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## Risk-Sensitive Adaptive Tactics: Models and Evidence from Subsistence Studies in Biology and Anthropology

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*Risk-sensitive analysis of subsistence adaptations is warranted when (i) outcomes are to some degree unpredictable and (ii) they have nonlinear consequences for fitness and/or utility. Both conditions are likely to be common among peoples studied by ecological anthropologists and archaeologists. We develop a general conceptual model of risk. We then review and summarize the extensive empirical literatures from biology and anthropology for methodological insights and for their comparative potential. Risk-sensitive adaptive tactics are diverse and they are taxonomically widespread. However, the anthropological literature rarely makes use of formal models of risk-sensitive adaptation, while the biological literature lacks naturalistic observations of risk-sensitive behavior. Both anthropology and biology could benefit from greater interdisciplinary exchange.*

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**KEY WORDS:** risk; adaptation; subsistence economics; behavioral ecology.

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### INTRODUCTION

As they seek more refined models of nonmarket economic behavior and ecological adaptation, archaeologists (see Halstead and O'Shea, 1989; Tainter and Tainter, 1996) and ethnographers (Cashdan, 1990; de Garine and Harrison, 1988) have turned attention to questions of stochasticity and subsistence risk. This parallels a trend in biology, where a large body of literature now has shown sophisticated risk-sensitive behavioral capacities in a variety of organisms (see below; summaries by Bernstein, 1996; Ellner and Real, 1989; Kacelnik and Bateson, 1996;

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McNamara and Houston, 1992; Real and Caraco, 1986; Stephens and Krebs, 1986, pp. 128–150; and *American Zoologist*, Vol. 36, 1996). The taxonomic ubiquity of risk-sensitive tactics suggests that they are a common evolutionary phenomenon, thus one of potential importance to hominid evolution as well. We seek through this review to demonstrate that ecologically minded ethnographers and prehistorians could benefit substantially by greater attention to the conceptual developments and comparative potential found in the broader behavioral ecology literature on risk.

Although we focus on subsistence economics, especially foraging, the conceptual developments surveyed should transfer to any behaviors that produce more-or-less unpredictable outcomes with nonlinear consequences for utility or fitness. This includes habitat choice and territoriality, life history, and reproductive and social behaviors (see Bednekoff, 1996; Benton *et al.*, 1995; Caraco and Chasin, 1984, p. 81; Rubenstein, 1982; Winterhalder and Leslie, 1998). O'Connell (1995) has made the case that archaeology requires an evolutionary theory of behavior; risk-sensitive models seek to advance that theory with respect to subsistence adaptations.

We begin with definitions. Next we develop a conceptual framework for risk-sensitive analyses. These sections are followed by reviews of empirical studies in biology and anthropology, drawing only occasionally on literature from economics and psychology. Although this ordering—concepts, biology, and only then anthropology—may seem perverse to an anthropological readership, it in fact is essential to one of our most important findings: neglect by anthropologists of formal models and comparative materials from biology threatens our ability to accurately appraise the role of risk in shaping behavioral adaptations.

Throughout we attempt to develop an integrated view of existing models, whether they have been used in biology or anthropology. In the concluding section, we compare and assess the present state of knowledge in the focal disciplines and direct attention to gaps and to promising avenues for future study. For economy of presentation, the empirical studies we summarize are described in Tables I through IV.

## DEFINITIONS

Risk is unpredictable variation in the outcome of a behavior, with consequences for an organism's fitness or utility. Subsistence outcomes that by chance fall short of needs are an example. Neodarwinian theory predicts that creatures tend to adapt so as to avoid harmful dietary shortfalls by minimizing them to the degree possible. Thus, behavioral ecologists treat risk with some of the same analytical tools as other adaptive problems—optimization premises (Foley, 1985; Parker and Maynard Smith, 1990), simple models (Levins, 1966; Richerson and Boyd, 1987), and a hypotheticodeductive methodology (Smith and Winterhalder, 1992). Utility theory, the basis of much economic and biological modeling on this subject, makes

additional, axiomatic assumptions that choice is rational and logically consistent (see Friedman and Savage, 1948, pp. 287–288; von Neumann and Morgenstern, 1944). For brevity, in what follows we present the relevant models in graphical form. Readers are referred to the relevant citations for the underlying assumptions and mathematics.

Common usage sometimes confounds the economic meaning of risk with related concepts that we wish to distinguish. With *risk* the probability distribution of outcomes is in some sense known to the organism, but stochasticity makes any particular outcome unpredictable. Outcomes can be assigned odds but not determined in advance. *Uncertainty* refers to incomplete knowledge of outcome probabilities (Knight, 1921). Uncertainty can be overcome by acquiring information about an environment (see Stephens, 1987, 1989); risk cannot. An organism can have certain knowledge (know precisely the probability distribution of outcomes) but still face risk. As well, in economics and behavioral ecology, risk does not mean exposure to danger (e.g., a “risky” situation). We use *hazard* to refer to potential sources of harm to an organism. Inadequate food is a hazard. As we demonstrate below, an organism can seek to avoid the hazard of food shortfalls by being risk averse (avoiding behaviors linked to unpredictable outcomes in favor of more certain ones) or risk prone (favoring behaviors linked to unpredictable over more certain outcomes). Finally, biological theory uses fitness as its ultimate “currency,” whereas economic theory has developed in terms of utility. Because we draw from literature in both fields we gloss these two currencies with the word *value*. Fitness and utility differ in important respects, but the generality of the concepts discussed here will bear the refinements that might be required by their more specific use.

## THE THEORY OF RISK SENSITIVITY

In this section we review and synthesize the concepts and models necessary to analyze risk-sensitive adaptations. It is our experience that much of this literature is unfamiliar to anthropologists (as it was to us, until fairly recently). This is an unfortunate state of affairs and an impediment to progress in human ecological studies, ethnographic and archaeological. The atheoretical approach adopted in much of the anthropological literature on subsistence risk is a handicap. Our subsequent discussion of empirical analyses is organized around concepts introduced in this section. We highlight those biological and anthropological case studies that draw on the appropriate theoretical tools.

Deterministic optimization models of subsistence decisions assume that an organism continuously experiences the average conditions of its behavior and environment. Each behavioral option has a predictable outcome with an associated value. In contrast, risk-sensitive models allow for the stochasticity that characterizes most real situations, to greater or lesser degrees. An organism cannot count

on a particular result. It faces a range of possibilities, their frequencies given by a probability distribution. In moving from deterministic to risk-sensitive models, a predictable average outcome gives way to odds over a known range of outcomes. We wish to understand to what extent this stochasticity matters to the adaptive problems that organisms must solve.

A risk-sensitive analysis entails two steps. We must first associate each behavioral option with its probability distribution of outcomes. We must then specify the relationship between outcomes or rewards (say net acquisition rate of resources) and their values (utility, fitness). The set of cultigen varieties and field locations chosen by the farmer has an associated probability distribution of yields. Each yield has a particular fitness or utility (value).

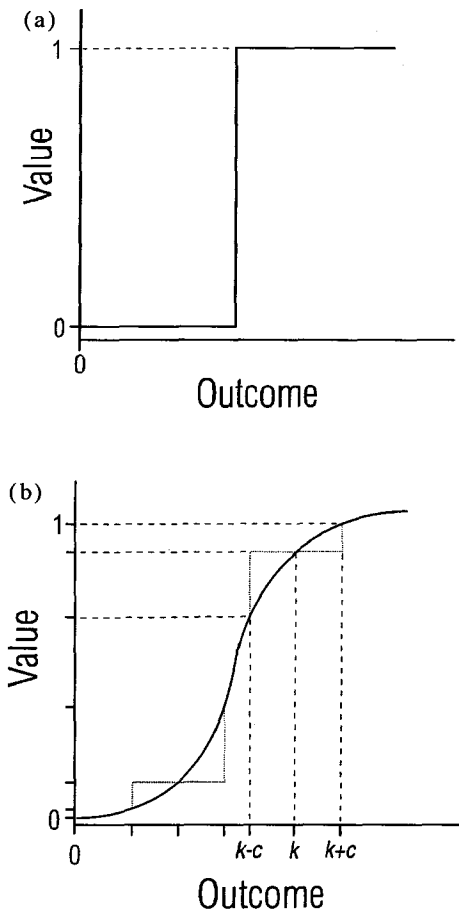
The overall value of a behavioral option is given by the sum of the weighted likelihood of each possible outcome multiplied by its value. This distinction between a distribution of values and a probability distribution of outcomes is implicit in Pascal's Wager (ca. 1669) but was first formalized by Bernoulli [1954 (1738)]. We have

$$E_i[V(x)] = \int V(x)f_i(x)dx \quad (1)$$

The expected value of alternative  $i$ ,  $E_i[V(x)]$ , is the product of the value function  $V(x)$  and the outcome probability distribution  $f_i(x)$  specific to alternative  $i$ , summed over each possible outcome ( $x$ ). The best choice among the alternatives is that having the highest expected value. In the language of economics: the objective probabilities of the outcome distribution  $f_i(x)$  must be weighted by their subjective utilities  $V(x)$ . To minimize confusion, we consistently use *outcome* or *reward* when referring to the probability distribution and *value* when referring to the utility or fitness function.

### Relationship Between Outcome and Value in Terms of Fitness or Utility

A sigmoid or convex-concave value function is likely to be especially important with respect to subsistence adaptations (Fig. 1b) (see Rubenstein, 1982; Schaffer, 1978; Smallwood, 1996). Value always rises with increasing resources (e.g., kcal/hr acquired), but it does so at an accelerating marginal rate when resources are scarce (to the left of the inflection point) and a decelerating marginal rate when they are abundant (to the right of the inflection point). Consider the fitness function relating atmospheric oxygen concentration (a needed metabolic resource) to the work capacity of a mammal. Food operates similarly: with too little, added increments have high value; with too much, added increments count for little. Some portion or variant form of the convex-concave value function covers most of the circumstances for which we require hypotheses about subsistence risk.



**Fig. 1.** Functional relationships between resource outcome and value (fitness, utility). (a) The step function, adopted by the Z-score model. (b) A general sigmoid function. The sigmoid function illustrates the basic logic of risk sensitivity. For the concave portion, in which marginal returns are decreasing, an organism will prefer a constant outcome ( $k$ ) to equal probabilities of a variable outcome ( $k + c$ ,  $k - c$ ). For the convex portion of increasing marginal returns, it will do better with the variable outcome.

Consider an organism with a simple, two-way choice: a fixed reward ( $k$ ) or an unpredictable reward with equal probability of being either ( $k - c$ ) or ( $k + c$ ), for small values of  $c$  (Fig. 1b). The average outcome of these two options is equal but their values are likely to be different. To the right of the inflection point the

value gained from alternative  $(k + c)$  does not offset the larger loss of value when  $(k - c)$  is the outcome. The mean or expected value of the variable reward is less than the value of the constant reward. The organism optimizes fitness or utility by avoiding the variable option. It is variance or risk averse. In contrast, to the left of the inflection point, the expected value of the variable tactic is the greater:  $(k + c)$  more than offsets  $(k - c)$ . Given choices of equal expected value, the organism doing relatively poorly opts for the tactic producing variable outcomes. It is variance or risk prone. Jensen's inequality formulates the mathematics underlying these relationships (Smallwood, 1996).

Daniel Bernoulli [1738] (1754), p. 25] first stated the generality and importance of the concave (risk averse) portion of this function:

*... the utility resulting from any small increase in wealth will be inversely proportionate to the quantity of goods previously possessed. Considering the nature of man, it seems to me that the foregoing hypothesis is apt to be valid for many people to whom this sort of comparison can be applied. (italics in original 1738 translation)*

Economists did not formally recognize arguments for a convex segment until over two centuries later (Friedman and Savage, 1948). The applicability of this function is not limited to *Homo economicus*. In an important experimental study, Caraco *et al.* (1980) show that the utility function for yellow-eyed juncos (*Junco phaeonotus*) has the sigmoid form.

