1-1-1982

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Recommended Citation

Behavioral Ecology and Sociobiology 10:215-263

Behav Ecol Sociobiol (1982) 10:251–263

Behavioral Ecology and Sociobiology

Optimal Foraging: Some Simple Stochastic Models

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Received November 9, 1981 / Accepted April 24, 1982

Summary. Some simple stochastic models of optimal foraging are considered. Firstly, mathematical renewal theory is used to make a general model of the combined processes of search, encounter, capture and handling. In the case where patches or prey items are encountered according to a Poisson process the limiting probability distribution of energy gain is found. This distribution is found to be normal and its mean and variance are specified. This result supports the use of Holling's disc equation to specify the rate of energy intake in foraging models. Secondly, a model based on minimization of the probability of death due to an energetic shortfall is presented. The model gives a graphical solution to the problem of optimal choices when mean and variance are related. Thirdly, a worked example using these results is presented. This example suggests that there may be natural relationships between mean and variance which make solutions to the problems of 'energy maximization' and 'minimization of the probability of starvation' similar. Finally, current trends in stochastic modeling of foraging behavior are critically discussed.

Introduction

Foraging animals search for, encounter, and handle their prey according to rules which are most accurately described by statements of probability. That is, we expect stochastic models of foraging behavior to resemble nature more closely than deterministic models. However, many models of optimal foraging behavior are deterministic. There are two reasons for this. Deterministic models are nearly always simpler than their stochastic counterparts, and it is often easy to convert deterministic into stochastic models by representing distributions of random variables by their expectations (or mean values).

However, stochastic models have an important place in optimal foraging theory for three reasons.

1. Many biologically important phenomena are fundamentally stochastic, so that deterministic models do not make sense (e.g. sampling).

2. Stochastic models can be compared to deterministic models to tell us how good, as approximations, these simpler models are. This comparison is useful both for models of inherently stochastic problems as well as for models that can reasonably be modeled deterministically.

3. Conversion of deterministic to stochastic models by replacing deterministic variables with expectations of random variables may be inappropriate because characteristics of the random distribution other than the expectation may be critical; for example, both expectation and variance of food intake may be important.

The most valuable stochastic models may be useful in all three (or other) ways. To make this clear we give examples of these uses of stochastic models below.

Inherently Stochastic Problems

Some foraging problems are essentially stochastic and cannot be modeled deterministically. For example, deterministic models usually assume that the forager 'knows,' in some sense, the relevant characteristics of its environment. This might be reasonable in a relatively static environment, such as those usually provided in experimental tests of foraging theory (cf. Krebs et al. 1977). However, in a stochastic world, parameters such as encounter rate may change unpredictably. Some time and energy will have to be invested in sampling the environment because real environments will often have unpredictable and hence stochastic characteristics. The trade-

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off between the information gain and the energy gain due to a foraging decision can only be analyzed stochastically.

Comparison and Analysis

Simple deterministic models may be reasonable approximations to more realistic stochastic models. One use of stochastic models, and perhaps the most valuable one, is to explore the extent to which deterministic approximations are reasonable. Excellent examples of this are the re-analyses of Oaten's (1977) 'information by patch exploitation' model by Green (1980) and McNamara (1982). Green and McNamara demonstrated not only that the optimal patch residence for Oaten's naive (stochastic) forager may differ from Charnov's (1976a) knowledgeable (deterministic) forager, but they have also shown which factors influence the degree of this difference, for example, variance in the distribution of patch quality.

In this paper we present a stochastic argument which allows us to compare conventional deterministic models with a stochastic case. We use ideas from the mathematical theory of renewal (Cox 1962) to make a generalized model of the combined processes of search, encounter, capture and handling. We use these results to derive expressions for the mean and variance of energy gain due to foraging for a fixed time. We find the limiting distribution of energy gain due to foraging.

Stochasticizing by Expectations

Recent empirical (Caraco et al. 1980; Real 1981; Caraco 1981; Waddington et al. 1981) and theoretical work (Caraco 1980; McNamara and Houston, in press; Real 1980a, b; Stephens 1981) suggests that conversion of deterministic models by simply considering deterministic variables to be the means of probability distributions may be inappropriate: foragers are, and should be, sensitive to both the mean and variance of the distribution of food reward. This has been called risk-sensitive foraging by Caraco et al. (1980). Following the terminology of economics (e.g., Keeney and Raiffa 1976) Caraco et al. called preference for variance in food reward risk-proneness and preference for certainty risk-aversion.

Both risk-prone (Leventhal et al. 1959; Pubols 1962; Herrnstein 1964) and risk-averse (Real 1981; Waddington et al. 1981) preferences have been demonstrated in foraging animals. It may surprise biologists that both risk-prone and risk-averse preferences occur. Real (1981a, b), for example, suggests that risk-aversion ought to be universal. The key evidence is provided by Caraco et al. (1980) and Caraco (1981). Caraco et al. were able to manipulate the energy budgets of yellow-eyed juncos (*Junco phaenotus*), and offered them a constant and a variable food reward, where the expected value of the variable reward was equal to the value of the constant reward. The juncos preferred the constant choice when their expected energy budgets were positive, but preferred the variable choice when their expected energy budgets were negative. Caraco et al. demonstrated the following simple empirical rule: Be risk-averse if your expected daily energy budget is positive; be risk-prone if your expected daily energy budget is negative.

Caraco (1980) suggested that risk-sensitive foraging behavior would be predicted by a model minimizing the probability of starvation. Stephens (1981) has shown analytically that a simple model minimizing the probability of falling short of some threshold food requirement predicts the expected energy budget rule. In these cases there are compelling reasons to abandon simple conversion by expectations and develop full scale stochastic models which allow foragers to choose between variances as well as means.

We present a graphical generalization of the Stephens (1981) model of risk-sensitive foraging preferences. We consider how a forager minimizing its probability of starvation might best choose from a relatively complex set of mean-variance pairs.

