OPTIMAL FORAGING: SIMULATION STUDIES OF DIET CHOICE IN A STOCHASTIC ENVIRONMENT

BRUCE WINTERHALDER

Department of Anthropology and Curriculum in Ecology
University of North Carolina at Chapel Hill
North Carolina 27514

ABSTRACT.—Foraging models are a growing part of the ethnobiological study of hunter-gatherers. Highly simplified for analytic reasons, the early "classical" versions of these models excluded consideration of several relevant factors. Among them is the possibility of maladaptive food shortages due to the effects of stochastic environmental fluctuations on food capture rates. To remedy this deficiency, the present simulation study develops a stochastic, risk-minimizing analog to the widely used but deterministic and rate-maximizing diet choice model. The results indicate that optimal efficiency-maximizing and risk-minimizing choices are quite similar. However, even with the optimal risk-minimizing choice, the forager in a stochastic environment will experience large variations in food capture rate from one time interval to the next. This and other studies using and developing foraging theory hold the promise of a micro-ecological theory of hunter-gatherer economies, past and present.

INTRODUCTION

Human and evolutionary ecology have met in the study of hunter-gatherers. The result is a modest but promising and growing place in the ethnobiological niche, one where anthropologists and biologists are applying common theories to the study of like topics. Research on the foraging behavior of human and non-human organisms is a prominent part of this effort. This work, based in optimal foraging theory, typically uses highly simplified models to examine food or habitat choice, time allocation, the use of space, or group formation and structure.

The theory and methodology of foraging models and applications in anthropology recently have been reviewed elsewhere (Pulliam 1981; Winterhalder and Smith 1981; Smith 1983; Winterhalder 1986a). A lucid and comprehensive review of the biological literature on this subject can be found in Stephens and Krebs (1986). Applications of interest to ethnobotanists are quite diverse, and include hominid paleoecology (Hill 1982; Kurland and Beckerman 1985), archaeology (Bettinger and Baumhoff 1982; O'Connell, Jones and Simms 1982; Webster and Webster 1984) and human ecology (Hames and Vickers 1982; Beckerman 1983; O'Connell and Hawkes 1984; Hill *et al.* 1985; Pate 1985; Sih and Milton 1985; and Smith 1985). Thomas' (1985) attention to this body of ideas, in his paper on the 'state-of-the-art' in hunter-gatherer studies in archaeology, highlights its growing importance.

Here I would like to focus on an extension of a key component of foraging theory, the diet breadth model. Although its analytical utility is well established, the diet breadth model excludes a long list of variables which might affect resource selection. In fact, on first encounter, the set of missing considerations appears more impressive than the caloric benefits and costs, search and pursuit times, and prey densities which are the actual stuff of the model. It includes the effects on foraging behavior of: (i) non-foraging activities; (ii) environmental stochasticity and risk; (iii) group interactions, including sharing; (iv) resource depletion; (v) incomplete information (uncertainty); and, (vi) non-

energy utilities (e.g., nutrients and non-food materials). While this tally of omissions might seem a staggering debility, it also can be viewed as an exciting queue of questions, hard on the heels of a promising analytic beginning.

This paper is one of a series which attempts to refine understanding of the diet breadth model by examining the role of factors excluded in the original formulation. Two previous publications (Winterhalder 1983, 1986a) have looked at the interaction of foraging and other behaviors by modelling the effects of opportunity costs on diet choice. The present paper posits a risk-minimizing (rather than the usual rate-maximizing) goal for the forager, and thus begins to incorporate stochasticity of environmental variables into the diet choice model. A subsequent paper (Winterhalder 1986b) examines the effects of food sharing on foraging choices. This series is an attempt to develop more fully a micro-ecological understanding of human diet selection.

BACKGROUND AND DEFINITIONS

Current analysis of foraging behavior is based largely on deterministic models, those assuming that an average or expected value for each of the relevant parameters suitably characterizes it. The emphasis is on efficiency, defined as maximizing a net rate of intake while foraging. Such models are relatively easy to devise and test, and they may sometimes approximate the results of their more complex stochastic analogs (Poole 1979; Stephens and Charnov 1982). Nonetheless, what is convenient for the analyst may be alien to the forager. Environmental variability may be the more apposite factor in selection for behavior (Winterhalder 1980). Random variation may be common in nature and broadly significant in the analysis of evolutionary phenomena like foraging (Real 1980; Real et al. 1982). For the organism, effectively avoiding risk due to this variability may be more important than efficiently adapting to its circumstances, viewed normatively.

In this paper I report the results of a study in which parameters in the diet breadth model (MacArthur and Pianka 1966; Schoener 1971) are treated as stochastic variables. This model predicts which among a set of potential prey an optimal forager will elect to pursue. It has been used extensively in studies by ecologists and anthropologists (reviews in Pyke et al. 1977; Krebs et al. 1983; Smith 1983; Stephens and Krebs 1986; Winterhalder 1986a). According to the model, the parameters central to foraging decisions are encounter rate (based on search rate and prey density) and pursuit and handling time for each species. The forager has energy costs associated with search and pursuit; benefits are determined by the net energy value of the prey captured. This analysis will introduce a stochastic element into each of these two basic components of the model, encounter rate and pursuit time. Although conceivably there are other ways to approach the question of diet choice and risk, this particular entry to the problem has the advantage that it begins with simple modifications in the structure of a familiar deterministic model. I have adopted a simulation methodology for finding the stochastic solutions to the diet breadth model (equation 3) because a direct analytic analysis proved unwieldy.