We make several observations about the sigmoid value function. First, its precise form is time sensitive. If value is expressed as a rate, it must be determined in relation to a set duration ( $d_{R_{min}}$ ) of time that fixes the consequences of that rate. The same result can be achieved with greater conceptual transparency if the  $x$ -axis has units of absolute amount/ $d_{R_{min}}$ . For example, the fitness consequences for a large mammal given an option between  $k$  liters/hr water acquisition and equal probabilities of 0 or  $2k$  liters/hr depend on the duration over which it must live with its choice. Consider a 0-liter/hr result suffered for 6 hr, 6 days, or 6 weeks before the choice and outcome are iterated. Similarly, given a  $d_{R_{min}} \approx$  week, the value functions for key metabolic resources vary from a near step function (oxygen) to more smoothly curved sigmoid (water and calories) to a curve more nearly linear in form (trace minerals). Responses to risk depend on the time frame, urgency, and consequences of decisions that cannot be reversed over some interval.

Second, the ongoing experience of the organism with respect to resources determines its preferences with respect to reward variability or constancy. To get a qualitative sense of this relationship, compare the magnitude of upside gain of the variable reward  $(k + c)$  to the downside loss  $(k - c)$  as  $k$ , or the average anticipated reward, moves from left to right (Fig. 1b). Because organisms presumably spend most of their time in positive energy balance, to the right of the inflection point, they typically will avoid variable options in favor of more certain results having the same average.

Third, using Fig. 1b we have compared a constant reward to a symmetrical, two-outcome choice ( $k \pm c$ , with equal probabilities) with an equal mean. Even this very simple situation has impressive generality. For instance, we will get the same qualitative predictions as above if the variable reward has multiple outcomes, as long as they are symmetrically distributed about their mean—for example, when they are normally distributed. In the next section we show how this same logic is used to compare behavioral alternatives that differ by both mean and variance.

### *The Z-Score Model*

For analytical convenience, we can approximate the sigmoid curve with a step function (Fig. 1a). Below the resource level set by ( $R_{\min}$ ) the value is zero; above ( $R_{\min}$ ) it is 1. By this simplification we fully characterize the value function with a single parameter, ( $R_{\min}$ ), while preserving a semblance of the sigmoid form. We also can invoke the central limit theorem to suggest that over large time intervals the distribution of energy gains (a continuous, random variable) from a particular subsistence choice approximates a normal distribution. Consistent with this result, we describe the outcome of each subsistence option by its mean ( $\mu$ ) and standard deviation ( $\sigma$ ). The expected value [Eq. (1)] of each option then is the summed product of the step function [ $V(x)$ ] and the normal curve representing that option's outcomes [ $f_i(x)$ ].

The step function and normal outcome distribution are the basis for the widely used Z-score model of shortfall minimization (Stephens, 1981; Stephens and Charnov, 1982). In this model the shortfall-minimizing alternative is the choice that reduces to the extent possible the likelihood of zero fitness, the area beneath the outcome distribution that lies to the left of  $R_{\min}$ . Because the area beneath normalized distributions are symmetric around the mean, this is equivalent to maximizing the high-fitness area to the right of  $R_{\min}$ , or

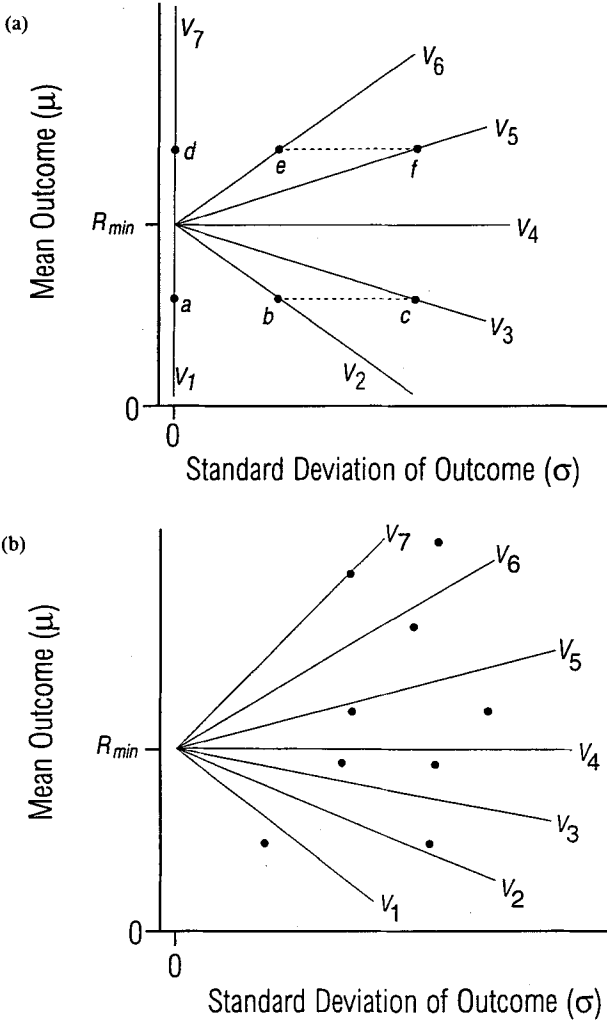
$$Z = (\mu - R_{\min})/\sigma \quad (2)$$

Rearranging terms, we have  $\mu = R_{\min} + \sigma Z$ , the slope–intercept equation for a straight line (Figs. 2a and b). Here  $\mu$  is the y-axis coordinate,  $\sigma$  is the x-axis coordinate,  $R_{\min}$  is the y-intercept, and  $Z$  is the slope of the line. The decision maker intent on minimizing the harmful consequences of risk will choose the outcome with a mean/SD pair ( $\mu, \sigma$ ) on the line of highest possible slope. Because all points on a particular line have a fixed  $Z$ , they represent ( $\mu, \sigma$ ) pairs among which the forager should be indifferent. The set of lines emanating from  $R_{\min}$  constitutes a risk indifference or isovalue map, with value increasing from  $v_1$ , to  $v_2$ , etc. (Figs. 2a and b).

The Z-score isovalue map gives us several rules of shortfall minimization widely used in biology. The *expected energy budget rule* predicts that organisms



in negative energy balance ( $\mu < R_{min}$ ) always prefers a variable to a constant reward, if the means of the rewards are equal (b preferred over a; Fig. 2a). Those in positive balance ( $\mu > R_{min}$ ) prefer the constant reward (d preferred over e). The *extreme variance rule* compares options with a constant mean and nonzero



**Fig. 2.** Isovalue maps for two risk-sensitive models and normal outcome distributions: (a) the Z-score model, showing expected energy budget and extreme variance rule; (b) Z-score, showing a general distribution of outcomes; (c) the linear variance discounting (LVD) model. The variables  $v_1$  through  $v_n$  designate isoclines of increasing value. Each of the dots in b represents the mean and standard deviation (the  $\mu, \sigma$  pair) of one alternative with the set of behavioral options.

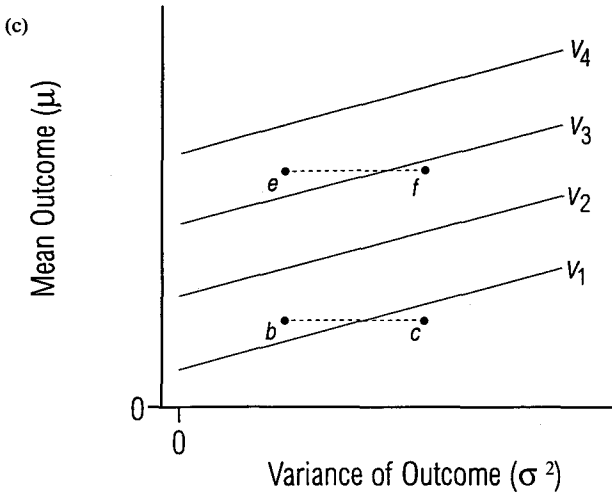


Fig. 2. (Continued)

variances. Organisms in negative energy balance maximize variance (c preferable to b), whereas those in positive energy balance minimize it (e preferable to f). More generally, the *Z-score rule* (Fig. 2b) identifies the shortfall-minimizing alternative from any array of  $(\mu, \sigma)$  combinations. It is that alternative with an outcome  $[(\mu, \sigma)$  pair] tangent to the indifference line of highest value (steepest slope).

The *Z-score* model has been used widely in biology and occasionally in anthropology. However, it has several important limitations. (i) It is based on the discrete interval,  $d_{R_{min}}$ . At the start of a time period the organism selects the tactic most likely to surpass  $R_{min}$  at its conclusion. The organism does not adjust tactics dynamically according to its ongoing experience during that period.  $d_{R_{min}}$  is partly a modeling artifice. Ideally it also reflects the organism's natural history. For a small song bird nightfall ends foraging, and the requirements of overnight survival set the fitness consequences of the day's yield. A logical  $d_{R_{min}}$  is the diurnal cycle. Onset of a migratory (see Moore and Simm, 1986) or reproductive season that requires a minimum body weight for success or onset of a lean season requiring a minimum-sized food cache might determine other potentially significant intervals. (ii) The *Z-score* approach makes no provision for carryover of a surplus to a successive interval. The outcome that surpasses  $R_{min}$  by a wide margin is treated as if it is no more valuable than the outcome that exceeds it only by a hair's breadth. (iii) Additionally, the model performs poorly as outcome variability approaches zero. The value of all possible tactics for which  $\sigma = 0$  is set at either 0 ( $v_1$ ; Fig. 2a), for all  $\mu < R_{min}$ , or 1 ( $v_7$ ; Fig. 2a), for all  $\mu > R_{min}$ . This violates our intuition that fitness or utility should be a more continuous function of mean outcome ( $\mu$ ). Put simply, the *Z-score* model is not effective in comparing constant or near to constant food rewards. It also predicts complete indifference to variance (represented

by  $\sigma$ ) if  $\mu = R_{\min}$ . The significance of these limitations depends on the behavior in question, on the natural history of the organism, and on its environment.

### *Linear Variance Discounting*

A second model, linear variance discounting (LVD), is used widely in economics and occasionally in biology (Ellner and Real, 1989; Real, 1980). It assumes that the value function  $V(x)$  is a negative exponential (concave, with a shape roughly like that of the sigmoid curve to the right of the inflection point; Fig. 1b). LVD organisms are indifferent among normalized mean/variance combinations given by

$$v = \mu - k\sigma^2 \quad (3)$$

The value ( $v$ ) is a function of the expected reward ( $\mu$ ), discounted to a fixed extent ( $k$ ) by the variance ( $\sigma^2$ ). In effect,  $k$  measures the undesirability of variance. The formula shows the increase in mean reward required for indifference to a certain increase in variance. By rearranging terms to  $\mu = v + k\sigma^2$ , the LVD formula can be represented like the Z-score model, but with variance ( $\sigma^2$ ) rather than standard deviation ( $\sigma$ ) on the abscissa (Fig. 2c). A value-minded forager always prefers higher to lower lines but should be indifferent among choices lying along a line ( $v_1, v_2$ , etc.).

Whereas the Z-score model predicts that risk sensitivity changes as mean intake increases, the LVD model assumes constant aversion, irrespective of the mean (Caraco and Lima, 1985). Stephens and Paton (1986) use this divergence in an ingenious test to evaluate which model better fits experimental results with risk-sensitive, rufous hummingbirds (*Selaphoruous rufus*). They examined food intake choices between two options with the same low mean but different variances (e.g., b and c; Fig. 2a). They then added a constant amount of food to each reward in the experimental schedule. This elevates the average intake but does not change  $\sigma$  or  $\sigma^2$  (e.g., e and f; Fig. 2a). From the first to the second test the birds switched their preference from the higher to lower variability. Such a change is predicted by the Z-score model (extreme variance rule; Fig. 2a) but contrary to the prediction of the LVD model (Fig. 2c). Rufous hummingbirds do not behave as if  $k$  is the constant assumed by the linear variance discounting model.