Results

Our results consist of three models. Firstly, we attempt to establish a fairly general framework for comparing conventional deterministic models to a stochastic case. To do this we use results from renewal theory to find the limiting (i.e., time large) distribution of energy gain. Secondly, we consider a simple case in which elements of this distribution of energy gain, other than its mean, may be important; that is, when natural selection minimizes the probability of death due a short-fall. Finally, we sketch an example which applies both of these results to a conventional foraging problem, the choice of an optimal patch residence time. To aid continuity brief discussion and summary paragraphs follow each model.

The Limiting Distribution of Energy Gain

Earlier papers (Charnov 1976a, b) used deterministic arguments to derive equations for the rate of energy intake by a predator attacking individual prey items or traveling between patches or clumps of prey. In this section we formulate the problem as a stochastic process through time (Charnov 1973; McNair 1979). The random variable of interest is the net energy intake in some time interval, 0 to τ. As general results, the mean and variance of this variable, may be obtained, at least for large τ. Since the basic argument is similar for patches or prey types, we shall develop it only for prey types.

The Model. Our basic technique is to consider the time from leaving one prey item until leaving the next as a random event. Suppose that the predator began hunting at time zero and has just finished handling a prey item. Let this be the $r-1^{\text{th}}$ item handled. Let T_r be the time elapsed between leaving the $r-1^{\text{th}}$ item and leaving the r^{th} item. T_r is the sum of the search time for the r^{th} item and its handling time. The beginning of the search for the next item can be called a renewal point or event. Renewal theory (Cox 1962) is the study of the properties of this type of process. The T_r are drawn from the same probability distribution and are assumed to be independent of one another. This is a repeating environment assumption (MacArthur 1972).

To make this more precise, we shall use the following definitions: h_r = handling time for the r^{th} prey item. T_{sr} = the search time between leaving the $r-1^{\text{th}}$ and encountering the r^{th} prey items (thus $T_r = h_r + T_{sr}$). $E(X)$ = expectation of an arbitrary random variable X. $V(X)$ = variance of an arbitrary random variable X. N_τ = number of prey items encountered and handled in a time interval of length τ. ξ_r = the net energy gain associated with prey item r. The ξ_r are identically distributed and independent with finite mean and variance. In general, the ξ_r are not independent of the T_r.

$G_\tau = \sum_{r=1}^{N^\tau} \xi_r$, the sum of the ξ_r for N_τ

prey encountered and handled during τ. We shall not count in G_τ any prey the predator has encountered, but has not yet finished handling as this prey is not counted in N_τ. G_τ is the net energy intake during τ.

Because they will be used in several final results we define the following simplified notation:

$$E(G_\tau)=\mu_\tau \quad E(T_r)=\mu, \quad E(h_r)=\mu_h \quad E(\xi_r)=\mu_e,$$

$$V(G_\tau)=\sigma_\tau^2 \quad V(T_r)=\sigma^2, \quad V(h)=\sigma_h^2 \quad V(\xi)=\sigma_e^2,$$

$$Cov(T_r, \xi_r)=\sigma_{re}.$$

G_τ can be considered as a cumulative renewal process and Smith's theorems (Smith 1955) may be used to obtain the asymptotic (τ goes to infinity) mean and variance. The basic results may be found in Cox (1962, p. 100). We simply quote them here:

$$\mu_\tau = E(G_\tau)_{\tau\to\infty} \approx \frac{\tau\mu_e}{\mu} \tag{1.1}$$

$$\sigma_\tau^2 = V(G_\tau)_{\tau\to\infty} \approx \tau\left[\frac{\sigma_e^2}{\mu} + \frac{\sigma^2\mu_e^2}{\mu^3} - 2\frac{\mu_e\sigma_{re}}{\mu^2}\right]. \tag{1.2}$$

Paloheimo (1967, 1971) was the first to use these results to model predator behavior, although he did not consider the accumulated catch $[E(G_\tau)]$ in terms of energy intake. Even though these are derived under the assumption that τ is large, the approximations may be good for 'small' intervals, depending on how fast the stochastic process converges. G_τ can also be shown to follow a normal distribution as a result of the central limit theorem. To see how these results may be used to generate energy intake equations, consider the case where prey items are encountered 'at random.'

Let there be k prey types, with type i having associated with it two random variables. The first is the handling time (h_i), the second is the energy value (e_i) associated with the handling time events. These have been previously discussed (Charnov 1973, 1976b). Their means are h_i^* and e_i^*. Each type forms an encounter process with the predator. The encounter processes are assumed to be independent Poisson processes through time with encounter rates λ_i ($i=1,2,\ldots,k$). During the handling of a prey item, no new item may be encountered. It is important to notice that it is the *encounter* process which is Poisson, that is we expect the number of encounters in a fixed search time to fit a Poisson distribution not the number of prey captured in a fixed time foraging.

If we look at the encounter process formed by pooling the k processes (i.e., look at an encounter regardless of type), the resulting pooled process is still Poisson and the new rate parameter is $\lambda^* = \sum_{i=1}^{k} \lambda_i$. The probability that an encounter is with a prey type j is λ_j/λ^* and is independent of search time (T_{sr}) (Cox 1962).