Risk commonly refers to the potential for a significant decrement to the fitness of an organism associated with a particular situation, choice or activity (see below). Environmental stochasticity can but need not induce risk; it is only one among the factors (e.g. predation or exposure) which might be considered more generally as hazardous. Further, this paper considers risk (from stochastic variation or unpredictability) rather than uncertainty (from incomplete information). Lack of appropriate information may contribute to unpredictability in an organism's environment, but the analytic and evolutionary implications of this situation are different from the case of stochasticity (Stephens and Krebs 1986). In order to keep these questions clearly separated, here I assume that the organism "knows" the environment to the extent possible—it has complete information on the probability distributions for the stochastic foraging parameters.

Because unsuccessful foragers can exist for some period on endogenous reserves, with only gradually increasing costs to adaptive performance, risk assessments must include a temporal dimension. Short-falls may not matter, or may matter to varying degrees, depending on their severity and duration, and on the nutritional state of the organism at their onset. The model presented here assumes that there is a critical foraging interval which will end to the detriment of an organism experiencing a relatively low or negative energy balance. Foraging benefits will be measured by the net acquisition rate for energy (see Smith 1979).

The formulation of a stochastic foraging model requires three steps: Step 1, specify how fitness (through a currency or utility) will be defined for a particular problem (e.g. avoiding starvation, maximizing net acquisition rate); Step 2, specify the relationship between that aspect of fitness and the structure of the food reward (e.g. mean, variance); and Step 3, specify the relationship between the structure of the food reward and behavior (e.g. patch residence time, diet breadth). For clarity, these steps will be identified in the analysis which follows.

In the existing economic and ecological literature risk has two meanings, best kept separate. As above, it sometimes refers to fitness by identifying the possibility that some subsistence decisions in an unpredictable environment may threaten survival and reproduction. In this use risk is probability of loss. This is a Step 1 consideration and in deference to colloquial use will be designated risk. In other cases risk has been used to refer to choice among possibilities with differing variances (e.g. "risk-prone" or "risk-averse," Caraco 1981), meaning to choose or avoid reward variability. To also use risk in this context invites ambiguity. Hence, for this second case I will speak of variance-prone or variance-averse (cf. Caraco 1983). This is a Step 2 consideration. By these definitions, all organisms should be risk-averse, but one interesting prediction of models described below is that to achieve this goal they may seek, or try to avoid, variability, depending on circumstances. With reference to foraging, risk-sensitive means generally that the variance of food capture rates associated with resource decisions affects fitness.

RISK-SENSITIVE BEHAVIOR

Selection is expected to generate adaptive strategies which compensate for environmental variation, if it affects fitness. Experimental study has revealed that two species of juncos (Caraco et al. 1980; Caraco 1981) have consistent preferences in simple tests with reward variability. Given a choice between a variable and fixed reward with equivalent means, birds feeding at a rate *above* their requirements choose the constant reward (the are variance-averse), while those feeding *below* intake requirements choose the variable reward (they are variance-prone). Further experiments with white-crowned sparrows, and a choice between two degrees of variability at a fixed mean, led to similar results (Caraco 1983): consistency of choice in a pattern predictable from the overall energy budget.

To help explain these observations, Stephens (1981) assumed that the organisms were trying to minimize their probability of starvation, and he derived rules for risk-sensitive foraging which predicted Caraco's results. For the same expected (average) intake, a forager in positive energy balance will choose the minimum variance; the forager in negative energy balance will choose maximum variance. This has been termed the "extreme variance rule" by Stephens and Charnov (1982).

Stephens and Charnov (1982) argued that the conditions for the extreme variance rule are unlikely in nature. Rarely would an organism face a choice between fixed and probabilistic food awards *at the same mean.* These authors derived a more realistic and general solution for the risk-sensitivity problem which analyzes sets of mean/variance

combinations. In their "Z-score model" encounter rates are given by a poisson distribution, but they assume a limiting distribution for net acquisition rate that is normal.

The fitness goal of the risk-sensitive organism in this model is to avoid falling short of some threshold, a starvation net acquisition rate, given as R_{min}. This is a Step 1 procedure. A simple graphical model (Fig. 1) depicts the optimal choice from among complex mean/standard deviation (s.d.) sets. Formally, the chance of starvation increases with the function

$$(R_{min} - \mu_t)/\sigma_t \qquad (1)$$

where R_{min} is the minimum net acquisition rate tolerable, and μ_t is the average and σ_t the s.d. of the food reward distribution. It is evident that increasing the tolerable minimum, or decreasing the average reward, will increase the organism's risk. The role of the variance is more complicated: when the numerator is negative, increasing variance increases risk; when positive, increasing variance reduces risk.

If Z' is set equal to (1), then minimizing Z' will offer the forager the greatest chance of avoiding its crisis threshold. By rearranging terms the relationship can be depicted in the form of the familiar quadratic (or slope-intercept) equation.

