}, 0, n] + E[t_{s_{1}}|t_{s_{1}} \leq t_{1}, 2, n] + t_{2}\right)$$

$$+ \dots$$

+
$$P[C=n|n]$$
 · $\left(E[t_s|t_s \leq t_0, 0, n] + \cdots + E[t_s|t_s \leq n-1, n-1, n] + t_n\right)$

(A.14)

(A.15)

For simplicity let the successive giving-up times be a constant, t, i.e.,

$$t_0 = t_1 = t_2 = \dots = t_n = t_n$$

In a more compact notation,

or,

$$E[t_{s}|n] = \begin{cases} n \\ t + \sum P[C=i|n] \\ i=1 \\ t \end{cases} \begin{pmatrix} i=1 \\ \sum E[t_{s}|t_{s} \leq t,r,n] \\ r=0 \\ for n=0 \\ (A.16) \end{cases}$$

If one knows the distribution of prey among patches, then the expected total search time per patch can be computed. Multiply the expected search time given n prey per patch by the probability that there will be n prey per patch, and sum over all possible values of n. Let E[n] = x, the mean number of prey per patch.

$$E[T_{s}] = \sum_{n=0}^{\infty} P[N=n]E[T_{s}|n]$$

or,

$$E[T_{s}] = t + \sum_{n=1}^{\infty} P[N=n] \begin{pmatrix} n \\ \sum P[C=i|n] \\ i=1 \end{pmatrix} \begin{pmatrix} i-1 \\ \sum E[t_{s}|t_{s} \leq t,r,n] \\ r=0 \end{pmatrix}$$

or,

$$E[T_{s}] = t + \sum_{n=1}^{\infty} P[N=n] \begin{pmatrix} n & i-1 \\ \sum (e^{-(n-i)pt}) & \prod (1-e^{-(n-j)pt}) \\ i=1 & j=0 \end{pmatrix}$$

$$\begin{pmatrix} i-1 \\ \Sigma & \frac{1}{(n-r)p} & - & \frac{t}{e^{(n-r)pt}} \end{pmatrix}$$

(A.17)

Expected Capture Rate Per Patch

One can now compute E[R], the expected capture rate, using an equation from Murdoch and Oaten (1975); see also Oaten (1977b).

$$E[R] = \frac{E[C]}{E[T_s] + b \cdot E[C] + m}$$
(A.18)

where E[C] is given by (A.10), and

 $E[T_{c}]$ is given by (A.17),

- b is the mean handling time per prey, (seconds), and
- m is the mean transit time between patches
 (seconds).

The particular distribution of prey among patches will determine the specific expression for P[N=n] which is used in computing E[C] and $E[T_s]$.

APPENDIX B

CALCULATION OF EXPECTED CAPTURE RATE FOR A POISSON DISTRIBUTION OF PREY AMONG PATCHES AND A GUT STRATEGY

APPENDIX B

CALCULATION OF EXPECTED CAPTURE RATE FOR A POISSON DISTRIBUTION OF PREY AMONG PATCHES AND A GUT STRATEGY

For the GUT model and assuming a random search within a patch, Appendix A gives formulae for calculating the expected number of prey captured in a patch E[C|n](A.9), and the expected search time per patch $E[T_s|n]$, (A.16), conditional on there being n prey initially present in the patch. These equations are equivalent to those of Murdoch and Oaten (1975), though the notation is modified slightly.

If the distribution of prey among patches is known, then equations (A.10), (A.17), and (A.18) can be used to compute the overall expected capture rate (the overall functional response of Murdoch and Oaten, 1975).

