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PREFERENCES FOR FIXED AND VARIABLE FOOD SOURCES: VARIABILITY IN AMOUNT AND DELAY

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Much research has focused on the effects of environmental variability on foraging decisions. However, the general pattern of preference for variability in delay to reward and aversion to variability in amount of reward remains unexplained at either a mechanistic or a functional level. Starlings' preferences between a fixed and a variable option were studied in two treatments, A and D. The fixed option was the same in both treatments (20-s fixed-interval delay, five units food). In Treatment A the variable option gave two equiprobable amounts of food (20-s delay, three or seven units) and in D it gave two equiprobable delays to food (2.5-s or 60.5-s delays, five units). In both treatments the programmed ratio [amount/(intertrial interval + latency + delay)] in the fixed option equaled the arithmetic mean of the two possible ratios in the variable option (ITI = 40 s, latency = 1 s). The variable option was strongly preferred in Treatment D and was weakly avoided in Treatment A. These results are discussed in the light of two theoretical models, a form of constrained rate maximization and a version of scalar expectancy theory. The latter accommodates more of the data and is based on independently verifiable assumptions, including Weber's law.

Key words: optimal foraging, choice, risk sensitivity, rate maximization, Weber's law, scalar expectancy theory, key peck, European starling

Foraging decisions are affected by environmental variability. Animals choosing between options that provide the same rates of energy gain over time, but with different variances, generally show a preference for one option over the other. A review of the literature suggests that which option is preferred is often explained by the dimension that is variable. When variance is in the number of responses, the searching time, or the delay to reward, animals invariably prefer the higher variance option (Ahearn & Hineline, 1992; Cicerone, 1976; Davison, 1969, 1972; Ha, 1991; Ha, Lehner, & Farley, 1990; Logan, 1965; Morris, 1986), but when variance is in the amount of food per reward, the picture is less clear. Animals often prefer the lower variance option (Barkan, 1990; Clements, 1990; Hamm & Shettleworth, 1987; Logan, 1965; Real, 1981; Reboreda & Kacelnik, 1991; Tuttle, Wulfson, & Caraco, 1990; Waddington, Allen, & Heinrich, 1981; Wunderle, Santa-Castro, & Fletcher, 1987), but are occasionally indifferent to variance (Staddon & Innis, 1966) and sometimes show a state-dependent switch in preference for variability in amount (Caraco et al., 1990). In functional terms such preferences can be interpreted as adaptive responses to the fitness consequences of foraging on unpredictable food sources in different physiological states (see McNamara & Houston, 1992, for a review of risk-sensitive foraging theory). However, although this adaptationist approach can account for state-dependent switches in preference, it does not explain the more obvious pattern of differences in preference for variability in time and amount. In this paper we shall begin by describing two recent models that can potentially explain this difference. Both of these models are based on forms of reward-rate maximization but produce sensitivity to variance as the result of psychological properties of the subject animals' systems for processing information. We summarize the predictions that these models make about the effects of variability on preference and present an experiment designed to discriminate between the two accounts.

Rate Currencies

Classical rate-maximizing models in optimal foraging theory do not predict effects of variability on preference. This is because they assume that animals maximize the ratio of ex-

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pected gain over expected foraging time, or ratio of expectations (RoE), where

$$\mathrm{RoE} = \frac{\sum_{i=1}^{n} Gi}{\sum_{i=1}^{n} Ti}. \qquad (1)$$

In this equation, *Gi* is the energy gained from the *i*th food item, *Ti* is the time taken to acquire this item, and *n* is the total number of food items on which the calculation is based. In the majority of experiments examining the effects of variability (see citations above), this currency takes equal values in the fixed and variable options, and therefore maximization of RoE cannot explain the systematic preferences observed. RoE is assumed to be the basic currency of foraging decisions on the grounds that natural selection should favor animals that on average collect more energy during the time dedicated to foraging (Stephens & Krebs, 1986). However, there has been some controversy about the most appropriate way of calculating rate of gain. An alternative to maximizing RoE advocated by some authors (e.g., Templeton & Lawlor, 1981) is to maximize the expected ratio of amount over time, or expectation of ratios (EoR), where

$$\mathrm{EoR} = \frac{\sum_{i=1}^{n} \left(\frac{Gi}{Ti}\right)}{n}. \qquad (2)$$

If there is no variability in *T*, then the RoE and EoR algorithms give identical rates. However, when *T* is variable, for any set of values of *G* and *T* it will be true that EoR > RoE (Caraco, Kacelnik, Mesnik, & Smulewitz, 1992). Thus, the finding that animals prefer options that yield the same RoE but are more variable in delay could indicate that they maximize EoR rather than RoE. In addition, because larger rewards often take longer to collect or to transport (Cuthill & Kacelnik, 1990; Schmid-Hempel, Kacelnik, & Houston, 1985), variability in amount could also have an effect on preference through the associated variability in time (Caraco et al., 1992).

