JOURNAL OF ANTHROPOLOGICAL ARCHAEOLOGY 5, 369–392 (1986)

Diet Choice, Risk, and Food Sharing in a Stochastic Environment

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Received May 15, 1986

Foraging models can predict the optimal diet selection for an organism which has the goal of maximizing its net acquisition rate for energy while hunting and gathering. Here a simulation methodology is used to determine the optimal diet selection under the assumption that the forager's goal is to minimize the risk of an energy shortfall. The results show that the rate-maximizing and risk-minimizing diets are similar; that sharing is more effective than changes in diet in reducing risk; and that the risk-reduction which can be obtained from sharing requires quite small numbers of participants. Food sharing may be an ancient and pervasive feature of hominid foraging adaptations. © 1986 Academic Press, Inc.

INTRODUCTION

Foraging theory is attaining a prominent position in the ecological analysis of ethnographic and archaeological materials on foragers (reviews in Smith 1983; Winterhalder 1986a; Thomas 1986). The primary value of this approach is heuristic; it provides a systematic means of arguing from widely accepted premises to specific, testable predictions about foraging behavior.

The basic procedure entails several steps (Winterhalder 1981; Maynard Smith 1978). One first postulates an optimization criterion; for example, foragers will attempt to maximize their net acquisition rate (NAR) of energy while foraging. This is an operational statement about the selective forces believed to have shaped the foraging behavior. It brings the assumption about energy or another "currency" into the analysis as part of the hypothesis being tested. One continues with a description of constraints. Some of these are parameters held constant for purposes of the analysis. Others, commonly some environmental factor and behavioral option, are allowed to change as independent and dependent variables. Thus, one may hold constant factors like prey value and forager pursuit costs, in order to investigate the relationship between changes of prey

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density and forager diet breadth. A model is the concrete expression of this set of fixed and variable parameters. It establishes the constraints as another part of the hypothesis to be assessed. Finally, the model is used to generate predictions about the relationships between the independent and dependent variables.

Foraging models developed by this approach address issues of diet or prey choice, habitat or patch selection, foraging movement, time allocation, central place aggregation, territoriality, and group formation and size (reviews in Winterhalder and Smith 1981; Krebs and Davies 1984; Stephens and Krebs 1986).

The evaluation of foraging theory takes several forms. One first can ask if the predictions follow from the premises and constraints. This assesses the logical integrity of the modeling procedure. Secondly, one can ask if the model generates predictions like those arising from other models that are constructed differently but meant to answer the same question. In Levin's (1966) terms, such overlap gives us "robust" hypotheses. Third, one can attempt to evaluate the reality of the model's premises and constraints in actual cases, and their generality. For the diet breadth model this would mean asking—among other things—if energy efficiency, defined as net acquisition rate (Smith 1979), has been a significant adaptive consideration to the foragers analyzed, or foragers in general. Finally, one can assess the model's predictions against observed foraging behavior, using comparative or quantitative methods. A judgment about this whole set of analytical and empirical assessments determines the standing of an evolutionary ecology model.

SIMPLE MODELS, PROGRESSIVELY EXTENDED

Foraging theory attempts to obtain reliable answers to limited questions. This accounts for the artifice of separating the behavior into the categories cited earlier. The goal of generality is retained in two ways. First, the models are allied to evolutionary ecology and economic theory. This allows us to assemble families of models which coherently and broadly address the multifaceted nature of hunting and gathering. Second, the models are built around concepts and parameters which are not case specific; any model can be applied in diverse circumstances. As an example, the diet breadth model stems from neo-Darwinian and microeconomic postulates; its formulation in terms of prey density and value, and predator search and pursuit costs, makes it applicable to nearly any foraging population.

Despite this generality, our simplified model forager begins with a destitute, unreal form. He or she is fully informed about a well-behaved environment, has only one set of behavioral choices oriented toward reaching a single goal, and acts in isolation from other foragers. Early foraging

models set aside questions of uncertainty (How do foragers get and maintain information about their environment?); unpredictability (How does risk from environmental stochasticity affect foraging choices?); the interacting demands of behaviors other than foraging (What are the opportunity costs of choices among different types of behaviors?); complex resource benefits (Are diet choices based on complicated nutritional needs in addition to energy?); resource renewal (How does resource selectivity interact with resource depletion?); and issues of group behavior (How does food sharing affect foraging choices?). The predictions for this "stripped down" forager may appear fanciful, but his or her heuristic value lies precisely in their clear single-mindedness. We can observe how and by how much predictions diverge from observations, and then have hope of isolating the reasons for the divergence.

Foraging behavior variability is complex and multicausal, but unless we can predict the effects of its causes taken separately, we have no hope of disentangling their respective effects when taken together. Likewise, early foraging models were simple and monocausal, and it is important to learn how well their predictions withstand the incorporation of factors and options we know to exist.

RISK

In this paper I will present an extension of the simple diet breadth model (MacArthur and Pianka 1966). The environmental parameters incorporated into that model are averages. The goal of the forager is to maximize its net rate of energy acquisition while foraging. My extension raises this question: What is the result if we build the same model with environmental parameters that are allowed to vary stochastically, and with the premise that the forager's goal is to avoid the risk of starvation or serious food shortages? That is, how do our diet choice predictions change if we assume a risk-minimizing rather than efficiency or rate maximizing organism?

I will develop an answer to this question in five steps:

(1) I begin with an example of a diet breadth analysis using the deterministic, efficiency-maximizing model. This example is the basis for later comparisons, and it demonstrates the approach discussed rather abstractly thus far.

(2) I then describe a general method (the "z-score" model) for depicting how the mean and variation in food capture rates associated with different foraging choices can be related to the goal of risk minimization.

