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CHAPTER EIGHT

Risk-Sensitive Foraging: Decision Making in Variable Environments

MELISSA BATESON AND ALEX KACELNIK

8.1 INTRODUCTION

Analysis of foraging has greatly benefited from the integration of evolutionary, ecological, and cognitive research. In this chapter, we focus on risk sensitivity, the area of foraging theory that concerns how and why animals respond to variability in food sources. Our intention is to show how optimality modeling and cognitive research can and need to operate in unison if we are to understand risk sensitivity. For many years, data collection and theoretical developments regarding risk sensitivity have progressed in parallel in the behavioral ecology and psychology literatures. The lack of interchange between these two disciplines reflects a difference in the types of questions asked and the types of explanations sought. In behavioral ecology, research has centered on theoretical predictions that under certain ecological conditions, natural selection should favor foragers that are sensitive to environmental variance. Conversely, research in psychology has been driven by animals' observed responses to variance and, more recently, by hypotheses about the information-processing mechanisms that underlie foraging. We demonstrate the necessity of both approaches and advocate a program of research that simultaneously considers evolutionary ecology and cognitive mechanisms.

8.1.1 What Is Risk Sensitivity?

We begin with three examples that introduce the phenomenon of risk sensitivity. In the first experiment, bumblebees (*Bombus edwardsi*) were allowed to forage on an array of two types of artificial flowers. One color of flower always contained a constant volume of 0.1 μ l of nectar, and the other color of flower contained either 1 μ l of nectar (10% of flowers) or no nectar (90% of flowers). Once the bees had experienced both flower types and presumably learned something about their different properties, the bees showed a strong preference for the flowers that contained the constant volume of nectar (Waddington et al. 1981). In the second experiment, thirsty pigeons (*Columba livia*) were given

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repeated choices between two keys. The keys were arranged such that pecks on one key led to water delivery after a fixed 15-second delay, and pecks on the other key led to water delivery after a variable delay averaging 15 seconds. After training, the birds preferred water delivery with the variable delay (Case et al. 1995). In the third experiment, yellow-eyed juncos (*Junco phaeonotus*) were given repeated choices between two feeding stations, one of which offered four millet seeds on every visit, and the other either one or seven seeds with equal probability. The birds' preferences depended on the ambient temperature: At 1°C, they preferred the variable option; however, at 19°C, they preferred the constant option (Caraco et al. 1990).

In all three experiments, the animals faced two options that offered equal average rates of gain. The animals' preferences appeared to be influenced by the variance in the rate of gain that differed between the two options. In all cases, the variable option was programmed such that it was impossible for the animals to know exactly the gain that would result from choosing this option; with the variable option, the animals could learn only the probability distribution of possible outcomes. In the foraging literature, this type of environmental variance is referred to as *risk*, and an animal with preferences that are affected by the variance in the rate of gain is called *risk sensitive*. When two options offer the same long-term rate of gain, animals that prefer the less variable option (e.g. Waddington's bumblebees) are *risk averse*, and animals that prefer the more variable option (e.g. the pigeons of Case et al.) are *risk prone*.

Thus in foraging theory, risk has a very specific meaning. Risk should not be confused with the problem faced by an animal that has incomplete information and knows neither the mean nor variance of the foraging options it faces; this problem is often referred to as uncertainty. Also, risk should not be confused with risk of predation, which some authors prefer to call danger.

8.1.2 Patterns of Risk Sensitivity

In a recent review (Kacelnik and Bateson 1996), we collated the results of 59 experimental studies of risk sensitivity in 28 animal species including insects, fish, birds, and mammals. In most of these studies, we found evidence for sensitivity to risk, and a number of consistent patterns emerged. A brief review of our findings follows.

Most of the variation in the direction of risk-sensitive preferences is explained by the component of rate of gain that is programmed to be risky. Because rate of gain is a function of the amount of food obtained and the time taken to obtain it, variation in either of these components can generate risk

in the rate of gain. When risk is generated with variance in amount, as in the bee example described, animals are usually risk averse (fig. 8.1a). By contrast, when risk is generated with variance in the time associated with getting food or water, as in the pigeon example described, animals are almost universally risk prone (see fig. 8.1a).

In some species (for example juncos), the direction of preference appears to be dependent on the relationship between the energy needs of the animal and the average rate of energy gain available from the foraging options (the *energy budget*). Usually, if an animal's rate of gain exceeds its needs (i.e. the animal is on a *positive energy budget*), then risk aversion occurs. However, if the rate of gain is insufficient for the animal to meet its needs (i.e. the animal is on a *negative energy budget*), then risk proneness occurs (fig. 8.1b). This effect of the energy budget seems to be restricted to experimental situations in which risk is generated with variance in food amount. As yet, there is virtually no evidence that preference for variable time delays is affected by the energy budget; however, this lack of effect has not been thoroughly tested. There is also some evidence that a response to the energy budget may be dependent on the typical body weight of the species; lighter species appear more likely to respond to changes in the budget than heavier species (fig. 8.1c).

In this chapter, we will present a critical review of the main theories that have been proposed to account for risk sensitivity. We will concentrate on identifying which of the above findings the different theories can and cannot explain. However, before we proceed with these theories, we need to explain why risk sensitivity challenges classical optimal foraging theory, which until recently has provided the dominant framework for the modeling of animal decision making.

8.1.3 Classical Optimal Foraging Theory Predicts Indifference to Risk

In Charnov's (1976a, 1976b) two seminal optimality models, he assumed that foraging animals make decisions that maximize their rate of energy gain. In these models, rate of energy gain is computed as the ratio of the expected energy obtained from food to the expected time spent foraging. This form of rate is also known as *long-term rate*, or the *ratio of expectations* (Bateson and Kacelnik 1996). Thus,

$$\text{long-term rate} = \frac{E\{\text{energy obtained from food}\}}{E\{\text{time spent foraging}\}}, \quad (8.1)$$

where $E\{\}$ designates an expectation or average. The choice of long-term rate is justified on the grounds that it makes sense to start with the assumption that natural selection should favor animals that maximize this currency. The

rational is that both the survival and reproduction components of fitness have an obvious relationship with the long-term rate of energy gain. The more energy gained, the greater the probability of survival and the greater amount of energy that can be put into reproduction. Also, the less time spent feeding, the more time there is for other activities such as predator avoidance and reproduction. Therefore, animals may be expected to maximize their long-term rate of energy gain because, by doing so, they obtain the most energy per unit of time that is devoted to foraging (see Ydenberg, this vol. section 9.2, for further discussion of currencies).

As equation 8.1 shows, only expectations or averages enter the computation of long-term rate. Therefore, in most risk-sensitivity experiments in which the average amount and time are the same in the two options, long-term rate should be identical and foraging decisions should be unaffected by risk. However, the results summarized in figure 8.1 clearly show that considering only the average values of these variables is insufficient because risk has considerable effects on preference in most studies. Thus, maximizing long-term rate cannot be all that is involved in decision making. In the following section, we will introduce Jensen's (1906) inequality, a mathematical result that helps us understand why risk affects foraging decisions.

8.1.4 Jensen's Inequality

Let us start by imagining a function $y = f(x)$. Although it is mathematically irrelevant what x and y are, we will assume that y represents fitness and x represents the amount of food an animal gains from a foraging option. Thus, for example, the function allows us to determine how many units of fitness (y) a junco will obtain from four millet seeds (x). In the case of a risky foraging option in which there are two or more possible values of x (either one or seven seeds in the case of the juncos), we need to calculate the average fitness value of the option; however, there are two different ways to calculate the value. We can compute the average value of x (with use of the same notation described, $E\{x\}$) and use this value to obtain a single value of y (written $E\{y\} =$

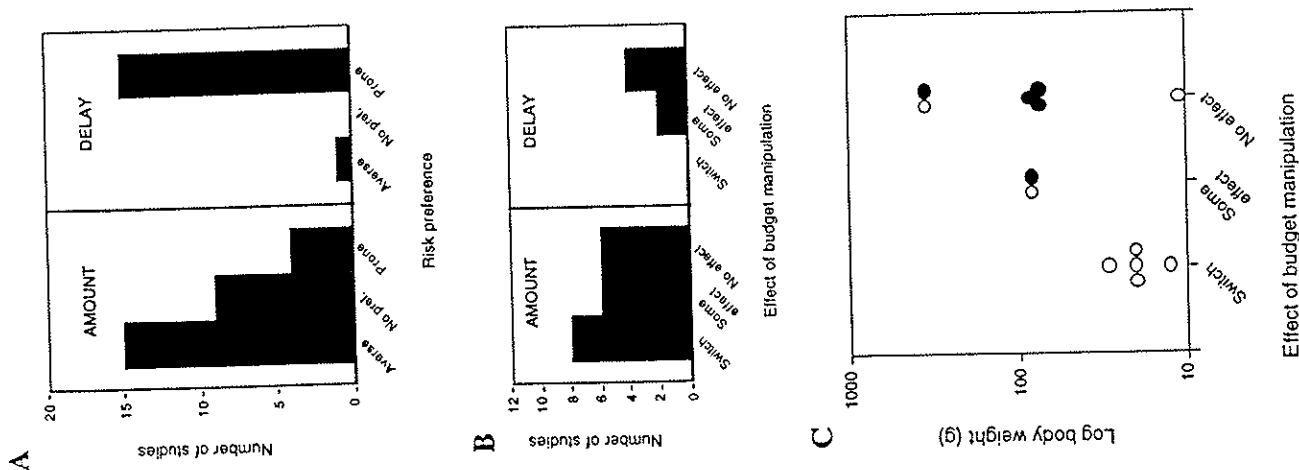


Figure 8.1. The responses of animals to risk. Data are from 28 species of insects, fish, birds, and mammals. (a) The differential effects of variability in amount and delay on risk-sensitive preferences. (b) The effects of energy-budget manipulations on risk-sensitive preferences. "Switch" indicates that subjects switched from being risk averse on positive budgets to risk prone on negative budgets. "Some effect" indicates there was a similar, but smaller shift in preference as that of the switch group. "No effect" indicates that manipulations of energy budget did not change the direction or degree of preference. (c) The response of bird species to energy-budget manipulations versus body weight. Empty circles indicate studies examining risk in amount, and the filled circles indicate studies examining risk in delay (replotted from Kacelnik and Bateson 1996).

$f(E\{x\})$). Or we can compute the y value obtained with each value of x and take the average of the resulting values of y (written $E\{y\} = E\{f(x)\}$). In other words, we can either average the values of x before applying the function or average the values of y obtained after applying the function to each value of x .

If $f(x)$ is a linear function, then averaging may be performed at either stage because the outcomes will be equal: $E\{f(x)\} = f(E\{x\})$. However, if $f(x)$ is nonlinear, then the stage at which averaging occurs matters because *Jensen's inequality* applies, and $E\{f(x)\} \neq f(E\{x\})$. Specifically, if $y = f(x)$ is increasing and decelerating, then calculating $E\{x\}$ first and applying the function to the result produces a higher value than calculating the average of the y values obtained after applying the function (i.e. $E\{f(x)\} < f(E\{x\})$). By contrast, if $y = f(x)$ is increasing and accelerating, the opposite is true, and $E\{f(x)\} > f(E\{x\})$.

If we make the assumption that fitness is the ultimate currency of all decisions, then the above results produce the following consequences for animals that must choose between fixed and variable foraging options with equal long-term rates of gain. In cases in which the fitness function is linear, risk sensitivity is not predicted because both options offer equal fitness. However, if the fitness function is nonlinear and animals average the fitness they obtain after applying the function, then risk sensitivity will occur, and the direction will depend on the shape of the function. If $y = f(x)$ is increasing and decelerating, then risk aversion is predicted; if $y = f(x)$ is increasing and accelerating, then risk proneness is predicted (fig. 8.2).