Proposals for the use of EoR were originally rejected on theoretical grounds because of the assumed advantage of collecting more food in a given length of time given by maximizing RoE (Gilliam, Green, & Pearson, 1982; Possingham, Houston, & McNamara, 1990; Turelli, Gillespie, & Shoener, 1982). However, there is mounting experimental evidence (Brunner, Gibbon, & Fairhurst, 1994; Cuthill, Kacelnik, Krebs, Haccou, & Iwasa, 1990; Harder & Real, 1987; Mazur, 1984, 1986, 1987) that animals may in fact maximize something related to EoR. One explanation for the use of this currency is that animals may not be able to perceive or process the amount (*G*) and time (*T*) associated with the acquisition of each prey item separately, and may instead perceive the rate (*G*/*T*) directly (e.g., Real, 1991). Given this constraint, it is not possible to compute RoE, and EoR may be maximized as the nearest approximation. In the absence of any variability in time this estimate is perfect, but in its presence it leads to preference for variable delays and possibly also to variable amounts when these covary with delay.

In summary, given options with equal RoE, maximization of EoR makes the following predictions: (a) Variability in delay to food should be preferred, and (b) variability in amount per se should have no effect on preference. The idea that rate may be perceived directly as a single dimension adds (c) that consumers ought to be unable to use information on amounts and delays separately, and should behave as if they "know" only their ratio. If they are shown to possess and use separate information on amount and delay, then the use of EoR cannot be justified on the grounds that information processing limitations act as a constraint.

Weber's Law in Memory

Reboreda and Kacelnik (1991) suggest an alternative framework for explaining animals' responses to variability. According to their model, amounts and delays are perceived independently, but Weber's law affects memory for both dimensions. Weber's law, the principle that the accuracy of perception decreases proportionally to stimulus value, applies to the ability to discriminate stimuli in various sensory dimensions. It is prevalent in the discrimination and reproduction of time intervals, and it is the basis of a theoretical framework for decision making with respect to time variables known as scalar expectancy theory (SET; Gibbon, 1977; Gibbon, Church, Fair-