(3) I follow with an application of that general method to the question of diet choice, using simulation techniques to provide a stochastic analog to the initial deterministic example.

(4) This exercise leads me to consider how pooling and dividing the catch of independent foragers can mitigate risk.

(5) Finally, I will present a more general mathematical analysis of foraging and food sharing. It will show how risk reduction through sharing is affected by (a) intraforager variability of capture from one time period to the next; (b) interforager correlations in food capture; and (c) number of independent foragers participating in the sharing.

To anticipate four important conclusions of this effort, it appears (i) that risk-minimizing diet choices are not too different from those that maximize efficiency; (ii) that sharing is more effective than changes in diet choice in reducing risk; (iii) that the relatively large degree of risk reduction which can be gained by sharing is realized by a quite small number of participants; and (iv) that the circumstances in which this is possible can be precisely specified in ecological terms.

The reader should consult Kaplan and Hill (1985) for a more comprehensive review of evolutionary ecology explanations of food sharing, and for additional references on this subject.

(1) DIET BREADTH: THE DETERMINISTIC MODEL[1]

The diet breadth model has faced logical scrutiny for 18 years. It also is a paragon of robustness. Pyke et al. (1977) claim that it has been independently derived on nine occasions. Field studies (reviews cited earlier) show that it has broad but usually partial or imperfect applicability. By the tests cited earlier, it has achieved a central role in foraging theory. I have chosen a version developed by Schoener (1974) because it has an intuitively clear format and variables.

The model specifies that a prey type should be added to the diet only if its net return relative to pursuit and handling cost (e_x/t_x) is greater than the average efficiency for the diet containing all resource types of higher rank. Represented mathematically:

$$e_x/t_x > \frac{\sum p_i e_i - C_s T_s}{\sum p_i t_i + T_s} \tag{1}$$

with the variables defined as follows:

e_x net energy (kcal) of prey type x
t_x time (min) required to pursue and handle x

[1] The programs for the deterministic and stochastic analyses of diet breadth were written in Turbo PASCAL and run on an IBM XT microcomputer by Sara DeGraff. The stochastic simulation used the pseudorandom number generator available in the language software. The pooling and exchange analyses presented in Table 4, and Figs. 3–5 were calculated and graphed using SYMPHONY software on the same computer.

p_i	relative frequency of prey type i, as encountered, for prey in the diet
e_i	net energy (kcal) of prey type i
C_s	cost (kcal/min) of searching for prey
T_s	average search time (min) required to encounter an acceptable prey type
t_i	time (min) to pursue and handle i
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	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 Eq. (1) reverses.

To demonstrate this model and to establish a basis for later comparisons, I have generated a hypothetical data set (Table 1). It populates an environment with six prey types, with differing energy values, pursuit times and costs, and densities. The forager searches at a velocity of 8 km/hr while expending a 2 kcal/min and scanning a radius of 200 m to either side.

The resulting calculations are presented in Table 2. The prey types are ranked by their net return relative to pursuit and handling time (e_x/t_x); each diet breadth generates a foraging efficiency (E/T). The optimal diet contains three types (A, D, and E). Pursuit of the fourth ranked item (C) when encountered has a lower net rate of energy return ($e_C/t_C = 6.0$ kcal/min) than if it is ignored in favor of the three types of higher rank

TABLE 1
PREY AND PREDATOR PARAMETERS

	Energy value (kcal)	Pursuit time (min)	Pursuit cost (kcal/min)	Density (no./area)
Prey parameters				
APREY	200	4	3	0.4
BPREY	150	30	3	0.8
CPREY	80	10	2	1.0
DPREY	40	1	3	4.0
EPREY	20	1	3	8.0
FPREY	100	40	2	10.0
Forager parameters				
Velocity:	8 km/hr			
Search radius:	0.2 km			
Search cost:	2.0 kcal/min			

TABLE 2
OPTIMAL FORAGING ANALYSIS, DETERMINISTIC CASE

Prey type	Rank (e_x/t_x, kcal/min)	Foraging efficiency (E/T, 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

(E/T = 9.94 kcal/min). Note as well that the foraging net acquisition rate (E/T) declines with diet breadths beyond the optimum of three types.

It is worth adding that neither large size nor relatively great abundance is a reliable indicator of what prey should be pursued. In this example, the least abundant resource, APREY, has the highest rank, whereas the most abundant resource, FPREY, is outside of the optimal diet. Similarly, the smallest item, EPREY, is in the optimal diet while two relatively large items, FPREY and BPREY, are not.

By selectively altering the environment parameters or forager capacities in Table 1, we could observe the effects of changing conditions on foraging efficiency and optimal diet breadth. Qualitatively, the results would show that factors decreasing search time for highly ranked prey will cause the optimal diet to contract; factors decreasing pursuit time will cause the optimal diet to expand. Converse conditions have the converse results. To cite an example from my field work in the boreal forest, the introduction of snowmobiles, which are efficient for locating but not for pursuing prey, decreased search time costs. As predicted the diet breadth contracted (Winterhalder 1983).