With the above in mind, the search time between encounters (T_{sr}) has a negative exponential distribution with mean and variance:

$$E(T_{sr}) = 1/\lambda^* \qquad V(T_{sr}) = 1/\lambda^{*2}. \tag{1.3}$$

We have for the r^{th} renewal

$$E(h_r)=\mu_h=[\sum\lambda_i h_i^*]/\lambda^* \qquad (1.4)$$

$$E(\xi_r)=\mu_e=[\sum\lambda_i e_i^*]/\lambda^* \qquad (1.5)$$

$$V(\xi_r)=\sigma_e^2=[\sum\lambda_i E(e_i^2)]/\lambda^*-\mu_e^2 \qquad (1.6)$$

$$V(h_r)=\sigma_h^2=[\sum\lambda_i E(h_i^2)]/\lambda^*-\mu_h^2 \qquad (1.7)$$

$$\begin{aligned} Cov(T_r,\xi_r)&=\sigma_{re}=Cov(h_r+T_{sr},\xi_r)\\ &=Cov(h_r,\xi_r). \end{aligned} \qquad (1.8)$$

Now:

$$T_r=T_{sr}+h_r, \quad \text{so} \quad \mu=E[T_{sr}]+\mu_h$$

or

$$\mu=1/\lambda^*+[\sum\lambda_i h_i]/\lambda^*. \qquad (1.9)$$

Since

$$Cov(T_{sr},\xi_r)=0, \qquad \sigma^2=V[T_{sr}]+\sigma_h^2$$

$$\sigma^2=1/\lambda^{*2}+\sigma_h^2. \qquad (1.10)$$

If we substitute (1.5) and (1.9) into (1.1) the following results as $\tau\to\infty$.

$$\frac{\mu_\tau}{\tau}\approx\frac{\sum\lambda_i e_i^*}{1+\sum\lambda_i h_i^*} \qquad (1.11)$$

substituting (1.5) and (1.10) into (1.2) gives the variance for G_τ as $\tau\to\infty$.

$$\sigma_\tau^2\approx\tau\left[\frac{\sigma_e^2}{D}+\frac{\mu_e^2(1+\sigma_h^2\lambda^{*2})\lambda^*}{D^3}-\frac{2\mu_e\sigma_{re}}{D^2}\right]$$

$$\text{where} \quad D=1+\sum\lambda_i h_i^*. \qquad (1.12)$$

Expressions (1.11) and (1.12) completely specify the limiting distribution of energy gain, G_τ, because Smith's theorems (Smith 1955) show that the limiting distribution of a cumulative renewal process approaches normality according to the central limit theorem.

Implications of the Model. The chief importance of this result is to specify the distribution of energy gain. However, this result is also important as further stochastic justification of expression (1.11). Expression (1.11) is the form of Holling's disc equation (Holling 1959) most commonly used in models of optimal foraging. Many authors have used expression (1.11) as a currency of maximization in deterministic models of optimal diet choice (Charnov 1976b; Maynard Smith 1974; McNair 1979; Pearson 1974; Pulliam 1974; Schoener 1969, Werner and Hall 1975) and models of optimal patch use (Charnov 1976a; Orians and Pearson 1979; Pyke et al. 1977 for a review of this and other currencies), when encounters are assumed to be at random. Previously expression (1.11) has been justified for stochastic situations because it is equal to the expected gain per prey encounter, $E(\xi_r)$, over the expected time spent per encounter (including interprey time), $E(T_r)$. The average amount of energy gained per time unit approaches $E(\xi_r)/E(T_r)$ as the number of encounters becomes infinite, according to the law of large numbers (Gilliam et al. 1982; Turelli et al. 1982; McNair, personal communication). The result presented here adds the weight of the central-limit theorem to the use of this formulation for foraging models. Usually, the central-limit theorem implies faster convergence to the limiting state than the law of large numbers. However, the comparison is not perfect because the renewal justification is asymptotic in time, while the law of large numbers justification is asymptotic in the number of prey encountered. Important unanswered questions are: How fast is the asymptotic distribution reached (but see Turelli et al. 1982) and what affects the speed of approach?

Conclusions. In this section we find the limiting probability distribution of energy gain for a foraging animal when encounters with prey items (or patches) occur at random. This distribution is normal and we give its mean and variance. The results also support the use of Holling's disc equation to represent the rate of energy intake in foraging models.

The Risk of Starvation and Optimal Preferences

Many species have nonbreeding seasons in their life histories; during these periods survival until the next breeding season may be the most important attribute of fitness. Stephens (1981) has shown that when death due to starvation is defined as falling short of some threshold food requirement, both the mean and variance of the food reward distribution are important in determining optimal behavior. However, Stephens's formulation only considers the case where the mean is fixed and the forager is allowed to choose from a set of different variances. In this section we present a graphical model which extends this formulation by specifying sets of mean-variance pairs which provide equal probabilities of starvation.

The Model. To illustrate the model we consider a small bird foraging in winter. Many small birds suffer significant overnight mortality in winter (e.g., Prys-Jones 1979) and most must stop feeding at nightfall. Assume that the bird's main problem is surviving from day to day, by acquiring sufficient energy reserves to survive the night.

Let R be the amount of food required to survive the night, and let S_0 be the random variable which describes the bird's energy supply when it must stop foraging for the night. The probability of starvation is $P(S_0<R)$. Assume that the forager makes decisions about how to forage at intervals. Let k be the number of decision intervals left in the day. Let S_k be the bird's reserves when there are k foraging decisions left in the day. Let X_i be the net amount of food gained in the i^{th} interval, where X_i is a random variable with distribution

$$f(x_i|\mu_i,\sigma_i^2)\ \mu_i=E(X_i) \quad \text{and} \quad \sigma_i^2=V(X_i).$$

Assume that the X_i are independently distributed. Then

$$S_0=S_k+\sum_{i=1}^{k} X_i \tag{2.1}$$

therefore

$$P(S_0<R)=P\left(S_k+\sum_{i=1}^{k} X_i<R\right)=P\left(\sum_{i=1}^{k} X_i<R_{\text{net}}\right)$$

where R_{net} is the net food requirement, ($R_{\text{net}}=R-S_k$). Now if k is large we can use the central limit theorem for independent random variables to find the distribution of the sum of random variables $\sum_{i=1}^{k} X_i$. For convenience, we define: $\mu_\tau=\sum_{i=1}^{k}\mu_i$, the total expected gain due to the decisions made in the remaining time, τ $\sigma_\tau=\left[\sum_{i=1}^{k}\sigma_i^2\right]^{1/2}$, the standard deviation of the distribution of the remaining food reward. The central-limit theorem states that

$$Z=\frac{\sum_{i=1}^{k} X_i-\mu_\tau}{\sigma_\tau} \tag{2.2}$$

has an approximately standard normal distribution, with mean zero and variance one. We use Z algebraically to show that $\mu_\tau+\sigma_\tau Z$ is probabilistically equivalent to $\sum_{i=1}^{k} X_i$, that is

$$\begin{aligned} &=P(\text{Starvation})=P\left(\sum_{i=1}^{k} X_i<R_{\text{net}}\right)\\ &=P(\mu_\tau+\sigma_\tau Z<R_{\text{net}})\\ &=P[Z<(R_{\text{net}}-\mu_\tau)/\sigma_\tau]\\ &=\Phi[(R_{\text{net}}-\mu_\tau)/\sigma_\tau]. \end{aligned} \tag{2.3}$$