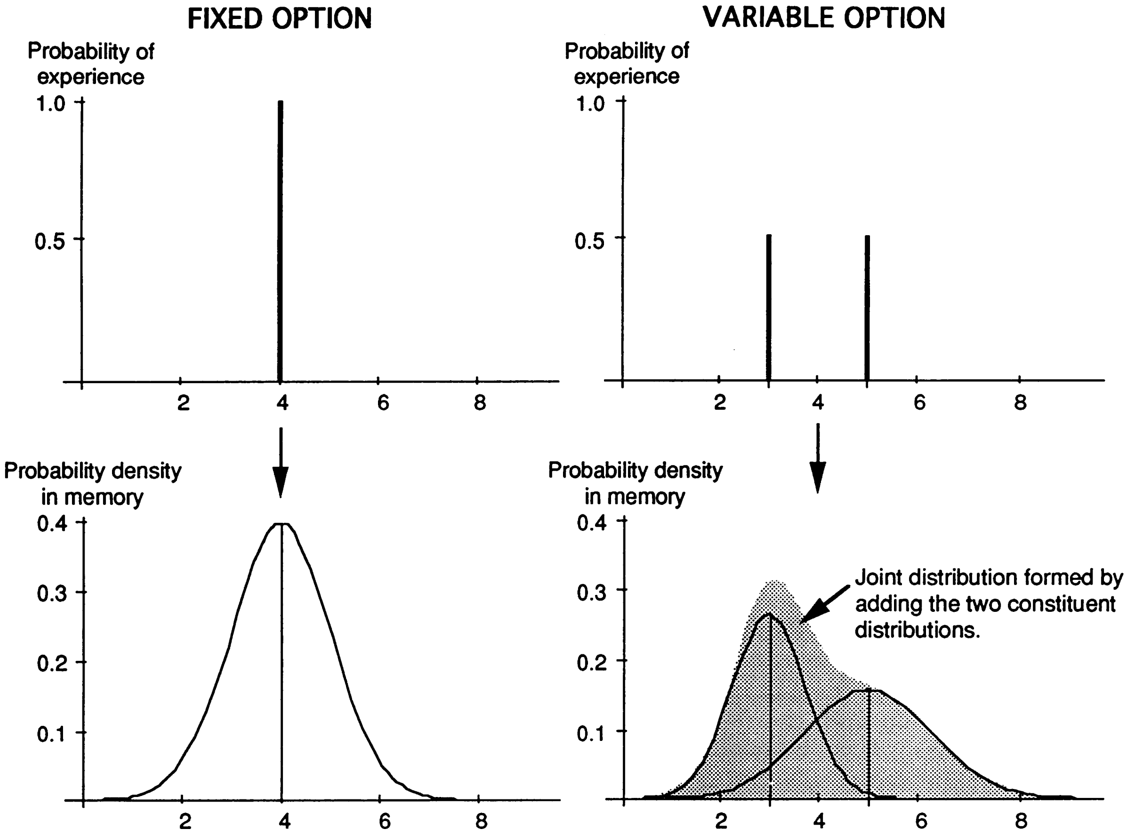

Fig. 1. The upper two panels represent the experienced distribution of outcomes in a fixed (left) and variable (right) option. The lower two panels represent the distributions that are assumed to be formed in memory as a result of the above experiences. Note the skew in the distribution of the memory for the variable option that results from the constant relative accuracy with which the constituent stimuli are represented.

hurst, & Kacelnik, 1988; Gibbon, Church, & Meck, 1984). Reboreda and Kacelnik extend SET to include memory for amount. In their model the memory formed of each time interval or amount of food has the value of a random sample drawn from a normal distribution with a mean equal to the real value of the stimulus and a standard deviation proportional to the mean. The constant of proportionality relating the mean to the standard deviation (i.e., the coefficient of variation) is assumed to be constant for a given subject in a given experiment (hence Weber's law). Thus, the value remembered for a large interval or amount is drawn from a distribution with a larger mean and standard deviation than that for a smaller interval or amount. If the same time interval or amount is experienced repeatedly, it will be represented in memory as a normal distribution centered on its true value. However, a uniformly distributed mixture of intervals or amounts is represented in memory as a positively skewed distribution. This skewed distribution is generated by combining the normal distributions that represent each of the constituent elements of the mixture, as demonstrated in the lower right graph of Figure 1.

Once a memory representation has been formed, the value of the original interval or amount can be recalled by taking a single random sample from its associated memory distribution. Subjects are assumed to choose between two options by retrieving one sample from memory for each option, comparing these samples, and preferring the option offering the better sample (bigger reward size or shorter delay). A random sample from the representation of a fixed option or a variable option (a mixture of two equally probable val-

Table 1

Schedule parameters used in the experiment. The programmed rates in the RoE and EoR columns can be obtained by substituting the values given in the table for G and T into Equations 1 and 2, respectively.

		Time foraging (T)					
Option	Units of food (G)	Delay (s) (D)	Assumed latency (s) (L)	Intertrial interval (s) (ITI)	Food delivery time (s) (F)	RoE (units per second)	EoR (units per second)
Fixed	5	20	1	40	5	0.08	0.08
Variable amount (Treatment A)	3 or 7 delivered with 50% probability	20	1	40	3 or 7 with 50% probability according to the units of food	0.08	0.08
Variable delay (Treatment D)	5	2.5 or 60.5 given with 50% probability	1	40	5	0.06	0.08

ues with a mean equal to the fixed option) will on average equal the mean value of the actual amount or interval. However, because the representations of variable options are skewed to the right, in more than half of comparisons the sample from the representation of the variable option will be smaller than the sample from the representation of the fixed option. Thus, for options with equal RoE, the above model makes the following predictions: (a) Variability in delay to food should be preferred because the variable option will yield shorter samples more than half of the time, (b) variability in amount of food should be avoided because the variable option will yield smaller samples more than half of the time, and (c) foragers should have separate information on the amounts and delays associated with each option.