(2) A GENERAL RISK-AVOIDANCE MODEL

The key to a general risk-minimizing model lies in recognizing that each foraging choice has a mean or "expected value" food reward *and* a variation about that mean. The variability is due to fluctuations in prey encounter rate or other stochastic factors affecting foraging success over time. For simplicity, I will represent this situation by a normal distribution, mean (μ) and standard deviation (SD = σ) (Fig. 1; see McCloskey 1976). Consistent with the colloquial definition of risk ("probability of loss"; see Winterhalder 1986b), risk is defined as the probability of falling below a fixed minimum requirement (m). This might be starvation or some less catastrophic but significant cost to fitness or adaptation. By

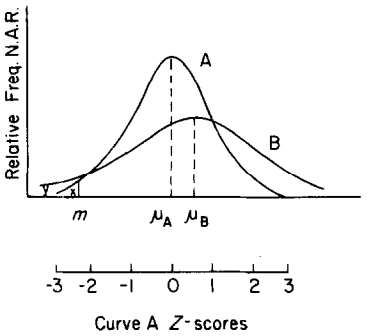

FIG. 1. The distribution of net acquisition rate (NAR) outcomes for two diet choices (A and B), with expected average return rates of μ_A and μ_B. The starvation threshold is given by m. The optimal risk-minimizing forager makes the choice which minimizes the probability of dropping below m in a foraging interval.

standardizing this curve we can measure risk with the standard normal deviate (Z). Graphically, the probability of dropping below the minimum requirement is the area beneath the curve and to the left of m. The optimal risk-reducing strategy is that which minimizes this area by minimizing the standardized Z value associated with m.

Figure 1 makes it evident that risk depends jointly on the mean and SD of the food capture rate. The foraging choice generating distribution B has a higher average value than that for distribution A, but it also is riskier (probability of starvation $= x + y$) than choice A (probability of starvation $= x$) because of its relatively large variance.

Stephens and Charnov (1982; also Stephens and Paton 1985) give a more elaborate and formal derivation of the same result, calling it the z-score model. They also develop a convenient way of depicting the interrelationships among μ, m, and Z. It begins with the formula for calculating Z, the standard normal deviate:

$$Z = (m - \mu)/\sigma. \tag{2}$$

This can be rearranged to the format of the linear slope-intercept equation:

$$\mu = m - Z(\sigma). \tag{3}$$

This allows us to represent the three variables of the z score model on an x–y plane. The minimum intake (m) is the y intercept, Z is the slope of the line. Each point in the plane is a SD/mean combination (σ, μ), representing the food reward distribution associated with a particular foraging choice (see Fig. 2).

Three considerations will complete the argument: (1) How does the

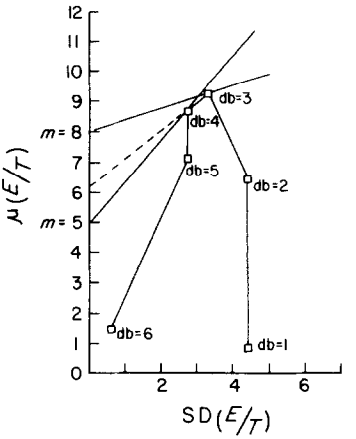

FIG. 2. Optimal diet selection analyzed with the z-score model of risk minimization (Stephens and Charnov 1982). The mean ($=\mu$), SD combinations for the foraging efficiency (E/T) at six diet breadths (db = 1 to 6 prey types) are shown, along with several possible starvation thresholds ($=m$). If $m = 5$, the optimal risk minimizing diet includes four prey types; if $m = 8$ the optimal choice drops to three prey types.

slope of Z correspond to risk? (2) How is the risk-minimizing SD/mean combination chosen? And, (3) How can we find these (σ, μ) combinations for the array of foraging choices to be examined?

Reference to Fig. 1 will show that risk diminishes as Z becomes a large negative number. However, negative values of Z correspond in our general risk-minimizing Eq. (3) to positive slopes. Thus, risk is minimized as the slope of the line in the diagram increases, i.e., as it rotates counterclockwise. This answers the first question.

The answer to the second question now is apparent: the optimal risk-minimizing choice is the available SD/mean pair intersected by the line of greatest slope extending from m (Fig. 2).

The last step is more difficult. We must establish the mean and SD of the food reward for each of the foraging choices to be analyzed.

Stephens and Charnov (1982) solved this problem by mathematical derivation for a key foraging model, the marginal value theorem (MVT) (Charnov 1976). The MVT assumes a forager moving randomly among a set of patches within which it seeks food. The patches are dispersed in an intervening space without prey. Within each patch initially high capture rates decline as the prey are depleted. The model answers this question: How long will the optimal forager stay in a patch? At what point in the process of depletion should it abandon its present location to search for another, more productive spot, given a trade-off between lost travel time and the higher capture rates when a new, undepleted patch is found? The original, deterministic version used average values for the travel costs to

a new patch. In the risk-minimizing version these are allowed to vary stochastically, as they might for a forager trying to locate randomly placed food aggregations. The stochastic form of the model generates a mean and SD for the NAR, as a function of the time spent in each patch.

The resulting (σ, μ) curve has the interesting and very useful property that the optimal choice in a stochastic environment (over a wide range of minimum requirements) is not very different from the optimal choice predicted by the deterministic model. The time allocated to a patch in order to minimize risk is quite close to that which maximizes the net acquisition rate. Because organisms generally can expect to capture more food than their minimum needs ($\mu > m$), in most cases the optimal time allocation for the risk-minimizer will differ by being somewhat longer than that for the efficiency maximizer.

(3) DIET CHOICE AND RISK AVOIDANCE

Stephens and Charnov compare the deterministic and stochastic versions of the marginal value theorem. My objective here is a similar comparison, using the diet breadth model. This requires establishing the mean/SD pairs associated with each possible diet breadth.

Examination of Eq. (1) will show that two variables are likely to exhibit stochastic properties: prey enounter rate (relative density) and prey pursuit time. These in fact are the key components of the model. A direct solution for the stochastic version of the equation is mathematically unwieldy; simpler, less elegant results can be obtained using a computer to simulate the solution. Basically this means iterating the calculation of foraging net acquisition rate at each diet breadth, with the prey densities and pursuit costs for each iteration determined stochastically. A set of these iterations will provide the mean and SD of the foraging NAR for various diet choices. The details of this procedure are given in Winterhalder (1986b).