Thus, risk sensitivity is predicted if two conditions are met. First, the function that relates the amount of food gained to fitness must be nonlinear. We will refer to this condition as the *nonlinearity condition*. Second, averaging of outcomes from variable options must be performed with the fitness values obtained after the fitness function has been applied. We will refer to this condition as the *averaging condition*. Classical optimal-foraging models do not predict risk sensitivity because average long-term rate of gain is computed by averaging outcomes before the fitness function is applied (i.e. the averaging condition is not met).

Most existing models of risk sensitivity rely on Jensen's inequality. The models differ, however, in a number of respects that can obscure this underlying link. A major difference concerns the identity of the function $y = f(x)$. We introduced Jensen's inequality with use of the function to relate energy gain to fitness. However, alternative explanations of risk sensitivity focus on different functions. The alternative explanations also differ in the biological justifications they provide for the nonlinearity and averaging conditions. We divide the explanations into two types. The explanations presented in sections 8.2–8.4 are called *functional* because they assume that risk sensitivity has

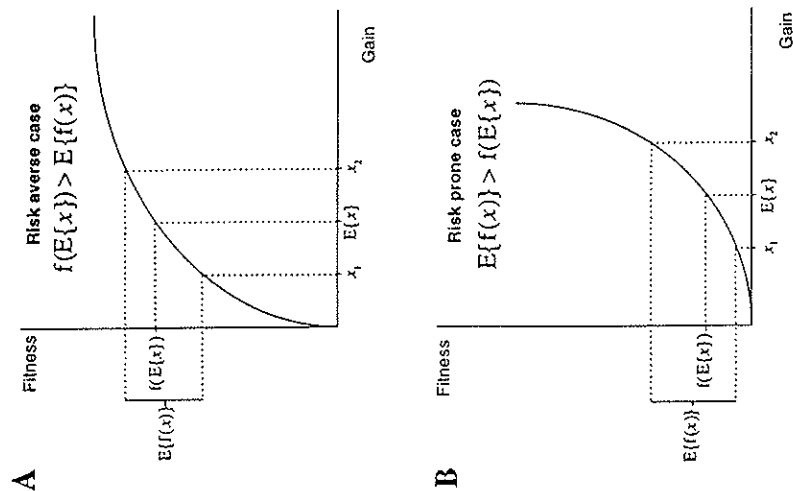


Figure 8.2. Graphics demonstrating Jensen's inequality. (a) $f(x)$, increasing and decelerating, leads to risk-averse behavior. (b) $f(x)$, increasing and accelerating, leads to risk-prone behavior.

evolved because of its fitness consequences. By contrast, the explanations in sections 8.5 and 8.6 are called *mechanistic* because they explain risk sensitivity as arising from basic psychological processes such as associative learning and perception. As Tinbergen (1963) made clear, these are logically distinct kinds of explanations, both of which are needed to fully understand behavior. Every behavioral phenomenon has a functional and mechanistic explanation; therefore, one type of explanation does not substitute for the other. Thus, we expect functional and mechanistic models of the same phenomenon to lead to identical predictions about behavior. We shall see, however, that differences in the background and motivation of behavioral ecologists and psychologists—who are responsible for the functional and mechanistic models, respectively—result in models that address different aspects of risk sensitivity and make very different predictions about behavior.

8.2 FUNCTIONAL EXPLANATION 1: LONG-TERM RATE MAXIMIZATION

In section 8.1.3, we argued that risk sensitivity is not explained by classical optimal-foraging models that assume maximization of long-term rate. However, this is only the case if the long-term rate of gain is equal in the fixed and variable options of a risk-sensitive foraging experiment. In this section, we suggest that there are a number of reasons why the long-term rate of gain experienced by a forager may differ from that intended by the experimenter.

In most risk-sensitivity studies, a tacit assumption is made that there is a linear relationship between the characteristics of the foraging option programmed by the experimenter and what is experienced by the forager. Thus for example, it is assumed that if one millet seed results in a net energy intake of 1 calorie, then seven seeds will provide 7 calories. However, the programmed amount of food may not have a linear relationship to the amount ingested by the animal, and the programmed time delay before food is obtained may not have a linear relationship to the delay experienced by the animal. It is also possible that the gross amount of food ingested by the animal may not have a linear relationship to the net energy derived from it. Because it is impossible for an animal to average quantities not yet experienced, the averaging condition is bound to be met and Jensen's inequality will apply if any of the functions we described is nonlinear. We, therefore, have a potentially trivial explanation for some cases of risk sensitivity.

The different techniques for generating risk can affect the shape of the function that relates what is programmed to what is experienced by the forager. Of the studies that generate risk by varying the amount of reward, most manipulate either the number of similarly sized food items, the duration of access to a food hopper, or the volume or concentration of nectar delivered. Although it is usually claimed that the average amounts obtained from constant and variable options are equal, evidence is rarely presented. In many cases, it is possible that animals may not consume the entire reward available or may not consume rewards of different sizes at the same rate. In cases in which amount is controlled by the time of access to food, the linear relationship assumed between programmed access time and the amount of food taken is usually not verified. It has been demonstrated that the amount of grain consumed by pigeons feeding from a hopper is an increasing, but decelerating function of the time of hopper access (Epstein 1981) (fig. 8.3). Jensen's inequality predicts that given an increasing, decelerating function, pigeons should be risk averse if they are offered a choice between two foraging options with the same average time of hopper access but with different variances in the length of access. In order to eliminate this possible source of risk-sensitivity, linearity between programmed and experienced reward needs to be proved in each study. For

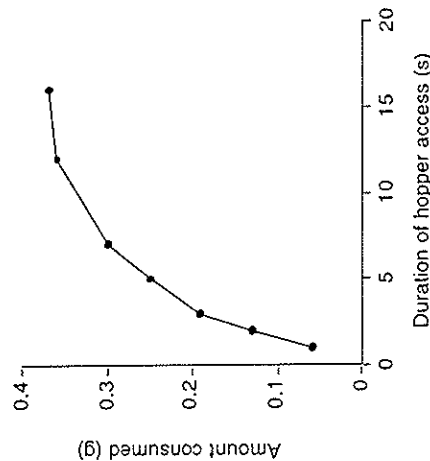


Figure 8.3. An example of nonlinearity in the relationship between the programmed duration of hopper access and the amount of grain consumed by pigeons. The nonlinearity is probably produced by two factors: the maximum amount of food the bird can retrieve from the hopper during one episode of reinforcement and the decreasing accessibility of grain as the pigeon eats (replotted from Epstein 1981). This graph shows that if a pigeon is given a choice between a fixed reinforcement of a 10-second duration versus a risky reinforcement equally likely to be 5 or 15 seconds in duration the bird maximizes its long-term rate of food intake by choosing the fixed option.

example, Reboreda and Kacelnik (1991) reported risk sensitivity in starlings (*Sturnus vulgaris*) despite the establishment of a linear relationship between time of hopper access and grams of food consumed in this species.

Experimenters that explicitly claim to vary the amount of food almost always also vary the time taken to acquire the food; large rewards usually take longer to deliver, handle, and consume than small rewards. This source of variability is usually ignored because it will not cause differences in the long-term rate of gain that is available from a fixed and variable option if the function that relates the reward size to handling time is linear. However, if there is a nonlinear relationship between the reward size and handling time, then differences in long-term rates can result because of Jensen's inequality. For example, Possingham et al. (1990) argued that a bumblebee presented with a choice of a flower type that offers a fixed 3 μ l of nectar versus a variable flower type that offers 1 or 5 μ l should be risk prone if the bee is maximizing its long-term rate of energy gain. This prediction is based on the observation that in bumblebees there is an increasing, but decelerating relationship between the volume of nectar taken from a flower and the time spent on the flower (fig. 8.4) (Hodges and Wolfe 1981). The effect of this relationship is that—although, on average, the volume of nectar taken from the fixed and variable flowers will be identical—the average time taken to get the nectar

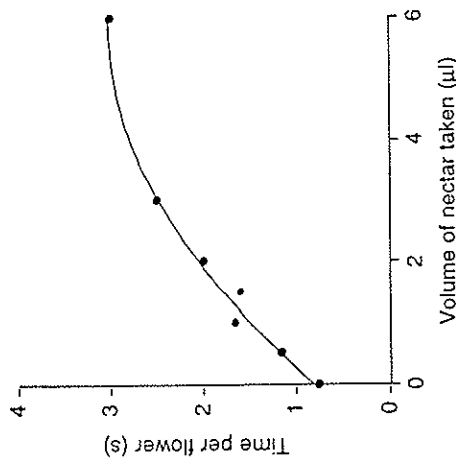


Figure 8.4. The relationship between volume of nectar taken and handling time per flower in the bumblebee, *Bombus appositus* (replotted from Hodges and Wolfe 1981). Bees extract larger volumes of nectar proportionately more quickly; initially, more of the hairy tongue comes into contact with the nectar, and lapping is more efficient (Harder 1986).

from the variable flowers will be less than that taken with the fixed flowers. Hence, the variable flowers will provide a higher long-term rate of nectar intake than the fixed flowers. This effect of handling time ought to be important in animals such as bees because handling takes up a substantial portion of total foraging time. However, the argument presented does not help us understand risk sensitivity in bees because the reported cases show risk aversion (Real 1981; Waddington et al. 1981; Real et al. 1982) and not risk proneness (we will return to the problem of why bees are sometimes risk averse in section 8.5). Despite this specific problem, the general point remains that nonlinearities in handling time can generate differences in the long-term rate of intake that is provided by fixed and variable food sources (which ostensibly should provide the same rate).

As with food amount, the delay to obtain food can also be controlled in a number of ways. Most studies use schedules of reinforcement, in which reward is programmed on the basis of either the number of responses performed (*ratio schedules*), the amount of time elapsed (*time schedules*), or a combination of these (*interval schedules*). With time schedules, the timing of reward is independent of the behavior of the animal; however, with interval or ratio schedules, reward is contingent on the animal completing the required responses. Thus, a programmed interval or ratio need not have a linear relationship to the actual delay experienced by the animal. For example, Ha et al. (1990) used fixed and variable ratio schedules to examine risk sensitivity in grey jays (*Perisoreus canadensis*) and reported risk proneness. However, to

assess the source of risk sensitivity in this experiment it must be established if the rate of responding is constant over the range of programmed ratios. If, for instance, animals worked faster when the ratio was higher, then the average time taken to complete a variable ratio would be less than the time taken to complete a fixed ratio with the same average value. Thus, animals that appear to be risk sensitive with respect to the programmed ratios may simply be rate maximizers when experienced times are taken into account.

The examples we have discussed all relate to nonlinearities in the functions that relate the parameters programmed by the experimenter to those experienced by the forager. Fewer data exist on the shape of the function that relates the gross rate of energy gain to the net rate of energy gain because obtaining this information requires measurements of energy expenditure. However, it is theoretically feasible that this function may also be nonlinear. For instance, in the case of honeybees that collect nectar by hovering from one flower to the next, the cost of staying aloft per unit time increases with the load already collected; successive equal volumes of nectar collected have different net values to the bee (Schmid-Hempel et al. 1985; see also Ydenberg, this vol. section 9.2).