Here we present an experiment designed to discriminate between these two models. Starlings' responses to fixed and variable options were studied in two treatments, A and D. The fixed option was the same in both treatments, but in Treatment A the variable option consisted of two equally probable amounts of food, and in Treatment D the variable option consisted of two equally probable delays to food. Unlike previous experiments of this type (with the exception of Reboreda & Kacelnik, 1991), the delays were calculated such that the EoR was equal in all of the options. Thus any differential response to the fixed and variable options cannot be attributed to maximization of the programmed EoR. When EoR is equated, it is still the case that the SET approach predicts preference for variability in delay and aversion to variability in amount. We show this in the Appendix by proving that according to Reboreda and Kacelnik's version of SET, a variable option consisting of two equally probable values should be chosen as often as a fixed option that always yields the geometric mean (i.e., the square root of the product) of the two alternative values of the variable option. It follows that as long as the fixed option is greater than the geometric mean of the two alternatives in the variable option, then the model predicts preference for variable delays. For the schedule parameters we chose (see Method and Table 1), the value of the fixed delay (20 s) was well above the geometric mean (12.3) of the two alternatives in the variable delay (2.5 and 60.5 s).

Reboreda and Kacelnik (1991) provided some evidence consistent with the SET model: Starlings preferred variable over fixed delays to food and were weakly averse to variability in amount of food. They rejected the EoR account because the programmed EoR was equated in the different options. However, their results were not conclusive, and an important assumption was not tested. Reboreda and Kacelnik used three measures of preference: proportion of choices, latency to accept rewards in forced trials, and pecking rate during the delays between choice and delivery of the rewards. These measures gave significant results in favor of delay variability but only marginal trends (.05 < p < .10) for aversion to variability in amount. The study provided no evidence for the assumption that delays are remembered independently of their contribution to the ratio of gain to delay. Here we replicate and extend this study to address these problems.

We examined pecking patterns during delays to food to exclude the possibility that in our experiment the subjects may have been unable to process delays independently of the amount/delay ratio. The ability to remember mixtures of delays is known from other procedures and other species (e.g., Catania & Reynolds, 1968). We also introduce methodological differences designed to reduce individual variation. In Reboreda and Kacelnik's experiment there were two design features that might have contributed noise. First, rewards were given using pigeon grain hoppers, and subjects showed idiosyncratic differences in the amount of food scooped per unit of time of hopper access; here, we used pellet dispensers that delivered programmed amounts of food to all birds. Second, in the earlier experiment, each session had a block of forced trials followed by a block of choice trials, with the result that biases in choice led to individual variation in amount of experience of each option within the block of choice trials. Here, choice trials were interspersed between forced trials, ensuring that before each choice all birds had experienced both options a virtually identical number of times.

METHOD

Subjects

The subjects were 6 wild-caught first-year European starlings (*Sturnus vulgaris*). After capture they were housed together in an outdoor aviary for approximately 2 months with free access to water and food. During the experiment the birds were housed and tested in individual cages measuring 120 cm by 50 cm by 60 cm. The birds were visually but not acoustically isolated. Temperature in the laboratory ranged between 7 and 13 °C, and the lights were on between 6 a.m. and 6 p.m. The birds were food deprived from 5 p.m. until the start of each session at 8 a.m. the following morning. During the experimental sessions the birds' responses were reinforced with turkey starter crumbs, and after the session the birds were given four mealworms and ad lib turkey crumbs until 5 p.m. This regime resulted in the birds being maintained at approximately 90% of their ad libitum feeding weights.

Apparatus

Each cage had an operant panel in the center of the back wall, with two response keys (3.5 cm in diameter), one on each side of a central food hopper. The keys could be illuminated from behind with yellow, red, or green light. The food hopper was connected to a pellet dispenser (Campden Instruments) filled with turkey crumbs sieved to an even size. The standard reward used in both training and the experiments consisted of five units of crumbs. Such a reward had a mean weight of 0.06 g (SD = 0.0072 g) and took 5 s to deliver (1 s per unit). A BBC Master microcomputer running SPIDER experimental control language controlled the stimulus events and response contingencies and recorded the data.