$$\mu_t = R_{min} - \sigma_t Z' \qquad (2)$$

Given a set of mean/s.d. pairs, the line of greatest slope (-Z'), drawn from R_{min} and intersecting a point in the set, represents the organism's best chance of avoiding starvation (Fig. 1). In effect, this procedure allows the Z-score of a standard normal distribution to accomplish Step 2 of a risk-sensitive foraging analysis. It also identifies the optimal mean/s.d. pair, and by working backwards from that combination it is possible to identify the appropriate behavioral choice (Step 3).
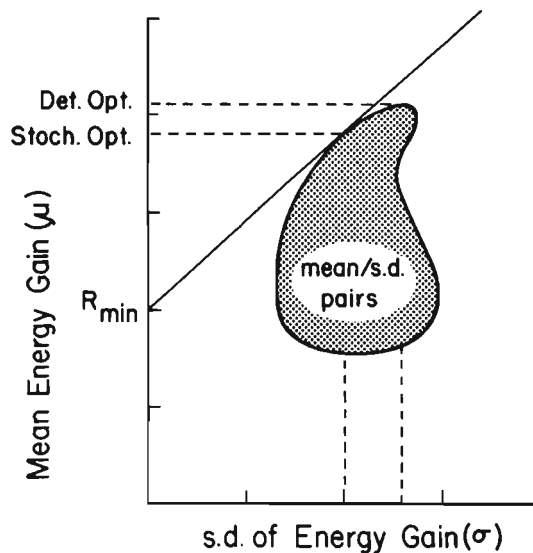

FIG. 1.—Stephens and Charnov (1982) risk-sensitive foraging model. The steepest line extending from R_{min} and intersecting a point in the feasible set of mean/s.d. pairs gives the optimal risk-minimizing solution, with a mean and standard deviation (E/T) as shown (stoch. opt.). Also shown are the mean and s.d. of the rate-maximizing solution (det. opt.).

Stephens and Charnov (1982) show that the extreme variance rule is a special case of their formulation, in which the feasible set is given by horizontal lines (fixed μ_t, but differing σ_ts), either above or below the organism's threshold R_{min}.

Stephens and Charnov apply their general result to the analysis of optimal patch residence time, given stochastic variation in the search time required to find a new patch. This is the stochastic analog to the marginal value theorem (Charnov 1976). The result is an oblong mean/s.d. set which leads to these inferences: (i) the optimal patch residence time in the stochastic or risk-sensitive case is near to that for the deterministic, rate-maximizing solution; and, (ii) if the organism is in positive energy balance (net acquisition rate $\rangle$ R_{min}) then the optimal residence time is somewhat longer for the stochastic case (the organism is variance-averse), whereas for a net acquisition rate $\langle$ R_{min} it is somewhat shorter (and the organism is variance-prone).

The convergence between the efficiency-maximizing and risk-minimizing choices is an important result of this analysis. But, the unusual shape of the mean/s.d. set associated with this particular foraging model suggested to Stephens and Charnov (1982:259) that "it may be misleading to try to find general relationships between mean and variance . . . this relationship may depend critically on the nature of the foraging problem at hand".

The present analysis will use simulation methods to generate stochastic variation in the parameters of the diet breadth model in order to test this proposition.

METHODS[1]

The objective is to calculate the mean/s.d. pair associated with each possible diet breadth in a resource choice situation (Step 3). The set of these pairs then can be used to identify the optimal, risk-sensitive diet choice (Step 2), using the Z-score model. I will assume that the fitness-related goal of the organism (Step 1) is to avoid falling below some minimum level of food intake, measured as energy net acquisition rate.

The methodology and results will be described in three steps, first with stochasticity in encounter rates only, second with stochasticity in pursuit times only, and lastly, with stochasticity in both search and pursuit. Some species may face unpredictability in encountering potential prey, but little stochastic variation in the time required to pursue and handle an item. Others may experience regular encounters, but face unpredictability in pursuit times. Yet others, perhaps most foraging species, will face some degree of stochasticity in both parameters affecting diet breadth decisions.·

The Diet Breadth Model.—The diet breadth (db) model specifies that a prey item should be added to the diet only if its net return relative to pursuit and handling costs (e_x/t_x) is greater than the average efficiency for the diet containing all items of higher rank. This statement can be represented mathematically (see Schoener 1974):

$$e_x/t_x \ \rangle \ \frac{\Sigma p_i e_i - C_s T_x}{\Sigma p_i t_i + T_s} \ \approx \ E/T \qquad (3)$$

with variables defined as follows:

e_x net energy (kcal) of prey item x (its energy value less the energy required to pursue and handle it).

t_x time (min) required to pursue and handle prey type x.

p_i the relative frequency of prey type i, as encountered, calculated for those prey in the diet at a particular diet breadth.

e_i net energy value (kcal) of prey type i (see e_x).

C_s the cost (kcal/min) of searching for prey.

T_s the average search time (min) required to encounter an acceptable prey item (one included in the diet at a particular diet breadth).

t_i the time (min) required to pursue and handle prey type i (see t_x).

Σ sum from prey type i = 1 to i = (x - 1), with prey ranked from most to least valuable by e_i/t_i.

E/T   overall foraging efficiency at a particular diet breadth.

The optimal diet includes all ranked prey items down to but not including the type x for which the inequality in equation 3 reverses.

Search time (T_s) is derived for each diet breadth by the formula

$$T_s = \frac{1}{(V_s 2r_s) \, \Sigma \, d_i} \tag{4}$$

where

d_i prey density (#/km^2) for prey type i.

V_s search velocity (km/min).

r_s search radius (km).

Σ sum for those prey types in the diet at that diet breadth.

This equation assumes that the search time to locate an acceptable prey type is inversely related to the velocity and radius of the search, and to the aggregate density of the prey types that will be pursued when encountered.

Stochastic Search.—The model assumes that prey are encountered randomly. In the deterministic version this means that the d_i for each type is the average density. In the stochastic analog, any finite interval of searching will cover a fixed area which is a sample of the randomly located resources. Prey densities actually encountered in that interval will be distributed as a stochastic poisson variate (d^*_i) with $\lambda_i = d_i$, for i = 1 to n potential prey types.