Starting from Murdoch and Oaten's (1975) version of (A.9), I developed the following recursive formula for calculating E[C|n]:

E[C|0] = 0 $E[C|n] = (1 + E[C|n-1])(1 - exp{-npt})$ (B.1)

The expected search time per patch, given n prey initially present also has a recursive form:

$$E[T_{s}|n] = T_{a}(n) + tT_{b}(n)$$
 (B.2)

where
$$T_a(0) = 0$$

 $T_a(n) = (T_a(n-1) + 1/np)(1 - exp{-npt})$ (B.3)

and $T_b(0) = 1$

$$T_{b}(n) = (1 - exp\{-npt\})T_{b}(n-1)$$
 (B.4)

In the calculations using equations (A.8) and (A.16) the summations were not taken to infinity, of course, but were truncated whenever the bound on the error for E[C|n] became very small. As Murdoch and Oaten (1975) show, when n gets very large, then E[C|n] gets close to E[C|n-1] + 1, i.e., the derivative of E[C|n] with respect to n gets close to 1, so that E[C|n] is essentially a straight line. Thus, if the summation for E[C] in equation (A.10) is taken from n = 0 to n = j, then the bound B_j on the error for E[C] is approximately equal to

If there is a Poisson distribution of prey among patches, then the probability function of the Poisson is used for P[N=j]:

$$P[N=j] = \frac{x^{j}e^{-x}}{j!}$$
 (B.6)

$$B_{j} \stackrel{\sim}{\sim} (E[C|N=j]-j) \stackrel{\infty}{\Sigma} \frac{(x^{n}e^{-x})}{n=j+1} + \stackrel{\infty}{\Sigma} \frac{n(x^{n}e^{-x})}{n!} (B.7)$$

where x is the mean number of prey per patch.

Since the summations will be done over 0 to j,

$$\sum_{n=0}^{\infty} \frac{x^n e^{-x}}{n!} = S_j \text{ will be known, and so}$$

$$\sum_{n=j+1}^{\infty} \frac{x^n e^{-x}}{n!} = 1 - S_j \text{ will be known.}$$
(B.8)

Also, note that

$$\sum_{\substack{n=j+1}}^{\infty} \frac{n}{n!} \frac{x^n e^{-x}}{n!} = \frac{x^{j+1} e^{-x}}{j!} + j \sum_{\substack{n=j+1}}^{\infty} \frac{x^n e^{-x}}{n!}$$
(B.9)

Hence the bound B_j on the error for E[C], given that the summations in equations (A.8) and (A.16) are taken from n=0 to n=j rather than to infinity, is approximately equal to

$$B_{j} \sim (E[C|N=j] - j + x)(1 - S_{j}) + \frac{x^{j+1}e^{-x}}{j!}$$
(B.10)

In all computations involving E[C] or E[T_s], the summations were terminated when either this approximate bound B_j was less than 0.0001, or P[N=n] was less than 10^{-38} .

With E[C] and $E[T_s]$ computed as described above, the expected capture rate E[R] for a Poisson distribution of prey among patches is easily found from equation (A.18). APPENDIX C

PROOF OF A GUT WHICH MINIMIZES RISK

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PROOF OF A GUT WHICH MINIMIZES RISK

(Thanks to Dave Ruppert of the Statistical Consultation Service at Michigan State University for the following proof.)

Let the number of prey in patches 1,2,3,...be identically and independently distributed random variables. Let p[n] = Prob[n prey in the ith patch] Let P[n,t] = Prob[predator will find no prey in t seconds given that there are n prey in patch] where t is the Giving-Up-Time. Let N = T/(t+m)

where T is some long search time, T >> (t+m), and m is the transit time between patches.