On the ground this method envisions a forager moving through a habitat of randomly distributed prey. In an interval of foraging time the hunter–gatherer encounters the sample of prey species which reside within the area searched. The actual density of each prey type found in this area will be a stochastic, poisson variate, with a mean equal to the average density for all such samples in the habitat. Likewise, the time it takes to pursue and capture a prey item is sure to vary. This can be examined by assigning each episode of pursuit a stochastic time cost drawn from a normal distribution. The mean of the distribution is the average pursuit time for a prey type; the standard deviation is set by assuming a constant coefficient of variation (= .33).

Our simulated forager minimizes risk to the extent that its prey selec-

tion avoids the chance of a very poor NAR in each of a string of foraging intervals.

Table 3 gives the results for one simulation of 100 iterations. The mean values approximate those for the deterministic case, as is expected. They peak at a diet breadth (db) = 3. The SD of the NAR declines irregularly as the diet expands to include more prey types. I have also included the range, to show that the minimum and maximum NAR experienced by this hypothetical forager are quite divergent.

These results are presented in the format of the general z-score model in Fig. 2. Note first the configuration of the SD/mean set: it is narrowly concave downward. The diet choices from 1 to 6 are positioned around it counterclockwise. This gives us a result much like that for the marginal value theorem: the optimal risk-minimizing diet choice converges with the rate-maximizing choice. In normal circumstances, i.e., the forager's minimum requirement is below what it can expect, the risk-minimizing diet might expand somewhat. Conversely, if the organism is in negative energy balance, it is expected to contract its diet breadth and specialize.

More specifically, above a minimum of about 6.3 kcal/min (NAR) our risk-minimizing forager will choose the deterministic diet breadth of three prey. If its minimum requirement is below that value, then it will shift to four prey types.

This is a good occasion to emphasize that, contrary to a much repeated rule, generalizing a particular strategy (e.g., by including more prey types) may increase rather than reduce the chance of a shortfall. Generalizing may lower variance, but at such a high cost in average foraging efficiency that it actually increases risk. Also note that if our forager were in dire circumstances, needing a minimum of 18 kcal/min in the next foraging interval, then its best (but not good) chance is to specialize on two prey types.

TABLE 3
OPTIMAL FORAGING ANALYSIS, STOCHASTIC CASE

	Foraging efficiency (E/T) by diet breadth for ranked prey types 1 through 6					
	1	2	3	4	5	6
Mean	0.9	6.5	9.2	8.7	7.1	1.5
SD	4.4	4.4	3.3	2.7	2.7	0.6
Min	−2.0	−0.1	1.4	1.4	1.4	0.2
Max	13.1	17.8	18.1	16.0	13.6	3.7
Deterministic value[a]	1.8	7.6	9.9	9.0	6.5	1.4

[a] From Table 2.

(4) SHARING

Assume that our hypothetical forager has a minimum requirement of 5 kcal/min NAR for each foraging interval, and that it makes the optimal choice of four prey types. Of the 100 foraging intervals simulated, 10 had values below this minimum. In effect, the best choice will not always be a good one, or even good enough. If the threshold is one of starvation and our forager's life span covers some large fraction of 100 foraging intervals, its chances of survival to old age are slim. Even if the threshold (m) carries a lower cost, this might still be an intolerable frequency of shortfall. To minimize risk, even optimally, is not always to avoid it.

This brings us to the effect of sharing on this residual variation. Imagine a group of (N) individuals who hunt and gather independently, but pool and then equally divide the catch at the end of each foraging period. We can observe the effects of this sharing process by combining and averaging separate stochastic foraging simulations. The data from such an experiment are given in Table 4, and shown graphically in Fig. 3, for a diet breadth of three prey types. Sharing essentially has no effect on the average intake, but it does reduce the SD of the NAR. The rate of reduction is large at small N and diminishes as group size grows. Note also that the maximum and minimum values converge toward the mean as the number of sharing foragers increases.

These data allow us to make a rough comparison of the efficacy of diet breadth changes and sharing in reducing risk. It already has been observed that the optimal risk-minimizing choice available to a forager may not constitute risk avoidance. In the set of simulations used to construct Table 4, the lone, risk-minimizing forager choosing a db = 4 (rather than

TABLE 4
SHARING AND RISK REDUCTION

	Number of independent foragers in sharing group					
	1	2	3	4	5	6
Simulated[a]						
Mean (E/T)	9.5	9.6	9.6	9.6	9.8	9.7
SD	3.6	2.7	2.1	1.8	1.6	1.5
Min	3.1	3.8	5.6	5.8	6.4	6.4
Max	21.4	17.9	15.3	14.6	14.6	13.8
Derived[b]						
SD (E/T)	3.6	2.5	2.1	1.8	1.6	1.5

[a] For a db = 3.
[b] See text, page 381.

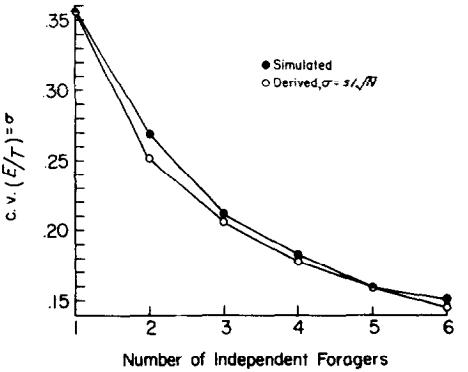

FIG. 3. The coefficient of variation (c.v.) for net acquisition rate (E/T) achieved by sharing foragers, as a function of the number of persons pooling and dividing their catch. The solid circles show the empirical results of summing and averaging separate stochastic foraging simulations; the open circles show the theoretical expectation.

the rate-maximizing db = 3) gains an average reduction of 8% in the SD of its NAR. The cost for this is a 6% reduction in mean foraging efficiency. By contrast, only two sharing foragers (at db = 3) can attain a 30% reduction in their joint NAR SD, and preserve the maximum foraging efficiency of a db = 3. Six foragers sharing their catch attain a 58% reduction in their pooled SD.