Salient limitations of the LVD model are as follows. (i) The model violates our intuition that an organism's response to variability will be a function of its mean expectations. Constant risk (variance) aversion seems unlikely. The exchange rate fluctuations that doom the impoverished student traveler may be little more than a nuisance to the affluent vacationer. (ii) Because it draws only on a concave value function, LVD predicts universal risk aversion. Unlike the Z-score model, it forces us to conclude that risk-neutral or risk-prone behavior is always irrational.

(iii) Because the predictions of LVD are independent of  $\mu$ , it ignores the forager's current energy budget. There is no equivalent of  $R_{\min}$  in this model. (iv) In contrast, the LVD model solves one shortcoming of the Z-score approach. It can represent relative value as a continuous function of mean outcome even at  $\sigma^2 = 0$  (see Fig. 2c).

### *General Variance Discounting*

General variance discounting (GVD) draws on the full flexibility of Eq. (1). For normally distributed outcomes, GVD produces an isovalue map according to the formula

$$v = \mu - G(x)\sigma^2 \quad (4)$$

This is Eq. (3) with a discounting function  $G(x)$  in place of the constant ( $k$ ). We might, for instance, specify that variance is to be discounted as a function of the mean [ $G(x) = f(\mu)$ ] and thereby avoid the assumption of constant risk aversion.

Using variant forms of the sigmoid value function, we show how the Z-score and LVD models serve as special cases of the GVD approach (Fig. 3). This substantiates our earlier claim that a sigmoid curve has a high level of generality in the analysis of subsistence adaptations. The value function,  $V(x)$ , is shown in Fig. 3 as a near-step function (Fig. 3d), a smooth sigmoid function (Fig. 3e), and a near-linear function (Fig. 3f), with their corresponding isovalue maps (Figs. 3a–c). Figure 3a approaches the indifference topography of the Z-score model (rotated 90°), including its relative insensitivity to mean outcomes when  $\sigma = 0$ . As the value function approaches the linear, the isovalue curves become more vertical (Fig. 3c). The expected value is determined almost solely by the mean of the outcome distribution. The smoothed sigmoid function (Fig. 3b) produces a risk-sensitive indifference map that responds to both  $\mu$  and to  $\sigma$  over their full ranges. It thus avoids many of the counterintuitive features of the Z-score and linear variance discounting models.

The various approaches to shortfall minimization can be integrated by observing that as the sigmoid value function is transformed toward a step function (Fig. 3d), the corresponding isovalue map shifts toward the fanlike form in Fig. 3a, pinching off, at low variance, its sensitivity to mean outcome. As the sigmoid value function becomes increasingly linear (Fig. 3f), the indifference map becomes increasingly vertical and thus insensitive to outcome variance (Fig. 3c). Comparison of Figs. 3a through 3c demonstrates when we should expect the simplified Z-score or LVD models to make qualitatively sound predictions (that is, predictions closely matching those of the more robust sigmoid function). For instance, the Z-score indifference map (Fig. 3a) is like that for the sigmoid value function (Fig. 3b) for values of  $\sigma$  not located near 0. In this range it sheds some of its limitations

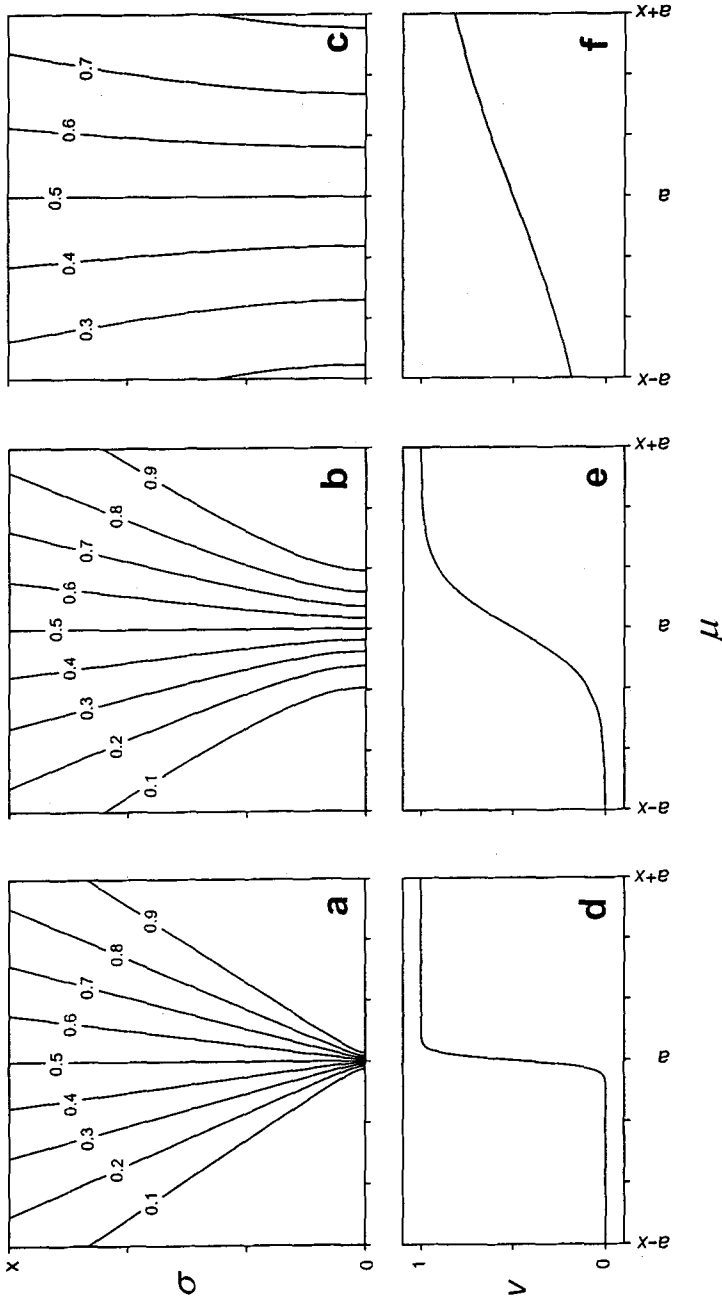


Fig. 3. Isovalue maps for a general risk-sensitive model, based on variant forms of a sigmoid value function and normalized outcome distributions. Each of the value functions, which range from a near-step function (d), through a smooth sigmoid (e), to a near linear-form (f), has a corresponding isovalue map, a through c, respectively. At  $\sigma = 0$  the isovalue map is congruent with the value function. As  $\sigma$  increases from zero, it spreads the value function into a fan-shaped form. [The sigmoid curve used here was generated by the formula  $y = 1/(1 + e^{-\alpha/\beta})$ , where  $\alpha =$  (outcome - inflection point of the fitness function) and  $\beta$  is assigned values of 3, 22, and 100 for d, e, and f, respectively].

by reliably mimicking the more complicated but more general model. The utility function governing the LVD approach is like that for the segment of the sigmoid function to the right of the inflection point. Note that the corresponding portion of Fig. 3b (that for which  $\mu > R_{\min}$ ) would give indifference curves like the linear ones of the LVD model were the  $x$ -axis transformed to  $\sigma^2$  (see Fig. 2c). In qualitative terms, the LVD model fits situations in which behavior is not affected by a convex or accelerating segment of the value function.

### Confounding Factors

Various factors can complicate the predictions of these simple risk-sensitive models. We mention four of them.

#### *Variable Reward Versus Variable Delay*

Risk-sensitive subsistence may arise from unpredictably sized outcomes encountered on a regular schedule, from regularly sized outcomes at intervals of unpredictable duration, or from some combination of these possibilities. If intervals are unpredictable, reward value may be complicated by future discounting (see Rogers, 1994). Because (positive) discounting decreases the present value of a delayed reward, it favors immediacy (Kagel *et al.*, 1986a). Consequently, it shifts preferences toward temporally variable outcomes compared to a same (average) reward at regular intervals. Variable delay favors risk-prone choices. Research with pigeons indicates that they typically are risk prone in time and risk averse in quantity (Hamm and Shettleworth, 1987). This is a growing research area in biology (Benson and Stephens, 1996; Green and Myerson, 1996; Kacelnik and Bateson, 1996; Rebores and Kacelnik, 1991).

#### *Skew Outcome Distributions*

Normal distributions have two useful attributes: they are robust in the face of potentially restrictive assumptions and they are symmetrical. Caraco and Chasin (1984) show that if the outcome distribution is nonsymmetrical, foragers with constant or decreasing risk aversion generally benefit by electing positive over negative skew for reward distributions with equal means and variances. Negative skew may be preferred for  $R_{\min}$  equal to or very close to the mean outcome. A dearth of naturalistic studies forestalls knowing if skew (third-moment) outcome distributions are needed for realism.

#### *Continuous Risk-Sensitive Adjustments*

The Z-score approach envisions risk sensitivity as a sequence of choices that are set for the duration of the critical interval ( $d_{R_{\min}}$ ) rather than as a continuous

process of adjusting tactics to conditions. Analysis of continuous adjustments requires the more complicated technique of dynamic optimization. Houston and McNamara (1985; see also Bednekoff, 1996) model the dynamic choices of a risk-sensitive forager with two resources. The organism continuously monitors its energy reserves and remaining foraging time. It has the twin goals of maintaining positive energy balance and surmounting an end-of-day threshold of reserves. Its best tactic is risk averse (take both prey) except if low reserves late in the day create the possibility of ending below its threshold. Then it must gamble and switch to the higher variance, one-prey option. The trade-off here acts like the extreme variance rule applied within the foraging interval.

### *Uncertainty*

Uncertainty also may affect risk sensitivity, especially in an environment in which the basic parameters of subsistence choices are changing rapidly. McNamara (1996) argues that selecting an unpredictable option in order to sample its outcome distribution accurately is costly, and the usefulness of the information may be ephemeral. Such appraisal difficulties bias choices toward less variable outcomes, making the uncertain organism more risk averse than would be predicted from a pure, risk-sensitive model.

### **Summary**

The analysis of risk-sensitive subsistence adaptations requires a two-step procedure: outcome distributions for each alternative behavior must be specified, and appropriate values must be assigned to the outcomes and then summed. The Z-score, LVD, and GVD approaches each accomplish this, albeit with important limitations. Using isovalue maps (Fig. 3), we have shown how these models relate to one another, how their respective limitations affect their performance, and how these limitations can sometimes be overcome. The Z-score and LVD approaches are restricted cases of a convex-concave, GVD, model. The Z-score approach is poorly suited to situations of zero or near-zero variances but allows for changes in variance discounting as a function of mean outcome. The LVD approach requires constant discounting of variance but gives more satisfactory results for comparisons involving constant (nonvarying) outcomes. Compared to the Z-score model, the more general curvilinear form of the sigmoid value function has significant advantages. We can assign the inflection point of the sigmoid value function a role comparable to that of  $R_{\min}$  in the Z-score model. This places the minimum requirement within a smoothed or graded set of changing marginal values. Compared to the Z-score mode, it also allows us to represent the enhanced value that arises from a carryover surplus. The exact form of the sigmoid can be varied to represent the behavior of interest and the natural history of the organism and its environment in a wide variety of circumstances.

### Relationship Between Tactic and Outcome

Applying risk-sensitive models also requires that we understand (or speculate about) reward distributions. Assuming normality, this entails specifying the mean and standard deviation of each alternative within a set of behavioral options. The set of  $(\mu, \sigma)$  pairs makes an array of shortfall-minimizing possibilities on the isovalue map (Fig. 2b). Its shape and the distribution of the pairs with respect to tactics determine how risk sensitivity affects choice. If the array is narrowly concave or sharply pointed on its upper surface (with greater dispersion about  $\mu$  than  $\sigma$ ), then the shortfall-minimizing tactic (i) converges with the rate-maximizing option, (ii) is relatively insensitive to  $R_{\min}$  or the sigmoid inflection point, and (iii) is also relatively insensitive to the precise form of the value function. A narrowly concave outcome array also makes it difficult to observe risk-sensitive choices in naturalistic or experimental settings [e.g., Cartar and Abrahams (1996, Fig. 2c)]. The contrasting set of statements apply if the array has a relatively shallow and broad upper surface (e.g., greater dispersion about  $\sigma$  than  $\mu$ ). The shortfall-minimizing option (i) will likely diverge from the deterministic optimum, (ii) will be sensitive to  $R_{\min}$ , and (iii) will be sensitive to the precise form of the value function.