The explanations for risk sensitivity discussed in this section may seem uninteresting because they do not require anything beside long-term rate maximizing; thus, these explanations are consistent with the classical optimal-foraging theory. In many experimental studies, however, risk is programmed without consideration for the shape of the functions that relate what is programmed to what is experienced, and nonlinearity in these functions must be acknowledged as a candidate explanation for some reports of risk sensitivity.

From the ecological perspective that examines how resource characteristics affect the exploitation of the resource by foragers, the cause of risk sensitivity is irrelevant. What matters is that foragers may treat food sources that provide the same average quantity of food differentially depending on the variance in food quantity. This differential treatment could have consequences for the evolution of food species. For example, in the only risk-sensitive foraging study that used a natural food source, Cartar (1990) showed that bumblebees' choices between two flower species were influenced by variance differences in the rate of gain associated with the species. Such behavior should place selective pressures on the distribution of nectar between flowers because a plant can theoretically attract more pollinators with simply a change in this distribution.

8.3 FUNCTIONAL EXPLANATION 2: RISK-SENSITIVE FORAGING THEORY

Risk-sensitive foraging theory is the main, functionally based framework developed to explain why animals are sensitive to risky food sources. This theory

focuses on the function that relates the energy gained, as the result of a foraging decision, to fitness and provides biological justifications for both the non-linearity and the averaging conditions.

8.3.1 The Energy-Budget Rule

The simplest and best known risk-sensitive foraging model (Stephens 1981) concerns a small endotherm, such as a bird, that has to attain a minimum reserve threshold by dusk to survive the night. This threshold provides the necessary nonlinear relationship between rate of gain and fitness. If the animal has more than the threshold level of reserves, it survives until the next day; however, if the animal has less, it dies and has a fitness of zero. Consider a bird faced with two foraging options that differ only in the variance of the expected number of seeds available per reward (for example the junco experiment described in section 8.1.1). If the fixed option offers a rate of gain that is sufficiently high to take the bird above the threshold (i.e. it is on a positive-energy budget), then the bird should be risk averse; however, if the rate is not sufficiently high (i.e. the bird is on a negative energy budget), then the bird's only chance of survival is to be risk prone and gamble on the variable option that gives an above average rate of gain (fig. 8.5). These options have been summarized in the *daily energy-budget rule*, which states that a forager on a positive budget should be risk averse and a forager on a negative budget should be risk prone (Stephens 1981). Note that "budget" is not equivalent to the animal's absolute level of reserves; budget refers to the relationship between an animal's needs and its potential rates of gain. A hungry animal close to starvation could be on a positive budget if it is currently facing a rich food source. By a similar argument, a well-fed animal could be on a negative budget. If everything else is assumed to be constant, however, a subject with low reserves has higher needs and is therefore more likely to be on a negative budget than a counterpart with high reserves.

Many investigators have sought to test the energy-budget rule directly by experimentally manipulating the energy budget of the subjects. Relatively few studies, however, have produced convincing support for the theory. In our recent review, we examined 24 studies that manipulated energy budget: In 18 of these studies, risk sensitivity was investigated when amount was variable. Time was variable in five studies, and both amount and time were variable in one study. Among the experiments with variable amount, 14 showed a shift toward risk proneness when energy budgets were reduced and risk aversion when energy budgets were increased; although, only eight of these studies showed a complete switch in preference between significant risk proneness and significant risk aversion (Caraco et al. 1980; Caraco 1981; Caraco 1983; Barnard and Brown 1985; Moore and Simm 1986; Caraco et al. 1990; Young

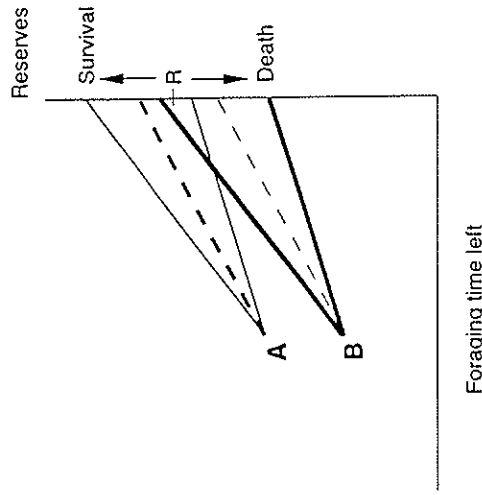


Figure 8.5. Graphic demonstration of the logic that underlies the energy-budget rule. *A* and *B* represent two foragers that differ in their energy reserves. Both have to make one foraging decision before nightfall and must choose between a fixed option (*broken line*) that gives a certain amount of food or a risky option (*solid line*) that gives with equal probability a small or large amount of food. *R* represents the level of reserves needed by dusk if the foragers are to survive the night. The optimal choices for *A* and *B* are different: *A* is on a positive budget and ensures its survival by choosing the fixed option; however, *B* is on a negative budget, and its only chance of survival is provided with the variable option. Optimal choices for each forager are shown in bold.

et al. 1990; Croy and Hughes 1991). Despite this apparent support for the energy-budget rule, we suspect that the real number of failures to obtain the predicted switch in preference with budget manipulations is actually greater; studies that fail to reject the null hypothesis (lack of effect of budget) are harder to publish and probably seldom submitted for publication. Some studies that show failure may be salvaged for publication if a convincing post hoc argument can be made for why a switch in preference was not predicted. A possible example is Barkan's (1990) study of black-capped chickadees (*Parus atricapillus*), which examined two very different rates of intake; the continuing risk aversion of the birds despite apparent budget changes was justified on the basis of careful calculations that showed birds were, in fact, always on positive budgets.

Of the few budget-manipulation experiments with variability in delay, all have failed to demonstrate convincing shifts in preference. Ha and colleagues (Ha et al. 1990; Ha 1991) tried unsuccessfully to induce a preference switch in gray jays; we failed also to show a preference switch in starlings (Bateson and Kacelnik, 1997). Similar failure was met by Case et al. (1995) with use

of water as a reward for pigeons and manipulation of water budgets. A study of rats by Zabudoff et al. (1988) showed some evidence for a preference switch; the rats became risk prone as their body weights dropped from 85% to 75% of their free-feeding weights. This study, however, is difficult to interpret because the decrease in body weight is confounded by an increase in the variance of the more variable option; other studies have shown increasing risk proneness with increasing variance in delay to reward. Reboresda and Kacelnik (1991) found that individual starlings that were less efficient at using hopper access time (and as consequence got smaller food rewards) were significantly more risk prone than more efficient birds. This observation agrees with the prediction that needier animals should be more risk prone. However, because the amount of food the birds obtained was not manipulated experimentally, this evidence is only correlational. Thus, there is little direct evidence that energy budget affects risk sensitivity when the delay to receive food is variable. Instead, risk proneness with variable delays seems universal.

Differences in body weights of the various species of birds and mammals used in risk-sensitivity studies may explain the species that respond to budget manipulations and those that do not. Smaller species may be more likely than large species to be subject to selection for short-fall minimization, and thus, smaller species may be more likely to show energy budget-associated switches in risk sensitivity. In support of this prediction, studies of larger species of birds such as pigeons (Hamm and Shettleworth 1987; Case et al. 1995), jays (Ha et al. 1990; Ha 1991), starlings (Bateson and Kacelnik 1997), and rats (Leventhal et al. 1959; Kagel et al. 1986) have failed to find support for the energy-budget rule. In an attempt to reduce the impact of phylogenetic confounds (such as differences in metabolic rate) between birds and mammals, we analyzed the relationship between body weight and the effects of budget on risk sensitivity in birds only. In small birds, we found that changes in budget were more likely to cause appropriate switches in foraging preferences (fig. 8.1c). A closer inspection of the data, however, reveals that all studies with variability in delay have been conducted on larger species such as pigeons, jays, and starlings. Thus, it is not presently clear if the lack of an effect of budget in these studies is due to the component of rate of gain that was varied or the body weights of the experimental species because these two variables are confounded.

It is interesting to speculate if differences in energy budget were responsible for the differences in responses to amount and delay variability observed (fig. 8.1a). When food amount is variable, some of the variation in behavior is potentially attributable to the energy budget. Among the risk-averse animals, some were certainly on positive budgets (Caraco 1982; Stephens and Ydenberg 1982; Caraco and Lima 1985; Tuttle et al. 1990); however in one study, the subjects were probably on negative energy budgets (Wunderle et al. 1987).

Among the risk-prone animals, the shrews of Barnard et al. (1985) were probably on negative energy budgets. In the other three studies (Essock and Rees 1974; Young 1981; Mazur 1985), pigeons were maintained at 80% of their free-feeding weights and could also have been operating on negative budgets. However, the difficulty of explaining the variation is exemplified with the studies on pigeons. Despite the similar procedures employed and the maintenance of all birds at 80 or 85% of their free-feeding weights, two studies showed risk aversion (Menlove et al. 1979; Hamm and Shettleworth 1987) and three showed indifference (Staddon and Innis 1966; Essock and Rees 1974; Hamm and Shettleworth 1987) (in addition to the studies that showed risk proneness mentioned). This variation cannot be explained with any obvious differences in procedure that may have resulted in budget differences.

If delay is variable, animals are almost universally risk prone (the only exception has been shown in the concurrent schedule study of Rider [1983] in which a questionable measure of preference was used) (see Kacelnik and Bateson 1996). Given that most studies were performed by psychologists with pigeons maintained at body weights as low as 75% of free-feeding body weights, it is possible that subjects may have been on negative energy budgets. However, this seems unlikely because pigeons are relatively large birds that can be maintained at 75%–80% of their free-feeding weights for long periods of time. Moreover, given that most of the daily ration is generally received in the experiment, the rate of intake experienced must be sufficient to result in a positive energy budget.

Three studies (Logan 1965; Reboresda and Kacelnik 1991; Bateson and Kacelnik 1995a) directly compared responses to variability in amount and delay under the same conditions of energy budget. All showed that animals (rats in the first study and starlings in the other two) were risk averse when variability was in amount but risk prone when variability was in delay. These results suggest that the difference in response to variability in amount and delay is not attributable to energy-budget differences.

8.3.2 Beyond the Energy-Budget Rule

The energy-budget rule is insufficient to explain the patterns of risk sensitivity reported in the literature. Most experimental tests have focused on the energy-budget rule; however, this rule is not a universal prediction of all risk-sensitive foraging models. Stephens's (1981) original risk-sensitive foraging model inspired the creation of a number of variant models that explore the modification of his various original assumptions. It is not our intention to give an exhaustive review of the theory because an excellent review is available (McNamara and Houston 1992); however, we want to present the current level of sophistication and complexity of the theory's predictions.

One of the most important constraints in Stephens's model is that the forager is allowed to make only a single foraging decision and is then required to stick with this choice for the rest of the day. This constraint led to the criticism that risk proneness would be very rare in nature because it would occur only if the forager's probability of dying was over 50% that day (Krebs et al. 1983). However, if the forager is allowed to make sequential decisions that can vary according to its current state, then risk proneness becomes far less dangerous and therefore more likely. A risk prone forager with a run of good luck that creates a positive trajectory can capitalize on this luck by switching to risk aversion instead of chancing the creation of a negative budget again (Houston and McNamara 1982; McNamara 1983; McNamara 1984). Whether a single- or sequential-choice model is more realistic for a given foraging situation will depend on the degree to which an animal commits itself when it makes a choice. Single-choice models may be more appropriate to large-scale habitat choices, and sequential-choice models will be appropriate to the modeling of prey choices within a habitat. Most experiments on risk sensitivity probably approximate the sequential-choice model more closely due to their small-spatial scale and the large number of choices per session.