The opportunities for a single forager to reduce risk by adjusting prey choice are constrained by the SD/mean linkage. Pooling and division are an effective way of circumventing this limitation.

(5) A GENERAL MODEL OF SHARING AND RISK REDUCTION

We can generalize this approach to sharing by adapting a formula used by McCloskey (1976) in a study of risk and nineteenth-century field dispersion in the Midlands of England. The objective is to determine how variation in the NAR of sharing foragers is affected by three factors: (i) intraindividual variation in NAR from one time period to the next; (ii) the number of foragers participating in the group; and, (iii) the average interforager correlation of NAR in each foraging interval. This last variable adds a quite interesting element to the analysis. It allows us to examine temporal synchronism in the stochastic environmental conditions experienced by foragers hunting and gathering at different locations in their group range.

The exact solution to this question is quite complex. However, with little loss of accuracy (see McCloskey 1976), it reduces to

$$\sigma = s\left[\frac{1 + (N - 1)R}{N}\right]^{0.5} \tag{4}$$

where

σ = average NAR c.v. for an individual forager, after sharing
s = average NAR c.v. for an individual forager, before sharing
N = number of individuals foraging separately but pooling and dividing their catch
R = average correlation of NAR between any two foragers in a given time period.

To get a sense of the behavior of this equation, note that in the trivial case of $N = 1$, $\sigma = s$. If foragers experience perfect correlations in their before-sharing NAR (i.e., if $R = 1$), then $\sigma = s$ and pooling and division cannot reduce day to day fluctuations in their catch. With no interforager correlation ($R = 0$), $\sigma = s/\sqrt{N}$. In this case variation falls off but at a decreasing rate. In fact, this is the general expression for the result derived earlier by pooling stochastic simulations (Fig. 3). For positive values of R not equal to 1 or 0, as N gets large there is an asymptotic limit to the reductions achievable through sharing at $\sigma = sR^{0.5}$. Finally, if $R = -1$, then an N of 2 reduces σ to zero. With a perfect inverse correlation in their capture rates, it takes only two foragers to eliminate any variation from their after-sharing NAR.

Figure 4 graphs the product of this equation for different group sizes ($n = 1 \ldots 20$) and a range of negative and positive interforager correlations ($R = -0.4, -0.2, 0, 0.2, 0.4, 0.6, 0.8$, and 1.0). I have set s, the before-sharing c.v., at 0.35, approximately that experienced by the risk-minimizing forager simulated earlier (at a diet breadth of three prey; see Table 3). For all positive values of R other than 1, there is a continuous decrease in the after-sharing consumption c.v. as group size grows. Note, however, the asymptotic form of the curves and that the major part of the risk reduction occurs at small values of N. At $R = 0.2$, for instance, 80% of the potential risk reduction from pooling and division can be gained by only six foragers. For modestly negative values of R, even smaller numbers of foragers (e.g., 3–5 individuals) can gain dramatic reductions in the variation of their pooled catch. Negative correlations require that independent foraging trips encompass regions which are asynchronous in the stochastic conditions affecting hunting and gathering success.

There is a simple and more general way of demonstrating this point about small group size. As the foraging unit grows in numbers, the marginal reduction in NAR variation diminishes rapidly. Because of the asymptotic form of the curves (for positive values of R) significant gains

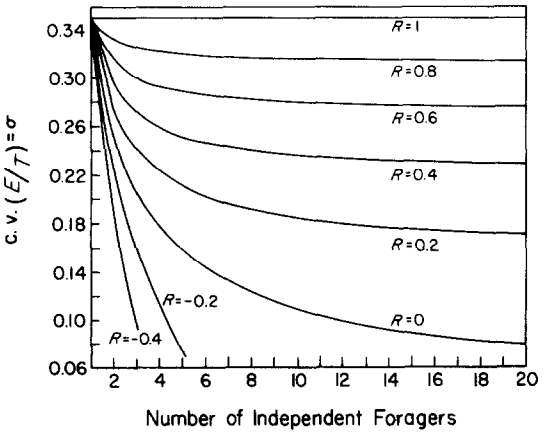

FIG. 4. The coefficient of variation (c.v.) for net acquisition rate achieved by sharing foragers, as a function of the number of participants and the correlation (R) among their individual capture rates.

are exhausted quickly. At some point the *disadvantages* to increasing group size (e.g., more rapid localized depletion of prey) will offset the small marginal increments of benefit gained by sharing. It is reasonable, then, to ask this question: What number of pooling foragers is necessary to obtain some fixed proportion of the gains which potentially can be achieved by sharing? Posing the question in this form has the handy mathematical result that it eliminates both σ and s from Eq. (4), allowing expression of N directly as a function of R.

Mathematically the argument is as follows. For positive values of R, set

$$\sigma = s - [k(s - sR^{1/2})]$$

where k is the fractional reduction in s relative to the potential reduction at the asymptote ($\sigma = sR^{1/2}$). The right side of this equation can be substituted for σ in Eq. (4). The result eliminates s (and σ), and reduces to

$$N = \frac{R^{1/2} + 1}{(1 - k^2)R^{1/2} + (1 - k)^2}. \tag{5}$$

For negative values of R, set $\sigma = s - k(s) = s(1 - k)$. Note here that zero has replaced the asymptote as the maximum reduction possible. In this case, substitution in Eq. (4) gives the following result:

$$N = \frac{1 - R}{(1 - k)^2 - R}. \tag{6}$$

For both Eqs. (5) and (6), if $R = 0$, then $N = 1/(1-k)^2$.