#### *Patch Residence*

Risk-sensitive variants of two key foraging models are available. The first is a stochastic variant of the marginal-value theorem (Charnov, 1976). The marginal-value theorem specifies how long an organism should continue harvesting a patch of declining value before incurring the travel costs to find a similar location not depleted of resources. Stephens and Charnov (1982) derive the  $(\mu, \sigma)$  pairs of energy gain for a shortfall-minimizing forager faced with stochastic variation in the time required to locate a fresh patch. The Z-score model result produces these qualitative predictions: (i) for a wide range of  $R_{\min}$  values, the safety-first (risk-sensitive) residence time will be close to the rate-maximizing time ( $\mu_{\max}$ ) that would be specified by the deterministic version of the model; (ii) if  $R_{\min} < \mu_{\max}$ , the risk-sensitive forager will remain longer than would be predicted by the deterministic model; and (iii) if  $R_{\min} > \mu_{\max}$ , the forager will depart sooner.

#### *Resource Selection*

Two analyses examine outcome distributions for the encounter-contingent resource selection model (Stephens and Krebs, 1986). Winterhalder (1986a,b) simulated stochastic variation in prey encounter rates and handling times for six resource species, ranked and harvested in the six combinations of "diet breadth" given by the deterministic version of the model. Diet breadths 1 through 6 were arrayed counterclockwise around a concave parabola. Tucker (1996) has identified



several shortcomings in this analysis. Most importantly, there is no *a priori* reason that the optimal shortfall-minimizing combination of resources will be found among the six options that are adequate for the deterministic form of the model. Tucker found several combinations (among the 64 possible permutations of a data set of six resources) that outperformed any of those used by Winterhalder. Weissburg's (1991) simulation examined  $(\mu, \sigma)$  arrays for encounter-contingent diets under a variety of assumptions about the functional relationships between prey size, profitability, and encounter rates. However, like Winterhalder, Weissburg looked only at resource combinations given by the deterministic model, leaving the generality of his results uncertain.

### Summary

The very limited progress in analyzing stochastic outcome distributions for subsistence adaptations stands in sharp contrast to the advanced analytical work on value functions. Theoretical efforts are few. They are limited to patch and resource selection models and are compromised by known limitations. We are unaware of any empirical studies that would allow us to formulate and compare outcome distributions empirically, or to assess the fidelity of modeling efforts to field conditions. This is a serious gap. Given basic similarities in the value functions examined above (Figs. 3a–c), predictions about risk-sensitive subsistence choices may depend largely on the shape of  $(\mu, \sigma)$  arrays, about which we know little. Further, only the most general of statistical principles give us any assurance that these distributions are normal, as is assumed in the models that are used most commonly.

## APPLICATIONS IN BIOLOGY

Table I lists and describes biological research reports that specifically test for shortfall minimization with respect to resource selection (see also Kacelnik and Bateson, 1996; Stephens and Krebs, 1986, p. 135). Table II lists biological papers describing how other behaviors function to mitigate the subsistence consequences of unpredictable environmental variability. Our comments are given in summary form, drawing on these tables and the literature that they cite. We begin our review of cases with the nonhuman literature because it illuminates both the logic and the widespread applicability of the risk-sensitive models just summarized.

In biology, most research motivated by shortfall minimizing models of resource choice has been experimental and laboratory based. Field experiments or naturalistic observations are rare (for exceptions see Barkan, 1990; Cartar, 1991; Gillespie and Caraco, 1987; and Uetz, 1996). Biological studies of risk-sensitive resource selection now are of sufficient duration, number, and variety that

methodological pitfalls have become evident (Kacelnik and Bateson, 1996), alternative models are available (Bednekoff, 1996; McNamara, 1996), and competing explanations for some results have been proposed (Smallwood, 1993, 1996). The expected energy budget rule has gained in importance because it makes predictions that appear to be unique to a risk-sensitive framework (Kacelnik and Bateson, 1966, p. 419).

Following pioneering work by Caraco *et al.* (1980), the majority of papers test the expected energy budget rule. Organisms are given a choice between a fixed interval to constant or stochastically variable rewards with equal means. Analyses of the extreme variance rule or multioption, *Z*-score trade-offs are less common. In such experiments, virtually all the species (but sometimes not all individuals) observed in laboratory and field studies demonstrate fairly consistent, risk-sensitive behavior. Indifference to reward variability is rare. It is clear that risk-sensitive behaviors have taxonomically widespread evolutionary significance, which suggests that they may be present in primates as well as our hominid ancestors.

Risk-prone resource selection under negative energy balance is predicted and is regularly observed in passerines (e.g., juncos, sparrows), shrews, and other small, temperate-zone endotherms. These species tend to be solitary, feeding specialists with low reserves, high metabolic requirements, and periodic and relatively lengthy interruptions of foraging (e.g., long, cold nights). Bitterlings, an ectothermic fish, can be induced to make risk-prone choices only if they are far below energy balance (Young *et al.*, 1990).

Two examples illustrate this work. Caraco *et al.* (1990) recorded seed consumption of juvenile and adult yellow-eyed juncos (*Junco phaeonotus*) at ambient temperatures of 19, 10, and 1°C. The birds ate significantly more seeds at each drop of temperature, signaling increasing energy requirements. The birds were then offered a choice between a constant reward and a variable reward (equal mean). With a negative energy budget at 1°C, only one bird showed significant risk aversion; 42% were risk prone. With a positive energy budget at 19°C, there was only one case of risk proneness, and 61% of the birds were risk averse. The response under each condition is largely consistent with the expected energy budget rule, thus with adaptive risk sensitivity.

Moore and Simm (1986) proposed that yellow-rumped warblers (*Dendroica coronata*) would become risk prone during the premigratory fattening period, when they are under pressure to gain weight rapidly. In their experiment five birds served as controls and five were stimulated to anticipate migration by manipulating the photoperiod of their laboratory environment. After forced-choice (learning) trials, the birds were given open-choice trials with a fixed delay to the option of a constant or variable reward (same mean). Consistent with the expectation, premigratory birds chose the variable rewards, whereas controls preferred the constant reward. Notably, when the experimental (risk-prone) birds attained maximum weight they shifted back to the risk-averse (constant) outcome.

Table I. Summary of Risk-Sensitive Foraging Studies in Nonhuman Organisms

Study	Species	Varied quantity	Test and result	Interpretation: Support for hypothesis? Specific challenge?
Banschbach and Waddington, 1994	Honeybees	Nectar concentration	Expected energy budget rule: indifference to variability despite manipulation of colony reserves	No (extreme eusociality and large numbers of foragers may moot applicability of risk-sensitive hypothesis)
Barkan, 1990	Black-capped chickadees	Sunflower seed, variable quantity	Expected energy budget rule (field): dominants, assumed to be in positive energy balance, were risk averse	Yes
Barnard and Brown, 1985	Common shrews ( <i>Sorex araneus</i> )	Mealworm segments	Expected energy budget rule	Yes
Battalio <i>et al.</i> , 1985	Laboratory rats	Food pellets, variable quantity	Expected energy budget rule (along with effects of mean-preserving spreads on choice and tests of independence axiom)	No (risk averse despite negative energy budget; could be due to large body size)
Caraco, 1981	Dark-eyed juncos ( <i>Junco hyemalis</i> )	Seed, variable quantity	Expected energy budget rule: risk prone when negative; risk averse when positive	Yes
Caraco, 1982, 1983	White-crowned sparrows ( <i>Zonotrichia leucophrys</i> )	Millet seed, variable quantity	Expected energy budget rule, and Z-score model: risk prone when negative; risk averse when positive	Yes
Caraco <i>et al.</i> , 1990	Yellowed-eyed juncos ( <i>Junco phaeonotus</i> )	Millet seed, variable quantity	Expected energy budget rule, using ambient temperature to manipulate energy balance	Yes (procedure corrects earlier problems of methodology)
Caraco and Chasin, 1984	White-crowned sparrows ( <i>Zonotrichia leucophrys</i> )	Millet seed, variable quantity	Test for risk sensitivity to reward skew, for outcome distributions with equal means and variances	Yes (positive skew preferred)
Caraco and Lima, 1985	Dark-eyed juncos ( <i>Junco hyemalis</i> )	Millet seed, variable quantity	(1) Test for sensitivity to mean-variance trade-offs; and (2) for diminishing vs. constant aversion	(1) Yes; (2) Nonsignificant results

Caraco <i>et al.</i> , 1980	Yellow-eyed juncos ( <i>Junco phaeonotus</i> )	Millet seed, variable quantity	Expected energy budget rule: risk prone when energy budget negative; averse when it is positive	Yes (experimental derivation of utility map for juncos)
Cartar, 1991	Bumblebees ( <i>Bombus melanopygus</i> , <i>mixtus</i> , and <i>sitkensis</i> )	Nectar volume and variability	Expected energy budget rule: depleting or augmenting colony stores led to switching between more and less variable nectar sources (dwarf huckleberry versus seablush)	Yes
Cartar and Abrahams, 1996	Bumblebees ( <i>Bombus occidentalis</i> )	Nectar volume	Patch departure threshold, manipulation of energy stores in colony; departure patterns not predicted by shortfall minimizing	No (narrowly concave outcome array may have obscured risk-sensitive behavior)
Cartar and Dill, 1990	Bumblebees ( <i>Bombus occidentalis</i> )	Nectar volume in colony store	Expected energy budget rule: switch from risk averse to risk prone as colony reserves fall below its requirement	Yes (but see Banschbach and Waddington, 1994)
Clements, 1990	Blue jays	Mealworms, variable quantity	Expected energy budget rule: risk averse under negative energy budget	No (omnivores may have less need for risk-prone behavior)
Ekman and Hake, 1988	Greenfinches ( <i>Carduelis chloris</i> )	Solitary versus group foraging	Risk-averse social foraging under positive energy budget, shifting to risk-prone solitary foraging under negative energy budget	Yes
Gillespie and Caraco, 1987	Long-jawed, orb-weaving spider ( <i>Tetragnatha elongata</i> )	Creekside (impooverished) versus lakeside (rich) habitats	Naturalistic/experimental test of expected energy budget rule using web movement frequency in habitats providing capture rates below and above female reproductive requirements	Yes (but see Smallwood, 1993)
Ha, 1991; Ha <i>et al.</i> , 1990	Gray jays ( <i>Perisoreus canadensis</i> )	Standardized food pellets, variable time	Expected energy budget rule: risk prone, irrespective of energy balance	No (inconsistency perhaps explained by time discounting)
Hamm and Shettleworth, 1987	Pigeons	Food pellets, variable quantity	Risk sensitivity and expected energy budget rule; preference for constant outcome decreased as food intake decreased	Yes (risk aversion sensitivity to mean and variance)
Hastjarjo <i>et al.</i> , 1990	Albino rats	Amount of food	Expected energy budget rule	Inconclusive (but see Houston, 1991)

(Continued)

Table I. (Continued)