P[predator finds no prey in time interval [0,t]] \cong

$$\sum_{n=0}^{\infty} \frac{T/(t+m)}{e} defn$$

To minimize log f(t) (for 0 < t < T):

$$\frac{d}{dt} \left[\log f(t) \right] = \frac{-T}{(t+m)} 2 \qquad \log \begin{pmatrix} \infty \\ \Sigma \\ n=0 \end{pmatrix} p[n] P[n,t]$$

$$+ \frac{T}{t+m} \begin{pmatrix} \frac{1}{\sum p[i] P[i,t]} \\ n=0 \end{pmatrix}^{\infty} \sum_{i=0}^{\infty} p[i] \frac{d P[i,t]}{dt}$$

Example: Let $P[n,t] = e^{-ptn}$ and $p[n] = \frac{\mu^n e^{-\mu}}{n!}$

$$\sum_{n=0}^{\infty} p[n] P[n,t] = e^{\mu(e^{-pt}-1)}$$

Thus
$$f(t) = e^{(e^{-pt}-1) \mu T/(t+m)}$$

Now
$$\frac{\log f(t)}{\mu T} = \frac{(e^{-pt}-1)}{t+m}$$

And
$$\frac{d}{dt}\left(\frac{\log f(t)}{uT}\right) = \frac{(t+m)(-pe^{-pt}) - (e^{-pt}-1)}{(t+m)^2}$$

$$= \frac{1 - [p(t+m) + 1] e^{-pt}}{(t+m)^2}$$

Let $h(t) = [p(t+m) + 1] e^{-pt}$

Then
$$\frac{d}{dt}$$
 (log f(t)) = $\left(\frac{1-h(t)}{(t+m)^2}\right) \mu^T$
 $\begin{cases} > 0 \text{ if } h(t) < 1 \\ = 0 \text{ if } h(t) = 1 \\ < 0 \text{ if } h(t) > 1 \end{cases}$

Now
$$h(0) = pm + 1 > 1$$

and $h'(t) = -p^{2}(t+m)e^{-pt} < 0$

and $h(\infty) = 0$

Therefore h(t) decreases monotonically from pm + 1 to 0 as t goes from 0 to ∞ .

$$\frac{d \log f(t)}{dt} \begin{cases} < 0 \text{ if } t < t^* \\ = 0 \text{ if } t = t^* \\ > 0 \text{ if } t > t^* \end{cases}$$

Therefore f(t) has a minimum at t*

APPENDIX D

EXPECTED NUMBER OF PREY REMAINING

IN THE PATCH

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APPENDIX D

EXPECTED NUMBER OF PREY REMAINING IN THE PATCH

It would be very useful to the predator to be able to estimate the number of prey remaining in the current patch. Assuming that the mean prey number per patch is known (perhaps after much experience with a particular prey distribution), the expected number of prey in the patch upon first arrival would be the mean. Assuming that there are no other reliable environmental cues to estimate prey abundance, the predator can use the sequence of search times between captures as information about prey density in the patch: if times between captures are short, the patch probably is a high-quality patch; if times between captures are long, the patch is probably a low-density patch.

Since the number of prey remaining is simply the initial prey number minus the number caught, the problem can be changed to that of estimating the initial prey number. Assume for simplicity that each prey found is captured, so that $X_{(1)}$ denotes the search time to the first prey capture (the pursuit time required to capture the prey

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is included with handling time). The probability that the patch initially contained n prey given that the first prey capture occurred at t_{s1} is given by Bayes' law:

$$P[N = n | X_{(1)} = t_{s_1}] = \frac{P[X_{(1)} = t_{s_1} | N = n] P[N - n]}{\sum_{\infty} P[X_{(1)} = t_{s_1} | N = j] P[N = j]}$$

$$\sum_{j=0} P[X_{(1)} = t_{s_1} | N = j] P[N = j]$$
(D.1)

where X₍₁₎ is the random variable for search time before the first prey capture (to the first prey sighting),

t is a possible value for
$$X_{(1)}$$
,

N is the random variable for number of prey initially in the patch, and n is a possible value for N.