The graph produced by these equations is displayed in Fig. 5, for values of k ranging from 0.5 to 0.8 (a 50 to 80% reduction of the before-sharing c.v.), and for values of R from -1.0 to $+1.0$, virtually the full range of environmental possibilities. Although there is a sharp narrow peak as R approaches zero, it is striking that small and relatively constant numbers of sharing foragers can achieve a large proportion of the potential reduction in intake variation. For example, six or fewer sharing foragers can achieve 60% of the potential reduction in variation, whatever the environmental correlations. In effect, the conclusion about small group size is relatively insensitive to R, and it holds over a wide range of reasonable expectations about the marginal gains to be expected of sharing.

DISCUSSION

I will comment on several assumptions in the model, with the goal of assessing its generality. I then raise but address only briefly an important question which also bears on the generality of the result: If pooling and division is so effective at reducing risk, why is it not more common cross-specifically? Some attention to definitions has precedence.

Risk

Defining risk precisely is like juggling a porcupine: whatever way you throw it up, it comes down prickly. Risk has (at least) two distinct

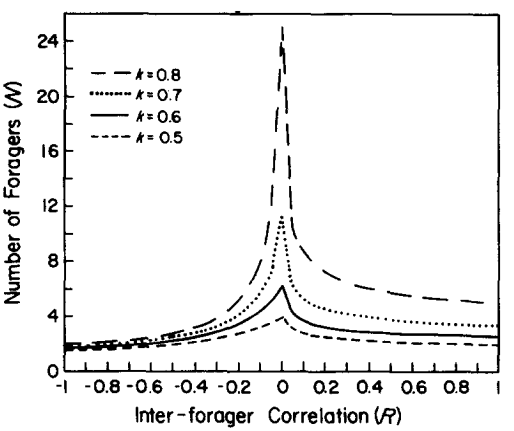

FIG. 5. The number of sharing foragers (N) required to obtain fixed proportions ($k = 0.5$ to 0.8) of the potential reduction of variation in food capture rates, for differing levels of interforager correlation (R).

meanings in the ecological and economic literature. It sometimes refers to the probability of loss, of fitness, or in economics, loss of profit or utility. This is the colloquial definition as well—juggling porcupines is risky. However, risk also can refer to the magnitude of the stochastic variance associated with particular choices. Thus a person who prefers (or an organism which selects) an option with high variance is sometimes called risk prone, whereas one selecting (perhaps at some cost in the average or expected value of the outcome) an outcome with low variance is called risk averse. He or she avoids variance. For mean-preserving changes in variance the two definitions often will coincide; otherwise they may not, and ambiguity and confusion may ensue.

In deference to colloquial understandings, I have used risk for probability of loss. Since the second and more specialized meaning is synonymous with variance (or some related measure of dispersion), variance seems an appropriate substitute. All organisms then should be risk averse, but to achieve this they may be either variance averse or variance prone (cf. Caraco 1983). This convention keeps meanings clear without inventing new words or changing old ones.

Stochasticity and Diet Breadth

The approach adopted here, which makes search and pursuit times stochastic, has the advantage that it begins with simple, intuitive modifications in the structure of a familiar deterministic model. However, there are other manipulations of the model which possibly are relevant to the question of diet selection and risk. Dave Stephens (personal communication) has suggested two: the risk-sensitive forager may rank prey differently than is assumed by the deterministic model and my stochastic adaptation of it; and the risk-sensitive forager may exhibit partial preferences, a possibility again not predicted in the original model or encompassed in my adaptation. A more thorough exploration of risk and diet breadth awaits exploration of these additional factors.

Probability Distributions

The foraging simulation used here assumes that encounter rates approximate a stochastic poisson distribution, whereas pursuit and handling times approximate a stochastic normal distribution. Qualitatively, each distribution is logically appropriate to its role: the poisson gives the frequency distribution of relatively rare and randomly dispersed events sampled from a temporal or spatial field. The normal distribution characterizes those situations in which many small random factors interact to generate symmetric dispersion about a mean. The empirical fidelity of

these distributions to the actual circumstances of foragers should be tested, but minor deviations are unlikely to affect the qualitative interpretation presented.

The stochastic search assumption clearly is more appropriate for mobile animal prey than for plants, at least for foragers familiar with their ranges. If animals are regularly spaced or otherwise associated with fixed and known locations (e.g., particular habitats or patches), then their location will be somewhat predictable and the poisson will *over*estimate the variability of encounter rates. On the other hand, if they are randomly dispersed but in an unknown clumped or contagious pattern, then the poisson will *under*estimate the variability of encounter (see Whittaker 1970: 11). It is clear that the model does not address the ethnographically established use of low quality but sometimes abundant and low risk "fallback" foods.

Use of the normal distribution for pursuit and handling appears appropriate for both plants and animals. Although the model uses the same coefficient of variation for all prey, it would be more realistic to assume that this parameter is unique to each type. On average it probably is lower for plants than for animals.

The adoption of the poisson distribution as one of only two sources of stochasticity in the simulation does create an analytic problem. The simulated NAR sometimes deviates (significantly) from a normal distribution if some prey types are quite rarely encountered (see Winterhalder 1986b). This of course obviates precise interpretation of the mean/SD sets by the z-score method, which assume normality. In specific applications, it thus is important to know the actual form of the stochastic conditions faced by foragers. Stephens and Charnov (1983) have shown that in the general case the limiting distribution of acquisition rates is normal.