A second assumption of Stephens's model is that the only way to die is by failing to meet the critical level of reserves by nightfall. The possibility of starving while foraging is not included, even though for small mammals (such as the shrew) starvation during foraging is a very real danger. If the model is modified so that a forager is assumed to forage continuously to maintain reserves above a lethal level, then it can be shown that the optimal policy is always to be risk averse, if the mean net gain from a foraging choice is positive (Houston and McNamara 1985). Houston and McNamara (1985) combined in a single model the possibility of death (by allowing reserves to fall below a lethal level) during foraging with the need to build reserves to survive the night. In this case, the optimal policy was a compromise between those results in the separate models: A forager is risk averse at all levels of reserves except for a wedge-shaped region in the reserves-versus-time-of-day space near dusk when it is optimal for animals on negative budgets to be risk prone so that the required level of reserves may be achieved (fig. 8.6a).

A third limitation of Stephens's original model (and of all the others mentioned) is that the optimality criterion is restricted to maximization of probability of survival. There may be animals, particularly insects, that have the option of using energy for immediate reproduction. McNamara et al. (1991) modeled the situation in which reproduction occurs above a certain level of reserves and causes a reduction in reserves. They showed that the policy that maximizes lifetime reproductive success is different from one that minimizes mortality. In these reproduction models, risk proneness can occur at high levels of reserves because there are conditions in which a risk-prone decision could take a for-

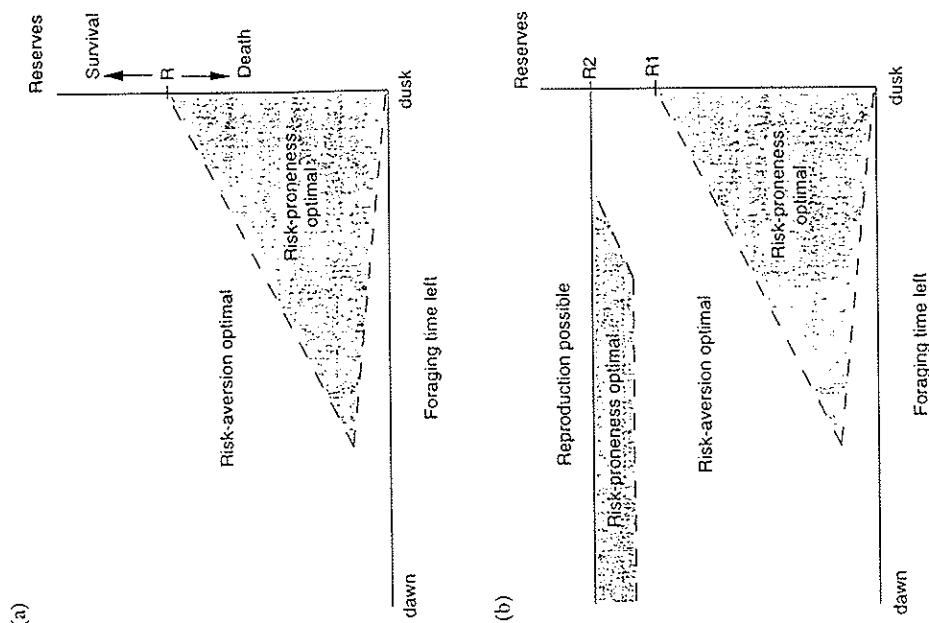


Figure 8.6. Optimal policy. (a) Diagram shows the wedge-shaped region near dusk in which it is optimal to be risk prone. R is the level of reserves required to survive the night (redrawn from Houston and McNamara 1988). (b) Diagram shows the effect of introducing the possibility of reproduction: If reserves are above the R_2 , then reproduction is possible. This second threshold gives rise to risk proneness at high levels of reserves in addition to the wedge-shaped region (see McNamara et al. 1991).

ager over a threshold above which it can reproduce (fig. 8.6b). Given certain parameters, it can be shown that as reserves increase, the optimal policy changes successively from risk aversion (to escape an immediate lethal level) to risk proneness (to have a chance of meeting a daily requirement) back to risk aversion (when the requirement can be reached but there is no chance of

reproduction) and finally back to risk proneness again (when this offers the possibility of reproduction).

A final deficiency of the models discussed is that they only consider variance in amount of food; yet, clearly variability in the time associated with obtaining food can also produce risk in the rate of intake. Zabludoff et al. (1988) modeled choice between a foraging option in which there was a fixed delay to food and one in which the delay had the same mean but was variable. In this situation they showed that if the forager must reach a critical level of reserves by nightfall, then the energy-budget rule describes the optimal policy. However, McNamara and Houston (1987) showed that, under some circumstances, the effects of variability in amount and time are not equivalent. Variability in amount and time affect variance in rate of intake; however, unlike variable amounts, variable delays additionally introduce variance in the number of choices that can be made because the length of the delay affects the amount of time remaining.

The message from our brief overview of risk-sensitive foraging theory is that, as Houston and McNamara stressed (Houston 1991; McNamara et al. 1991; McNamara and Houston 1992), there is no single model of risk-sensitive foraging and no single prediction. Notably, the energy-budget rule is not a universal prediction of risk-sensitive foraging theory. This complexity has a number of ramifications for how the risk-sensitive foraging theory can be tested.

8.3.3 Problems with Testing Risk-Sensitive Foraging Theory

Failure to find evidence supporting the energy-budget rule is inconclusive because it is always possible that the wrong model has been tested. Even if the correct model can be chosen for a given situation, there still will be too many unknowns to predict quantitatively how an animal should respond to a given manipulation. For example, the juncos of Caraco et al. (1990) switched from an average of 60% preference for variability in a cold regime to an average of 37% preference for variability in thermoneutral conditions; however, risk-sensitive foraging theory predicts only the direction of the switch, and not the magnitude of the switch.

An additional problem with testing of risk-sensitive foraging theory (and most purely functional models) is that assumptions must be made about the mechanisms an animal uses to assess variables such as the energy budget or rate of intake. Although the many different manipulations tried can theoretically modify energy budgets, modification does not mean that a shift in budget will necessarily be registered by the animal; registration of the shift depends on the proximate mechanism used by the animal to assess its budget. For example, in the natural habitat, ambient temperature may be easy to measure

and provide a reliable correlate of energy requirements. An animal, however, that has evolved a rule-of-thumb to change its risk preference with use of ambient temperature may fail to register a change in energy requirements induced by other means, such as a period of restricted access to food. At present, we do not know how animals assess their energy budgets; a failure to demonstrate an effect of an energy-budget shift on preference does not imply that the energy-budget rule will not predict behavior in the wild. A similar argument can be applied to the assessment of variance in rate of gain. These problems are only partially solved with experimentation in the field (e.g. Cartar 1991) because under natural conditions it is very difficult to control and measure the experience of individual foragers and thus a different set of problems are introduced.

From this discussion, it should be clear that testing the ecological validity of risk-sensitive foraging theory will be exceedingly difficult by rejecting predictions of specific models; the rejection of a model can always be attributed to some cause other than the general validity of the theory. Given this difficulty, we must rely on confirmation of predictions of risk-sensitive foraging models. If a theory makes original and counterintuitive predictions that are later confirmed, we gain confidence in the theory. The energy-budget rule emerges as the best candidate for a prediction that is currently unique to risk-sensitive foraging theory. We suggest that a sound empirical demonstration of this rule would provide strong evidence for the theory. The demonstration by Caraco et al. (1990) of the predicted switch in juncos may provide such evidence (Houston and McNamara 1990), but wide replication of their results is needed.

Another specific prediction of risk-sensitive foraging theory is that all risk-sensitive foraging models necessitate an unpredictable environment instead of just a variable environment. A starving junco is predicted to prefer a risky option because the possibility of a run of large seven-seed rewards will create a positive trajectory. A variable, but predictable option in which the junco receives one and seven seeds alternately offers no benefits over a fixed option that always yields four seeds because the total number of seeds obtained is the same. Thus, we can predict that if the observed preferences have evolved for the reasons proposed by risk-sensitive foraging theory and psychological mechanisms tightly match fitness consequences, then animals should be risk sensitive in the context of unpredictable variance but not predictable variance. We recently tested this idea in starlings. We reached the tentative conclusion that the birds appeared not to treat predictable and unpredictable variable delays differently in the manner predicted by risk-sensitive foraging theory (Bateson and Kacelnik, 1997). However, this negative result may be another example of a difficulty already mentioned. The prediction may have failed because predictable variance is uncommon in the natural world; animals may

d seconds in the future is $\exp(-\alpha d)$. Therefore, if the subject is fully informed of all the parameters of the problem, then the discounting function $f(r, d) = \exp(-\alpha d)$. This is a linear function of reward amount and a negative exponential (i.e. decreasing and decelerating) function of delay. This prediction has been made independently in the literature on economics (Samuelson 1937) and foraging (Kagel et al. 1986; McNamara and Houston 1987).

We will now examine the effects of introducing inexact knowledge of reward arrival. This situation can be treated as mathematically equivalent to the existence of variability in the expected delay to reward. Consider a fixed option in which a reward of fixed magnitude, r , is promised for delivery after a fixed delay, d_f , and a variable option in which a reward also of fixed magnitude, r , is promised after a delay of either $d_f - \delta$ or $d_f + \delta$ with equal probability. The expected delay in the variable option is $d_v = 0.5 [(d_f - \delta) + (d_f + \delta)] = d_f$. The discounted value of the fixed option is $v_f = f(r, d_f)$, but the subject may employ different algorithms to assign value to the variable option. The subject may use either

$$v_{v1} = f(r, d_v) \quad (8.2a)$$

or

$$v_{v2} = 0.5[f(r, d_f - \delta) + f(r, d_f + \delta)]. \quad (8.2b)$$

In equation 8.2a, the subject discounts reward value with use of the expectation of the delay; in equation 8.2b, the subject averages the discounted value of each possible outcome. Thus, we discriminate between the order in which averaging and attributing value are performed. If the averaging of the two possible delays is performed first and the discounting function is applied later, we have equation 8.2a. If the discounting function is applied to each possible delay and the averaging is performed later, we have equation 8.2b. We encountered the same distinction when we introduced Jensen's inequality (section 8.1.4). We are, therefore, familiar with the various outcomes: If the discounting function is linear, then these two equations produce the same result and $v_{v1} = v_{v2}$. If the discounting function is decreasing and accelerating, then $v_{v1} > v_{v2}$. If the discounting function is decreasing and decelerating, then $v_{v1} = v_{v2}$. If the assumptions involved in predicting the discounting function are valid and the function is a negative exponential, then the third case applies and the value computed for the variable option according to equation 8.2b will be higher than that of the fixed option. In the case of a subject facing an isolated choice between a fixed and variable delay option, it is possible to prescribe equation 8.2b, because this equation maximizes the expected fitness consequences of the decision. To illustrate the effect of variability in delay, let $\alpha = 0.1$ and compare a fixed delay of 5 seconds with a variable delay that is either 1 or 9 seconds with equal probability. In the fixed option, the probabil-

have evolved a general rule to treat all variability as risk regardless of its predictability or unpredictability.

8.4 FUNCTIONAL EXPLANATION 3: TIME DISCOUNTING

It is possible that not all cases of risk sensitivity will be explained with the same theory, and this may be particularly true for the difference in response to variability in amount and time. We will discuss a completely different functional explanation for why animals may be sensitive to variance in food delay based on the probability of being interrupted while foraging. We will introduce the argument by considering a choice between an immediate reward and another reward of the same magnitude that is delivered later. After this we will investigate the effects of adding variance to the time before a reward is delivered.