Expected Number of Prey Remaining Given a Poisson Distribution of Prey Among Patches

For the Poisson distribution of prey among patches,

$$P[N = n] = \frac{x^{n} e^{-x}}{n!}$$
 (D.2)

where X = E[N] is the mean number of prey per patch. The probability density function for search time before the first capture for a given number of prey in the patch is given by (A.3):

$$P[X_{(1)} = t_{s_1} | N = n] = pne^{-pnt}s_1$$
 (A.3)

Given these relationships, then one can compute the probability that the patch initially had n prey, given that the search time to the first capture was t_{s_1} .

$$P[N - n | X_{(1)} = t_{s_1}] = \frac{\left(pne^{-pnt}s_1\right)\left(\frac{x^n e^{-x}}{n!}\right)}{\sum_{j=0}^{\infty} \left(pje^{-pjt}s_1\right)\left(\frac{x^j e^{-x}}{j!}\right)}$$
(D.3)

After a little algebra the result is

$$P[N - n | X_{(1)} = t_{s_1}] = \left(\frac{-pt_{s_1}}{xe^{-pt_{s_1}}}\right)^{n-1}$$

$$(n-1)! \sum_{j=0}^{\infty} \frac{j\binom{-pt_{s_1}}{j!}}{j!}$$

(D.4)

Note that

$$\sum_{k=0}^{\infty} \frac{w^k}{k!} = e^w,$$

(D.5)

so that a closed form expression is:

$$P[N - n | X_{(1)} = t_{s_1}] = \left(\frac{-pt_{s_1}}{xe}\right)^{n-1} \left(\frac{-pt_{s_1}}{e}\right)$$
(D.6)

The probability that there were N prey initially in the patch given that one prey was found at t_{s_1} equals the probability that there are N-1 prey remaining given that one was found at t_{s_1} .

$$P[N = n|t_{s_1}] = P[K = n-1|t_{s_1}]$$
 (D.7)

where K is the random variable for number of prey remaining in the patch.

To find the expected number remaining, E[K], multiply each possible number remaining by its probability and sum over all possible numbers remaining. If one prey was found then the smallest possible initial number was n-1. One can label the summation index as k = n-1 so that it runs over all possible remaining numbers of prey.

$$E[K|t_{s_1}] = \sum_{k=0}^{\infty} kP[K = k = n-1|t_{s_1}]$$

$$= \sum_{k=0}^{\infty} \frac{k \left(-pt_{s_1} \right) k \left(-xe_{s_1} \right)}{k!}$$
(D.8)

After a little algebra, any applying the relationship (D.5), one obtains the desired result.

$$E[K|t_{s_1}] = xe^{-pt_{s_1}}$$
(D.9)

where K is the number of prey remaining in the patch,

x is the mean number of prey per patch, p is the searching effectiveness parameter, t_{s1} is the time at which the first prey was found.

APPENDIX E

DERIVATION OF EXPECTED CAPTURE RATE FOR THE TIME EXPECTATION STRATEGY

APPENDIX E

DERIVATION OF EXPECTED CAPTURE RATE FOR THE TIME EXPECTATION STRATEGY

Interpret X_1, \ldots, X_n as the search times required to find each of n prey. As in <u>Appendix A</u>, there is no restriction on the order in which these prey may be found. Assume, as before, that search within a patch is a Poisson process. Then the search time to find each individual prey has a common probability density function (p.d.f.). That is, the p.d.f. for each search time X_i is given by

$$f(t_s) = pe^{-pt}s$$
 (E.1)

(Notice that this, again, is analogous to Feller's (1971) problem of parallel waiting lines, where the X_1, \ldots, X_n are interpreted as the lengths of n service times commencing at time 0 at a post office with n counters.)

It follows from (E.1) that the probability that the search time required to find a specific prey exceeds a given time is given by

 $P[X_i > t] = e^{-pt}$ for each i = 1, ..., n. (E.2)

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Since the X_i are independent, one can treat the capture of prey during some fixed time t as a set of Bernouilli trials, where one defines for each prey

"failure" =
$$P[X_i > t] = e^{-pt}$$

and "success" = $P[X_i < t] = 1 - e^{-pt}$ (E.3)

for all
$$i = 1, ..., n$$
.