The Risk Threshold ("Starvation")

Another point at which we might question the generality of this model lies in the operational definition of risk as a stepfunction, or a threshold effect. Above (m) there are no fitness or utility costs, at and below (m) the costs jump to some constant, positive value. The analytic virtues of the simplification are evident, but what has been lost?

Actual organisms probably experience continuously increasing costs to fitness or utility as NAR declines below a certain level. This can be stated mathematically—the risk minimizing choice is the particular mean/SD distribution which minimizes the function

$$\int(\mu, \mathrm{SD})_i(f_d)d\mu, \tag{7}$$

where f_d is the fitness decrement curve. The optimal choice is that which

minimizes the summed probabilities of risky outcomes weighted by the fitness consequences of those outcomes. The precise relationship between this formulation (7) and the step function used in this paper (and in the z-score model generally) awaits further study.

Carry-over vs Exchange Averaging

Interpretation of the marginalist modification of Eq. (4) requires simultaneous attention to Figs. 4 and 5. There is a relative observation: *to the extent* that interindividual pooling and division can reduce consumption variance, it can do so with quite limited numbers of participants (see Fig. 5). And there is also an absolute observation about the potential magnitude of this benefit: for negative or low positive values of R, small group sharing is very effective at reducing pooled consumption variance, whereas for high positive values of R it is ineffective (see Fig. 4).

In the right circumstances relatively small numbers of foragers can dramatically reduce their food availability variance by pooling and dividing separate catches. But observe that somewhat the same functional result is available to one forager able to store and carry over a surplus. The group consumes a pooled average, the individual a running average. Ignoring time constraints, within-interval pooling among three foragers has the same functional result as sequential pooling by one forager over three intervals. However, these are not exactly equivalent because of the factor of time: the individual practicing sequential pooling may not be able or willing to tolerate the accumulated effects of a run of several bad intervals, whatever the statistician's reassurances about the "long term." Because group pooling averages within time intervals, the benefits of such reassurance are gained more quickly (in fact, as many times faster as there are individuals in the pooling group). Further, group pooling still allows for carry-over when surpluses are available. Thus, where both are effective, exchange pooling has advantages for risk reduction when compared to carry-over pooling.

Equation (4) provides further insight into this question of carry-over versus exchange averaging. I have plotted the key variables of that equation in a 2 × 2 table (Fig. 6): high and low levels of intraforager SD (from one foraging interval to the next) versus high and low levels of interforager correlation (degree of synchronism within a region, among the foraging trips and perhaps the territories or ranges of the different hunter–gatherers).

In situations (Case A) of high intraforager SD (high s) and high interforager correlations (high R), everyone does unpredictably well or poorly in synchrony. Sharing is of little absolute advantage and we would expect carry-over storage. If the spatial correlations (R) diminish immediately

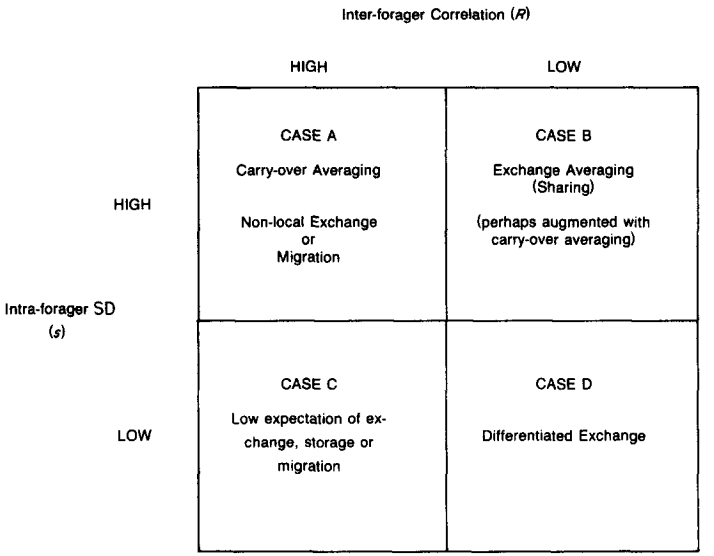

FIG. 6. Expected behavioral responses to the combination of high and low levels of (i) intraforager variation (s) and (ii) interforager correlation (R) in food capture rates.

beyond the group's foraging range, nonlocal exchange, or temporary migration, are possibilities. Which of these alternatives to predict is a question of specific constraints, cost and benefits.

In the other situation of high individual risk (Case B), high s and negative or low positive values of R generate a prediction of localized exchange, perhaps augmented by carry-over averaging or storage, for reasons outlined above. This is the case most directly addressed in the paper.

The two remaining cases (C and D) present low individual risk, but have implications for equity of consumption and for exchange and reciprocity. In Case C everyone gets close to the average intake from one to the next time interval, and all do more or less equally well. A predictable habitat with hunting ranges of like quality would be an example. There is little risk and little differentiation of NAR among individuals or foraging ranges. In Case D everyone gets close to their own average from one to the next time interval, but some do consistently above the group average and some consistently below, perhaps due to differences in skill or to access to ranges of differing qualities. Here there is predictability, but also individual differentiation and we might expect forms of exchange involving goods or services in addition to food.

Taken as a separate cause, environmental stochasticity should generate selective tendencies in the direction of the behaviors depicted in Figure 6.

And, in actual cases in which stochasticity is a significant ecological factor, we can predict that these behaviors will be the evolutionary consequence. Note, however, that a *comprehensive* model relating environmental fluctuations to features like sharing, storage and migration would also include *non*-stochastic patterns, perhaps viewed as autocorrelation (Harpending and Davis 1977) or predictability (Goland 1983).

