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# An Introduction to Risk Sensitivity: The Use of Jensen's Inequality to Clarify Evolutionary Arguments of Adaptation and Constraint[1]

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SYNOPSIS. I review the basic rationale for risk-sensitive foraging, and present a few of the most common expressions of risk-sensitivity theory. A simple heuristic, the energy-budget rule, and the z-score model are explained. These functional models of risk sensitivity assume or explicitly model fitness as a nonlinear function of an animal's energy state. For such nonlinear relationships, Jensen's inequality predicts that the fitness realized by an animal with a more constant energy state may be higher or lower than the fitness resulting from a variable energy state with the same mean, depending on the shape of the fitness function. Predictive functional models of behavior, like the energy-budget rule and the z-score model, depend on specific features of the function relating energy state to fitness, which may or may not be general features for most organisms. While behavioral ecologist have studied the functional significance of animal responses to variation in foraging rewards, psychologists have long studied the psychological mechanisms by which preferences for variable or constant rewards are expressed. Jensen's inequality is applied here too; psychologists propose nonlinearities in the perception and processing of information. The growing number of different relationships that might account for risk-sensitive behavior is a potential source of confusion. I advocate "returning to the basics," *i.e.*, that hypotheses to explain risk-sensitive behavior should specify precisely the assumed nonlinear relationships.

## INTRODUCTION

Behavioral ecology was already a well-defined discipline in 1980, when Caraco (1980) and Real (1980) independently introduced the concept of risk-sensitive foraging. Behavioral ecologists were mostly concerned with developing and testing functional models of behavior. They constructed models of the relative costs and benefits of the alternative behaviors available to the animal under study. By assuming the animal behaves so as to maximize its net benefit, they could derive predictions from these models. Costs and benefits were usually calculated in some proximate currency thought to correlate with evolutionary fitness (*e.g.*, rate of net energy intake, number of matings obtained). By 1980, this approach had been remarkably successful at explaining a variety of foraging, reproductive, and social behaviors, as textbooks from that time make clear (Krebs and Davies, 1978, 1981). Prior to 1980, functional models of behavior focused on the average net benefit of the behavioral options under study.

The key contribution of risk-sensitive foraging theory is its consideration of the variation about average rewards associated with different strategies. Specifically, consider an animal that has a choice between two foraging strategies that yield the same average amount of food, but with different variances about that average. Should the animal choose the strategy with the lower variance in the amount of food, or the higher variance? Risk-sensitive foraging theory is a collection of models that consider the effects of variance about the average re-

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ward. As such, it might more accurately be named "variance-sensitivity theory," but the current name is well established. The term "risk-sensitive" is occasionally used to refer to animals that change their behavior in response the risk of predation (*e.g.*, Pierce, 1988), but here I use the term exclusively to refer to sensitivity to variation.

Risk-sensitive behavior has been well documented in response to variations in the amount of rewards for particular strategies, and for variations in the delay to the delivery of the reward. Animal responses to variations in delay are often quite different from their responses to variations in amount (Hamm and Shettleworth, 1987). Several papers in this volume consider risk-sensitive behavior in response to delays (Green and Myerson, 1996; Benson and Stephens, 1996; Kacelnik and Bateson, 1996, all in this volume). Merely for brevity, I will restrict my discussion to variations in amount of reward.

The theoretical treatments in Caraco (1980) and Real (1980) were ground-breaking; however, it was the experimental results from that time that drew the attention of behavioral ecologists to risk sensitivity. For example, Caraco *et al.* (1980) conducted laboratory experiments with wild-caught birds, demonstrating: a) that the birds were sensitive to the magnitude of variation in rewards associated with different foraging options, and b) that the birds switched their preference from a high-variation option to a low-variation option, in accordance with risk-sensitive foraging theory. That animals could detect and respond to different levels of variation was of great interest to behavioral ecologists, and inspired many theoretical and empirical studies of risk-sensitive behavior (see reviews in Stephens and Krebs, 1986; McNamara and Houston, 1992; Kacelnik and Bateson, 1996).