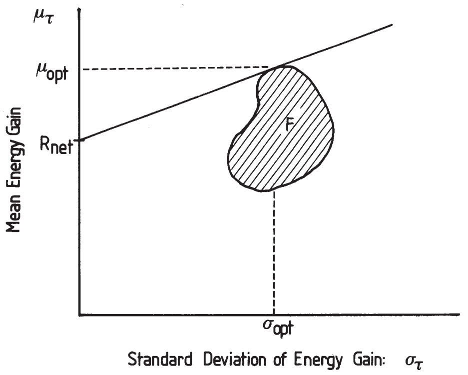

Fig. 1. The general graphical solution for optimal preferences from complex sets of mean and variance. The *hatched shape*, marked *F*, represents an arbitrary feasible set of mean-standard deviation pairs. The pair which minimizes the probability of death due to an energetic short-fall is found by constructing the line originating at R_{net} (the net energy requirement) on the mean axis and which passes through, or touches, the feasible set with the greatest slope possible

Where $\Phi(\ )$ is the cumulative distribution function (*cdf*) of a standard normal. This means that the probability of starvation strictly increases with the term $(R_{\text{net}}-\mu_\tau)/\sigma_\tau$.

Let $Z'=(R_{\text{net}}-\mu_\tau)/\sigma_\tau$. Any fixed value of Z' defines a set of pairs (μ_τ,σ_τ); all members of such a set give the same probability of starvation. A forager minimizing its risk of death due to starvation should be indifferent to a choice between any two points lying on the line

$$\mu_\tau=R_{\text{net}}-\sigma_\tau Z'. \tag{2.4}$$

When Z' is fixed, (2.4) is the familiar slope-intercept equation of a straight line in $\mu_\tau-\sigma_\tau$ space. This suggests the simple graphical method of solution illustrated in Fig. 1. In general, the forager will be able to choose from a limited feasible set of mean-variance pairs, which is illustrated by the hatched blob in the figure. Consider the family of lines, each of which intersects the μ_τ axis at R_{net}. The line of greatest slope which can be drawn through the feasible set gives the smallest possible probability of starvation, and the point, or points, (μ_τ,σ_τ) of the feasible set through which this line passes is (are) the optimal mean-standard deviation pair (or pairs). The line of greatest slope gives the solution, since when the slope, $-Z$, is largest, the value Z (which we want to minimize) is smallest. In a particular optimality problem we would have calculated the feasible set by considering the effects of varying some behavioral parameter of interest, e.g., patch residence time, or the probability of pursuit upon encounter. These calculations would allow us to work back-

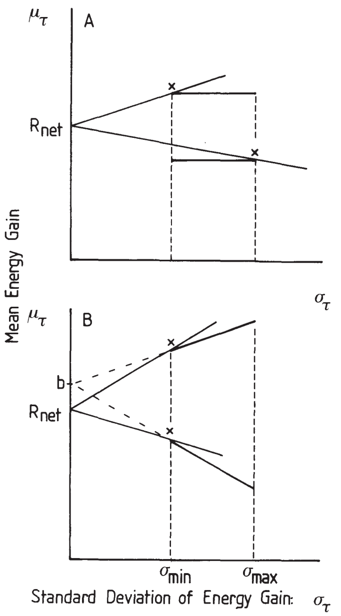

Fig. 2A, B. Linear Feasible Sets. **A** Two horizontal feasible sets, i.e., sets in which the forager chooses from a range of variances (standard deviations in the graph) at a constant mean. This illustrates that the extreme variance rule, discussed in the text, is a special case of this graphical model. *Crosses* indicate the optimal choices. **B** Example of the general rules for linear feasible sets, i.e., when $\mu_\tau = m\sigma_\tau + b, \sigma_{min} \leqq \sigma_\tau \leqq \sigma_{max}$. The optimal preference depends only on the position of the intercept b relative to the net requirement, R_{net}. Note that in the lowest feasible set the extreme variance rule does not hold because all possible means are less than the net requirement, R_{net}, but the optimal policy is still to minimize variance (and consequently to maximize the mean)

ward from the optimal (μ_τ, σ_τ) pair to find the optimal behavioral (or choice) parameter. This procedure is illustrated by a worked example in the next section.

The simple behavioral rule for minimizing the probability of starvation proved by Stephens (1981) can be derived as a special case of this model. Stephens showed that at a given mean a forager would minimize its probability of starvation due to a short fall by: (A) Always minimizing variance if its expected gain is greater that its requirement; (B) always maximizing variance if its requirement is greater that its expected gain. We call this the extreme variance rule. It follows from the general graphical solution because the feasible set is a horizontal line (i.e., μ_τ is constant). Figure 2A shows that when $\mu_\tau > R_{net}$ the line of greatest slope passes through the smallest possible σ_τ in the feasible set (condition A above). But when $\mu_\tau < R_{net}$ the line of greatest slope passes through the largest possible σ_τ in the feasible set.