Study	Species	Varied quantity	Test and result	Interpretation: Support for hypothesis? Specific challenge?
Kagel <i>et al.</i> , 1986b	Albino rats	Water, variable quantity	Expected energy budget rule; water in place of energy. Risk averse despite severe water deficit	No (negative result perhaps due to relative large size)
Koops and Giraldeau, 1996	European starlings ( <i>Sturnus vulgaris</i> )	Patches of food pellets, varying clump density	Frequency of scrounging relative to clump density and expected energy budget rule	Yes (risk-sensitive rather than rate-maximizing expectations were supported)
Lawes and Perrin, 1995	Round-eared elephant shrews ( <i>Macroscelides proboscideus</i> )	Mealworms, variable quantity	Expected energy budget rule: risk averse under short-term negative energy budget	No (facultative torpor and generalist feeding may be alternatives)
Moore and Simm, 1986	Yellow-rumped warblers ( <i>Dendroica coronata</i> )	Larvae, variable quantity	High energy accumulation requirement of premigratory period predicted to increase risk-prone foraging	Yes
Perez and Waddington, 1996	Carpenter bees ( <i>Xylocopa micans</i> )	Nectar volume and sugar concentration	Expected energy budget rule. Result: risk indifference, unaffected by energy budget	No (perhaps due to the large number of foraging episodes in this solitary, nonstoring species)
Real, 1981, Real <i>et al.</i> , 1982	Bumblebees ( <i>Bombus sandersoni</i> ); wasps ( <i>Vespula maculifrons</i> )	Nectar volume/flower	Linear variance discounting risk averse under positive energy budgets	Yes (result debated by Harder and Real, 1987; Possingham <i>et al.</i> , 1990)
Reboreda and Kacelnik, 1991	Starlings ( <i>Sturnus vulgaris</i> )	Grain, variable amount and delay	Indifferent or risk averse to varying amount; indifferent or risk prone to varying delay; negative correlation of intake rate and risk proneness	Mixed (discounting or mechanisms of memory may help to explain results)
Stephens and Paton, 1986	Hummingbirds ( <i>Selasphorus rufus</i> )	Sugar solution, variable quantity	Choice behavior consistent with Z-score but not linear variance discounting	Yes

Tuttle <i>et al.</i> , 1990	White-throated sparrow ( <i>Zonotrichia albicollis</i> )	Thistle seed, variable quantities	Expected energy budget rule: risk aversion increased over trials (that is, with experience)	Yes (albeit constrained by frequency-dependent preference for rare types)
Uetz, 1996	Colonial, web-building spiders ( <i>Metepetra incassata</i> )	Site richness	Facultative, colonial web building is a shortfall-minimizing response to rich environments; solitary webs are a risk-prone response to poor environments	Yes
Waddington <i>et al.</i> , 1981	Bumblebees ( <i>Bombus edwardsii</i> )	Continuous vs. intermittent nectar	Risk averse to temporal reward variation	Importance of variance of rewards in choice models; differences in individual preferences due to "learning"
Wunderle and O'Brien, 1985; Wunderle <i>et al.</i> , 1987; Wunderle and Cotto-Navaro, 1988	Bananaquits ( <i>Coereba flaveola</i> )	Nectar volume; nectar quality	Risk sensitivity demonstrated and tested for conformity with Z-score (expected energy budget rule) vs. linear variance discounting	Mixed (results consistent with LYD but not with Z-score model; e.g., varying risk aversion but risk-prone behavior not demonstrated)
Young <i>et al.</i> , 1990	Bitterlings ( <i>Rhodeus sericus</i> )	Trout pellets, variable quantity	Expected energy budget rule: variable reward selection increased with duration of deprivation	Yes
Zabludoff <i>et al.</i> , 1988	Laboratory rats ( <i>Rattus norvegicus</i> )	Food delay	Test of temporal discounting versus energy budget rule; results inconclusive	No (large size may account for results)

**Table II.** Behaviors Hypothesized or Demonstrated to Minimize Subsistence Shortfalls in Nonhuman Species, in Relation to Z-Score Model Parameters

Behavior	Example(s)	Effect on Z-score variables		
		$R_{\min}$	$\mu$	$\sigma$
Resource selection; foraging tactic	See Table I	—	—	Increase or decrease
Torpor	Lawes and Perrin, 1995; Reichman and Brown, 1979; Wrazen and Wrazen, 1982	Decrease	—	—
Fat reserves	Ekman and Hake, 1990; Lima, 1986; Rogers, 1987	Decrease	—	—
Group foraging	Binford and Rypstra, 1992; Brown, 1988; Brown <i>et al.</i> , 1991; Ekman and Hake, 1988; Ekman and Rosander, 1987; Pulliam and Millikan, 1982; Uetz, 1996	—	—	Decrease
Pooling (social insects)	Banschbach and Waddington, 1994; Harder and Real, 1987	—	—	Decrease
Pooling/sharing (other species)	Heinrich and Marzluff, 1995; Hoelzel, 1991; Packer and Rutan, 1988; Stanford, 1995; Wilkinson, 1988	—	—	Decrease
Hoarding/caching (storage)	Ágren <i>et al.</i> , 1989; Clarke and Kramer, 1994; Daly <i>et al.</i> , 1992; Formanowicz <i>et al.</i> , 1989; Hurly and Robertson, 1990; Jenkins <i>et al.</i> , 1995; Nilsson <i>et al.</i> , 1993; Shaffer, 1980; Smith and Reichman, 1984; Vander Wall, 1990	—	—	Decrease

In contrast to studies like those summarized immediately above, it has proven difficult to induce risk-prone resource selection in omnivorous species (e.g., bananaquits, blue jays, elephant shrews), those with larger body size (laboratory rats, gray jays), or those with alternative shortfall-minimizing tactics such as torpor (e.g., elephant shrew) or nocturnal hypothermia [some chickadees (Rogers, 1987)]. Likewise, it has been difficult to show risk-prone resource selection in some social insects, perhaps because an individual's food intake is not dependent on its own, immediate foraging success. These studies suggest that the expected energy budget rule may apply only rarely to hominids, nonhominid primates, and modern humans, which are omnivorous and relatively large species.

Animals are commonly risk averse when quantity is variable. They often are risk prone when the time to reward is variable. This is observed both across studies and within them when both treatments have been used (e.g., Bateson and Kacelnik, 1995). Trials manipulating delay before reward provide less evidence for the expected energy budget rule than those manipulating the amount of reward (Kacelnik and Bateson, 1996). As we noted earlier, such results suggest that these species are discounting the value of delayed rewards.

It should be noted that risk-prone behavior is a desperation measure in which the best choice available nonetheless has low odds of success ( $<50\%$  chance of making  $R_{\min}$  for a cumulative normal distribution). The ability to induce this tactic in some species offers a striking confirmation of the importance to them of subsistence risk. However, the environmental setting that leads to risk-prone choices obviously will have placed strong selection pressures on tactics that would forestall the need for them. That is, a ready shift to risk-prone food selection may be characteristic only of species with severely constrained alternatives. Because quantitative tests in the field are rare, we do not know the extent to which the risk-prone choices that can be observed in the laboratory are used in nature. For instance, uncertainty due to environmental change in field settings may have the consequence of greater risk aversion (McNamara, 1996).

Finally, biologists have proposed and investigated a variety of alternative behaviors believed to minimize the likelihood of shortfalls. In order to demonstrate the organizing potential of the theory introduced in the prior section, we have grouped these by their presumed effect on variables of the Z-score model (Table II). For instance, torpor and related physiological states, as well as acquisition of fat reserves, lessen  $R_{\min}$ . Group foraging, pooling, theft (scrounging, scavenging), and hoarding (caching, storage) reduce  $\sigma$ . Table II (see also Table IV) presents each of these tactics in its risk-averse orientation. Thus, if we assume a concave value function, joining a group of increasing size may lessen an individual's chance of a shortfall by reducing consumption variance. Table II does not explicitly show but we emphasize that the inverse of each behavior also may serve as a shortfall-minimizing tactic when risk-prone behavior is the better adaptive option. For instance, if leaving a group increases individual variance, then it may



be a risk-sensitive adaptive tactic when the value function is convex (if  $\mu < R_{\min}$ ). Other of these variance related behaviors may be similarly reversible, although this has been little investigated.

There has been relatively little work on cost-benefit trade-offs among the various shortfall-minimizing alternatives in Table II (see Smith and Reichman, 1984; Wrazen and Wrazen, 1982) and, to our knowledge, no attempt to place such studies within the formal framework of outcome functions and isovalue maps. Although experimental demonstration of the switch from risk-averse to risk-prone behavior offers impressive confirmation of sensitivity to risk, more subtle cost-benefit trade-offs among various types and degrees of risk-averse behaviors are likely to dominate the behavioral repertoire of an organism. In model terms, most of the adaptive action, most of the time, will be among behavioral alternatives whose outcomes lie to the right of the sigmoid inflection point (e.g., those above  $v_4$ ; Fig. 2b).

In the following paragraphs we briefly discuss some of the other shortfall-minimizing tactics described in the biological literature. These studies provide archaeologists and anthropologists with a diverse set of models, concepts, and comparative evidence that are potentially applicable to primates, hominids, and prehistoric/historic human foragers.

Organisms able to drop their basal metabolic requirements can use torpor to wait out temporary periods of limited food availability. Endogenous storage of fat reserves is a related option. Rogers (1987) found lower fat reserves in bird guilds exploiting more predictable resources. Similarly, Ekman and Hake (1990) found that greenfinches put on more reserves in situations of lower temperatures and less predictable foraging success.

Group foraging is common in cliff swallows feeding on ephemeral swarms of insects, a clumped, patchy resource of short duration and high density. Brown (1988) compared solitary- and group-foraging sparrows and found that food intake "variance declined markedly with increasing group size" (p. 787). Pulliam and Millikan (1982) and Ekman and Rosander (1987) gave various ways in which gregarious foraging can mitigate variance. In *local enhancement*, swallows (Brown, 1988) and greenfinches (Ekman and Hake, 1988) reduce intake variability through observational learning as naïve members watch the more knowledgeable group members locate prey. Information sharing about the location of ephemeral food patches also reduces variance in individual food intake (Caraco and Pulliam, 1984). It can be incidental and passive [colonial spiders monitoring web vibrations (Uetz, 1996)]. Or it can be active. For instance, on cold, cloudy, calm days when foraging success is poor, cliff swallows use a "squeak call" to alert conspecifics that a mass of insects has been found (Brown *et al.*, 1991). The caller benefits by watching others track the erratic swarms.

Prey that bounce off one spider's web may be entangled in another's (Uetz, 1996); insects flying out of the path of one bird end up in the beak of its neighbor

(Pulliam and Millikan, 1982). This is known as the "ricochet" effect. In addition, group foragers sometimes share in vigilance efforts (Binford and Rypstra, 1992; Pulliam, 1973). More effective predator detection increases the time that individuals are able to spend feeding. Finally, scrounging from successful foragers reduces intake variance (see Beauchamp and Giraldeau, 1996; Binford and Rypstra, 1992; Koops and Giraldeau, 1996).

Social insects are masters at variance reduction through the "pooling" of resources. Honeybees are risk indifferent to the choice between constant and variable levels of nectar in artificial flowers (Banschback and Waddington, 1994). Because hundreds, if not thousands, of foraging workers may be active at any given time, colony survival is not dependent on the risk-sensitive foraging of individual workers (see debate by Cartar and Abrahams, 1996; Cartar and Dill, 1990; Harder and Real, 1987). Food sharing has been proposed to reduce consumption variance of separately foraging group members in social carnivores (Packer and Ruttan, 1988), chimpanzees (Stanford, 1995), common ravens (Heinrich and Marzluff, 1995), bats (Wilkinson, 1988), and killer whales (Hoelzel, 1991).

Storage (also known as hoarding or caching) is a common tactic during periods of unreliable or low productivity (Vander Wall, 1990). It is more common in variable environments [e.g., high latitude, terrestrial (Smith and Reichman, 1984)]. *Larder hoarding* concentrates a food store in one protected location. *Scatter hoarding* disperses small caches within a home range (Formanowicz *et al.*, 1989; Hurly and Robertson, 1990, p. 95). Hoard recovery itself is prone to stochastic variation as a result of theft, rot, mildew, or insect infestation. For example, European nuthatches retrieve more sunflower seeds from a larder hoard as the temperature decreases. On days with high temperatures they meet needs with ordinary foraging (Nilsson *et al.*, 1993). Scatter hoarding may reduce variation in recovery if at least some hoards escape loss (Daly *et al.*, 1992; Jenkins *et al.*, 1995). Scatter hoarding also may minimize the loss of food due to theft (Formanowicz *et al.*, 1989; Shaffer, 1980). Clarke and Kramer (1994) propose that the decline of scatter hoarding with age in eastern chipmunks is explained by their growing ability to defend a centralized larder.