Psychological examinations of animal responses to variation in rewards preceded this burst of interest in risk sensitivity among behavioral ecologists. Psychologists were interested in the mechanisms of perception that influenced animal choices. However, behavioral ecologists drew more inspiration from the field of economics than from psychology in their functional models of risk sensitivity (Real and Caraco, 1986; Bednekoff (1996) briefly reviews the importance of risk sensitivity in economics). It is therefore interesting that some behavioral ecologists are now trying to synthesize the mechanistic models of psychology with the functional models of behavioral ecology (*e.g.*, Real, 1991, 1996; Kacelnik and Bateson, 1996).

This paper is written with two objectives in mind; to provide a tutorial on risk-sensitivity theory, and to comment on the value of re-examining the assumptions underlying explanations of risk-sensitive behavior. I introduce the basic logic and mechanics of risk sensitivity, first with a simple heuristic, and then by examining rules of behavior derived from this logic. Next, I examine the underlying assumption of these functional models: a non-linear relationship between fitness and the energy state of the animal. Careful attention to this underlying assumption can clarify (or invalidate) evolutionary arguments. Psychologist also hypothesize nonlinear relationships in their mechanistic explanations of risk-sensitive behavior. One might account for risk-sensitive behavior by hypothesizing nonlinearity at any one of several functional or mechanistic relationships linking environmental input with behavioral output. I suggest that any clear explanation of risk-sensitive behavior should specify precisely which relationship(s) are hypothesized as nonlinear.

## MODELS OF RISK-SENSITIVE BEHAVIOR

### *A simple hueristic*

In nature, animals seldom obtain the average reward associated with a particular strategy; there is usually variation in the rewards. Some strategies may yield more consistent rewards than others. Consider an animal that has two foraging strategies available to it. Each strategy yields the same mean reward in terms of net energy intake/foraging bout, but one strategy's rewards vary more than the other (Fig. 1). Would the animal benefit more by choosing the strategy with the variable or more constant rewards? The answer depends on the animal's requirements. If an animal requires relatively little to satisfy its requirements

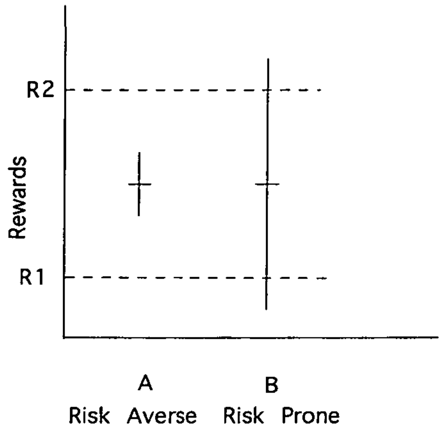

FIG. 1. A simple heuristic. Strategies A and B each provide the same mean reward, but the reward for strategy B is more variable. The vertical line for each strategy represents the spread of possible rewards for playing that strategy (*e.g.*, the range of possible rewards, or the variance for normally distributed rewards, or some other measure of variation). If an animal requires a minimum reward level of R2, it is more likely to obtain its requirement by playing the more variable risk-prone strategy.

(before turning its attentions away from foraging to mate acquisition, territory defense, etc.), it is safer for the animal to chose the more constant strategy, as the average rewards of this strategy satisfy the requirements of the animal. If the animal chooses the more variable strategy, it risks not meeting its energetic requirements for that foraging bout. If there is no great benefit for exceeding the required amount of energy (a possibility considered later), there is no reason for the animal to accept such risks, and it should be risk-averse: meaning it should prefer the strategy yielding more constant rewards.

The situation is different if the animal's requirements exceed the average reward of the two strategies (Fig. 1, $R_2$). Now, choosing the low-variance strategy minimizes the chance that the animal will meet its requirement for rewards in this foraging bout. The best option available to the animal is the variable strategy. This risk-prone behavior maximizes the probability (however small) that the animal meets its requirements. This is the logic of the energy-budget rule introduced by Caraco (1980). According to this rule, animals expecting to exceed their energy requirements should be risk-averse, and those expecting to fall short should be risk-prone.