If the feasible set is linear, but not in general, horizontal, there is a simple extension of this rule. Assume that the feasible set is defined by the linear equation $\mu_\tau = m\sigma_\tau + b$, where $\sigma_{min} \leqq \sigma_\tau \leqq \sigma_{max}$. It is easy to show that the probability of starvation due to a short fall is minimized by: choosing σ_{max} if $R_{net} > b$, and choosing σ_{min} if $R_{net} < b$. The direction of preference for variance is independent of the slope of the feasible set. Consequently, the optimal mean value may be either the maximum possible mean or the minimum possible mean in the two cases above (the case where $R_{net} < b$ is illustrated in Fig. 2B). We have shown that the assumption of a fixed expected reward is critical to the extreme variance rule. In the lower feasible set in Fig. 2B, all possible means are less than the minimum requirement R_{net}, but the optimal choice is maximum mean and *minimum* variance.

Linearity is only the simplest kind of nontrivial relationship which might exist between μ_τ and σ_τ. This general linear solution is an advance over the special case of fixed expected gain, because it makes the point that the nature and degree of a forager's preferences over variance are changed when the forager has a restricted choice of mean-variance combinations.

Implications of the Model. Caraco (1980) suggested that a forager should be risk-prone if it has 'no available allocation strategy' which produces an expected net reward greater than expected requirements. However, Caraco used the term 'risk-proneness' to mean that a forager would prefer to draw a realization from a probability distribution than to be given the mean value of the same distribution with certainty. This usage is in line with economics and mathematics (cf. Keeney and Raiffa 1976). That is, the definitions of risk-proneness and risk-aversion have built into them the assumption that a forager is offered a choice between variances at the same mean. As we have argued above, and as the results of the first section suggest, foragers are unlikely to be offered such choices in nature. A useful theory of risk-sensitivity will need to go beyond these strict definitions of risk-proneness and risk-aversion to consider which distribution should be preferred from an arbitrary set of distributions. The model we have presented does this for an animal minimizing its probability of death due to a short fall.

In this model we begin by relating energy intake to survival. The assumption that there is some fixed threshold requirement is only the simplest possible relationship. There may, for example, be unpredictable elements in the threshold (e.g., if the overnight temperature is unpredictable, in our small bird example); or the probability of survival may be an increasing sigmoid function of daily food reward

(McNamara and Houston, in press). The results will be more complicated if the distribution of daily food reward is not normal. Departures from normality may be relatively common, especially in the tails of the approximated distribution. Perhaps most dubiously, we assume that all amounts of energy gained greater than the requirment are equivalent in terms of fitness; that is, we tacitly assume that there is no advantage to a large energetic 'carry-over.' McNamara and Houston (in press) present an interesting discussion of this problem.

These assumptions may not always make sense. The model may fit the case of an over-wintering bird, foraging on an especially cold day; but it will not fit the same bird in the breeding season. Real (1980a, b) and Caraco (1980) have presented more general models of risk-sensitivity. However, the relationship between the natural history of foragers and these general models is not always clear. Despite the limitations of our model, it is useful as a simple and analytical alternative to mean maximization models.

Conclusions. In this section we present a simple model of risk-sensitive foraging preferences. The model is based on minimization of the probability of energetic short-fall. Our model suggests that preferences between distributions of food reward ought to be sensitive to relationships between mean and variance. Our graphical model provides a technique for finding optimal preferences from complex mean-variance sets.

Patch Use and the Risk of Starvation – A Worked Example

An important question raised in the last section is what mean-variance relationships are most common and most general? In this section we apply the results of the two previous sections to finding the optimal patch residence time for an animal minimizing its risk of starvation. This illustrates how the relationship between mean and variance may be found in a foraging problem.

The Model. Consider an animal foraging in discrete patches in a manner which minimizes its probability of starvation. Assume that time spent in a patch completely specifies the net amount of food acquired from the patch. Patches are identical, and numerous enough that environmental depletion due the forager's behavior is not significant, i.e., the forager is always entering undepleted patches. The only stochasticity is due to random variation in the time required to find a new patch.

Our problem is to find a patch residence time, t, which minimizes the probability of starvation, as discussed above. Let T_s be the random variable which represents the time between leaving one patch and entering another. Assume that T_s is exponentially distributed with parameter q, that is patches are encountered at random. Let t be the residence time, which is the parameter over which we wish to optimize, and let $g(t)$ be the negatively accelerated gain function (a deterministic function) which relates the net amount of energy gained from a patch to the residence time. We use Eq. (1.1) and (1.2) to give specific expressions for the asymptotic mean and standard deviation of energy gain. This example is simple, because for a fixed residence time, the variance in energy gain within a patch is zero, as is the covariance of the interrenewal interval and the energy gain per patch. The required terms are:

$$\mu_e = g(t)$$

$$\mu = E(T_s) + t = 1/q + t$$

$$\sigma^2 = V(T_s) = 1/q^2$$

$$\sigma_e^2 = 0$$

$$\sigma_{re} = 0.$$

By substitution we find the required mean and variance terms:

$$E(G_\tau | t) = \mu_\tau(t) = \frac{g(t)\tau}{(1/q)+t} \tag{3.1}$$

$$V(G_\tau | t) = \sigma_\tau^2(t) = \frac{\tau(1/q^2)[g^2(t)]}{[(1/q)+t]^3}. \tag{3.2}$$

It is a standard result of patch-use theory that μ_τ is maximized where

$$g'(t) = \frac{g(t)}{(1/q)+t}. \tag{3.3}$$

This result is a special case of Charnov's (1976a) marginal value theorem. Consider the derivative of the standard deviation, σ_τ, with residence time,

$$\partial\sigma_\tau/\partial t = (\tau^{1/2})\left\{\frac{g'(t)\,[(1/q)+t]^{3/2} - (3/2)\,g(t)\,[(1/q)+t]^{1/2}}{q[(1/q)+t]^3}\right\}.$$

Since the term in the denominator is always positive the sign of the derivative is determined by the difference in the numerator. The standard deviation increases with t as long as

