RISK-SENSITIVE FORAGING THEORY AND OPERANT PSYCHOLOGY

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Hastjarjo, Silberberg, and Hursh (1990) have presented data on the foraging behavior of rats and discussed it in terms of risk-sensitive foraging theory. Because risk-sensitive foraging theory is comprised of several different models, it does not lead to general predictions about when an organism should prefer a foraging option with high variance to a foraging option with low variance. Any comparison of data with the predictions of the theory must be based on an appropriate model. I draw attention to various experiments that are potentially relevant to the results reported by Hastjarjo et al. and show how the time period over which the organism must survive can influence a model's predictions about risk sensitivity.

Key words: risk-sensitive foraging, variability, rats

Hastjarjo, Silberberg, and Hursh (1990) have presented data on the behavior of rats faced with a variable and a constant source of food. They argued that risk-sensitive foraging theory cannot explain their results. Although it is true that the data are challenging, I do not feel that Hastjarjo et al. give an adequate account of risk-sensitive foraging theory and the associated data, especially those aspects of it that relate to their experiments. In this note I offer a summary of risk-sensitive foraging theory, together with a brief account of some previous experiments that are relevant to the results of Hastjarjo et al. (For a more technical review of the theory, see McNamara & Houston, in press.) I emphasize that although there is a general principle that accounts for the evolutionary advantage of risk-sensitive foraging, different models of risk-sensitive foraging can lead to a variety of predictions about behavior.

Risk-Sensitive Foraging (RSF)

The basis of RSF is that choice depends not only on mean amounts of food but also on the variability in the amount of food. The importance of variability has long been recognized in operant psychology (e.g., Davison, 1969; Fantino, 1967; Herrnstein, 1964; Killeen, 1968), but only started to receive serious at-

tention in behavioral ecology in the 1980s (e.g., Caraco, 1980; McNamara & Houston, 1982; Real, 1980a, 1980b). Much of the empirical work in operant psychology has tended to investigate variable delay to food, whereas empirical work in behavioral ecology is concerned with variable amounts of food (see McNamara & Houston, 1987, for a discussion of both sorts of effect). Theoretical work in behavioral ecology has largely been concerned with the advantages, in terms of Darwinian fitness, of RSF.

In this context it is important to realize that there are several RSF models, so it is not meaningful to say "RSF theory predicts such and such." The different models are based on different biological assumptions, and so are relevant to different organisms. The essence of RSF is a nonlinear relationship between fitness and energy. Although an organism's fitness depends on survival and reproduction, the models have concentrated on survival; in particular, on avoiding starvation. (For a model that includes reproduction see McNamara, Merad, & Houston, 1991.) The model that is most frequently cited was described by Stephens (1981). It gives rise to a simple rule known as the daily energy budget rule.

The Daily Energy Budget (DEB) Rule

Consider an organism that forages during the hours of daylight and rests at night. Let the organism have two sources of food and assume that it uses a given source throughout the day. Each source provides the same mean

rate of energetic gain, but one has a high variance and the other has a low variance. If the mean rate of gain is sufficient to achieve the amount of energy that the organism needs to survive the night (i.e., the DEB is positive), then survival probability is greater if the low-variance option is chosen. Conversely, if the mean is insufficient (DEB is negative), then survival probability is greater if the high-variance option is chosen (Stephens, 1981). Given the choice between two equal means, an organism is said to be risk-prone if it prefers the more variable option and risk-averse if it prefers the less variable option. Thus the the rule can be summarized: If DEB is positive, then be risk-averse; if DEB is negative, then be risk-prone. For an extension to unequal means, see the "z-score" model described by Stephens and Charnov (1982).

The DEB rule is based on interrupted foraging; the organism forages to build up its energy to survive a period during which it cannot forage. An obvious example is provided by small birds foraging during the winter. Some organisms (e.g., shrews) continue to forage at night. As an alternative to models based on the day–night cycle, Houston and McNamara (1985) introduced a model based on "continuous" foraging. The subject can always forage but may die of starvation while foraging if its reserves fall to zero. If the mean gain while foraging is positive, then it is always advantageous to minimize variance (McNamara & Houston, 1990). If the mean gain while foraging is negative, then it can be advantageous to be risk-prone when reserves are low but to be risk-averse when reserves are high (McNamara & Houston, 1990; McNamara et al., 1991).