The program determines the stochastic density variate (d^*_i) for each prey type by generating a random number (range 0.001 to 0.999) which is matched to intervals of the cumulative poisson distribution for the associated λ_i. Each cumulative interval is associated with an integer value for d^*_i. This procedure generates 100 unit area samples in which the density of each species is a stochastic poisson variate, d^*_i. Foraging efficiencies are calculated for each diet breadth in each interval, followed by the mean and the s.d. of the foraging efficiency at each diet breadth for all one hundred intervals. The value of the input parameters and the size of the unit area searched have been set arbitrarily (see Table 1). If no prey are encountered, then the foraging efficiency for that interval is set at the negative of the search cost ($-C_s$).

In effect, this procedure envisions an organism which must allow for foraging efficiency variation due to stochastic encounter rates among sequential foraging periods.

TABLE 1.—*Prey and predator parameters used in the deterministic and stochastic analyses.*

Name	Energy Value (Kcal)	Pursuit Time (Min)	Pursuit Cost (Kcal/min)	Density (#/km²)
Prey Parameters:				
APREY	200.0	4.0	3.0	0.4
BPREY	150.0	30.0	3.0	0.8
CPREY	80.0	10.0	2.0	1.0
DPREY	40.0	1.0	3.0	4.0
EPREY	20.0	1.0	3.0	8.0
FPREY	100.0	40.0	2.0	10.0
Forager Parameters:				
Velocity: 8 km/hr				
Search Radius: 0.2 km				
Search Cost: 2.0 Kcal/min				

Its risk-sensitive foraging goal is to avoid a critical net acquisition rate in each unit area searched. The procedure assumes that encounter rates are not correlated from one interval to the next, nor are densities among prey types within an interval correlated. This may generate greater degrees of randomness than a forager actually would experience, given the possibility of co-variation among contiguous samples of habitat, or local interactions among prey species in the use of food or space. However, if prey are clumped relative to the scale of the forager's search area, then it could underestimate unpredictability.

Stochastic Pursuit.—In the deterministic model, encountered prey within a particular diet breadth are always pursued; there are no "partial preferences." This assumption is retained in the stochastic case. Consistent with the assumption of unpredictability, the organism is assumed to know the probability distribution for pursuit of an encountered species, but is assumed not able to estimate pursuit time in any given encounter. Pursuit times are given as a stochastic variate t^*_i, with a normal distribution, $= t_j$. The s.d., $\sigma = 0.25\mu$, is scaled positively with the mean by a constant coefficient of variation.

Random numbers (range 0.00003 to 0.99997) are matched to intervals of the cumulative normal distribution, generated by taking Z-scores in half-unit increments from $-4 \leqslant Z \leqslant +4$. The Z-score at the mid-point of the randomly selected interval is then converted to the pursuit time variate by the standard formula ($t^*_i = \mu_i + Z\sigma_i$). In effect, this forager faces normally distributed stochastic variation in the time required to pursue, capture and consume a given prey item.

As indicated above, the program calculates foraging efficiency (E/T) at the end of a foraging interval based on a unit area of searching. Within that interval the forager may encounter and pursue zero, one or more of a particular prey type. If it pursues more than one, the pursuit time variate used to calculate the efficiency for that foraging interval is the average of the variates (t^*_i) for each of the encounters. This recognizes that the stochastic pursuit time variance for prey which are commonly encountered and quickly pursued will to some degree "even out" over the predator's critical foraging interval.

Stochastic Search and Pursuit.—This program joins the previous two procedures. For each of the 100 calculated intervals, the density of each prey type *and* its pursuit time(s) are treated as stochastic variates.

RESULTS

Table 1 shows the data set used in all simulations. Table 2 shows the prey ranking, the computed foraging efficiency at each diet breadth, and the optimal, deterministic solution. This data set was constructed with values which might characterize a small mammalian or avian predator, and then adjusted so that it gave (a) an optimum at an intermediate diet breadth and (b) a range of foraging efficiencies.

TABLE 2.—*Optimal foraging analysis for the deterministic case.*

Prey Type	Rank $(e_X/t_X,$ in Kcal/min)	Foraging Efficiency (E/T, in Kcal/min)
APREY	47.0	1.85
DPREY	37.0	7.63
EPREY	17.0	9.94
— — — — — — — — Boundary of Optimal Diet — — — — — — — — —		
CPREY	6.0	9.01
BPREY	2.0	6.48
FPREY	0.5	1.35

Stochastic Encounter Rate.—Table 3 gives the mean, standard deviation, and range for the foraging efficiencies at each diet breadth for three runs of the stochastic encounter rate simulation. Each run iterated the E/T calculation 100 times. The mean and standard deviation are graphed using the Z-score model in Fig. 2. The congruence among runs suggests that 100 iterations is an adequate sample.

It is evident in Figure 2 that the stochastic optimum and the deterministic optimum (db = 3) are the same for a wide range of R_{min} values, roughly 6 to 16. If the minimum tolerable intake is strongly below the expected, then the optimal (risk-sensitive) diet breadth will expand somewhat; if strongly above, then it will somewhat contract. These actions represent variance-averse and variance-prone behavior, respectively. Table 3 shows the results in more detail. Note that the range of E/T values is quite wide at all diet breadths. There is no choice available to this organism which can prevent it from experiencing some foraging intervals of only about 3 kcal/min net acquisition rate.