In a striking series of experiments, Caraco (Caraco, 1981, 1983; Caraco *et al.*, 1980) taught wild-caught birds to forage for seeds in covered dishes in a laboratory setting. The birds learned to associate covers of a particular color with either constant or variable numbers of seeds in the dish. When the average number of seeds in each dish exceeded that required to maintain a positive energy budget, the birds preferred the dishes with a constant number of seeds. When the average number of seeds was below that required for the birds to maintain a positive energy budget, the birds switched to a more risk-prone behavior. These experiments have been repeated with a number of bird and other animal species; the energy budget rule successfully predicted foraging behavior in a number of cases (see review by Kacelnik and Bateson, 1996).

### *The z-score model*

The preceding explanation illustrates the simplest situation, where the different strategies have the same mean reward. It is then easy to see which strategy maximizes the probability of meeting the animal's requirement. In more natural settings, different strategies are likely to differ in mean rewards as well as variation about the mean. Stephens (1981; Stephens and Charnov, 1982) developed the z-score model to determine which of the available strategies minimizes the probability of gaining less than the required reward when both means and variances differ. Consider an animal with an energetic requirement of R. Assume the animal has two foraging options available to it, each of which provides rewards according to a normal distribution, each with its own mean and standard deviation. In this circumstance, it can be shown that the option with the highest z-score—the highest ratio of [(R − mean)/standard deviation] is the option that minimizes the probability of energetic shortfall. The option with the highest z-score can be determined graphically (see Fig. 2). When the strategies differ only in the magnitude of variation, the results are the same as those

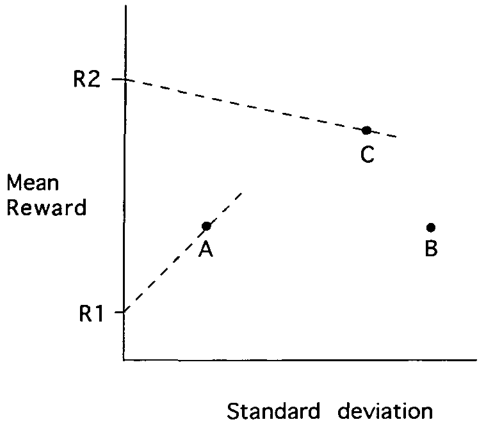

FIG. 2. The z-score model. Different strategies (A, B, C) are plotted by their mean reward and the standard deviation about that mean. Ri denotes the amount of reward required by the animal. For a given requirement, the strategy that minimizes the probability of gaining less than the requirement can be found by constructing lines from the requirement on the vertical axis to each reward. Assuming a normal distribution of rewards for each strategy, the strategy with the line of highest slope is the one with the highest z-score—the one that minimizes the probability of a shortfall. The z-score model allows easy comparisons of strategies that vary in both mean reward and standard deviation. Here, if the animal requires R2 rewards, strategy C minimizes the probability of a shortfall, even though its standard deviation is less than B's.

obtained by the energy-budget rule. Stephens and Krebs (1986) provide an accessible explanation of the details of the z-score model.

This model has been applied to the problem of patch departure: determining how long a forager should continue to exploit a particular patch before leaving (Stephens and Krebs, 1986). Here, a foraging strategy is the amount of time a forager chooses to continue exploiting a patch before departing. Foraging in a patch for, say, 90 seconds may yield rewards (*e.g.*, particular rate of energy intake) with a mean and a standard deviation about that mean. An exploitation time 120 seconds may yield a reward with a different mean and standard deviation. Again, if the rewards for staying a particular length of time in a patch are normally distributed, the exploitation time with the highest z-score is the length of time that minimizes the probability of the forager obtaining less than its required reward. This approach has been used to generate predictions for patch-exploitation times (patch departure rules) for bumblebees in an experimental foraging arena (Cartar and Abrahams, 1996).