This leads to a binomial distribution of number of "successes" during the search time t. The probability that i prey are found when n prey are present initially is:

$$P[C = i|n] = {n \choose i} (1-e^{-pt})^{i} e^{-pt (n-i)}$$
(E.4)

where C is the random variable for number of prey found per patch,

i is a possible value for C,

- n is the number of prey initially in the patch, and
- t is the total search time in the patch.

Due to the binomial distribution of C, the mean or expected value of C is

 $E[C|n] = n P["success"] = n(1-e^{-pt})$ (E.5)

and the variance of C is

 $Var[C|n] = n P["success"] P["failure"] = n(1-e^{-pt})e^{-pt}$

(E.6)

Expected Number of Prey Found per Patch When the Mean Number of Prey per Patch is Known

Suppose the statistical distribution of prey among patches is known, and one wants to know the expected number of prey found in a patch. Equation (E.5) gives the expected number of prey found per patch given n prey initially present in the patch, and one can multiply this by the probability that there will be n prey initially present and sum over all possible values of n.

Let P[N=n] describe the distribution of prey among patches, where E[N] = x, the mean number of prey per patch. Then

$$E [C] = \sum_{n=0}^{\infty} n(1-e^{-pt}) P [N=n]$$

$$= (1-e^{-pt}) \sum_{n=0}^{\infty} n P [N=n]$$

$$= (1-e^{-pt}) \sum_{n=0}^{\infty} (n-pt) P [N=n]$$

$$= (1-e^{-pt}) P [N=n]$$

 $= x(1-e^{-pc})$ (E.7)

This says that whatever the distribution of prey among patches, the expected number of prey captured per patch depends only on the mean of that distribution.

Expected Capture Rate per Predator: The Predator's Functional Response

The expected capture rate for the Time Expectation strategy will be the expected number of prey captured per patch divided by the expected time spent per patch. Total time per patch will include the total search time, t, a constant for this strategy; total handling time; and the transit time to the next patch.

$$E[R] = \frac{E[C]}{t + b E[C] + m}$$

$$= \frac{x(1-e^{-pt})}{t + bx(1-e^{-pt}) + m}$$
(E.8)

where R is the mean capture rate per patch,

b is the mean handling time per prey, m is the mean transit time between patches, t is the total search time per patch, x is the mean prey density per patch, and

p is the searching effectiveness parameter.

This capture rate depends on the mean prey density per patch, but is independent of the exact form of the distribution of prey among patches. For given values of t, p, b, and m, this expression for capture rate increases monotonically with mean prey density per patch, x, and approaches 1/b as an asympotote.

$$\frac{\lim_{x \to \infty} E[R]}{x \to \infty} = \frac{1}{b} \quad \text{for t, p, b, m constant} \quad (E.9)$$

APPENDIX F

OPTIMAL TOTAL SEARCH TIME TO MAXIMIZE CAPTURE RATE FOR THE TIME EXPECTATION STRATEGY

APPENDIX F

OPTIMAL TOTAL SEARCH TIME TO MAXIMIZE CAPTURE RATE FOR THE TIME EXPECTATION STRATEGY

The expected capture rate for the Time Expectation strategy was derived in <u>Appendix E</u> and was shown to hold for any distribution of prey among patches. As before,

$$\overline{R} = E[R] = \frac{x(1-e^{-pt})}{t + m + bx(1-e^{-pt})}$$
 (E.8)

Differentiating \overline{R} with respect to t, one obtains, after a little algebra:

$$\frac{d\bar{R}}{dt} = \frac{x[e^{-pt} (1 + p(t + m)) - 1]}{[t + m + bx(1 - e^{-pt})]^2}$$
(F.1)

A maximum (or minimum) of \overline{R} will occur where $\frac{d\overline{R}}{dt} = 0$. The first derivative will approach zero as t approaches infinity, and this leads to a value of \overline{R} that approaches zero, a minimum. Biologically stated, the mean capture rate will approach zero for a predator that stays forever in a single, depletable patch.