Three additional features of this simulation can be cited. First, while variance diminishes continuously from db = 1 to db = 6, the low end of the range of E/T values is highest at db = 4. This reinforces the observation that a risk-sensitive forager with a low R_{min} will increase its diet breadth above (but not much above) the deterministic optimum. Second, the distribution of foraging efficiencies over the 100 iterations is non-normal for some of the cases. Thus, it cannot always be assumed (see Stephens and Charnov 1982) that the distribution of stochastic food rewards will approach normality. Finally, at low diet breadths, the mean of the E/T values for each stochastic run is below that for the deterministic solution. This is a consequence of the fact that search costs

TABLE 3.—*Diet choice outcomes for the stochastic encounter rate simulations.*

	Foraging efficiency (E/T) by diet breadth for ranked prey items, 1 to 6					
Stochastic Model[1]	1	2	3	4	5	6
Run #1:						
Mean	1.26**	6.96**	9.35*	8.74*	6.99**	1.39**
s.d.	4.60	3.83	2.93	2.51	2.52	0.41
Range	(—2.00,12.65)	(—0.03,15.82)	(3.94,16.15)	(4.52,16.01)	(2.78,13.65)	(0.75,3.16)
Run #2:						
Mean	1.12**	6.80**	9.39	8.78	6.95	1.47**
s.d.	5.28	4.86	3.56	2.98	2.98	0.56
Range	(—2.00,17.12)	(—2.00,19.90)	(3.10,19.37)	(3.10,18.02)	(2.47,18.02)	(0.72,3.76)
Run #3:						
Mean	1.15**	7.04*	9.63	8.95	7.07*	1.43**
s.d.	4.67	4.00	2.88	2.44	2.59	0.45
Range	(—2.00,12.65)	(—2.00,17.11)	(2.84,17.09)	(3.78,14.87)	(3.04,14.86)	(0.72,3.73)
Deterministic Model[2]						
Value of E/T	1.85	7.63	9.94	9.01	6.48	1.35

[1]Parameter characteristics of prey and foragers as in Table 1, with prey density $(C/*_i)$ given as a stochastic poisson variate(λ_i = average prey density, d_i) over 100 sample iterations.

[2]See Table 2.

Kolmogorov-Smirnov test for a normal distribution; ** h_o (= normality) rejected, p < .01; * h_o rejected, < .05.
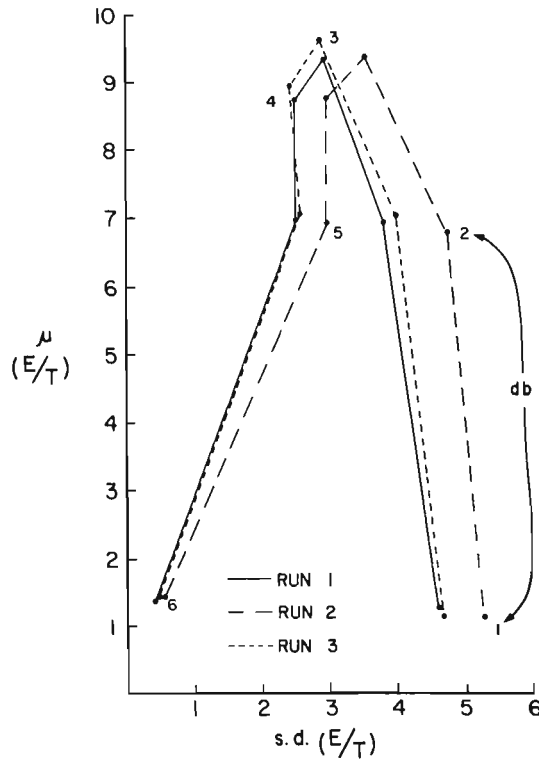
FIG. 2.—Mean/s.d. pairs at various diet breadths for the stochastic encounter rate simulations (db = diet breadth).

(—C_s) are charged to intervals which happen to be empty of prey. Failure to encounter an acceptable prey type in a foraging interval is more likely for narrow diet breadths and rare prey.

This last observation represents a case in which the predicted value of an averaging (deterministic) model does not match the expected (or mean) value of its stochastic analog (see Poole 1979).

Stochastic Pursuit.—Using the same input parameters (Table 1), three runs of 100 iterations each were simulated in which pursuit time was a random normal variate. The results (Fig. 3) can be interpreted to indicate that the optimal choice of a risk-sensitive forager is again strongly convergent with the deterministic, rate-maximizing solution (db = 3). However, a risk-sensitive forager with a low R_{min} will, in this case, reduce its diet breadth, whereas that with a relatively high R_{min} will expand its selection of prey. These responses are opposite to those deriving from the stochastic encounter simulation.

Table 4 presents the results in greater detail. The range of E/T values at a particular diet breadth is not large. At db = 3 this organism can expect a net intake of at least 8 kcal/min in a stochastic foraging interval. Three additional observations are pertinent. First, while the standard deviation steadily increases from db = 1 to db = 5, in each run the minimum end of the range reaches a peak at db = 3. An organism sensitive to this minimum value will not stray from db = 3. Second, the distribution of foraging