8.4.1 Interruptions and Temporal Discounting

Animals are expected to prefer immediate rewards over delayed rewards for a variety of reasons; however, we will focus on the effects of the probability of losing a reward because of an unpredictable interruption, such as the arrival of a predator or a change in weather, during the delay. If a predicted reward has a continuous chance of being lost before consumption, the longer the delay, the greater the cumulative probability that the reward does not arrive. Thus, a delayed reward will have a lower expected value than an immediate one because the value of a delayed reward is its immediate value multiplied by the probability that it materializes. Immediate rewards should also be preferred over delayed rewards because the time saved by accepting an immediate reward can be used to search for the next reward. This consideration, however, only should apply if an animal is making a sequence of foraging decisions and should not apply to an isolated choice. For clarity, we will restrict our discussion to the effects of the probability of interruption on an isolated choice and return to the additional considerations posed with sequential choices in section 8.5.

The value of a delayed reward, v , will be a function of the immediate value of the reward and its delay and can be written $v = f(r, d)$ where r is the value of the reward if it is obtained immediately and d is the delay from the point of choice; $f(r, d)$ is known as the *discounting function*, and there is much theoretical and empirical literature on the shape of this function (e.g. Myerson and Green 1995). If we assume that (1) the reason underlying discounting is probability of loss by interruption; (2) interruptions occur as a Poisson process with rate α (i.e. the chances of the reward being lost are constant per unit of waiting time); and (3) the rate of interruption, α , is constant for rewards of different magnitude, then the probability of getting a reward

ity of getting the reward is $\exp(-0.5) = 0.606$. The corresponding probability in the variable option is $0.5 [\exp(-0.1) + \exp(-0.9)] = 0.656$. Thus, we predict that animals should be risk prone if faced with an isolated choice between a fixed and variable delay to food when unpredictable interruptions have exerted an important selective pressure on the evolution of decision making.

In the case of an isolated choice between a fixed and variable amount of reward, the discounting function is assumed to be linear with respect to reward amount. Therefore, under the current theory of time discounting, variability in amount per se should have no effect on preference. If, however, r and d are correlated (as is the case if large food items take longer to handle than small ones), then variability in amount can affect preference by means of the variability's effects on delay (Caraco et al. 1992). We will return to this issue in section 8.5.

8.4.2 Time Discounting Is Not Exponential but Hyperbolic

There have been several attempts to explore how humans discount single delayed rewards. In a recent study, Myerson and Green (1995) gave subjects a choice between two notional sums of money: r_1 was delivered immediately, and r_2 was delivered after a delay, d . By systematically varying r_1 for each pair of values of r_2 and d , they found the value of r_1 at which each subject switched preference from one option to the other. This procedure gave estimates of the relative values of the immediate and the delayed rewards from which the shape of the time-discounting function, $f(r, d)$, could be derived. Like other similar studies, this experiment showed that the shape of the discounting function is hyperbolic and not exponential; for a given absolute increase in d , the fraction of value lost decreased as d increased. By contrast, with an exponential function, the proportional reduction in value with an increase in d is independent of the absolute value of d (fig. 8.7). Therefore, the empirically determined discounting function is inconsistent with the function predicted with our assumptions. We suggest that time discounting cannot be explained as a consequence of the probability of loss by interruption unless additional assumptions are invoked.

Nevertheless, the function that most closely fits the available data is

$$v = r/(a + kd), \quad (8.3)$$

where a and k are constants; a is small and k is close to $1s^{-1}$. In equation 8.3, value is also a linear function of reward and a decreasing decelerating function of delay. Therefore, whatever the reasons there are for devaluing delayed rewards, an isolated reward that is predicted to occur after a variable delay ought to be preferred to a reward that is predicted after a fixed delay of its arithmetic

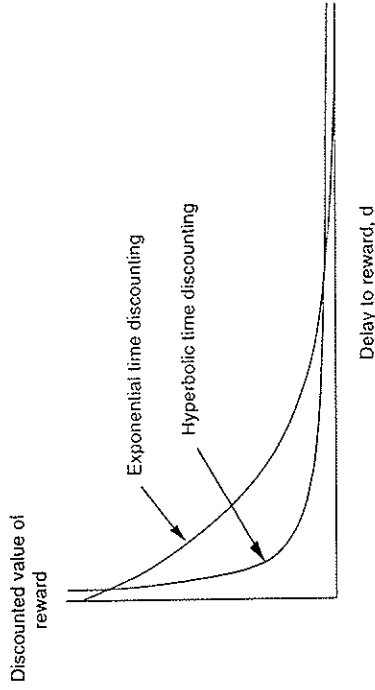


Figure 8.7. Exponential and hyperbolic time discounting functions. Both functions are decreasing and decelerating; however, their shapes differ.

mean. However, we have not been able to find empirical tests of this specific prediction.

8.4.3 Inadequacies of Purely Functional Accounts

All the functional explanations of risk sensitivity we have considered assume that animals can calculate accurate, unbiased estimates of parameters, such as their long-term rate of gain and the associated variance. In optimal-foraging models the tacit assumption is made that if adaptive behavior in animals necessitates accurate estimates of these parameters, then natural selection will provide the animals with the necessary cognitive equipment to obtain these estimates. When explaining subtle details of behavior, however, there are many reasons why a strictly adaptationist approach is insufficient.

In the following sections, we will discuss what is known about how animals process information while foraging. We will show how some of these findings may account for risk sensitivity with the generation of nonlinearities in the function that relates what is actually available to the subjective value the forager assigns to this. The explanations we will present differ from those in previous sections: risk sensitivity will be interpreted as a consequence of basic cognitive mechanisms instead of a direct functional response to external conditions. By promoting the development of mechanistically based models, we do not imply an anti-optimality stance. Behavioral mechanisms must also be the product of natural selection, and we hope that future work may help us understand why these mechanisms—which we regard as constraints in the context of the current discussion—have evolved. We believe natural selection is the main agent of evolutionary change, and we hypothesize that cognitive mechanisms, when viewed in a broader context, can be viewed as adaptations.

8.5 MECHANISTIC EXPLANATION 1: SHORT-TERM RATE MAXIMIZATION

Many experiments on nonhuman animals have examined the effects on choice of the length of delay to reward. It is tempting to generalize the ideas presented in the previous section and treat animal experiments as equivalent to the human experiments on time discounting. There are, however, problems with extrapolating from work in humans to that in animals; the preferences of animals can only be tested after training, which involves repeated exposure to the options. Repeated exposure introduces two differences between work in animals and that in humans. First, animals learn the probability of interruptions in the experimental conditions; because interruptions are typically not programmed, the subject can learn they do not occur. Therefore, whereas learned probability of interruption could influence the choices of humans who are instructed verbally to make an isolated choice, learned probability of interruption is less likely to explain animals' choices. Second, subjects learn to experience a sequence of choices; therefore, immediate rewards are more valuable than delayed rewards because the time saved with a short delay can be used to pursue the next reward. Thus, in animal experiments, a delay to reward can be viewed as a loss of foraging opportunity (Stephens and Krebs 1986).

From a functional point of view, an appropriate measure of value given a sequence of choices is long-term rate of gain (equation 8.1), which is the currency of classical optimal-foraging models. Notice the similarities between equations 8.1 and 8.3. The numerator of both functions is a measure of the immediate value of a food reward, and the denominator of both functions includes the time associated with acquiring the reward. Given that time spent foraging in equation 8.1 includes the delay to reward, d , long-term rate can be written as

$$\text{Long-term rate} = \frac{E\{\text{energy obtained from food}\}}{E\{\text{delay to food}\} + E\{\text{other time}\}}, \quad (8.4)$$

where "other time" refers to all periods in the foraging cycle other than the delay between choice and reward, such as intertrial intervals, postreward handling times, and travel times. Note that, like in equation 8.3, long-term rate drops hyperbolically with the delay to food. Long-term rate maximizing is therefore formally identical to hyperbolic time discounting. Animal experiments have demonstrated hyperbolic time-discounting functions (e.g. Mazur 1987; Rodriguez and Logue 1988). Therefore, if animals are offered a sequence of choices between two rewards—one immediate and another delayed—their choices are basically compatible with those in long-term rate maximizing. This fact has often been overlooked; authors have invoked time discounting when, in reality, rate considerations came into play. The two ap-

proaches could be combined because interruptions during a series of choices will affect the magnitude of the numerator and denominator in equation 8.4; although, an interruption may cause the loss of a reward, the interruption will release time to search for the next reward.

If variability is introduced and an animal must choose between rewards after fixed and variable delays of the same mean duration, the problem of whether to average first and assign value later or vice versa arises again. Unlike a human that faces an isolated choice, a maximizer of long-term rate should calculate averages first and assign value later as in equation 8.2a; this algorithm correctly characterizes the ratio of expected gain over expected time. As a consequence, this forager would be insensitive to risk as discussed in section 8.1.3. However, many experiments have demonstrated that animals, given sequences of choices, prefer variable over fixed delays with the same means (Herrnstein 1964; Davison 1972; Gibbon et al. 1988; Reboresda and Kacelnik 1991; Bateson and Kacelnik 1995a); the results are compatible with those from animals that assign value first and average later, as depicted with equation 8.2b. *Short-term rate* or the *expectation of the ratios* of amount to time is maximized (Bateson and Kacelnik 1995a, 1996):

$$\text{short-term rate} = E\left\{\frac{\text{energy obtained from food}}{\text{time spent foraging}}\right\}. \quad (8.5)$$

Note that the difference between short- and long-term rates is in the position of averaging: for long-term rate, averaging precedes the computation of the ratio of gain over time, whereas for short-term rate, averaging follows the computation of the ratio. "Short" and "long" are often mistakenly interpreted as referring to the "memory window"—the amount of previous experience on which a rate estimate is based.

Evidence for maximizing short-term rate comes from experiments in which animals had to determine when values of fixed- and variable-delay options were equivalent. For example, we performed a titration experiment in which starlings chose between fixed (initially 20 seconds) and variable (2.5 or 60.5 seconds with 50% probability) delays to food. The birds initially preferred the variable option, and we reduced the fixed delay to 5.61 seconds before the birds showed indifference between the two options (fig. 8.8) (Bateson and Kacelnik 1996). At this *indifference point*, short-term rate was approximately equal for the fixed and variable options; the hypothesis that the birds use this currency to value the options was supported.