## APPLICATIONS IN ANTHROPOLOGY

Studies of risk-sensitive behaviors of course are not limited to birds, insects, and rodents. Table III summarizes recent anthropological research on subsistence risk in a variety of human societies. Table IV categorizes the observed behavioral tactics in terms of their presumed effect on Z-score variables. Our comments again take summary form.

The number and diversity of these studies suggest a widespread anthropological interest in shortfall-minimizing tactics. Several of these papers use the

Table III. Summary of Anthropological Risk-Sensitive Subsistence Studies

Study	Population	Subsistence system	Proposed shortfall-minimization strategies
Bahuchet, 1993	Aka of Lobaye, Zaire (extant)	Hunter-gatherer	Pooling via two networks: <i>mutual aid network</i> for pooling meat within camp. <i>circulation network</i> : for exchange of iron tools and hunting labor between camps, along kin/marriage lines
Baksh and Johnson, 1990	Machiguenga of Peru (extant)	Hunter-gatherer, fishing, gardening	Foraging risk minimized by foraging, cooperative hunting, information sharing, and magic. Fishing: diversification of techniques, interhousehold fish exchange, storage, and magic. Gardening: crop and variety diversification
Bernus, 1988	Sahelian nomadic pastoralists (Twareg, Fulani, etc.), (extant)	Pastoralism; sheep, cattle, goats, camels	Annual migration and transhumance patterns change in drought years to take advantage of safe regions. Seasonally diminished milk supply compensated with cereals and wild grasses
Browman, 1987	Andean peasants (extant, pre-Columbian)	Agropastoralism	Five major strategies of shortfall minimization in the Andes: increasing land use potential through terracing or ridging; diversification of crops, varieties, activities, and locations; mobility; sharing and cooperative work; and storage
Cashdan, 1985	Semisedentary populations along the Nata River; Basarwa, Tswana, Kalanga (extant)	Basarwa = hunter-gatherer, agriculture, wage labor; Tswana and Kalanga = agropastoralist	Basarwa buffer risk by sharing while Tswana/Kalanga buffer risk through storage. Basarwa don't produce enough surplus to store, because they don't plant as large fields, due to higher mobility, due to cattle wage work ( <i>mafisa</i> system)
Chibnik, 1990	<i>Ribereños</i> , Amazonian floodplain farmers (extant)	Agriculture, fishing	Agricultural loans can potentially increase production and thus reduce risk but obtaining the loans and the risk of defaulting may counteract any risk-reducing benefits of the loan
Chibnik, 1994	<i>Ribereños</i> , Amazonian floodplain farmers (extant)	Agriculture, fishing	<i>Ribereños</i> raise a variety of crops on diverse land forms; high-yielding mudflats or <i>barrales</i> have high risk of flooding; some households use agricultural loans to cultivate rice, a high-price cash crop, on <i>barrales</i>

Colson, 1979	Makah of NW coast, 1940s; Gwembe Tonga of Central Africa, 1950s	Makah = hunter-gatherer-fishers; Gwembe Tonga = agropastoralist	Risk buffered by numerous behavioral "devices"; diversification of activities, storage, information storage about fallback foods/food prep techniques, conversion of foods into durables for storage and trade, social relations and exchanges with neighbors. Also, among the Gwembe Tonga, bad years may incite nonpublic and discrete food-processing techniques, stealing, raiding, migration, and hoarding relief subsidies. Foreign relief may weaken indigenous shortfall-minimizing devices
de Garine and Koppert, 1988	Massa and Mussey of northern Cameroon (extant)	Agropastoralist, fishing, occasional hunting and gathering	Risk of food and money shortage due to short rainy season and spatial variation in water and soil quality. Risk buffered by harvesting wild cereals, cash cropping cotton or rice, planting low-yield varieties that are flood resistant, selling livestock, cattle loans through prestige-enhancing social networks, eating cereals before they are ripe
Forbes, 1989	Modern Greek subsistence farmers	Agriculture	Farmers have different levels of "hazard response mechanisms": field fragmentation (scattering), polycropping trees and arable crops, deliberate overproduction, storage
Garnsey and Morris, 1989	Hellenistic age Greeks	Agriculture	Shortfall minimized through imperialism (increasing diversity of farmland through conquest); extension of farmland; intensification, colonization (emigration), trade, and regulation/redistribution
Goland, 1991	Ainu and Ju/'hoansi (extant)	Hunter-gatherer	Storage is preferred strategy if temporal variability is contingent, as with Ainu; sharing is preferred if low interforager correlation in hunting success, as with Ju/'hoansi
Goland, 1993a,b	Quechua peasants (extant)	Agriculture	Degree to which households scatter fields (reduce variance in returns) is related to the household's subsistence requirements ( $R_{min}$ ), consistent with Z-score model
Halstead, 1989	Thessaly, Greece, 6000-1200 B.C.	Agropastoralist	Shift from household-level risk-averse strategies (crop diversification, field scattering, storage, exchange, overproduction, herd diversification) to community-level storage and exchange of surplus managed by elite social class
Hames, 1990	Yanomamö of Venezuela (extant)	Horticulture, hunter-gatherer	Frequency and scope of sharing increases with riskiness of resource type (gardening < gathering < fishing < small game < large game)

(Continued)

Table III. (Continued)

Study	Population	Subsistence system	Proposed shortfall-minimization strategies
Hegmon, 1989	Hopi, early 20th century	Maize agriculture	"Restricted sharing" (sharing of surplus only between a few households) is the preferable shortfall-minimizing strategy to "pooling" (unrestricted sharing between all households) or no sharing, except when survival threshold is extremely high or low, when sharing is obviated
Jongman and Dekker, 1989	Classic Rome, early-modern Holland	Wheat-based market economy	Risks of poor wheat harvests and volatile markets mitigated by the state through "public intervention." Demand side strategies: (1) eviction of marginal people, (2) restrict nonfood uses of wheat (beer, starch). Supply side strategies: (1) drain lakes to create more farmland; (2) ban exports; (3) price fixing; (4) government/municipal storage; (5) donations by the wealthy; (6) imperialism; statewide diversification of land owning through conquest (Rome)
Kaplan <i>et al.</i> , 1990	Ache of Paraguay (extant)	Hunter-gatherer, agriculture in mission colonies	No correlation between amount of meat and honey produced (preshearing) and amount consumed (posisharing); thus tit-for-fat reciprocity not demonstrated. Better hunters consistently eat less than they procure, while poor hunters consistently eat more than they procure, without reciprocity. Good hunters may tolerate chronic losses in exchange for other fitness-enhancing favors, including better treatment from others and increased paternity
Kohler and Van West, 1996	Northern Anasazi (A.D. 901-1300)	Maize agriculture	Risk aversion (pooling) occurs during periods of high mean production and high spatial variability in production. Periods of low mean production and high temporal and/or spatial variability encourage noncooperative behaviors
Larson <i>et al.</i> , 1994	Coastal Chumash, 1780-1830	Maritime and terrestrial hunter-gatherer	Rapid missionization of coastal Chumash a risk-averse response to several years of high sea temperatures (low marine productivity) coinciding with several years of low rainfall (low terrestrial foraging potential)
Legge, 1989	Wodaabe of Niger, pre- and post-French colonialism	Pastoralism	Traditionally, risks managed by group mobility, diverse herd composition, controlled livestock breeding, livestock as storage, livestock loans, sharing, and combining pastoralism with agriculture and foraging. French colonial policies counteracted the effectiveness of these behaviors, leading to a decline in welfare of pastoralists
Ludwico <i>et al.</i> , 1991	Bari of Venezuela (extant)	Forager/horticulturalists	The Bari's choice of activities on a day are indifferent to the success of the previous day, thus, the Bari appear to be risk indifferent

Mace, 1990, Mace and Houston, 1989	Somali, Twareg, Meidob, and Turkana (extant)	Pastoralism	Herd composition depends on household subsistence requirements; invest in smallstock (fast reproductive rate, drought susceptible) if you are poor, invest in camels (slow reproductive rate, drought resistant) if you are wealthy
Mace, 1993	Gabbara (extant)	Pastoralism	Wealthy households control sheep breeding, poor households do not control breeding
Maihotra and Gadgil, 1988	Two nomad pastoral groups (Gavlis, Hatkar Dhangars) and three nonpastoral nomadic groups (Nandiwallas, Vaidus, Phasepardis), of India	Variety: pastoralism, foraging, fortune telling, etc.	Scarcity countered with job diversification and relaxation of hunting taboos; caste system previously obviated competition, but no longer the case due to the collapse of the resource base
Minc, 1986	Taremiut and Nunamiut of northwestern Alaska	Hunter-gatherer; sea mammals, caribou	Oral tradition used to transmit information vital to survival during periodic whale and caribou shortages. Secular forms (folklore and myth) effective against short-term fluctuations (seasonal, interannual), by emphasizing specialization, storage, redistribution, relocation, and trading; long-term fluctuation mitigated by taboos and rituals
O' Shea, 1981	Navajo, Tewa	Hunter-gatherer, agriculture	Regional exchange systems, a means for the indirect storage of perishable food surplus that allows the mobilization of food in times of scarcity, is a regular feature of semi- and fully-sedentary adaptations
O' Shea, 1989	Pawnee, Huron (protohistoric and historic)	Pawnee = maize agriculture with bison hunting; Huron = maize agriculture with anadromous fish	Where risks of agricultural failure cannot be buffered by raising domestic animals (the Old World pattern), farming is combined with foraging for wild resources (the New World pattern). Pawnee mitigate agricultural risk by hunting bison and exchanging hides; Huron mitigate agricultural risk by catching anadromous fish and through trade with fishing peoples
Olson, 1987	Malagasy (extant)	Agropastoralism, fishing	House structures, games, rituals, and forecasting (divining) demonstrate mental model of risk/probability that is consistent with catastrophe theory
Ortiz, 1990	Colombian hacienda managers, 1890-1920	Agriculture, cash cropping	Because the timing of harvests is uncertain, landowners hazard not being able to recruit sufficient labor for harvest. Landlords chose labor contracts, each of which have their own costs and risks (and thus changed with the political climate), to minimize the hazard of harvest failure

(Continued)

Table III. (Continued)

Study	Population	Subsistence system	Proposed shortfall-minimization strategies
Pagezy, 1988	Oto and Twa of Lake Tumba region, Zaire (extant)	Agriculture, fishing, communal hunter-gatherer, honey gathering	Rainfall has bimodal periodicity, local variations affect river and stream levels. Effective strategy for ensuring suitable diet by sharing, exchange, and purchase. Trade between Oto and Twa of spears, arrow tips, cassava, and fish
Rowley-Conwy and Zvelebil, 1989	Upper Paleolithic and Mesolithic European Hunter-gatherers	Hunter-gatherer	Storage predicted as shortfall-minimizing strategy in archaeological record when (1) sedentism (storage counteracts mobility), (2) mass capture technology and preservation technology, and (3) elite goods demonstrate "social storage." All found among Upper Paleolithic/Mesolithic European hunter-gatherers
Scarry, 1993	Native American communities in Black Warrior (Moundville) and Tombigbee river valleys, Alabama, A.D. 900-1250	Transition from gardening and nut gathering to intensive maize agriculture	Risk of maize underproduction could have been mitigated by household-level strategies: diversified maize varieties, field scattering. No need for central redistribution or "manager" (chief) to mitigate risk
Smith, 1978	Caribou-eater Chipewyan, Canada	Big game hunter-gatherer of taiga-tundra	Variation exists in caribou population sizes and migration routes; uncertainty mitigated through spatial placement of bands, flexible social organization linked by kinship that provides communication network for information sharing
Watts, 1988	Hausa peasants, Nigeria (extant)	Agriculture	Hausa peasants adjust agricultural decisions as timing and intensity of seasonal rains becomes more certain. Food shortage is present in normal years as well as famines. Inequities often exacerbated by incomplete market development
Wiessner, 1982	Dobe Ju/'hoansi, 1970s	Hunter-gatherer	<i>Hxaro</i> system is a formalized, balanced, delayed reciprocity system for storing social obligations that can be translated into food in times of need
Wright <i>et al.</i> , 1989	Sharafabad, Mesopotamia; Middle Uruk period	Agropastoral state	In bad years, livestock moved to better pasture; less recorded information about exchange and more about storage; reduced interest in public labor projects; increased craft production