TABLE 4.—*Diet choice outcomes for the stochastic pursuit time simulations.*

Stochastic Model[1]	Foraging efficiency (E/T) by diet breadth for ranked prey items, 1 to 6					
	1	2	3	4	5	6
Run #1:						
Mean	1.87**	7.67	9.98	9.11	6.60	1.38
s.d.	0.09	0.28	0.41	0.64	1.04	0.21
Range	(1.65,2.08)	(6.91,8.30)	(8.92,10.85)	(7.85,10.89)	(4.57,10.43)	(1.01,1.86)
Run #2:						
Mean	1.86**	7.66	9.96	8.99*	6.45	1.36*
s.d.	0.10	0.32	0.47	0.72	0.96	0.21
Range	(1.60,2.13)	(6.92,8.82)	(8.57,11.49)	(7.54,10.54)	(4.23,9.27)	(0.89,1.90)
Run #3:						
Mean	1.86**	7.60*	9.90	8.86	6.46	1.39
s.d.	0.10	0.29	0.41	0.70	0.89	0.24
Range	(1.60,2.08)	(7.13,8.62)	(8.93,11.37)	7.04,10.82)	(4.29,8.74)	(0.91,1.92)
Deterministic Model[2]						
Value of E/T	1.85	7.63	9.94	9.01	6.48	1.35

[1]Parameter characteristics of predator and prey as in Table 1, with prey pursuit times ($t^*{}_i$) given as a random normal variate (u = average prey density, s.d. = 0.25u) over 100 sample iterations.

[2]See Table 2.

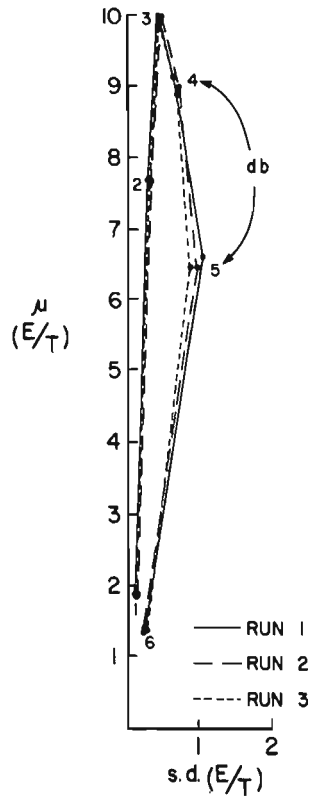**h_O rejected p < .01; *h_O rejected, p < .05; Kolmogorov-Smirnov test for a normal distribution.

FIG. 3.—Mean/s.d. pairs at various diet breadths for the stochastic pursuit time simulations (db = diet breadth).

efficiencies (E/T) at each diet breadth deviates from normality in relatively few instances. Finally, the mean for the stochastic runs matches closely that for the deterministic model. This is due to the symmetry of the normal distribution and the absence of uncompensated costs (i.e., all pursued prey are assumed to be caught, sooner or later).

Random Encounter Rate and Pursuit Time.—The results for the combined model are shown in Fig. 4. Because the qualitative outcome is similar to that for Fig. 2, the interpretation applied to that case fits this one as well. For the parameters used, the search component generally swamps that due to pursuit. Although it is not readily evident in Fig. 4, the combined model should result in a relative narrowing of the (more or less) parabolic set of mean/s.d. pairs. This is because the smaller pursuit variances (db = 1, 2 and 3) are added to the larger search variances, and the larger pursuit variances (db = 4, 5 and 6) are added to the smaller search variances. The result enhances the convergence of the deterministic and stochastic outcome. This qualitative result—combining the two sources of variance actually reduces the divergence between risk-sensitive and efficiency-maximizing diet choices—is probably more significant than the precise quantitative outcome.

Table 5 gives the numerical results for the combined model. They are rather like those of Table 3: (i) the stochastic means at narrow diet breadths are below those for the deterministic case; and (ii) the peak minimum value encountered is at db = 4 in
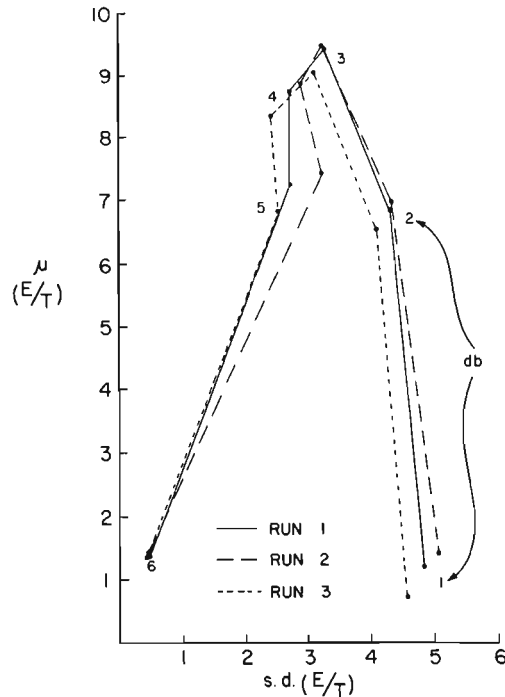
FIG. 4.—Mean/s.d. pairs at various diet breadths for the combined encounter rate and pursuit time simulations (db = diet breadth).

two runs and is equivalent at db = 3 or 4 in one run. Compared to Table 3, fewer of the distributions are non-normal. Adding an independent source of normal variation (stochastic pursuit times) should have this effect.

Even at db = 3 (optimal over a wide range of conditions), this organism will face some foraging intervals in which intake is only slightly above 2 kcal/min (those instances in which the few prey encountered are difficult to capture). For a db = 2 or 3, at least some foraging intervals will generate an intake of around 20 kcal/min, a 10 fold increase. Typically, both the range and standard deviation are larger in this combined model than for the stochastic encounter rate alone (compare Table 5 with Table 3), as is expected.