The energy-budget rule and the z-score model share an underlying assumption; they assume a specific relationship between the rewards gained by the animal and its fitness. That is, they assume that the animal experiences a higher fitness for satisfying its requirement, but no further gains in fitness for exceeding the requirement. In foraging terms, they assume that the forager benefits from meeting its energy budget, but that additional energy gained does not raise fitness further. This step function is actually a more extreme version of the sigmoidal relationship between energy state and fitness suggested by Caraco (1980) and Real and Caraco (1986). A nonlinear fitness function is an essential underlying assumption to functional explanations for risk-sensitive behavior in animals. An interesting property of nonlinear functions—referred to as Jensen's inequality—leads to the predictions of the energy budget rule and the z-score model.

### *Jensen's inequality, functional and mechanistic relationships*

Jensen was a mathematician from the 1700s, and unfortunately, very little is written about him beyond the inequality that bears his name. Jensen's inequality states that the average value of a function of a variable, E[F(x)], need not equal the value of the function evaluated at the average variable. One expression of his inequality is that for any concave-down (increasing, but decelerating) function,

$$F(E[x]) \geq E[F(x)] \qquad (1)$$

The opposite is true for a concave-up function (Feller, 1966).

To appreciate how Jensen's inequality applies to risk-sensitive foraging, consider the hypothetical fitness function in Figure 3. This concave-down function results if the benefit experienced by an animal for increasing its energy state becomes smaller at higher energy states. This relationship seems reasonable for a wide range of ani-

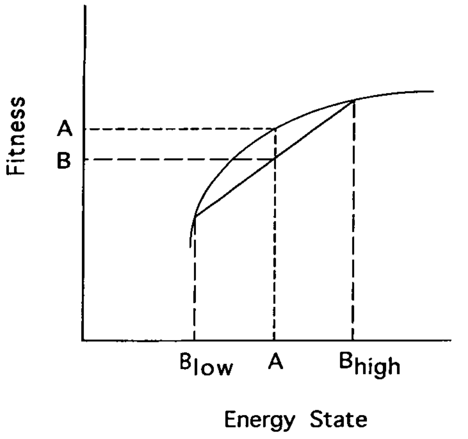

FIG. 3. Jensen's inequality. The concave-down curve represents the relationship between energy state and fitness. A constant energy state (A) yields a higher fitness than a variable energy state with the same mean (B). See text for further explanation.

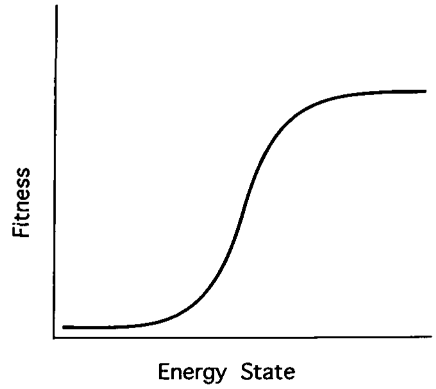

FIG. 4. A sigmoidal relationship between energy state and fitness. An animal with a low energy state (in the concave-up region) may be risk-prone because the average fitness for a variable energy state exceeds that for a constant energy state. An animal with a high energy state looses more than it gains by a variable energy state, which may lead to risk-averse behavior.

mals. It is consistent with the intuition that an animal with low energy reserves will benefit more from gaining a particular amount of energy than animal with higher reserves of energy. In marginal value terms, this relationship results when the value of an additional unit of energy declines as the energy in reserve increases.

Now consider an animal with the following choices available to it: strategy A, which yields a constant amount of energy to the forager and raises its energy state to point A in Figure 3: or strategy B, which yields a variable amount of energy. Strategy B either leaves the animal at $B_{low}$ or raises the animal's energy state to $B_{high}$ with equal probability. For either strategy, the animal has the same expected (mean) energy state, but the resulting fitness for the variable energy state is lower, because of the diminishing fitness returns associated with energy gains. The fitness gain from achieving an energy state x units above A does not offset the larger fitness loss from falling x units below A. Thus, the animal experiences higher average fitness for employing risk-averse behavior. The opposite is true for a concave-up fitness function.