Table IV. Behaviors Hypothesized or Demonstrated to Minimize Subsistence Shortfalls in Human Societies, in Relation to Z-Score Model Parameters

Behavior	Examples	Effect on Z-score variables		
		$R_{min}$	$\mu$	$\sigma$
Reducing group size	Jongman and Dekker, 1989	Decrease	—	—
Sending members to other locations, eviction of marginal members, infanticide				
Theft, raiding	Colson, 1979	—	Increase	—
Market behaviors	Chibnik, 1990, 1994; Jongman and Dekker, 1989; Ortiz, 1990	—	Increase	Increase
Agricultural loans, price fixing				
Agricultural intensification	Garnsey and Morris, 1989; Jongman and Dekker, 1989;	—	Increase	—
Draining lakes to make more farmland, terracing, ridging	Watts, 1988			
Diversification	Bernus, 1988; Browman, 1987; Chibnik, 1994;			
Field scattering, herd scattering, crop/variety/ herd composition, transhumance, mobility, conquest of new farmland, mixed economy	Colson, 1979; Goland, 1993a,b; Halstead, 1989; Mace, 1990, 1993; Mace and Houston, 1989; O'Shea, 1989; Watts, 1988	—	—	Decrease
Exchange	Bahuchet, 1993; Cashdan, 1985; Harnes, 1990;			
Sharing, pooling, intercommunity exchange	Hegmon, 1989; Kaplan and Hill, 1985; O'Shea, 1981; Pagezy, 1988; Wiessner, 1982	—	—	Decrease
Storage	Colson, 1979; Goland, 1991; Rowley-Conwy and Zvelebil, 1989; Wright <i>et al.</i> , 1989	—	—	Decrease
Storage by households, community-level storage, livestock as "banks"				
Premature consumption of crops	de Garine and Koppert, 1988; O'Shea, 1989	—	—	Decrease



concept of risk sensitivity to provide an alternative explanation for hunter-gatherer or peasant decisions that fail to conform to the rate-maximizing definition of rationality often espoused by development agencies (Browman, 1987; Cashdan, 1985, pp. 454–455; Colson, 1979; Forbes, 1989; Goland, 1993a, pp. 334–336; Legge, 1989; Ortiz, 1990, p. 303). Others relate risk to cultural change (Larson *et al.*, 1994), the frequency and prevalence of warfare (Ember and Ember, 1992), the origins of political complexity (Garnsey and Morris, 1989; Halstead, 1989), the origins of agriculture (Redding, 1988; Winterhalder and Goland, 1997), or pressures for imperialism and colonization (Garnsey and Morris, 1989; Jongman and Dekker, 1989).

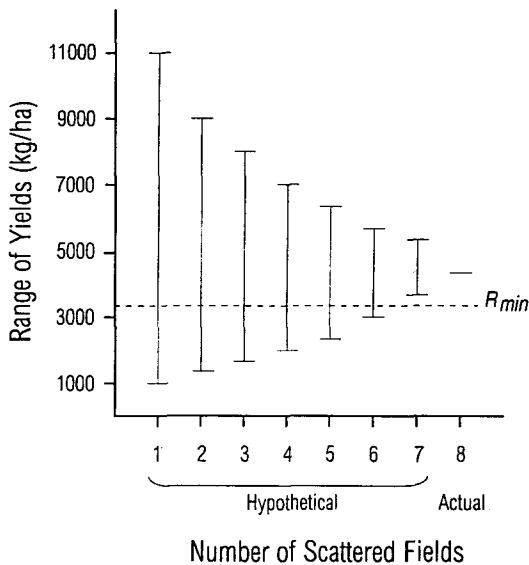
However, very few anthropological studies of subsistence risk have made use of formal models or concepts. This leaves many of the analytical arguments in this literature suggestive but inconclusive. For instance, it is routine to find statements that the adoption of a particular tactic (e.g., “generalizing” resource use) lessens the chance of a food shortfall, presumably because it reduces variance. The same argument may give no attention to the consequence of the tactic for *average* yield. But risk-sensitive models make it clear that both the mean and the average effect on outcome must be specified, and then assessed relative to the value function, in order to assess correctly the adaptive consequence of such a tactic. In many of these studies, such omission of key variables leaves critical gaps in the logic of shortfall minimizing. Variance reduction alone bears no unique relationship to shortfall minimization.

In contrast, we have located and here describe four studies that exemplify a full risk-sensitive argument. In the first, Mace and Houston (1989) use stochastic dynamic programming to model the mix of smallstock (goats, sheep) and camels that maximizes the long-term probability of household survival in a pastoral environment characterized by unpredictable droughts. Smallstock reproduce rapidly but are drought susceptible, while camels reproduce slowly but are drought resistant. Raising only smallstock is a high-mean, high-variance tactic, while an all-camel tactic has a lower mean and variance. The best risk-sensitive choice of herd composition depends foremost on household wealth. If wealth is less than household subsistence requirements (*h<sub>sr</sub>*), then the optimal strategy is to invest only in smallstock. If the household’s wealth is greater than its *h<sub>sr</sub>*, the optimal policy switches to “upstocking,” exchanging sheep and goats for camels and thus for the low-variance option. Note the parallels between this prediction and the expected energy budget rule: households below requirements are risk prone in their management practices, while those above requirements are risk averse. Although the authors are not explicit about a value function, it appears that they presume it to be sigmoidal, with an inflection point at *h<sub>sr</sub>*. Mace (1990) finds empirical support for the model’s predictions using data from four African pastoral groups (the Turkana, Twareg, Meidob, and Somali).

In another study, Goland (1993a,b) uses the Z-score model to examine why farming households in the Peruvian Andes disperse their agricultural production

into multiple, small, dispersed plots. She draws on a 2-year, quantitative sample of over 600 fields planted by 19 families. Using a GIS analysis and data on trail networks, field locations, number of visits (to till, fertilize, sow, weed, and harvest), and energy expenditure as a function of load, slope, and distance, she calculates that scattering imposes a mean cost of 7.5% of production, relative to 4% if fields were consolidated. Demographic, economic, and time allocation data for the 19 households allow her to calculate  $R_{min}$  for family agricultural production of potatoes. She uses data on yields and production inputs, along with regression analysis, to show that variability in management practices (seeding density, fertilization intensity, weeding effort, altitude, slope, exposure, etc.) accounts for only about 30% of the yield variance. The remaining variance constitutes risk, induced by unpredictable factors such as frost, rainfall surfeits or deficits, hail, pests, and trampling by livestock.

Figure 4 depicts the situation of 1 of the 12 families that effectively eliminated the chance of a shortfall through field scattering. This family planted eight potato fields and obtained a pooled (averaged) yield of 4477 kg/ha, somewhat above their  $R_{min}$  of 3100 kg/ha. Goland calculated and Figure 4 depicts the potential range of household outcomes had this family consolidated their total effort in any one of the locations they held (a one-in-eight chance of a disastrous 958 kg/ha to similar odds of a luxurious 11,818 kg/ha). This procedure was repeated for all combinations of two locations, all combinations of three, etc., up to the actual holding of eight



**Fig. 4.** Potential range of yields as a function of number of scattered fields, for a peasant farm household located in Cuyo Cuyo, Peru.  $R_{min}$  is the family's minimum requirement.

fields. The family scattered just beyond the degree necessary (seven fields) to make their minimum requirement with a high degree of assurance.

Hegmon (1989) simulated prehistoric Hopi exchange under three scenarios for interhousehold sharing: (i) complete household independence, (ii) restricted sharing (meet household needs and then pool the remainder to divide with neighbors), and (iii) unrestricted sharing (pool and redistribute equally the total yield of all households). Early 20th-century Hopi scattered corn production in different microecological zones to reduce unpredictable shortfalls from hail, floods, and grasshoppers. Yield variation was further reduced by obligatory exchange. Comparing effectiveness among scenarios, Hegmon found that only 46% of the independent households would survive 20 years (assuming that each household planted only 3.15 ha of corn in three fields). That number climbed to 73% for unrestricted sharing and to 92% for restricted pooling. In especially bad years, the tactic of restricted exchange protects marginally successful households from having to share in the catastrophic fates of a few of their neighbors.

Finally, Kohler and Van West (1996) interpret archaeological data on the Northern Anasazi population of the Mesa Verde region between A.D. 901 and A.D. 1300 using a risk-sensitive model. They assume a sigmoid utility function. In a prediction similar to the expected energy budget rule, Kohler and Van West hypothesize that cooperative (i.e., risk-averse) behaviors such as aggregation and exchange are expected so long as yields are adequate or better. Conversely, the best option for the Anasazi households in years of very poor yield would be risk prone, leading to the expectation that households would withdraw from intragroup exchange practices. In the extreme, this might lead to the breakup of village-based social units.

Kohler and Van West tested these predictions with detailed archaeological and paleoecological data. They found strong support for their model. For instance, the period with the highest expected value of cooperation coincides with the formation of the "Chacoan System," whereas its demise and subsequent abandonment of the region are associated with a period favorable to defection from exchange. Risk-based adaptive responses apparently contributed to the suprahousehold expansion and integration of this village-based agricultural society as long as times were fair to good. Under stressful environmental conditions, that same adaptive response may have destroyed socioeconomic cohesion. Households defected from exchange, making the best possible, risk-prone response to an extended run of poor harvests.

Although the majority of anthropological studies have focused on variance-averse strategies, there are occasional observations of what appear to be variance-prone behaviors in populations enduring exceptional economic stress (where  $\mu < R_{\min}$ ). The Kohler and Van West study just cited is an instance. Colson (1979) tells of a starving Makah boy who devised a method for processing crabs silently, so as to conceal the presence of food and avoid sharing. Gwembe Tonga agricultural households, in bad years, may bring their food-processing tasks inside so as to

restrict neighbors' knowledge of how much grain they have harvested and avoid sharing it (Colson, 1979).

Shortfall odds also may be reduced by decreasing  $R_{\min}$  or increasing the mean ( $\mu$ ) of an outcome distribution. For example, reducing the size of the consuming unit decreases its ( $R_{\min}$ ). Peasant households send family members to live with relatives in other regions or in urban areas during hard times (Thomas, 1973). States may forcibly evict marginal groups, as Emperor Augustus did to foreigners living in Rome in 6 B.C. (Jongman and Dekker, 1989, p. 118) or encourage emigration to distant colonies (Garnsey and Morris, 1989, p. 99). States also may reduce the demand for limited food by restricting nonfood uses. A poor wheat harvest in 1630 led authorities in Amsterdam to ban brewers and starch makers from purchasing the grain (Jongman and Dekker, 1989, p. 118).

Shortfalls in production may be mitigated by forcibly taking the production of others (presumably increasing  $\mu$ ). Raiding and theft increase among Gwembe Tonga agriculturalists when harvests are poor (Colson, 1979, p. 26). Hellenistic-age Greek polities used conquest and imperialism to increase grain stores in bad years (Garnsey and Morris, 1989). These observations are consistent with Ember and Ember's (1992) cross-cultural study of the determinants of warfare, in which the authors demonstrate through multivariate statistical comparison that anticipated future nonchronic resource scarcity is the strongest predictor of warfare in traditional, nonstate societies. They also found that in 73% of documented cases victors claimed the land of the defeated, while in 90% of cases victors took over nonland resources.