Training

After magazine training the birds were induced to peck the response keys by autoshaping. In this phase, delivery of standard rewards was preceded by 8 s of yellow light illumination of a randomly chosen key and was followed by an intertrial interval (ITI) of 60 s. After six sessions of 100 trials each (two sessions each day), all birds pecked at the illuminated key. In the second phase, the light signal was increased to 12 s if no peck occurred, but pecking at the illuminated key extinguished the light and produced immediate delivery of the standard reward. After 20 such sessions, all the birds were pecking the illuminated key on more than 75% of trials.

Experiment

A discrete-trials procedure with a fixed ITI of 40 s was employed. Rewards were dispensed according to response-initiated fixed-interval schedules programmed as follows. A trial started with a flashing light (on for 0.7 s, off for 0.3 s) on one of the pecking keys that, following the first peck, became steadily illuminated, indicating the start of the delay time. The first peck after the programmed

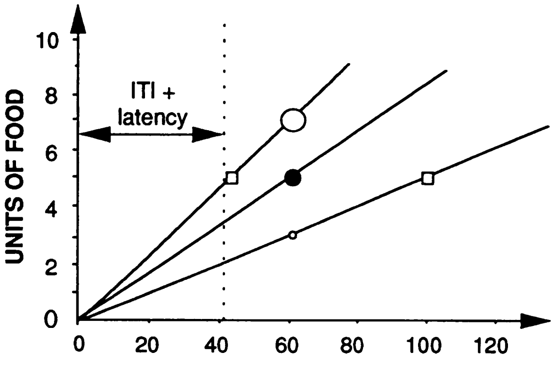

Fig. 2. The programmed contingencies in both treatments. In Treatment A the fixed option (filled circle) is compared with the variable-amount option (open circles) and in Treatment D with the variable-delay option (open squares). The slopes of the lines show the expectation of the ratios (EoR) offered by the various alternatives.

delay had elapsed extinguished the keylight and caused the delivery of food to the hopper. The ITI was timed from the end of food delivery, which lasted 1 s for every unit of food dispensed. The experiment involved forced trials, as described above, and choice trials that started with both keylights flashing, one red and one green. In choice trials the first peck caused steady illumination of the pecked key and extinguished the other keylight.

There were two treatments. In each the birds' preferences between a variable and a fixed option were examined. The fixed option always gave a standard five-unit reward after a delay of 20 s. In Treatment A the variable option led with equal probability to either three or seven units of reward after 20 s, and in Treatment D the variable option led with equal probability to five units of reward after delays of either 2.5 s or 60.5 s. These values were chosen so that in both treatments the programmed EoR was equal for the fixed and the variable options. This is shown graphically in Figure 2, and the rates and numbers from which they were calculated are given in Table 1. Although the variance in delay is greater than the variance in amount, we chose the values under the assumption that an EoR maximizing forager is sensitive only to the ratio of amount over delay and is unaffected by individual amounts and delays. On this basis, we chose the values so that the variance in EoR in the variable options of the two treatments was equal. This is incompatible with equalising the variance in the amounts and delays. Thus, using Equation 2, the following equalities held:

$$\frac{A_{\text{fixed}}}{L + D_{\text{fixed}} + F_{\text{fixed}} + ITI}$$

$$= \frac{1}{2}\left(\frac{A_{\text{fixed}}}{L + D_{\text{short}} + F_{\text{fixed}} + ITI} + \frac{A_{\text{fixed}}}{L + D_{\text{long}} + F_{\text{fixed}} + ITI}\right)$$

$$= \frac{1}{2}\left(\frac{A_{\text{small}}}{L + D_{\text{fixed}} + F_{\text{small}} + ITI} + \frac{A_{\text{large}}}{L + D_{\text{fixed}} + F_{\text{large}} + ITI}\right)$$

where A_{fixed}, A_{small}, and A_{large} stand for the fixed, small, and large amounts, respectively; D_{fixed}, D_{short}, and D_{long} stand for the fixed, short, and long delays, respectively; F_{fixed}, F_{small}, and F_{large} stand for the time taken to deliver the fixed, small, and large rewards, respectively; L stands for the latency to peck; and ITI stands for the intertrial interval. The first expression represents the EoR in the fixed option, the second is the EoR in the variable-delay option, and the third is the EoR in the variable-amount option.