The DEB in Stephen's model is conceptually distinct from the mean gain while foraging. If an organism has initial reserves x and can forage for a time T at mean rate μ, and requires an amount of energy R to survive the interruption, then the DEB is positive if

$$x + \mu T > R$$

and is negative if

$$x + \mu T < R.$$

The mean gain while foraging is μ, so the sign of μ does not by itself determine whether the DEB is positive or negative.

When the model based on continuous for-aging is modified to include reproduction, then under some circumstances it can be advantageous to be risk-averse when reserves are low and to be risk-prone when reserves are high (McNamara et al., 1991).

The derivation of the DEB provided by Stephens (1981) makes the following assumptions: (a) The subject cannot switch between the options during the foraging process. For a model that allows the organism to switch between the alternatives, see Houston and McNamara (1982). (b) The subject will not starve while it is foraging. For models that combine starvation while foraging with interruptions, see Barnard, Brown, Houston, and McNamara (1985), Houston and McNamara (1985), and McNamara and Houston (1986).

The Appropriate RSF Model

I hope this sketch of RSF theory makes it clear that there is no straightforward prediction about, say, mean gain and preference for variability. Much of the empirical work has been done on small birds (e.g., Caraco, 1981, 1982, 1983; Caraco et al., 1990; Caraco, Martindale, & Whittam, 1980) or shrews (e.g., Barnard & Brown, 1985a, 1985b; Barnard et al., 1985). The preoccupation with starvation in the models of RSF reflects the limited ability of such organisms to survive without food. The relatively superior abilities of pigeons and rats to store energy in their bodies may necessitate different models (see also Hamm & Shettleworth, 1987; Kagel, MacDonald, Battalio, White, & Green, 1986). Kagel et al. also draw attention to the problem of time scale in models. The models are based on a subject experiencing a given set of environmental parameters for a very long time. In practice, organisms may regard a period of low food availability as a temporary occurrence and behave in a way that would lead to certain starvation if this period persisted.

One way of shedding light on this question of time scale is to show how the optimal choice between variable foraging options depends on the time period over which the organism is trying to survive. The model described by McNamara and Houston (1990) can be used for this purpose. The model assumes that the organism's level of energy reserves, x, lies between zero and an upper limit, L. Any food that would have taken x above L is lost. If reserves fall to zero, then the organism dies of

starvation. At the start of each decision period, the organism can choose between two foraging options. If it chooses option i ($i = 1, 2$), there is a net increase of reserves by one unit with probability p_i, a net decrease of one unit with probability q_i, and no net change in reserves with probability $1 - (p_i + q_i)$. Thus the mean net gain if option i is chosen is $(p_i - q_i)$ and the variance is $p_i + q_i - (p_i + q_i)^2$.

Decisions are made at times $0, 1, 2, \ldots, T - 1$. We are interested in behavior over the time interval that maximizes the probability that the subject is alive (i.e., has reserves above zero) at the final time T. To find the behavior that maximizes survival at final time, we can work backwards in time from T using dynamic programming (e.g., McNamara & Houston, 1986; Mangel & Clark, 1986, 1988). This procedure finds the decision for an organism with reserves x (where $0 < x \le L$) at time t (where $0 \le t < T$) that maximizes the probability that the organism survives to T. An example of such an optimal policy is given in Figure 1. The figure plots the critical value $\tilde{x}(t)$, below which it is advantageous to choose Option 2 (the more variable option) and above which it is advantageous to choose Option 1 (the less variable option). It can be seen that when t is close to T, Option 1 should be chosen at all levels of reserves. As the time period to be survived increases (i.e., as t becomes further away from T) it becomes advantageous to choose Option 2 when reserves are less than a critical value $\tilde{x}(t)$. As the time until T becomes very large, $\tilde{x}(t)$ tends to a constant $\tilde{x}$ that is independent of time. McNamara and Houston (1990) concentrate on this "steady-state" region, in which the best decision does not depend on how close t is to T. The figure shows how this time can be relevant to the best choice of feeding option. Note that as long as reserves remain above $\tilde{x}(t)$, it is advantageous to choose the less variable option, even though reserves are decreasing.