The fitness function in Figure 3 predicts higher fitness for risk-averse behavior, regardless of the energy state of the animal. If the relationship between energy state and fitness is instead sigmoidal (Fig. 4), the most adaptive behavior depends on the energy state of the animal: risk-prone at low energy states, and risk-averse at higher energy states. Caraco assumes a this sort of sigmoidal relationship to justify the energy budget rule (Caraco, 1980; Real and Caraco, 1986), where the "requirement" of the forager is taken to be at or near the steepest part of the fitness function. As has been noted elsewhere (Ellner and Real, 1989), the z-score model can be regarded as a special case of this argument for the energy budget rule. By assuming the most extreme form of a sigmoidal curve (a step function, where fitness is zero below the required energy state and one above it), and by assuming a normal distribution of energy states associated with each strategy, Stephens derived the energy budget rule (Stephens and Krebs, 1986). Although Jensen's inequality is normally thought of in relation to continuous functions, the it applies to step functions as well, with the same results.

Although Caraco (1980) and Real (1980) are generally credited with conceptualizing the implications of a non-linear fitness function for foraging animals, Oster and Wilson (1978) made very similar arguments for ant colonies. Oster and Wilson considered the fitness of an ant colony as a whole, and the different strategies consist of different colony caste ratios. Nevertheless, their argument rest on a sigmoid-shaped curve relating net foraging yield to fitness. Oster and Wilson (1978, p, 214) delineated zones for "tychophile" and "tychophobe" colony caste ratios on their graph of colony fitness, which correspond precisely with risk-prone and risk-averse behavior. It appears that considerations of variance in foraging success was the next logical step for functional explanations of animal behavior (behavior broadly defined).

To this point, I have considered fitness functions associated with one aspect of survival of survival (*i.e.*, avoiding starvation). Of course, there are other components to fitness, and other ways that energy state might influence those components. For example, Moore and Simms (1986) consider a threshold energy state that birds must meet before they migrate, and include arguments for the effects of early or late migration in their model. In agreement with their model, they found that birds in a premigratory state were risk-prone until they reached their maximum migratory weight. Then they became risk averse. Bednekoff (1996) considers a threshold energy state that must be met before reproduction, with additional fitness benefits for achieving higher energy states beyond the threshold. He briefly reviews several other models of risk sensitivity and reproduction. Generally, the predictions of these models are more complicated than those of the energy budget rule or the z-score model. The different predictions of these models are due in part to the different shapes (other than sigmoidal or simple step function) considered for fitness functions. For example, a positive relationship between energy state and fitness beyond the threshold for reproduction may mean that risk-prone behavior yields higher fitness even when the expected energy state is above the threshold (Bednekoff, 1996).

I have presented only static models of risk-sensitive behavior. That is, the models consider the consequences of only one decision between risk-averse and risk-prone behavior, based on a particular set of parameters (*e.g.*, energy state relative to requirement, the shape of the fitness function). In natural settings, animals may be able to switch back and forth between risk-prone and risk-averse behavior. Dynamic optimization programming permits the consideration of multiple decisions based on changing state variables (such as energy state and time remaining to forage), particularly when the changes are due in part to the previous decisions of the animal. Dynamic optimization approaches to risk-sensitive foraging theory produce an even more diverse array of predictions for optimal risk-sensitive behavior (chpt. 7 in Mangel and Clark, 1988; Bednekoff, 1996; Kacelnik and Bateson, 1996).