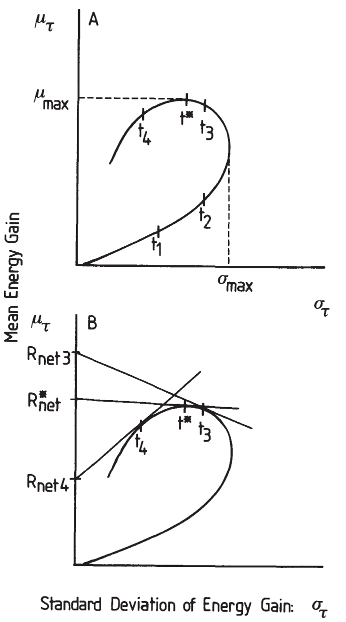

Fig. 3A, B. Patch residence time and the risk of starvation. The curve shown in **A** shows the shape of the feasible set for an animal foraging in discrete patches, and choosing an optimal patch residence time as discussed in the text. The patch residence times (t_i's) marked on the curve indicate how increasing residence time affects the mean and standard deviation, that is $t_4 > t^* > t_3 > t_2 > t_1$. **B** Application of the graphical model of the previous section to finding optimal patch residence times. R^*_{net} is the net requirement at which mean maximization is preserved. But, as with R_{net4}, if the requirement is less than R^*_{net} it is best to stay longer (i.e., $t_4 > t^*$); and as with R_{net3}, if the requirement is greater than R^*_{net} it is best to leave sooner (i.e., $t^* > t_3$)

$$g'(t) > \frac{(3/2)\,g(t)}{(1/q)+t} \tag{3.4}$$

the standard deviation decreases with t where this inequality is reversed, and is therefore at a maximum when t is such that,

$$g'(t) = \frac{(3/2)\,g(t)}{(1/q)+t}\,. \tag{3.5}$$

Notice the similarity between (3.3) and (3.5). We can conclude, because $g(t)$ is negatively accelerated, that the residence time at which the maximum standard deviation occurs is always less than the residence time at which the mean intake is maximized. We summarize the results of this analysis: (i) μ_τ and σ_τ are both unimodal functions of patch residence time, and (ii) that the maximum standard deviation will always occur at a smaller residence time than the maximum possible mean, and (iii) both μ_τ and σ_τ are zero when $t=0$. These points are enough to allow us to plot the feasible set in $\mu_\tau - \sigma_\tau$ space and use our earlier graphical treatment (Sect. 2) to make predictions about the qualitative differences between a forager choosing its patch residence time to maximize its intake rate, and a forager minimizing its probability of a shortfall.

Figure 3A shows the general shape of the feasible set. Figure 3B illustrates the qualitative deductions which can be made considering the general shape of the feasible set, and the graphical method of solution presented in Sect. 2. The optimal residence time for a forager minimizing its probability of starvation will have the following properties: (1) It will usually be near the residence time predicted by mean-maximization (the marginal value theorem) because of the feasible set's oblong shape. (2) There will be a critical level of requirement R^*_{net} at which the optimal residence time is exactly the same as in the mean-maximization case. (3) If the actual requirement is less than R^*_{net} then the optimal behavior is to stay longer than predicted by mean-maximization. (4) If the actual requirement is greater than R^*_{net}, the optimal residence time is shorter than predicted by mean-maximization. (5) As the requirement becomes larger the optimal residence time becomes shorter and approaches the time at which the maximum standard deviation is attained, but will never become smaller than this.

As a general rule we may say that if the requirement is low compared to expectations, then the forager should stay longer than expected by mean-maximization; if the requirement is high, the forager should stay for a shorter period than expected by mean-maximization, but never shorter than the time producing maximal variance. These predictions are only qualitative. There are indications from numerical examples that in many cases departure from the mean-maximization hypothesis may be small. The extreme variance rule does not hold in this example because neither the highest nor the lowest possible variance should be chosen, except in the limiting case. It does give us insight into why this result occurs. The forager chooses increasingly higher variance as requirements become large relative to expected gains. However, since the feasible set is not linear, the forager should never choose extremes of variance because it would have to accept a disproportionate loss in mean to do so.

Several authors have presented modifications of the marginal value theorem. Oaten (1977) and McNamara (1982) consider the case in which the forager also gains information while foraging. McNair (in press) considers a modification where the forager is allowed to encounter new patches while searching a patch. In both of these cases the optimal residence time is longer than predicted by the marginal value theorem (although the comparison with

Oaten's model requires a redefinition of the Charnov's marginal capture rate, cf. McNamara, in press). McNair (in press) also analyzes an optimal residence time model which minimizes the probability of starvation over an infinite time period. His model differs from ours in that he envisions no critical reckoning time (nightfall in our example). McNair's 'starvation' is simply running out of fuel during the foraging process. McNair finds that the probability of starvation is minimized by staying longer than the marginal value theorem would predict. McNair's infinite time model is similar to ours when net requirements are very small relative to expected gains. Our model suggests that over-staying may be the most common case; because requirements will normally be much less that expected gains. However, in the case of severe energetic stress relatively short stays may be optimal.

Conclusions. We consider the optimal patch residence time for a forager minimizing its risk of starvation. This requires that we specify the relationship between residence time, mean energy gain, and the standard deviation of energy gain. The surprising shape of the feasible set we find in this section suggests that it may be misleading to try to find general relationships between mean and variance. This is because we need to know how mean and variance are specified by a choice of foraging strategy (e.g., patch residence time). Our result suggests that this relationship may depend critically on the nature of the foraging problem at hand.

Discussion

The problem of stochasticity in optimal foraging is actually two problems. Firstly, in a stochastic environment a forager's behavior will not yield, for example, ten calories with certainty; instead a forager will at best be able to choose a probability distribution of calories. Choosing from a known set of probability distributions and choosing certain alternatives are clearly different problems. The first stochastic problem is how should foragers change their preferences when they are faced with known types of stochastic variability. Economists call this the problem of pure risk (Hey 1979).