Further evidence for maximizing short-term rate comes from studies of bumblebees, which are risk averse if there is variability in the volume of nectar in flowers (Real 1981; Waddington et al. 1981). Harder and Real (1987) showed this finding is compatible with bees maximizing short-term rate. In

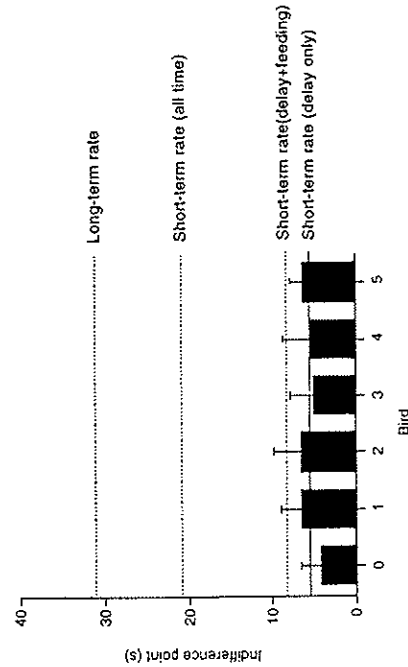


Figure 8.8. Indifference points derived from a titration experiment with six starlings. Bars show the mean (± 1 standard deviation) of the value of the fixed delay for which the birds were indifferent between the fixed and variable options. The variable option had two delay times (2.5 and 60.5 seconds) that occurred with equal probability. Lines show the predictions of the six currencies under consideration (only one line appears for long-term rate because the three predictions are identical). The data are significantly different from the predicted data (one sample t tests, $P < .05$) with the exception of expectation of ratios (short-term rate, shown as a solid line) that was calculated with only the delay to reward (from Bateson and Kacelnik 1996).

bees, the correlation between nectar volume, r , and handling time, d , results in the appearance of r in the numerator and denominator of $f(r, d)$; an increasing, but decelerating function that relates the volume of nectar taken to net intake rate from each decision results (fig. 8.9). This relationship does not lead to risk sensitivity if bees are maximizing long-term rate because volumes are averaged before the computation of rate. However, if bees are maximizing short-term rate, then risk aversion is predicted owing to Jensen's inequality. The magnitude of this effect of variability in reward amount will depend on the proportion of total foraging time that is spent handling the food item. In bees, this time is long; however, in many bird studies, the effects of handling time are likely to be overshadowed by longer delays to reward and intertrial intervals. Thus, variability in reward amount is unlikely to lead to detectable risk aversion even if there is a correlation between reward amount and handling time. In bees, risk aversion may be indicative of maximization of short-term rate given the measured correlation between nectar volume and handling time. In bees, risk aversion is abolished if the amount of reward is controlled with nectar concentration and not nectar volume; this occurs probably because there is no longer a correlation between r and d (fig. 8.9) (see Banschbach and Waddington 1994; Waddington 1995).

In animals, maximizing short-term rate is puzzling because an animal that

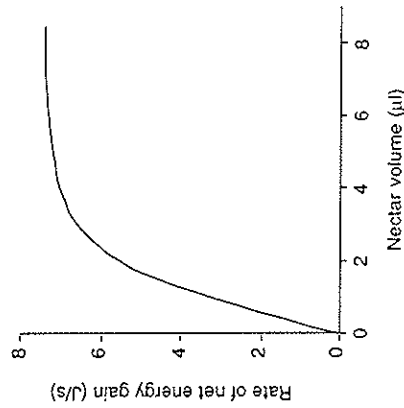


Figure 8.9. Function relating nectar volume to rate of net energy gain derived from the empirically established biomechanics of nectar extraction in bumblebees (replotted from Harder and Real 1987). The nonlinearity results from a correlation between nectar volume and handling time, (although Harder and Real assumed this function to be linear instead of nonlinear as shown in fig. 8.4 for the purposes of deriving this function).

maximizes this currency fails to account correctly for the loss of foraging opportunity and makes choices inconsistent with maximization of long-term rate.

8.5.1 Which Time Intervals Matter?

All time spent foraging including time lost traveling, pursuing, and handling prey items causes loss of foraging opportunity; this is why the denominators in equations 8.1 and 8.4 are the expectations of the sum of all time spent in foraging. However, in operant experiments, the delay between the choice of a foraging option and a reward has a much greater impact on the value of an option than similar time intervals after the reward (Snyderman 1987). A reward associated with a short choice-reward delay and a long postreward delay is preferred over a reward associated with two delay lengths that are reversed (such that the choice-reward delay is long and the post-reward delay is short). The strong impact of choice-reward delays is also found in studies in which one of the options has variable delays. For example, in the starling experiment described (Bateson and Kacelnik 1996), there were two additional times in the foraging cycle—the reward time (or handling time) and the intertrial interval. We calculated the indifference points predicted with the six algorithms that result from applying either short- or long-term rates; each calculated with three combinations of time intervals (choice-reward delay only, choice-reward delay plus handling time, and choice-reward delay plus handling time plus the intertrial interval). The indifference point was very close to that predicted

with short-term rate maximization calculated without only the intertrial interval (fig. 8.8). This apparently maladaptive behavior can be interpreted as follows: In the wild, animals never experience time delays between obtaining food and being able to make their next foraging decision. A wild starling is free to decide its next action the moment prey consumption is complete. Thus, starlings may fail to attend to the intertrial intervals because these time intervals do not occur in nature.

To those familiar with the foraging literature, it may seem strange that intertrial intervals have little impact on decision making when tests of the Marginal Value Theorem (Charnov 1976b) indicate that travel time between patches affects patch-leaving decisions (e.g. Kacelnik 1984). This apparent anomaly disappears when one understands that travel times are more analogous to choice-reward delays than intertrial intervals; the travel time *follows* the decision to leave a patch. Like choice-reward delay, travel time is between the forager's decision and its next reward (in the case of the Marginal Value Theorem, encounter with the next patch). In the laboratory, analogues of this foraging paradigm have led to the same conclusions as those from work with individual rewards. Kacelnik and Todd (1992) found that patch-residence time is shorter if travel time is variable than if travel time is fixed when average travel time is constant. This result contradicts maximization of long-term rate; however, this result is consistent with the birds paying attention to the intervals between decisions and their consequences. With this observation, we are strongly reminded of the theme of this book: Ecological models are inadequate without reference to the cognitive processes of animals in nature.

In summary, if animals are faced with sequences of choices, they maximize short-term rate. The only time intervals used to compute this rate are those between the choice and reward. If there is no risk in the choices, this currency results in behavior equivalent to long-term rate maximization. If there is risk, however, maximizing short-term rate can result in risk proneness when variability is in delay or risk aversion when variability is in reward amount (if there is a correlation between the reward amount and the handling time). Identifying short-term rate as the algorithm that best approximates the currency used by animals to attribute value to foraging options does not explain risk sensitivity. We have not yet identified a functional or mechanistic basis for the use of short-term rate. In the remainder of this section (8.5), discussion is devoted to some possible bases.

8.5.2 The Costs of Short-Term Rate Maximizing

The cognitive mechanisms that produce maximization of short-term rate in laboratory studies may produce behavior that maximizes something close to long-term rate in the natural environment. If this is the case, there would be

no need to explain why animals use a rate algorithm that results in suboptimal behavior in the laboratory. Maximization of short-term rate was initially rejected by optimal-foraging theorists because animals that used it appeared to make grossly maladaptive foraging decisions (Gilliam et al. 1982; Turelli et al. 1982; Possingham et al. 1990). In most experiments designed to separate the predictions of maximizing short and long-term rates, the discrepancy between the predictions was deliberately accentuated. Discrepancy between predictions is generated by programming very high variance in the variable-delay option. The lower the variance in delay, however, the smaller the difference in behavior predicted with maximizing short- and long-term rates. At the limit, when there is no variance in delay, short- and long-term rates are formally identical. Therefore, to determine the cost of maximizing short-term rate for a forager in its natural environment, we need to know the natural variability in the time it takes the animal to obtain prey items. If there is little variation in the natural environment, then the currency used will make little functional difference; even if the animal is maximizing short-term rate, behavior will be similar to that with maximization of long-term rate. To test this idea, measurements were made of the distribution of interprey intervals experienced by starlings that were foraging in natural pastures (Bateson and Whitehead 1996). These intervals were highly variable. Calculations proved that, given the observed level of variability, a maximizer of short-term rate would suffer a substantially lower daily food intake than a maximizer of long-term rate. Thus, at least in this case, maximizing short-term rate cannot be defended on the grounds that it generates adaptive behavior in the natural environment. We must look elsewhere for an explanation for why animals maximize short-term rate.

8.5.3 Associative Learning and Maximizing Short-Term Rate

In this section, we suggest that maximizing short-term rate can be explained mechanistically by considering the processes animals use to learn about causal relationships in the environment. We argue that the basic mechanisms of associative learning constrain animals' abilities to estimate the rate of food intake they are experiencing, and animals, as a result, behave suboptimally in some circumstances and display risk sensitivity.

In animal studies of risk-sensitivity, the foraging options are usually identified with stimuli such as differently colored flowers or pecking keys. When preferences are tested, the subjects choose among the stimuli instead of the rewards. It is therefore crucial to understand the process subjects use to attribute value to the stimuli, which have no worth before training because they are arbitrarily assigned to the foraging options. The training of subjects in foraging experiments follows a protocol that is analogous to that used in psy-

chological studies of conditioning. In a conditioning experiment, the subject is exposed to a neutral stimulus; after some time delay, the subject experiences a meaningful event (such as receipt of food) that has fitness consequences. The originally neutral stimulus is called the conditioned stimulus, or CS, and the meaningful event is called the unconditioned stimulus, or US. For the animal, the truly important event is the arrival of the US, and most of the changes in the animal's psychological state occur at this time. During training, the value of the CS changes every time an US is experienced. A variety of factors are known to affect the rate of acquisition and the asymptotic level of the value attributed to a particular CS (for a review see Dickinson 1980). We will be concerned with only two of these factors first, the delay between the onset of the CS and delivery of the US and, second, the value of the US.

In the following two sections, we will present models that produce maximization of short-term rate as a result of the conditioning process. The first model uses the effects of the CS-US delay on learning to provide a mechanistic explanation for risk proneness with delay. The second model uses the effects of the US value on learning to provide a mechanistic explanation for risk aversion with amount.

8.5.3.1 Risk Proneness in Birds and Mammals and the CS-US Delay

Since Pavlov's work early this century, it has been known that, usually, rewards presented shortly after the onset of the CS strengthen the association between the CS and US more efficiently than rewards presented after a longer delay. Also, the function that relates the speed of learning to the length of the CS-US delay is nonlinear and appears to be approximately hyperbolic for any given intertrial interval (for data in pigeons see Gibbon et al. 1977). We can explain these findings mechanistically as follows. If a naive subject is exposed to a stimulus (such as a red light [CS]), the stimulus leaves a trace in working memory that decays with time so that the strength of the memory is inversely proportional to the time elapsed since the occurrence of the stimulus. If a meaningful event (the US) then occurs, the subject attributes some value to the previously neutral stimulus it remembers and the magnitude of the change in value is proportional to the strength of the memory of the CS (fig. 8.10).

Compare what happens if a subject is trained with (1) a CS followed by a fixed delay to the US and (2) a different CS followed by a variable delay to the US. In the case of the fixed delay, the subject attributes value in proportion to its memory of the CS every time the US occurs, and this value is always the same. In the case of the variable delay, the value attributed to the CS in each trial depends on the length of the CS-US delay: If the delay is short, the change in value will be large; if the delay is long, the change in value will be smaller. Note that this mechanism of learning imposes value assignment

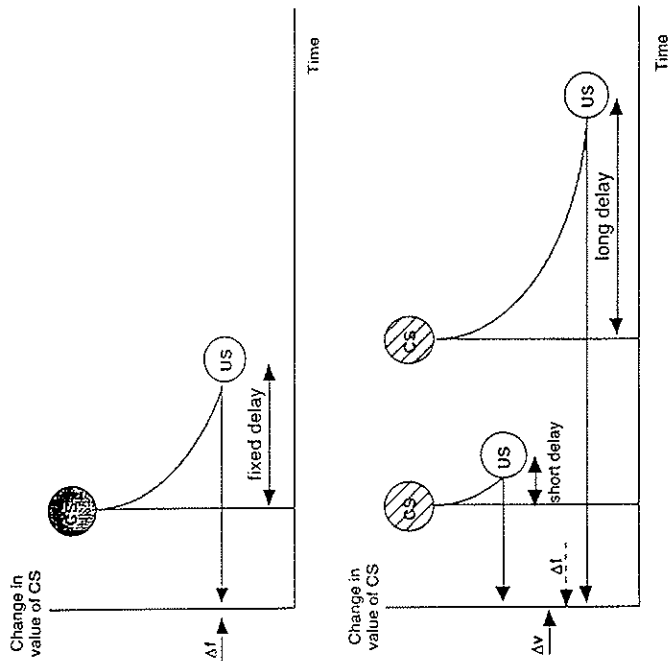


Figure 8.10. Model of how associative learning accounts for risk proneness if variability is in delay. *Upper panel:* the CS-US delay is fixed and results in a fixed change in value of Δf each time the US is experienced. *Lower panel:* the CS-US interval is variable (short or long with equal probability). The average change in the value of CS is Δv . If the function that relates the CS-US interval to the change in value of the CS is nonlinear, then $\Delta v > \Delta f$. The CS associated with the variable delay should be preferred over the CS associated with the fixed delay after similar exposure to the two options, because the CS associated with the variable delay will have a higher value.

before value averaging. If the function that relates the change in value to the CS-US delay is hyperbolic (as the literature suggests), then over a series of trials a CS followed by a fixed delay will acquire less value than a CS followed by a variable delay that has the same average length (another case of Jensen's inequality).