DISCUSSION

Rate-sensitive and risk-sensitive foragers.—For the marginal value theorem, Stephens and Charnov (1982) show that the optimal risk-sensitive choice in an unpredictable environment is similar to the rate-maximizing choice in a deterministic environment of averaged values. The risk-sensitive organism in positive energy balance somewhat increases patch residence time; that in negative energy balance somewhat reduces it. The convergence of the stochastic and deterministic optima is noteworthy. It allows us to retain the analytic simplicity of the original model, while appreciating its enhanced generality and realism. Stephens and Charnov observed that "there may be natural relationships between mean and variance which make solutions to the problems

TABLE 5.—*Diet choice outcomes for the combined (stochastic encounter rates and pursuit times) model.*

	Foraging efficiency (E/T) by diet breadth for ranked prey items, 1 to 6					
Stochastic Model[1]	1	2	3	4	5	6
Run #1:						
Mean	1.20**	6.82	9.41	8.73	7.22	1.39
s.d.	4.84	4.35	3.30	2.75	2.77	0.48
Range	(−2.00,18.69)	(−2.00,20.37)	(2.19,19.97)	(3.06,17.07)	(2.12,17.07)	(0.56,3.06)
Run #2:						
Mean	1.40**	6.93**	9.44	8.87**	7.42**	1.42
s.d.	5.05	4.35	3.26	2.93	3.29	0.46
Range	(−2.00,18.69)	(−0.04,20.04)	(2.26,19.85)	(3.76,19.85)	(2.61,19.85)	(0.60,2.94)
Run #3:						
Mean	0.72**	6.52	9.04*	8.33	6.80	1.35
s.d.	4.58	4.13	3.15	2.44	2.58	0.44
Range	(−2.00,13.58)	(−2.00,16.26)	(2.36,16.39)	(2.36,14.10)	(2.10,14.06)	(0.62,2.93)
Deterministic Model[2]						
Value of E/T	1.85	7.63	9.94	9.01	6.48	1.35

[1]Parameter characteristics of prey and forager as in Table 1, with prey density $(C/{}^*_i)$ given as a stochastic poisson variate (λ_i = average prey density) and pursuit time (t^*_i) given as a normal stochastic variate (u = average prey density, s.d. = 0.25u) over 100 sample iterations.

[2]See Table 2.

** h_0 rejected, $p < .01$; * h_0 rejected, $p < .05$; Kolmogorov-Smirnov test for a normal distribution.

of 'energy maximization' and 'minimization of the probability of starvation' similar" (1982:251). However, given only one concrete example (the marginal value theorem) they were hesitant to claim generality for this possibility.

The results obtained here strengthen the case for such a "natural relationship". In each of the three simulations—stochastic encounter rate, stochastic pursuit time, and the combined case—the risk-minimizing and efficiency-maximizing solutions were the same for a wide range of minimum intakes (R_{min}). Faced with stochastic encounter rates, the simulated forager strongly in positive energy balance (R_{min} ⟨⟨ net acquisition rate) will *increase* diet breadth somewhat. Faced with stochastic pursuit times, the forager strongly in positive energy balance (R_{min} ⟨⟨ net acquisition rate) will *reduce* diet breadth somewhat. The converse predictions hold for the case of negative energy balance. The predictions of the combined model are like those of the stochastic encounter simulation.

If an inverted "U" concave toward the x-axis found in this simulation represents the general case for diet breadth choices, then the ranked set of prey species available will occupy a counter-clockwise sequence of positions along the curve (Fig. 5). For an optimal diet which includes all available resource items (a to e), a risk-sensitive forager in positive energy balance is constrained to the efficiency-maximizing choice. There is no species to add, no increment of risk-minimizing to gain, even at the cost of efficiency. Likewise, if the optimal deterministic diet includes only one prey type from a potential set (e to i), then a forager in negative energy balance is constrained to the deterministic optimum. A complete generalist doing well, or a complete specialist doing poorly, can each do no better than the rate-maximizing choice.

It is also conceivable that several of the potential prey would rest at the peak of the curve (between d and f), generating a relatively broad but shallow segment in the set of mean/s.d. pairs. In this case, a small change in forager energy balance, one within a limited portion of the R_{min} range, would have a more dramatic impact on diet breadth.
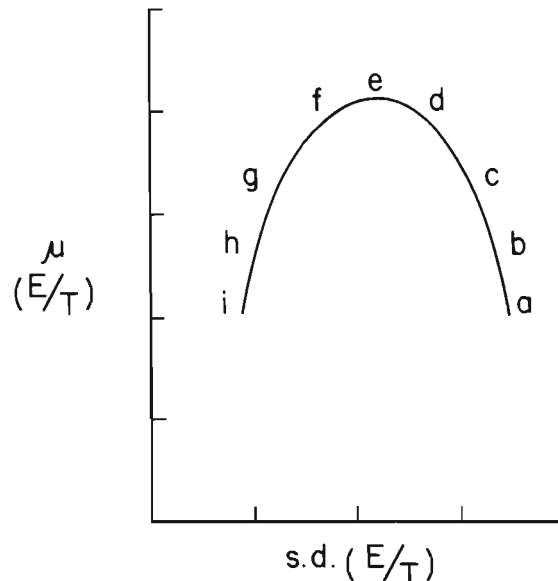

FIG. 5.—Generalized mean/s.d. set for diet choices in an unpredictable environment.

Taken to its limit this would approach the extreme variance rule (Stephens and Charnov 1982) as the set became linear. This situation probably is rare, as it would require that each sequentially added prey type have precisely those qualities which produce very little change in the average net acquisition rate of foraging while simultaneously producing a large reduction in the s.d. of the net acquisition rate.

These special cases reinforce the point made earlier: it may often be the case that the deterministic and stochastic optima will converge. Doing well seems to be the best way to not come up short, even in an unpredictable environment.