The second stochastic problem is more complicated and less direct. Imagine that the state of nature is represented by one of two possible overlapping probability distributions, A and B. Assume that the forager knows what the alternatives are, but cannot distinguish between them before deciding what tactic to use. Further, imagine that if the forager knew it was faced with distribution A it should use a different tactic than if faced with B. The tactic actually chosen should then reflect information (about the relative likelihoods of A vs B) gained while foraging. That is, the forager has a sampling problem, or in the terminology of economics a problem in pure uncertainty (Hey 1979), although it would probably be less confusing to call this a problem of information.

The separation of the stochastic problem into these two elements is logically important, not because animals face pure information or pure risk problems in nature, but because it suggests a sensible way for our study of stochasticity to proceed. In this paper we have discussed problems of pure risk. In more conventional terms we have made perfect information models. In this discussion we discuss risk and information and the controversies surrounding them, in turn. Finally, we consider the problem of rates in a stochastic environment.

Risk and Utility

The most general solution to the problem of risk is given by utility theory. In outline the procedure is simple. We have a utility function (exactly how we come to have it is an issue we discuss later), defined over all possible outcomes. The utility function specifies which outcomes are preferred and how much a given outcome is preferred over another. The fundamental result of utility theory is that a utility function *can* be defined so that distributions can be placed in order of preference by their expected utilities. The idea that such a function exists is called the expected utility hypothesis (cf. Raiffa 1968).

To help make the distinctions clear consider the form of a deterministic foraging problem. The steps in a deterministic analysis are: (1) choose a currency and (2) specify cost-benefit functions, (Schoener 1971). Expected utility is the same as Schoener's currency because it is the quantity we maximize. But in a risk problem cost-benefit functions do not relate behavior to expected utility. They relate behavior to the distribution of some intermediate reward (e.g., amount of food). The expectation of the utility function, given this distribution, provides the final link to the currency.

A utility analysis of foraging behavior would take the following form. (1) Choose a utility, for example, the probability of survival. All the considerations which apply to the choice of a deterministic currency apply to this decision, e.g., when is the probability of survival the most important fitness attribute? (2) Specify the relationship between the proposed utility and food. (3) Specify the relationship between behavior (e.g., patch residence time) and the distribution of food reward. Here, the effect of stochasticity is to require that we postulate (or measure) a second type of function; that is, we need not only relate behavior to food gains (Schoener's cost-benefit functions), but we must relate food gains to preference (utility functions).

Currency vs Expected Utility

There are two approaches to the problem of finding a forager's utility function. The conventional approach of utility theorists (cf. Raiffa 1968) is to allow the subject to specify its own utility function by giving it a series of preference tests. This approach has been adopted by Caraco et al. (1980) to make the important point that foraging animals have preferences over variance. The approach of deterministic foraging theory (cf. Pyke et al. 1977) has been to guess a reasonable currency based on our knowledge of the forager's natural hystory. These a priori currencies, with their connection to natural history, are one of the strengths of optimality analysis. Both approaches can be useful in the study of foraging behavior. But allowing the forager to specify its own utility function is, in a sense, the least satisfactory of the two alternatives because we want to know not only what a forager's preferences are, but why it has these preferences. We do not mean that these questions cannot be asked separately, but the second question is the biological one; utility theory, per se, sheds no light on the answer, only on the form the answer should take, i.e., a utility function.

Fitness and expected utility are both tautologically defined maximization criteria. To call them tautological is not a complete condemnation because they can both be interesting and helpful tautologies (see Maynard Smith 1969). Neither idea tells us much about the adaptive nature of foraging behavior. To say that selection has favored maximization of fitness or utility is simply too glib. We must go a step further and postulate how food and feeding are related to ultimate fitness. In the models we have presented, we postulated a simple connection between the forager's natural history and its risk-sensitivity: minimization of the probability of a short-fall. If our model fits natural foraging behavior, we can take satisfaction in having understood natural history well enough to have made an a priori guess about the appropriate utility, more so than if we had simply measured utility functions.

Description and Utility

The expected-utility hypothesis may fail; that is, no utility function may exist which describes the behavior. In economics there are famous examples of where humans show preferences which are inconsistent with the expected-utility hypothesis (e.g., Allais 1953). The reply of utility theorists is that their theory is prescriptive, not descriptive, of human behavior (Raiffa 1968). Utility theory tells us how rational human decisions *should be* made, not how human decisions are made. In foraging theory we do not want to prescribe animal preferences; we want to describe them. We do not want to instruct animals in how to make better decisions. We want to describe the decisions they do make. Perhaps we should consider whether animal decisions are more likely to satisfy the criteria of the expected-utility hypothesis than human decisions. When we adopt techniques from other disciplines, we should look hard at their internal difficulties. In the case of utility theory there is a large body of literature on the pros and cons of its application (e.g., Raiffa 1968; Keeney and Raiffa 1978, who provide discussions).

Variance Discounting

The formal machinery of utility theory may not be necessary in practice, especially if food reward is normally distributed. While normality cannot be guaranteed, it is likely to be the most general food reward distribution; this is suggested by the results in section one and less restrictively by the central limit theorem itself. When normality does occur, the intuitive idea of a trade-off between a measure of central tendency (mean) and a measure of variability (variance) can be justified by rigorous mathematics because the mean and variance provide a complete specification of a normal distribution. If we take normality to be general, we then have the problem of trying to find some general way to combine mean and variance to provide a measure of quality. Section two proposed that the Z-score of the standard normal distribution is a sensible currency for the case of acquiring a threshold food requirement.

Many authors have proposed that a straightforward linear combination of mean and standard deviation may be a generally useful currency (Oster and Wilson 1978; Caraco 1980; Real 1980a, b). This currency has the form:

$$\max(\mu - k\sigma)$$

where μ is the mean and σ is the standard deviation of the reward distribution, and k is a constant measuring the forager's risk-sensitivity. We maximize the mean, discounted by a certain amount for 'undesirable' variability, because k is usually positive. While this formulation is recommended by its simplicity, its claim to generality may be strong as well. Using arguments from utility theory, it has been shown that this formula is approximately correct under very general conditions using a series expansion argument (Oster and Wilson 1978; Real 1980a, b). It is exactly correct if the underlying distribution is normal and the utility function is a simple exponential function (Oster and Wilson 1978; Caraco 1980).