For the purposes of the rate calculations, it was necessary to assume a value for the latency, defined as the delay signaled by a flashing light between a trial becoming available and the bird actually initiating it by making the first peck at the key, because this period of time was under the control of the birds. Any model of rate maximization predicts that this latency should be as brief as physically possible. We therefore assigned a nominal value of 1 s to the latency.

The 6 birds were divided into two groups. Birds 0, 1, and 2 received Treatment D followed by Treatment A, and Birds 3, 4, and 5 received the treatments in the reverse order. In the first half of the experiment, the fixed option was signaled by green and the variable option by red. This was reversed in the second half.

A session comprised 12 blocks of nine trials

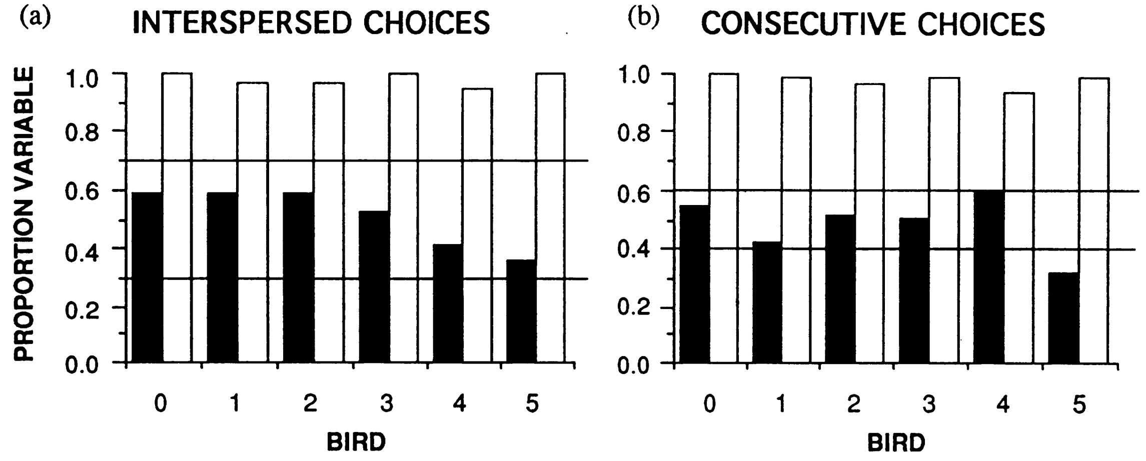

Fig. 3. Proportion of choices for the variable option made by each bird (a) in the last three sessions of interspersed choice trials for each treatment (total of 36 choices for each bird in each treatment) and (b) in the blocks of consecutive free-choice trials at the end of each treatment (total of 108 choices for each bird in each treatment). Filled bars are Treatment A and open bars are Treatment D. The horizontal lines indicate the 5% significance levels calculated using the binomial theorem with the null hypothesis that the birds are equally likely to choose constant and variable options. Thus results falling between the lines are statistically not significantly different from random choice.

each, a block consisting of eight forced trials followed by one choice trial. The eight forced trials of each block comprised four fixed and four variable trials in a different randomly chosen order for each block. Half of the fixed and half of the variable trials appeared on the left key, and the other half appeared on the right key. Two variable trials in each block were large/long and the other two were small/short, each type appearing once on each key. The forced trials ensured that the subjects experienced the two options a similar number of times and that the two outcomes of the variable option were experienced equally often. They also gave data on behavior towards both alternatives, including the less preferred one (latency to accept and rate of pecking during the delay). The choice trials gave a direct measure of preference.

Each half of the experiment consisted of 21 sessions run consecutively over 21 days. On the 22nd day of each half of the experiment, the birds were given a session of 108 choice trials with no forced trials, to control for the possibility that preferences were in some way affected by the interspersed forced trials.

Data Collection and Analysis

The following dependent variables were examined: (a) proportion of choices made to each option in the interspersed choice trials and in the final sessions of consecutive choices, (b) latency to start forced trials of each type (the duration of the flashing-light section of each trial), (c) number of pecks made during the delays in each trial type, and (d) pecking patterns. The pecks during the delays were collected into 1-s time bins to detect the accuracy of the birds' timing of rewards.