The preceding discussion has been restricted to functional models of risk-sensitive behavior. However, psychologists study animal responses to variation in rewards, and they also use Jensen's inequality in their explanations of animal preferences. Psychological models of risk-sensitive behavior generally focus on proximate mechanisms rather than functional explanations of the behaviors. Hence, psychologists propose and test psychological "laws" concerning how information is perceived and processed. For example, according to Weber's law, a standard difference between two stimuli becomes less noticeable as the magnitude of the stimuli increases (*e.g.*, a 0.03 g insect will appear much larger than a 0.01 g insect, but a 1.03 g insect may be very difficult to distinguish from a 1.01 g insect). One possible explanation for Weber's law is a concave-down relationship between the actual and perceived magnitude of a stimulus. Considering Weber's law in light of Jensen's inequality, it is possible that the mean value of a variable reward will be perceived as lower than the mean value of a more constant reward. Psychologists and behavioral ecologists have proposed Weber's law as an explanation for the apparent risk aversion of some foraging animals (Hamm and Shettleworth, 1987; Perez and Waddington, 1996).

## RETURNING TO THE BASICS: WHERE IS JENSEN'S INEQUALITY?

Functional models of risk-sensitive behavior generally follow the adaptationist's approach (also called the optimization research program: see Mitchell and Valone

1990). That is, animals are assumed to behave in ways that maximize fitness. The models are our attempts to clarify the fitness consquences that result from the choices available to animals. Rules like the energy-budget rule or the z-score model are in some sense "second-order models" in that they assume particular fitness functions implicitly, and generate rules for fitness-maximizing behavior based on those functions. Until recently, behavioral ecologists largely ignored information processing and psychological mechanisms involved in animal choices. Animals are typically assumed to be perfectly informed (or completely ignorant) of the relevant parameters, and assumed to choose the best available strategy. Recently, some behavioral ecologists have begun explicitly considering how psychological mechanisms may constrain animal choices (Real, 1991, 1996; Kacelnik and Bateson, 1996). Given this recent history, I see two important reasons for going "back to the basics," and explicitly examining the fitness functions implied by any explanation for apparent risk-sensitive behavior. I explain each of these points below with examples.

The first reason to return to the basics is that second-order models may conceal unlikely or unreasonable assumptions about the fitness function. Most empirical tests of functional hypotheses of risk-sensitive behavior begin with second-order models. That is, rather than assess the relationship between energy state and fitness, they test predictions of the z-score model or energy-budget rule, implicitly assuming the appropriate underlying fitness assumption (*e.g.*, Barkan, 1990; Bansbach and Waddington, 1995; Lawes and Perrins, 1995). This is problematic, because there are many reasonable alternatives to the standard sigmoid or step function of classic risk-sensitive models (*e.g.*, Bednekoff, 1996; McNamara, 1996). Second-order models do not allow consideration of other fitness functions. If an animal's behavior reflects a different fitness function, its risk-sensitive behavior may not conform to the energy budget rule, and the behavior may then be misinterpreted.

It may often be difficult to assess fitness functions directly. However, even in such situations, careful examination of the implied fitness function may be useful. Consider Rubenstein's (1987) argument for risk-sensitive reproductive strategies in spiders. Rubenstein studied a population of *Meta segmentata,* where female spiders are patchily distributed, and large male spiders realized the highest reproductive success by pursuing females in the densely populated patches. Because of their inability to win in male-male competition, small males had a higher reproductive success when they pursued females in the sparsely populated areas between dense patches (where a mating opportunity is unlikely to be contested). Mid-sized male spiders achieved approximately equivalent reproductive success (estimated as number of eggs fertilized) in either dense patches or sparsely populated areas. The variance in reproductive success is much higher in the dense patches: mid-sized males were almost assured of one mating opportunity in the sparsely populated areas, whereas the densely populated patches allow males to attempt to mate with multiple females. A mid-sized male pursuing matings in a dense patch may succeed, but risks losing all opportunities to a larger male. Rubenstein interpreted this situation as a classic risk-sensitive pair of options: equal mean reward with different variances. However, in this case, the reward is the number of eggs fertilized. For spiders (which have no paternal care) it seems unlikely that the relationship between number of eggs fertilized and fitness will resemble the sigmoidal functions of Figure 4. In fact, if the relationship is linear, then there is no difference in fitness between the variable and the constant strategy. Jensen's inequality becomes Jensen's equality if the fitness function is linear.