Uncertainty and Information in Patches

The marginal-value theorem (Charnov 1976a), a deterministic model finding optimal patch residence times, has been severely criticized because, according to Oaten (1977), sensible optimal leaving procedures 'must be based on a stochastic model'. Green (1980), Iwasa et al. (1981) and McNamara (in press) have all added mathematical weight to Oaten's criticism. It is unfortunate and misleading that Oaten and his colleagues have been so insistent in their campaign for stochasticity because the differences between Oaten's stochastic model and Charnov's deterministic model are not due to stochasticity per se.

Consider the following simple example. Imagine that a scientist is given two opaque urns, each containing different proportions of red to green balls, and is asked to obtain as many red balls as possible in some fixed number of draws, without replacement. If the scientist is told that the urn labelled A has initial proportion p_a of reds and the urn labelled B has reds in initial proportion p_b, the problem is closely analogous to Charnov's patch-use model where the urns are patches and the scientist is a forager. However, if the scientist is not told what the labels mean, he has Oaten's problem; because he cannot recognize patches he will do well to use knowledge gained while 'foraging' to improve his decisions. The difference here is not stochasticity. Both problems are stochastic. The difference is the amount of information the forager (scientist) is supposed to have. To call Oaten's model the stochastic case is to confuse the problems of risk and information.

Stochastic Rates

Pyke et al. (1977) have argued that maximization of the net rate of energy intake is the most sensible general currency of optimality in foraging because it subsumes both of the reasonable currencies proposed by Schoener (1971), energy maximization over a fixed time and time minimization to a fixed energy gain. Templeton and Lawlor (1981) have recently pointed out that in a stochastic world, maximization of the expected rate of energy intake is not necessarily equivalent to either of these strategies. In this case, what Templeton and Lawlor called the 'fallacy of averages' stems from the fact that the expectation of a quotient is not equal to the quotient of the expectations.

Let G be the random variable which specifies the net food gain over a random time T. Then each of following currencies of optimality is possible and generally distinct from the others.

1. Maximize $E(G/T)$.
2. Maximize $E(G)/E(T)$.
3. Maximize $E(G|T=t)$, where t is a fixed value.
4. Minimize $E(T|G=g)$, where g is a fixed value.

Currencies three and four are stochastic versions of Schoener's (1971) energy maximizer and time minimizer. However, a good deal of controversy surrounds the interpretation of currencies one and two (Templeton and Lawlor 1981; Gilliam et al. 1982; Turelli et al. 1982). Templeton and Lawlor claim that currency one is the average of energy intake and that models of optimal foraging which have claimed that currency two is the average rate of intake (specifically Charnov 1976b and Pulliam 1974) are wrong. Templeton and Lawlor are incorrect because both currencies are average rates of intake. The important question is which average is appropriate, not which is *the* average.

The precise meanings of these currencies depend on the definitions of G and T. If G is the amount of energy gained in time T, where T is the time from entering one patch until entering the next (Templeton and Lawlor's case), then as the number of patches visited becomes large, the average rate of energy intake *per patch* approaches $E(G/T)$ by the law of large numbers. By a similar argument, as the number of patches visited becomes large the average amount of energy gained *per unit of time* approaches $E(G)/E(T)$. These are both average rates. An animal using the $E(G/T)$ currency should choose foraging strategies where each patch yields the highest possible rate that particular patch can attain, regardless of the absolute amount of time spent in that patch. While the $E(G)/E(T)$ currency allows for the possibility that the rate attained within a particular patch might be less than the maximum possible if a higher overall rate can be had by moving on to better patches. There may be cases where $E(G/T)$ is a sensible currency: for example, if the forager is somehow limited to visiting only one patch per day (or whatever 'critical' period is applicable). However, we agree with Gilliam et al. (1982) that $E(G)/E(T)$ is a much better currency for nearly any forager.

Analysis and Simplicity

Our approach is to build simple models. Simple models are most useful because they allow us to see how the elements of the problem interact and to readily compare different conditions and assumptions. In a word, simpler models allow better analysis. The growing body of literature on stochasticity in foraging strongly argues that the additional complexities of stochastic models are worth it. But modelers should not lose sight of analysis. We have taken the time to discuss the controversies about stochastic rates and 'stochasticity' in patch use because we believe that these are cases where analysis has been lost in the shuffle. The cause of analysis is not well served by Templeton and Lawlor's (1981) surprising and self-contradictory statement that ecologists should be suspicious of 'conclusions that depend critically upon the precise form of the optimization criterion.' Not only are criteria critical by definition, if they are not they should have been removed from the model on the ground of parsimony inherent in the concept of analysis.

Modeling is just figuring out the implications of a set of assumptions. Templeton and Lawlor (1981) and Oaten (1977) seem to have elevated assumptions to the realm of metaphysics by insisting on right and wrong assumptions. Maximizing $E(G)/E(T)$ has different implications than maximizing $E(G/T)$, and a discussion of the these differences has proved helpful, despite Templeton and Lawlor's error (Gilliam et al. 1982; Turelli et al. 1982). Similarly, Oaten's important work has shown that foragers which cannot recognize patches should act differently from those which can. But this does not show that 'published strategies are not optimal,' as Oaten claims.

Acknowledgements. We are thankful to T. Caraco, T. Getty, R. Hegner, J. Horsfall, A.I. Houston, J.R. Krebs, D.W. Lendrem, J.M. McNamara, G.H. Orians, W.J. Sutherland, and R.C. Ydenberg for reading and thoughtfully criticizing all or part of the manuscript. We thank R.F. Green, J. McNair, J.M. McNamara, and N.E. Pearson for helpful discussion and several interesting manuscripts. We also thank H. Markl for his thoughtful editorial assistance. DWS is especially grateful to ELC for the many years he has spent as a teacher, commentator, and mentor. DWS is grateful to A.E. Sorensen for random assistance.

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