The first derivative will also be zero when t is chosen so that

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$$e^{-pt}$$
 (1 + p(t + m)) = 1. (F.2)

This must be at a maximum for \overline{R} . This is the only nonnegative, finite value of t for which the first derivative is zero. The first derivative is positive at t = 0, and approaches zero as t approaches infinity (where \overline{R} approaches zero). Since \overline{R} is non-negative for the range 0 < t < ∞ , then (F.2) must give the unique value of t where the sign of the first derivative changes from positive to negative. That is, (F.2) must give a maximum \overline{R} , and the optimal t.

Unfortunately, the optimal value of t specified by (F.2) cannot be calculated in a simple way. An iterative solution can easily be done by computer, however.

Notice that the optimal total search time t depends only on p and m; the optimal t is independent of prey density, and further, is independent of the distribution of prey among patches! A predator using this tactic need only estimate p and m to be able to find the optimal t and do as well as is possible for this tactic.

Since t = t_{opt} solves equation (F.2) the following expression can be used to simplify the formula for the maximum expected capture rate:

$$t_{opt} + m = (e^{pt_{opt}} - 1)/p$$
 (F.3)

Substituting the above expression into (E.8) and doing a little algebra the result is:

$$\overline{R}_{max} = E[R|t = t_{opt}] = \left(\frac{e_{opt}}{xp} + b_{opt}\right)^{-1} = \left(\frac{1 + p(t_{opt} + m) + b}{xp}\right)^{-1}$$
(F.4)

If the prey distribution among patches is Poisson, then this tactic, with optimal t, would be the best possible--it would yield the maximum capture rate.

FREQUENCY DISTRIBUTION OF OBSERVED GUT FOR THE TIME EXPECTATION STRATEGY

APPENDIX G

APPENDIX G

FREQUENCY DISTRIBUTION OF OBSERVED GUT FOR THE TIME EXPECTATION STRATEGY

What is the expected frequency distribution of observed GUT for the TE strategy? For the case when only one prey is found in a patch it is relatively easy to determine the frequency distribution, or, in other words, the probability density function (p.d.f.) for observed GUT. In this case the p.d.f. for search time to the first capture t has a negative exponential distribution, truncated at t, the total search time.

$$f(t_{s_1}) = \begin{pmatrix} -pt_s \\ 1 - e^{-pt_s} \end{pmatrix}^{-1} pe^{-pt_s} 0 \le t_s \le t_s \quad (G.1)$$

If the first prey is found after t_{s_1} seconds of search and a total of t_s seconds are allocated to searching, then the observed GUT must be $t = t_s - t_{s_1}$. Substituting $t_s - t =$ t_{s_1} into the above equation and multiplying numerator and t_{s_1} pt_s the result is the p.d.f. of the observed GUT, t, for the TE strategy when 1 prey is found in the patch.

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$$f(t) = \begin{pmatrix} pt_s \\ e^s - 1 \end{pmatrix} = pt \qquad 0 \le t \le t_s \quad (G.2)$$

Notice that this is a positive exponential curve, truncated at t = t_c.



Figure Gl. Probability density function of observed GUT for the TE strategy, given that one prey is found in a patch.

For the case where more than 1 prey is found the total search time to the last capture will be the sum of several independent intercapture times. Thus, when several independent variables (each with a different negative exponential p.d.f.) are added together, the sum will have a p.d.f. roughly like this:



Hence, the observed GUT, $t = t_s - t_{s_i}$, will have a p.d.f. that is the mirror image of $f(t_{s_i})$:



Figure G3. Probability density function of observed GUT for the TE strategy, given that i prey are found in a patch.