The second reason to return to the basics is that there are several potential relationships that may be cited as an explanation for any particular risk-sensitive behavior. Considerations of proximate mechanisms increases the number of relationships under consideration. This is a potential source of confusion. Nectivores have been used in a number of empirical investigations of risk sensitivity (*e.g.*, Cartar and Abrahams, 1996; Perez and Waddington, 1996) and illustrate this problem well. Consider a bee that exhibits risk-averse behavior when presented with two kinds of flowers: those with a constant volume of nectar, and those with a variable volume of nectar. The classical functional explanation for risk aversion here would be to assume a concave-down relationship between net energy state and fitness. However, there may be a concave-down relationship between nectar volume and the net rate of energy intake by the bee. If the latter were true and not the former (note, they need not be mutually exclusive possibilities), Perez and Waddington (1996) would not consider this situation to be an example of risk-sensitive foraging, while Real (1996) would.

To continue with the example, one might adjust the volume of nectar so that both variable and constant flowers provide the same expected net energy intake rate. If the bee were still risk-averse, one functional explanation might be the concave-down relationship between net energy intake rate and fitness mentioned above. Here, risk-aversion maximizes fitness. Alternatively, if there is a concave-down relationship between the actual volume of nectar in flowers and the bees perception of nectar, the bees may be maximizing their perceived rate of nectar collection. This mechanistic explanation does not exclude the functional hypothesis. Bee perception might be shaped by natural selection to promote risk-sensitive behavior, or it may reflect the constraints of the bee's neural architecture. In short, there are at least three different relationships involved in this behavior, any one of which might account for the risk-aversion observed, and none of which are mutually exclusive of the others. Rigorous tests of a risk-sensitive hypothesis is difficult or impossible if the roles of the different possible nonlinear relationships in the hypothesis are not clearly specified.

Hypotheses of adaptation and constraint are particularly problematic in this regard. Consider the different results obtained from studies of the risk-sensitive behavior of bumble bees (*Bombus* spp.). Real found bumblebees to be risk averse under a variety of experimental conditions specifically designed to elicit risk-prone behavior (see p. 384, Real and Caraco, 1986). He argues that the constant risk aversion of his bumble bees was due to an extremely short memory window in bumble bees (Harder and Real, 1987; Real, 1991). It is not clear whether the argument implies that the short memory is an adaptation to the natural foraging environment of these particular bumble bee species, or a neural constraint that prevents them from foraging in a way that would yield greater fitness. The distinction is important, particularly when these studies are compared with those of Cartar (Cartar and Dill, 1990; Cartar, 1991). Working with different, but congeneric species, Cartar elicited switching behavior between relatively risk-prone and risk-averse behaviors. While it is true that Cartar's experimental designs differ in several ways from those of Real, it is still the case that Cartar elicited changes in the bees' preferences for risk. This behavioral flexibility is consistent with a longer memory window for the bumblebees. If the short memory window advocated by Real is a psychological constraint of bumblebee neural architecture, it is apparently a rather specific constraint that operates in certain species of the genus, and not in others. If it is an adaptation to the local environment of the North Carolina peidmont where these experiments were done, we can test hypotheses as to the specific features of the environment that favor constant risk-averse behavior. Each of these possibilities may be developed into a viable hypothesis. However, until a specific hypothesis is put forward, it is not clear which critical nonlinear relationship is being proposed, nor where to look for applications of Jensen's inequality. No specific predictions can be derived or subjected to experimental test without first specifying an hypothesis.

## CONCLUSIONS

Theoretical work suggests that in a number of circumstances, risk-sensitive behavior should have fitness consequences (McNamara and Houston, 1992). The results from a large body of empirical investigations into risk-sensitive behavior suggest that many animals are sensitive to different levels of variation (Kacelnik and Bateson, 1996). Yet the empirical tests often do not conform with the predictions of the simplest functional models. Although this situation may be problematic, I view it as an opportunity: a set of problems yet to be solved. With a more diverse, realistic repertoire of functional models, and with the careful synthesis of functional and mechanistic models, I am hopeful that a clearer, general understanding of risk-sensitive behavior in animals can be achieved.

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