Unequal Means

Hastjarjo et al. (1990, pp. 155–156) cite various experiments on risk sensitivity and give the impression that they all involve equal means. This is not so; Battalio, Kagel, and MacDonald (1985) gave rats the choice between unequal means (Experiment 3, pp. 608–611). Furthermore, other experiments have investigated this topic.
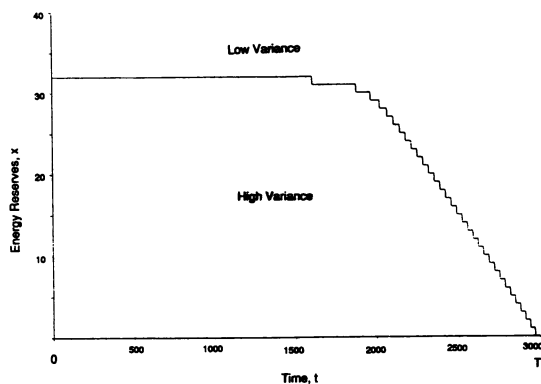

Fig. 1. The critical boundary $\tilde{x}(t)$, above which it is optimal to choose the less variable option (Option 1) and below which it is optimal to choose the more variable option (Option 2). The boundary is calculated from the model described in the text, with $p_1 = 0.08$, $q_1 = 0.1$, $p_2 = 0.49$, and $q_2 = 0.5$. Thus Option 1 has a mean of -0.02 and a variance of 0.148, whereas Option 2 has a mean of -0.01 and a variance of 0.01. The upper limit, L, on reserves is 40.

Barnard et al. (1985) report experiments in which the common shrew (*Sorex araneus*) could choose between a constant option (one mealworm segment per visit) and a variable option. Various treatments involved a mean at the variable option of 0.67, 1, or 1.33 segments per visit. The results suggested that the shrews preferred the variable option when its mean was high and its variance was low, but showed no significant preference when the variable option had high mean and high variance.

Caraco and Lima (1985) were able to demonstrate a trade-off between mean and variance in the dark-eyed junco (*Junco hyemalis*). If a constant option offered Y seeds, then a variable option that was chosen equally often had to have a mean greater than Y, and this mean was larger when the variance was larger.

Stephens and Paton (1986) investigated whether the behavior of rufous hummingbirds (*Selaphorous rufus*) could be accounted for by using a variance discounting rule based on the maximization of $\mu - k\sigma^2$, where μ is the mean amount of food, σ^2 is the variance, and k is a constant (see Real, 1980a, 1980b; Ellner & Real, 1989, for further details). The birds were offered alternatives that differed in mean and variance. The results did not agree with the predictions of the variance discounting rule, but were in agreement with the z-score model.

How Does Variance Vary with Treatment?

Hastjarjo et al. stated that

> ... the fewer the number of trials per day, the greater the variability in daily food consumption given that some portion of a rat's choices are to the risky alternative. Thus our results show that rats become more averse to risk as the day-to-day variance in the number of reinforcers earned increases. (1990, pp. 158–159)

Hastjarjo et al. used a procedure in which the organism received either an amount of food a with probability p or nothing with probability $q = 1 - p$. After n choices of this "risky alternative," the number of reinforcers obtained has a binomial distribution with parameters n and p. Thus the mean number of reinforcers is np, and its variance is npq. The mean amount of food is anp, and its variance is a^2npq. Thus, both the mean and the variance decrease as n decreases, but the coefficient of variation (=standard deviation/mean) increases. It is perhaps more relevant to consider the distribution of food that results from choices of the risky alternative. When $p = .33$, the probability of getting 10 or fewer reinforcers is about .97 when $n = 20$, .6 when $n = 30$, .18 when $n = 40$, and .03 when $n = 50$. Thus, in terms of the distribution of total amount of food, decreasing n increases the probability of getting less than a certain amount of food.

Discussion

The data currently available from studies of the response of rats to variable feeding options suggest topics for further investigation. For example, Battalio et al. (1985, Experiment 2) varied the number of forced-choice trials, whereas Hastjarjo et al. (1990, Experiment 1) varied the number of free-choice trials. Do these different sorts of manipulation have different effects? This cannot be determined by comparing these experiments because they differ in other ways (e.g., Battalio et al. used equal means, whereas Hastjarjo et al. did not).

Although workers in behavioral ecology and operant psychology have common interests, they also have different basic assumptions. In particular, for a behavioral ecologist a theoretical account of behavior involves a characterization of the fitness consequences of various possible actions. I hope that my outline of risk-sensitive foraging theory illustrates this point.

To an operant psychologist interested in uncovering regularities in behavior, this sort of theorizing may seem to be at best an irrelevance. But if operant psychologists are going to use the models of behavioral ecologists, they should be aware of their background and justification. Either an appropriate model should be chosen or an approach that does not involve fitness should be used.

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