Why Is Sharing Rare among Nonhuman Foragers?

There is nothing in this risk-minimization model to suggest that the striking benefits of sharing should be limited to human foragers. As with other evolutionary ecology models, this one should have broad, cross-specific applicability. Yet, the impression is that even in the primates and mammals, food sharing is exceptionally rare. Why is it so? Some possible answers to this question may give us further insight into why and to what extent the model applies to human foragers and hominids before them.

First, it may be the case that sharing or its functional equivalent does occur more frequently in nonhuman organisms, but we don't recognize or record it as such. Passive information exchange about rich food patches by colonial birds (Bertram 1978) might be an example of such functional sharing. Second, many organisms (e.g. herbivores) may face insignificant degrees of subsistence risk from the types of stochasticity modeled here. Others may face stochasticity, but in contexts which make alternative solutions (e.g., migration, storage) more effective. Yet others might conceivably benefit from localized sharing, but for reasons which are historical (e.g., competing goals, lack of preadaptations) or related to evolutionary processes (e.g., natural selection constraints, see Smith 1985; Kaplan and Hill 1985) have not evolved this particular social behavior, whatever its hypothetical advantages. Organisms selected to be solitary foragers have no recourse to sharing. Neither is it of any advantage to those foragers which search for prey *as a group*. The nomadic foraging unit may face risk, but capture variance is continually synchronized among the individuals ($R = 1$) because of their contiguity. Finally, sociobiological theory suggests possible evolutionary constraints: the genetical evolution of social behaviors like sharing will occur only when consistent with the inclusive fitness benefits of individuals, and when it is an evolutionarily stable strategy.

These limitations of observation and categorization, environmental context, alternative solutions, and constraints on the possibility or selective advantage of sharing return us to humans. Hunter–gatherers do their sharing in active and conspicuous ways; they often pursue mobile game in partially unpredictable environments and consequently they face some degree of stochasticity; they sometimes store food and migrate, in addi-

tion to sharing; and they often are organized into central-place (home base) subsistence systems, which provide the structural context for effective sharing. In addition, their behavior is affected by processes of cultural evolution perhaps not subject to the constraints which could impede the regular evolution of this kind of social behavior in nonhuman organisms (see Boyd and Richerson 1985). Thus, human foragers and hominids before them may regularly satisfy a set of necessary conditions for the evolution of sharing, the same conditions which other species commonly fail to meet. This indicates that food sharing is an ancient and pervasive feature of hominid lifeways.

CONCLUSIONS

Hunter–gatherers are renowned for living in small groups and for sharing food. Their environments presumably are stochastic to some degree; risk-minimization may have been prominent among their adaptive goals. Extension of foraging models to encompass risk adds to our understanding of the set of ecological factors which might have selected for (or against) particular patterns of diet choice and group formation in prehistoric and later foragers. A model which relates specific constraints and benefits to selection for food sharing puts us in a better position to evaluate the evolutionary origins of this feature in hominid prehistory (see review in Binford 1985). Some of the precise results presented here are specific to the data set employed, but the form of the analysis and the qualitative direction of the results should have broad applicability.

First-generation foraging models ignored risk, but in practice it may not matter much. By progressively extending the simple models it is possible to compare deterministic and stochastic assumptions and goals. In analyses of the marginal value theorem (Stephens and Charnov 1982) and the diet breadth model, it appears as if the rate maximizing choices predicted by deterministic models are similar to the most effective, risk-minimizing choices. This is a boon to those who live by foraging *and* to those who live by studying foragers.

The ecological link between the mean and SD in NAR which underlies this result has disadvantages for the foragers. The optimal risk-minimizing diet choice available to the individual organism may not avoid risk. The forager who both captures *and* consumes food independently may be able to reduce its variability of intake to only a limited extent by adjusting prey selection. However, pooling and division among a set of central-place foragers can significantly reduce the residual variation. By summing and apportioning equally the catch of two or more simulated foragers, I have shown that this takes relatively few individuals.

More generally, risk reduction is a function of intraforager variability,

interforager correlations (or synchronism), and number of foragers. The mathematical model depicting these relationships will help to identify field data relating the degree and patterning of sharing to the variety and range of environmental conditions which affect risk. The model demonstrates that major gains to risk reduction by sharing are achieved in relatively small groups. And it allows us to specify the circumstances in which such sharing can be effective. Both the form of this result and its magnitude are consistent with the view that risk reduction through pooling and dividing may have affected the type of groups observed ethnographically and archaeologically for hunter–gatherers.

In fact, by virtue of sharing, such groups would have the dual advantage of diet efficiency and security. As producers, individual hunter–gatherers can make prey choices that maximize their net acquisition rate; as consumers they can effectively minimize risk by sharing what they catch. It also is possible that individual members of a foraging group might elect to harvest a set of resources with high variance but lower than maximum acquisition rate (perhaps to obtain a critical nutrient), and to offset the increased risk through sharing. While first generation diet selection models also ignored sharing, this need not diminish confidence in their applicability to humans.

In conclusion, we can return to our "stripped down" forager and assert that although bare of realistic assumptions, the optimal diet breadth model still merits analytic attention. In this analysis, it has withstood well its relocation into a family of models which include stochasticity and risk, and the effects of group sharing.

ACKNOWLEDGMENTS

My appreciation to R. L. Bettinger, D. P. Braun, S. DeGraff, P. Gardner, E. A. Smith, J. Speth, and D. Stephens for their encouragement, comments, and criticism. R. Godoy introduced me to the economic literature on the English common field system. With special gratitude to Paul Winterhalder.

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