Consider what will occur if the subject, during the course of training, is allowed to choose between a CS associated with a fixed delay and one associated with a variable delay of the same average length. We predict that the subject will prefer the CS associated with the variable delay because this CS has a higher value, which reflects a stronger association with the US. We therefore can explain risk proneness as a product of the way animals learn if variability is in delay to reward. We can also explain why the CS-US delay,

which is equivalent to the choice-reward delay, should be particularly important to foraging animals. However, this idea needs further development because we do not know if risk-sensitive preferences that result from training can translate into the stable long-term preferences in the risk-sensitivity literature. Our explanation does not substitute for an optimality analysis; our explanation merely changes the optimality question asked. We are left to explain why a learning mechanism of this type has evolved.

8.5.3.2 Learning and Risk Aversion in Bees

In this section, we describe an artificial neural network that is designed to simulate how bumblebees learn the amount of nectar gained from flowers of different colors. Artificial neural networks are an increasingly popular tool for modeling the processes involved in learning and decision making. These models illustrate how a nervous system, composed of simple units, can produce seemingly complex behavior (Dukas, this vol. section 1.5). The network we describe is of interest because it produces risk aversion if there is variability in nectar volume. Risk sensitivity occurs as a result of how the volume of nectar obtained from a flower (i.e. the value of the US) affects the value attributed by the bee to flowers of that color (i.e. the CS).

In bumblebees, there is an increasing, decelerating function that relates the volume of nectar in a flower to the net rate of energy gain derived from the nectar (fig. 8.9). Montague et al. (1995) incorporated this finding into a simple neural network model. They assumed that the output, $r(t)$, of a reward neuron, R, is equal to the net energy derived from a flower (figure 8.11). Thus, there is an increasing, decelerating function that relates volume of nectar taken to $r(t)$. Neuron R is connected to neuron P by a nonmodifiable synapse such that neuron R affects the output of P [$=\delta(t)$] directly. Because of Jensen's inequality, flowers that contain a fixed volume of nectar cause a higher average value of $r(t)$ than flowers that contain variable volumes with a mean that equals the fixed volume. Neuron P also receives input by way of modifiable synapses from three neurons that carry sensory input about the colors of flowers currently in the visual field (Y = yellow, B = blue, N = neutral). The strength of the synapses W_Y , W_B , and W_N is modified according to the following learning rule. If the bee finds food, the change in weight that occurs at a particular synapse is proportional to the activation of that sensory neuron in the previous time step (i.e. how much of that color is in the visual field before the bee landed on the flower) and the current output of P [$\delta(t)$], which is controlled entirely by $r(t)$ at the time of reward and reflects the net energy gain). Thus, flower colors associated with fixed volumes of nectar result in higher synaptic weights than flowers associated with variable volumes (with Jensen's inequality).

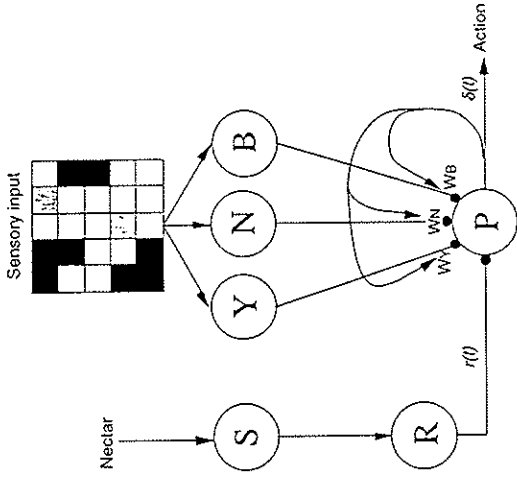


Figure 8.11. Architecture of a neural net that produces risk-averse behavior (redrawn from Montague et al. 1995). P is a simple linear unit that receives convergent sensory information and is hypothesized to correspond to the real bee neuron VUMmx1, which delivers information about reward during classical conditioning experiments (Hammer 1993). At the time (t) the bee gets a volume of nectar, $r(t)$ takes on the value derived from the utility curve shown in figure 8.9. The outputs of neurons N, Y, and B represent changes in the percentage of neutral, yellow, and blue colors in the visual field. These neurons influence the output of neuron P through weights W_N , W_Y , and W_B . The latter two weights are modifiable and W_N is fixed. The output of P, $\delta(t)$, controls the heading of the bee. As the model bee changes its heading above the array of flowers, the activity of these neurons change. Changing the weights with each encounter with a flower enables representation of information about the predictive relationship between sensory input and the amount of nectar obtained.

During the searching phase of foraging, the bee is not obtaining nectar and the output of P, $\delta(t)$, is equal to the weighted sum of the visual inputs [$r(t) = 0$]. This output controls the bee's probability of reorientation. If the bee is primarily looking at a flower color with a high synaptic weight, then $\delta(t)$ will be high and the bee will continue in the same direction. If the bee is looking at a flower color with a low weight, then $\delta(t)$ will be lower and random reorientation will occur. The higher synaptic weights associated with flowers containing fixed volumes inhibit random reorientation and thus promote approaches to these flower types. By contrast, the lower synaptic weights associated with variable-volume flowers result in random reorientation and make approach to variable flowers less likely. This simple model provides a mechanistic explanation for risk aversion in bumblebees. The behavior of the model closely resembles the risk aversion seen in experiments with bumble-

bees presented with different colored flowers associated with fixed or variable volumes of nectar (Real 1981; Waddington et al. 1981; Real et al. 1982).

Note that if the variability is in the concentration instead of the volume of nectar, the model does not predict risk aversion because the function that relates concentration of nectar to net rate of energy gain is linear. In bees, recent results have shown insensitivity to risk if variability is in nectar concentration (Bauschbach and Waddington 1994; Waddington 1995).

The learning models we described in this section and section 8.5.3.1 have three crucial features in common. First, both models assume that environmental variability (the CS-US delay or the volume of the US) affects the speed of learning about the CSs associated with the fixed and variable options. Second, in both models, learning is assumed to occur each time an US is encountered, and attribution of value to the CS occurs before the averaging of value. Third, both models assume that the strength of the association of a particular CS to reward affects the probability that the forager will choose, or move toward, this CS. The combination of these features results in maximization of short-term rate and consequent risk sensitivity.

8.6 MECHANISTIC EXPLANATION 2: PERCEPTUAL ERROR

We have not made any reference to the accuracy and precision with which environmental information is processed. In this section, we will first examine the types of errors animals make when they estimate environmental parameters, such as the length of time intervals and the size of food rewards. We will then consider how these errors could affect animals' responses to fixed and variable food sources and the role these errors may have in risk sensitivity.

8.6.1 Weber's Law and the Scalar Property

In the first example, we consider the accuracy and precision of starlings' memories for time intervals. The birds were given a task that simulated foraging in patches (Kacelnik et al. 1990; Brunner et al. 1992); the patch was a standard operant pecking key. Each patch contained an unpredictable number of food items (between zero and four) that could be obtained with pecking at the key. Once the patch was exhausted, the bird had to travel to the next patch by flying between two perches. Within the patch, the food items were delivered on a fixed-interval schedule; the first peck made by the bird after the programmed interval resulted in a food reward. No signal was given when the final food item in the patch was delivered, and therefore the birds could only detect patch exhaustion by timing the intervals between successive food items. When arriving at a patch, the bird would peck at the key, and its pecking frequency increased toward the time of completion of each interval. If a reward was not delivered because the patch was exhausted, pecking rate declined. The time

corresponding to the highest frequency of pecks, the *peak time*, provided an indication of how accurately the birds estimated the fixed interval. The variance in their peak times provided an indication of how precise their estimates were. This experiment was repeated with several different fixed intervals to examine how accuracy and precision varied with the length of the fixed interval. The birds' peak times were close to the fixed interval and showed the birds could measure times accurately. However, the standard deviations of their peak times were proportional to the fixed intervals and showed that precision is inversely proportional to the length of the time interval being estimated (fig. 8.12a).

In a second experiment (Bateson and Kacelnik 1995b), we examined accuracy and precision of starlings' estimates of food amounts. The birds faced a choice between two options indicated with colored pecking keys; each key was associated with a fixed quantity of food. To choose the option that offered the greater amount, the birds had to remember the quantity of food associated with each option. One option was a standard, and in the other, adjusting option, the quantity available was altered systematically from trial to trial. The amount of food available in the adjusting option was increased until the bird detected that the adjusting option yielded more food than the standard; then food yielded by the adjusting option was reduced until the bird detected that the adjusting option yielded less food than the standard. The variation in quantity of reward with the adjusting option therefore gave a measure of the accuracy of discrimination between the standard and the adjusting option. If the bird had perfect memory for all amount sizes, then the quantity of food available in the adjusting option would have ranged between one unit above and below the number of units available in the standard. If the bird only detected a difference when the two rewards differed by at least 3 units, then the adjusting option would have ranged within three units above and below the standard. We examined the range of values in the adjusting option for two differently sized standard values. In both cases, the range of values seen in the adjusting option centered around the same value as the standard value; therefore the birds had accurate memories for the size of food rewards. However, if the size of the standard was increased threefold, the range in the magnitude of the adjusting option increased by a similar factor; therefore, precision was proportional to the magnitude of the reward being remembered (fig. 8.12b).

Two properties apply to starlings' memories of time intervals and amounts of food. First, memories seemed to be centered around the true physical value experienced; the assumption that starlings are able to learn the foraging parameters accurately was justified. Second, even if the foraging parameter had no variance, starlings' estimates were imprecise, and most important, the standard deviations of their estimates were proportional to the value of the parameter being estimated. The phenomenon of proportional standard deviations is some-

tion for why animals are generally risk averse if variability is in amount and risk-prone if variability is in delay.

8.6.2 Scalar Expectancy Theory

Reboreda and Kacelnik (1991) (see also Bateson and Kacelnik 1995a) developed a model of risk sensitivity that is based on an information-processing model of timing known as scalar-timing theory (Gibbon et al. 1984; Gibbon et al. 1988). They assumed that the memory formed for a fixed time interval or amount of food can be modeled as a normal distribution with a mean that is equal to the real value of the stimulus and a standard deviation that is proportional to the mean (as suggested by the data presented). The memory representation for a variable option is formed from the sum of the memory distributions of its components. Thus, a food source that offers three or five seeds with equal probability will be remembered as the sum of the memory distributions of three and five seeds. Similarly, a stimulus followed by either a 3 or 5 second delay to food will be remembered as the sum of the memories of these two intervals. The memory representations of variable options will be positively skewed because the memory for the smaller stimulus has a smaller standard deviation than the memory for the larger stimulus (fig. 8.13).