Observed giving-up times measured in laboratory or field situations should have frequency distributions similar to these shown here if the animals are using the TE strategy. Further discussion of this point occurs in Chapters 5 and 6. APPENDIX H

DISCRETE TRIAL SEARCH: NUMBER OF

TRIALS BETWEEN CAPTURES

APPENDIX H

DISCRETE TRIAL SEARCH: NUMBER OF TRIALS BETWEEN CAPTURES

In several of the recent experiments studying foraging in a patchy environment the search by the predator within a patch involved discrete trials, e.g., removing foil caps from an array of cups (Smith and Dawkins, 1971; Smith and Sweatman, 1974), or removing sticky labels covering holes in artificial pine cones (Krebs, Ryan and Charnov, 1974). To model these situations and determine optimal predator behavior one of the first steps required is to specify the distribution of trials between captures. Truly optimal predators should search systematically, never revisiting a previously searched cell, e.g., a cup or hole. If a visit involves changing the appearance of a cup or hole, the covering is removed, then spatial memory of cell location need not be involved. For predators that search randomly, revisits to a cell can occur, reducing search efficiency. Best possible allocation of search trials can also be determined for these randomly searching predators.

Consider a situation where there are k prey distributed randomly among N cells, with no more than one prey per

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cell; N - k cells will be empty. What is the probability that r trials will be required to find a prey? That is, what is the probability that the predator will find r - 1cells empty, followed by a success on trial r?

Random Search

The search until the next prey is found can be considered a series of Bernoulli trials, where

$$P ["success"] = k/N, and (H.1)$$

$$P ["failure"] = 1 - k/N$$
 (H.2)

Thus, the probability of finding a prey on trial r, i.e., r - 1 "failures" followed by one "success," is

$$P[r|k, N] = (k/N) (1 - k/N) r - 1$$
 (H.3)

This is the probability function of the geometric distribution, a special case of the negative binomial distribution.

The mean number of trials required to find a prey, given k prey and N cells is

$$E[r|k, N] = \sum_{r=1}^{\infty} (rk/N) (1 - k/N)^{r-1} = N/k \text{ for } k < N$$
(H.4)

and when all cells contain prey

$$E[r|k, N] = 1$$
 trial. for $k = N$ (H.5)

To find the probability function and mean number of additional trials to the next capture, decrement k by 1, so that k equals the number of prey remaining, and use equations (H.3) and (H.4) above.

Systematic Search

For a predator that does not revisit any previously searched cells, the probability function of the hypergeometric distribution provides the probability that the first r - 1 trials will be unsuccessful.

P [first r-l cells empty|k, N] =
$$\begin{pmatrix} k \\ r-1 \\ N \\ r-1 \end{pmatrix} = \begin{pmatrix} N-r+1 \\ N-k \\ N \\ N-k \end{pmatrix}$$
 (H.6)

After searching r - 1 cells of the total N cells the probability that the next cell searched contains a prey is

$$P["success" | k, N - r + 1] = k/(N - r + 1)$$
(H.7)

Multiplying (H.6) by (H.7), one obtains the probability of finding a prey on trial r for a systematic searcher:

$$P[r|k, N] = \frac{\binom{k}{r-1}}{\binom{N}{r-1}} (N-r+1) = \frac{\binom{N-r+1}{N-k}}{\binom{N}{N-k}(N-r+1)}$$
(H.8)

The mean number of trials required to find a prey for this case is given by the following expression:

$$E[r|k, N] = \sum_{\substack{r=1 \\ r=1}}^{N-k+1} \frac{\binom{k}{r-1}}{\binom{N-r+1}{r-1}} =$$

$$\frac{kk!}{N!} \sum_{r=1}^{N-k+1} \frac{r(N-r)!}{(k-r+1)!}$$
(H.9)

To find the probability function and mean number of additional trials to the next capture, decrement k by 1 and decrement N by r, and use the formulae above. BIBLIOGRAPHY

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