Another way to increase  $\mu$  is to increase production by extending zones of cultivation or intensifying use of existing fields. Machiguenga gardeners cultivate twice the minimum that is required so as to ensure against crop failure (Baksh and Johnson, 1990, p. 215). Modern Greek communities overproduce for the same reason (Forbes, 1989). The early Greek state or *polis* sometimes mandated extending the area of land under cultivation (Garnsey and Morris, 1989, p. 99). Authorities in Amsterdam between 1590 and 1635 decreed the creation of more farmland by building dikes and draining lakes (Jongman and Dekker, 1989). Hausa farmers use ridging (Watts, 1988) and Pawnee and Huron cultivators use mounding (O'Shea, 1989) to intensify agricultural land use and increase production.

The majority of anthropological studies assert that shortfalls are minimized by lessening variance through diversification. Diversification typically takes four forms. The first is diversification of crop types or herd composition. Groups such as the Gwembe Tonga (Colson, 1979), the Massa and Mussey of northern Cameroon (de Garine and Koppert, 1988), the early 20th-century Hopi (Hegmon, 1989), 10th-century Native American communities in the Black Warrior and Tombigbee river valleys of Alabama (Scarry, 1993), Hausa peasants of Nigeria (Watts, 1988), Neolithic Greek farmers (Halstead, 1989), Hellenistic-age Greek farmers (Garnsey and Morris, 1989), and modern Greek farmers (Forbes, 1989) buffer drought risk by diversifying crop type and varieties. Pastoralists routinely diversify herd

composition (see previous discussion of work by Bernus, 1988; Legge, 1989; Mace, 1990; Malhotra and Gadgil, 1988).

The second is diversification of field and herd location. Crop failure due to spatially varying hazards is often buffered through field scattering (see Goland example, above). Field dispersion has been a part of agriculture in Neolithic Greece (Halstead, 1989), Hellenistic Greece (Garnsey and Morris, 1989), and modern Greece (Forbes, 1989; Thompson, 1963), among the 20th-century Hopi (Hegmon, 1989), among Amazonian floodplain cultivators (Chibnik, 1994), among Andean agriculturalists (Browman, 1987; Goland, 1993a,b), and for farmers in Ethiopia, Japan, Switzerland, Hungary (McCloskey, 1976, pp. 126–127), and the English Midlands during the Middle Ages (McCloskey, 1976, 1991). Pastoralists achieve the same result by placing livestock in the herds of spatially dispersed friends and family. This distributes household subsistence over locations with unsynchronized exposure to predators, disease, raiders, and lack of water and forage (de Garine and Koppert, 1988). Pastoralists also can diversify through mobility. In the Sahel of Africa migration routes change each year according to the variable conditions experienced in each of the environmental regions traversed (Bernus, 1988; Legge, 1989).

The third possibility is diversification of economic activities. Effective diversification may be achieved through the combination of economic activities not susceptible to the same environmental disruptions (Colson, 1979, p. 22). In the Old World, agriculture is often linked with pastoralism; in the New World, the Pawnee combined agriculture with bison hunting, while the Huron complemented maize cultivation with the harvest of anadromous fish (O'Shea, 1989). Andean farmers combine tuber and grain cultivation with camelid herding (Browman, 1987). Greek farmers of the Middle Neolithic (Halstead, 1989, p. 72) and Wodaabe pastoralists of Niger (Legge, 1989) combined agriculture with foraging in bad years.

Fourth, food transfers such as sharing and exchange diversify over unsynchronized sources. Hunter-gatherers, such as the Ache of Paraguay (Kaplan and Hill, 1985), the Navajo and Tewa (O'Shea, 1981), the Oto and Twa (Pagezy, 1988) and Aka of Zaire (Bahuchet, 1993), and the Ju/'hoansi (Goland, 1991; Wiessner, 1982) and other "Basarwa" of southern Africa (Cashdan, 1985; Kent, 1993; Lee, 1979), as well as some foraging horticulturalists [e.g., the Barí (Ludvico *et al.*, 1991) and Yanomamö of Venezuela (Hames, 1990)], mitigate production risk and consumption shortfalls by widespread sharing of foodstuffs among individuals and groups (Smith, 1988; Smith and Boyd, 1990). Sharing is effective even in small groups when there is a negative or low positive correlation in the success rates of individuals foraging separately (Winterhalder, 1986a).

In a related tactic, the food shortfalls can be mitigated by delaying or accelerating consumption. Hunter-gatherers in more seasonal environments, such as the Upper Paleolithic and Mesolithic European peoples (Rowley-Conwy and Zvebil, 1989), the Makah (Colson, 1979), and the Ainu (Goland, 1991), buffer

expected seasonal shortfalls as well as unpredictable aspects of their duration, timing, and intensity with storage. Storage averages consumption over time. Its efficacy is constrained by preservation costs and the sometimes conflicting need for mobility (Rowley-Conwy and Zvelebil, 1989). Storage also is integral to agricultural production (Cashdan, 1985; Forbes, 1989; Halstead, 1989; Wright *et al.*, 1989). In contrast, some agriculturalists, such as the Massa and Mussey of northern Cameroon (de Garine and Koppert, 1988), and the protohistoric Pawnee and Huron of North America (O'Shea, 1989), harvest and consume a sizable portion of their crop before it is ripe. "Green corn" is nutritionally inferior to ripe corn and requires more processing labor. However, the longer grain ripens in the field the greater the exposure to pests and the greater the chance of loss.

There have been only a few, tentative models of trade-offs among different risk-sensitive tactics. Rowley-Conwy and Zvelebil (1989) discuss trade-offs between storage and mobility, based on the effective spatial distances between resources and human settlements. Winterhalder (1986a) and Goland (1991) model the trade-off between storage and sharing among immediate-return hunter-gatherers. Winterhalder (1986a) notes that food sharing reduces consumption variance sufficiently that foragers, acting as producers, can opt for high-risk, rate-maximizing tactics, confident that end-of-day pooling will mitigate the consequences of an unexpected shortfall. Dwyer and Minnegal (1993) provide an example of this among the Kubo of Papua New Guinea.

The nearly exclusive attention in the anthropological literature on diversification (or "generalizing") as a means of variance reduction, and the apparent presumption that this automatically minimizes the chances of subsistence shortfalls, compels us to reiterate an earlier point: *without simultaneous attention to mean outcomes and to  $R_{min}$  or its equivalent, and without comparison of outcomes on an iso-value map, such proposals are logically incomplete and quite possibly mistaken.* Although much of the literature cited in Table III is plausible, diversification can serve many functions and conceivably might be neutral or harmful as a risk-sensitive adaptive tactic. This is a case in which the failure to take up formal models jeopardizes our capacity to assess correctly the functional benefits of behavior.

## CONCLUSIONS

Together, biology and anthropology offer substantial literatures on subsistence risk and impressive analytical and empirical resources for its analysis. However, these two fields are characterized by uneven progress in the areas of theory, models, laboratory, and field studies. We conclude with several summary observations.

A risk-sensitive analysis entails specification of a value function and a set of outcome distributions corresponding to the behavioral options. Theoretical work

on value functions is well advanced. Similar work on outcome distributions is yet quite limited. Empirical research is needed on both. For instance, it is critical whether the decision maker is to the left or the right of the value function inflection point (or  $R_{\min}$ ), yet we know little about how this point might be set.

Risk sensitivity should be presumed important if (i) the value function is nonlinear, and (ii) one or more of the behavioral alternatives is characterized by unpredictable outcomes. We do not yet have the experience to say how widespread are the behaviors and situations for which value functions are nonlinear. They may be more ubiquitous than is commonly perceived. For example, Winterhalder and Leslie (1998) argue that the long-term consequences of human fertility decisions are subject to nonlinear value functions. Although the specifics have received little empirical study, it also is a secure prediction that most if not all behavioral outcomes are characterized by some degree of unpredictable variability.

The existing literature contains several risk-sensitive models and not much guidance on choosing among them. We have shown with isovalue maps that two common approaches to risk sensitivity, the Z-score and linear variance discounting (LVD) models, are special cases of a general model with a sigmoid value function and normal outcome distributions. The LVD model operates qualitatively as if the value function is purely concave (to the right of the inflection point). In fact, this quite often will be the case. The Z-score model mimics the full range of the sigmoid, but in the highly simplified form of a step function. The more general sigmoid value function can be varied from a near-step to a near-linear function, and it predicts both risk-prone and risk-averse behavior as a continuous function of mean condition, giving it great versatility. These models set a framework within which it should be possible to make comparative appraisals of different shortfall-minimization tactics, although little such work has yet been done.

Outcome arrays may well be unique to the adaptive problem and setting. Their shape supplies valuable clues to the importance of risk sensitivity, the dependence of analysis on a precise understanding of the value function, and the applicability of different models for discounting variance. Unfortunately, we know very little about outcome arrays for subsistence choices. This should be a priority area for work, using computer modeling and field observations.

Most nonhuman organisms tested under laboratory conditions are risk sensitive in subsistence choices. To date, risk-prone resource choice under a negative energy balance (expected energy budget rule) appears to be common only for small homeotherms that are specialized feeders and that face regular, life-threatening interruptions to subsistence. Risk-prone choice appears to be less common for larger omnivores, perhaps due to endogenous reserves or to alternative food sources or behavioral tactics for avoiding shortfalls. This implies that risk- (or variance-) prone behavior will be rare among humans. In biology, there is a dearth of field observations of risk-prone behavior.

In natural settings, torpor, fat reserves, group foraging, sharing/pooling, and hoarding/caching appear to mitigate subsistence risk in nonhuman organisms, either by lessening  $R_{\min}$  or by reducing variance, relative to mean intake. Each of the variance-lessening mechanisms might be reversed when risk-prone behavior is optimal. All, to varying degrees, are potentially important in humans.

The extensive archaeological and anthropological literature on subsistence risk is largely qualitative and anecdotal. Little of it takes advantage of the formal theory discussed here. For both reasons specific claims must be interpreted with some caution. Nearly all studies document what appear to be risk-averse behaviors, although there are isolated observations of risk-prone choices under extreme dearth.

Most risk-sensitive tactics adopted by humans have analogues among nonhuman organisms. The exceptions appear to be recent institutional or market-based forms of insurance (Bernstein, 1996). Organisms can decrease consumption variance in subsistence efforts by (i) spreading exposure over *individuals* or other units through scrounging, sharing, or pooling; (ii) spreading exposure over *space* by such actions as mobility, field scattering, and scatter hoarding; (iii) spreading exposure over economic *activity types* by diversification; and (iv) spreading exposure over *time* by early or delayed consumption (storage). Consumption variance can be increased by the inverse of each of these tactics in situations calling for risk-prone responses.

There is an enormous and largely unexploited potential in this literature for interdisciplinary sharing of theory, concepts, models, and methodology and for comparative study of basic evolutionary and adaptive processes. This potential will be best realized if analysts from different disciplines begin working within a common theoretical framework like that of behavioral ecology.

Finally, behavioral ecologists working with nonhuman organisms are now seeking to synthesize and reconcile the evolutionary (functional, ecological) approach that we have reviewed here with the more mechanistic (perception, cognition) models of animal psychologists (see Green and Myerson, 1996; Real, 1991, 1996; Smallwood, 1996). Anthropologists could easily explore similar collaborations with psychologists (e.g., Kamil and Roitblat, 1985; Lopes, 1994) interested in human responses to risk. The statement by Kacelnik and Bateson (1996, p. 425)—“Our idea is that the general principles of associative learning have evolved under broader selective pressures than those acting on foraging decisions, and that they lead to deviations from optimality in some foraging tasks”—might easily have been made by cognitive (e.g., Tversky and Kahneman, 1992) or Darwinian (Barkow *et al.*, 1992) psychologists. We do not know to what extent humans are aware, or able to act as if aware, of underlying outcome distributions and value functions. The proximate cognitive and perceptual mechanisms by which individuals assess and respond to risk in various societies are a topic full of potential but scarcely touched in anthropological studies of subsistence.



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