It is assumed that subjects choose between two foraging options by (1) retrieving a sample from their memory for each available option; (2) comparing these samples; and (3) choosing the option that offers the more favorable sample (bigger reward or shorter delay). According to the previous description of memory representations, memory distributions for variable options are skewed to the right; however, memory distributions for fixed options with the same mean are symmetric around the true mean. If the subject makes a choice by picking a pair of samples—one from the variable and one from the fixed memory distribution—then in more than half of the comparisons the sample from the memory for the variable option will be smaller than the sample from the memory for the fixed option. Thus, the model predicts that an option that offers variability in delay to food should be chosen more often than a fixed alternative because the memory for the variable option will more often yield the shorter sample. An option that offers variability in amount of food should be chosen less often than a fixed alternative again because the memory for the variable option will more often yield a smaller sample. The difference in choice arises because options that offer short delays are good and should be preferred; options that offer small amounts are bad and should be avoided.

The major prediction of this model agrees with experimental observations because animals are usually risk averse if variability is in amount and risk prone if variability is in delay (fig. 8.1a) (Gibbon et al. 1988; Reboreda and

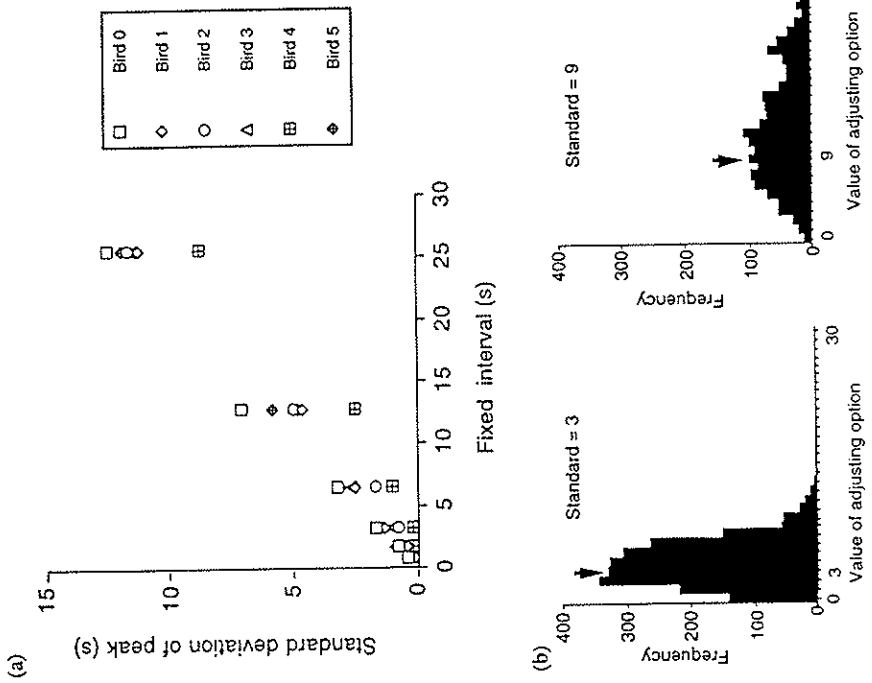


Figure 8.12. Demonstrations of Weber's law in starlings. (a) Memory for time. Graph shows the standard deviation of the peak time as a function of the fixed interval. Note the linear relationship between the standard deviation and the fixed interval: Short times are remembered more precisely than long times (replotted from Brunner et al. 1992). (b) Memory for amount of food. The range of values taken by the adjusting option with two different standards (three and nine units of food). Note the greater variability when the standard is nine units: Small quantities are remembered more precisely than large quantities (after Bateson and Kacelnik 1995b).

times known as the *scalar property*, which is a strong form of Weber's law. Weber's law is a very widespread phenomenon in discrimination and has been demonstrated for a number of different sensory modalities in many species including rats, pigeons, and humans. We will now examine how the scalar property interacts with environmental variance to give a mechanistic explana-

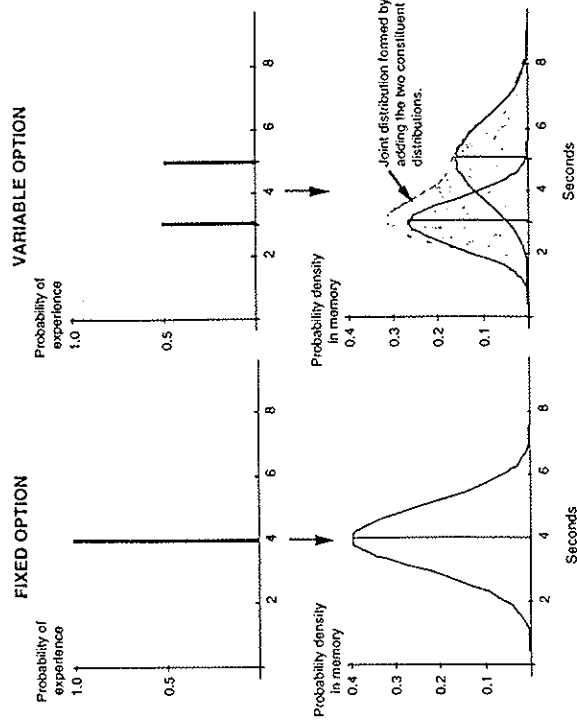


Figure 8.13. The scalar timing theory information-processing model. *Upper panels:* the experienced distribution of outcomes (delays or amounts) in fixed (*left*) and variable (*right*) options. *Lower panels:* the distributions that are assumed to be formed in memory as a result of the experiences (*upper panels*). Note the skew in the memory distribution for the variable option that results from the differing accuracies with which the constituent stimuli are represented (reproduced from Bateson and Kacelnik 1995a).

Kacelnik 1991; Bateson and Kacelnik 1995a). The model is also attractive because it predicts partial preferences, unlike the other models. The model, however, fails in some respects. First, although the qualitative agreement of data with the model is strong, there are quantitative discrepancies. For instance, the model predicts that animals should be indifferent between a fixed and variable option if the fixed option is equal to the *geometric mean* of the two alternative possibilities (amounts or delays) in the variable option (Bateson and Kacelnik 1995a) (i.e. the square root of the product of the two alternative possibilities in the variable option). Subsequent research, however, has demonstrated that, for delays at least, indifference occurs at approximately the *harmonic mean* (i.e. the outcome of maximizing short-term rate) (Bateson and Kacelnik 1996; Mazur 1984, 1986). Second, the model does not address the observed effects of energy budget on preference: It predicts universal risk proneness if variability is in delay and risk aversion if variability is in amount. Third, the model does not address what animals should choose if the two foraging options differ in the variance of both amount and delay simultaneously. A more recent version of scalar timing (Brunner et al. 1994)

deals with some of these problems; however, further developments are required to address all aspects of the data available in the risk-sensitivity literature.

8.7 CONCLUSIONS

The theories we have described rely on two types of explanations: functional (or evolutionary) arguments that consider the circumstances under which risk-sensitive behavior can be adaptive and mechanistic arguments that consider how risk sensitivity may emerge as a result of the cognitive processes used by animals to perceive, learn, and remember information about the environment. Functional and mechanistic approaches are complementary forms of explanation in animal behavior because all adaptive behavior must be implemented in some way (Tinbergen 1963). However, as we have presented with many examples, these alternative forms of explanation often produce different predictions about the details of risk-sensitive behavior. Different predictions occur because different approaches have been taken by behavioral ecologists and psychologists. Functional hypotheses are driven by the assumption that risk-sensitive behavior is adaptive. By contrast, mechanistic hypotheses indicate that risk sensitivity is a consequence of the cognitive mechanisms that underlie behavior. Although these mechanistic hypotheses are based on observations of how animals actually behave, these hypotheses do not address the adaptive importance of the mechanisms they postulate or the risk-sensitive behavior they predict. In the future, we hope to see a fusion of these two approaches with production of models that give equal weight to cognitive and evolutionary considerations.

By accounting for empirical observations of risk sensitivity, we found that all of the approaches have advantages and disadvantages, which strongly suggest that an integrated approach is the way forward. Risk-sensitive foraging theory is the only theory that can explain why the direction of risk-sensitive preferences should be affected by energy budget. However, this theory does not explain the many failures to obtain shifts in risk preference or why animals should more often be risk averse with amount but risk prone with delay. The theory is difficult to test conclusively because it has many variants. To make precise predictions about how manipulations will affect behavior, it is necessary to know the current status of an animal precisely. One effect of these uncertainties is that only qualitative predictions are being tested. For instance, the energy-budget rule predicts exclusive preferences; however, even the best examples of shifts in preference are only partial shifts in the predicted directions.

Time discounting that arises from the probability of interruption potentially explains why animals should be risk prone if variability is in delay. However,

time discounting fails quantitatively because with its simplest applications in isolated choices, it predicts exponential time discounting, and there is clear evidence that humans discount time hyperbolically. Also models that are based solely on time discounting do not address the effects on choice of variability in amount.

Maximizing short-term rate can account for the hyperbolic time discounting observed in animals and the consequent risk proneness if variability is in delay. However, assuming that animals maximize this currency does not explain all the data. The currency can only accommodate risk aversion with variable amounts if there is a positive correlation between amount and the handling time. Also maximizing short-term rate does not address the effects of energy budget. The major problem in maximizing short-term rate is explaining its functional and mechanistic bases. We suggested that maximizing short-term rate may emerge as a consequence of the basic mechanisms of associative learning that can be defended as adaptive in a context that is broader than that of risk sensitivity.

Scalar-timing theory can explain partial preferences and why animals are risk prone with variable delays and risk averse with variable amounts. However, the theory sometimes fails quantitatively and does not address the effects of energy budget.

Thus, whether risk-sensitive foraging preferences are largely the products of direct selection driven by the fitness consequences of variable food sources or whether they are consequences of selection for efficient cognitive mechanisms in broader contexts are unanswered problems. Of course, it is possible that the phenomena we categorize as risk sensitivity may only be superficially related; these phenomena may be the products of different underlying mechanisms, or they may have evolved under different selective pressures (in which case they will never be explained with a single unifying theory). Whatever the answers will be, it is unquestionable that satisfactory explanations for risk sensitivity will include ecological and cognitive considerations. This conclusion is not specific for risk sensitivity; however, its truth is particularly well exemplified with this area of research—perhaps because the field has attracted such extensive data collection and optimality modeling.

8.8 SUMMARY

Animals presented with foraging options that offer the same average rate of gain but differ in variance generally show strong preferences. This widespread behavioral phenomenon is known as risk sensitivity. Risk-sensitivity has implications for the ecological interaction of animals with their environments and the cognitive mechanisms that underlie foraging behavior. Several factors affect the direction of risk-sensitive preferences: the component of rate that

is variable (amount or time), the energy needs of the subjects, and possibly the typical body weight of the species. We reviewed explanations for these data arising from functional, descriptive, and mechanistic arguments. Animals can respond to environmental variance in ways that enhance fitness, and there is some evidence for use of adaptive policies such as the energy-budget rule. However, some well-documented cognitive processes also generate risk-sensitive behavior that does not appear to be directly adaptive. The broader adaptive importance of these cognitive processes remains to be established; however, we believe that cognitive processes cannot be ignored in any form of foraging research.

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