Disadvantages and Advantages of Simulation.—Simulation is a useful means of generating solutions to equations difficult to solve more directly. However, a simulation approach produces data that are not easily generalized, an important disadvantage. Without extensive experimentation, it is difficult to determine the sensitivity of the results to the peculiarities of the input parameters. Despite this limitation, the technique does produce actual values for a given set of inputs, and these may yield insights not readily evident in the more general solutions reached by mathematical derivation.

In the present instance, the simulation reveals details that might be missed in a purely qualitative application of the Z-score model. For instance, Fig. 4 indicates that a risk-sensitive forager with an R_{min} in the range of 5 to 17 kcal/min will choose a db = 3. In a qualitative interpretation, a change in R_{min} from 17 toward 5 might be interpreted to "increase" the optimal diet breadth of a risk-sensitive forager, but in fact, the number of prey items will not change. There is a broad plateau of stability for db = 3. Real prey choices are not continuously distributed along the curve; they are discrete and if limited in number, may be widely spaced.

How good are these optimal risk-sensitive solutions? Aggregating runs No. 1, 2 and 3 (Fig. 4) to give a total of 300 foraging intervals shows that db = 3 has intakes exceeding 17 kcal/min in 2 instances (0.67%) while a diet breadth of 2 items exceeds this value in only 3 cases (1.00%). An organism with an R_{min} > 17 increases its odds of avoiding starvation by 50% if it drops from 3 to 2 prey in the diet, but the chance of obtaining a net acquisition rate of 17 or greater is still very small. Similarly, for an R_{min} of 5, a diet breadth of 3 generates 20 intervals with shortfalls (6.67%), while a db = 4 decreases this to 16 such cases (5.3%), again only a small improvement. In effect, the best solution to a bad situation (R_{min} >> net acquisition rate) might rarely be good enough, and the best solution for a risk-sensitive organism in strong positive energy balance (R_{min} << net acquisition rate) might still be relatively precarious. No diet choice can prevent this organism from experiencing the rare interval below 3 kcal/min, nor help it above 21 kcal/min. The actual range of the food reward over some finite set of intervals thus is a salient consideration.

There is a semantic issue here worth noting because it is occasionally confused by critics of optimal foraging theory. The optimal solution in foraging theory is the *best possible* for a constrained situation and set of choices. It does not mean the most desirable outcome. Put differently, to minimize risk is not necessarily to avoid it. There is, after all, neither fitness nor consolation in making an optimal choice if the reward is still starvation, as it might well be in stochastic circumstances.

In actuality, the rare occurrence of a decidedly low value (or high value) may be less important than a series of intervals with low values. Extremely poor capture rates may be infrequent or perhaps of relatively short duration, and the unlikely and unusually poor interval tolerable. This suggests that distributional statistics are more important than range endpoints. A satisfactory (Step 1) goal may be to avoid the accumulated effect of poor foraging intervals which are frequent enough to clump together.

Stephens and Charnov (1982) showed that in the general case the foof reward distribution will approach normality. In the present simulation this was not always

true, probably because of the dominating effect of the search component of the model, hence of the poisson distribution. This distribution becomes highly skewed (right) as the mean drops from about 5 into fractional values, the range characteristic of most of the prey types used in this simulation (see Table 1). In fact, all of the distributions in Tables 3 and 5 are skewed to the right (positive g_1). This suggests that it is important to analyze the actual shape of the E/T distribution before advancing with inferences based on the Z-score technique (Fig. 1), if any of the prey types are rarely encountered during the foraging interval.

CONCLUSION

Because the environment of a species is always more or less stochastic it is important to know if foraging strategies must consider unpredictability in the capture rates associated with various choices. It is a boon to the forager, and to the human and evolutionary ecologist, that the structure of food choices and patch residence time appear to generate similar strategies for rate-maximizing and risk-minimizing goals. For the forager, one choice generally will cover the concurrent needs to maximize efficiency and minimize risk; for the analyst, the diet choice predicted by the simple efficiency-maximizing model also will approximate the risk-minimizing solution. In effect, the risk-sensitive forager is constrained to be highly rate-sensitive by the relationship between the mean and variance of energy capture rates. Empirical examination of this relationship should be a high priority in foraging studies.

The forager making a risk-sensitive choice in a stochastic environment still faces a rather large variation in intake from one interval to the next. Viewing nature through the model makes commonplace survival seem extraordinary. Several considerations may temper this conclusion: (a) minimum requirements (R_{min}) generally may be low relative to expected intake (average net acquisition rate); (b) the critical period may be long and not clearly bounded by a fitness threshold, perhaps because endogenous reserves or stored food are available (in fact, the concepts of positive and negative energy balance imply some ability to "average over" poor intervals); or, (c) there may be considerably more predictability in the environment that in simulations based on randomizing poisson and normal distributions. Each of these possibilities will lessen the impact of the abstract, statistical vagaries of the simulated food quest. A fourth possibility, perhaps especially important for hominids and prehistoric or extant hunter-gatherers, is central-place sharing by foragers who nonetheless hunt and gather independently (Winterhalder 1986b).

NOTES

[1]The programming and analyses were done on an Apple II + microcomputer in Apple Pascal by Sara DeGraff, using the pseudo-random number generator available in the language software. The distributions of prey densities and pursuit times were checked (by Chi-square) and none differed significantly from the expected poisson and normal frequencies. Statistical analysis of the distributions of foraging efficiencies (Tables 3, 4, and 5) were done on SAS.

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