RESULTS

Choices

Figure 3(a) shows the proportion of choices of the variable option made by each bird in Sessions 19 to 21 of each treatment. All 6 individuals were significantly biased towards variability in Treatment D but showed no preference in Treatment A. Figure 3(b) shows the data from the 22nd sessions (consecutive choice trials) in the same format. The results are essentially the same as in the interspersed free-choice trials, except that 1 bird was significantly biased against variability in Treatment A. For the purposes of statistical analysis, the choice proportions were arcsine square root transformed to correct heterogeneity in the variance of the residuals. Repeated measures ANOVA showed that the ef-

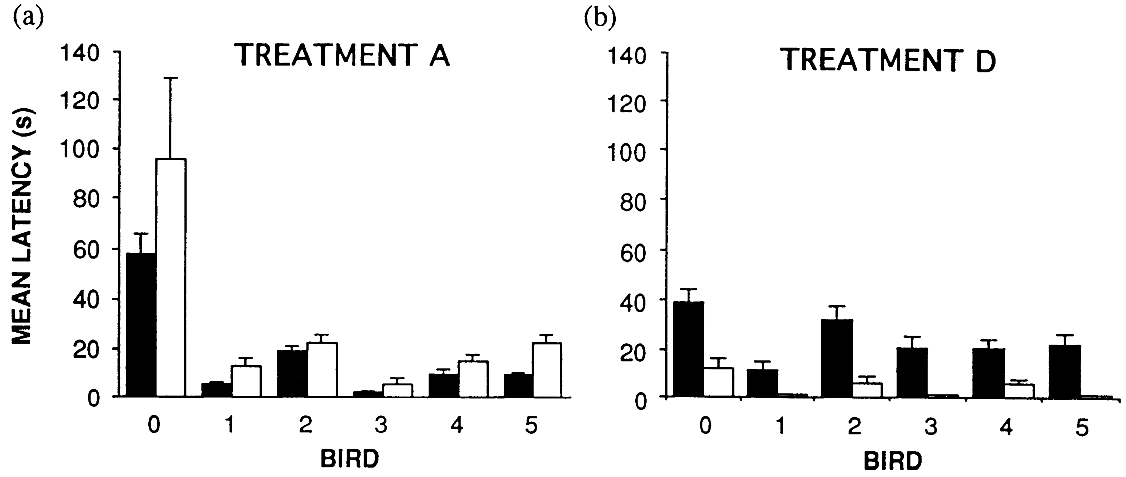

Fig. 4. Latencies to start fixed (filled bars) and variable (open bars) trials in Treatments A and D. Each bar is the mean ± 1 *SEM* of the data from each bird.

fect of treatment (A or D) on the proportion of choices for the variable option was significant in both the interspersed choice trials, $F(1, 5) = 123.70$, $p < .001$, and in the consecutive choice trials, $F(1, 5) = 113.80$, $p < .001$. In summary, the choice data show that when variability was in delay (Treatment D) the birds showed almost exclusive preference for the variable option, but when variability was in amount (Treatment A) choices were not significantly biased.

Latencies

For all birds, the mean observed latencies to peck were considerably longer than the latency of 1 s assumed in our calculations. The mean latency to peck in fixed and variable forced trials was calculated for each bird for the last three sessions of each treatment (thus each mean is based on 144 data points; see Figure 4). In Treatment A all 6 birds showed a greater mean latency in variable-amount trials than in fixed-amount trials (sign test, $p = .0312$), whereas in Treatment D the situation was reversed, and all 6 birds showed a greater latency to accept fixed-delay trials than variable-delay trials (sign test, $p = .0312$). Mean latencies were square rooted to correct for heterogeneity in the variance of the residuals. Two-way repeated measures ANOVA showed that treatment (A or D) did not have a statistically significant effect on mean latency; however, the effect of variance (fixed or variable) was significant, $F(1, 5) = 21.15$, $p = .006$: Across conditions, the birds showed greater latencies to peck on fixed ($M = 20.73$ s) than on variable trials ($M = 16.91$ s). The interaction between treatment and variance was significant, $F(1, 5) = 124.16$, $p < .001$, reflecting the fact that variance had the opposite effect on latency in the two treatments.

Pecking Patterns

The patterns of pecking during the delays shown by each of the birds in fixed-amount and variable-amount trials of Treatment A are summarized in Figure 5. All 6 birds showed an increase in their rate of pecking towards the end of the 20-s delay. For all birds the mean cumulative number of pecks made in the fixed-amount trials was greater than that in the variable-amount trials (sign test, $p = .0312$; see Table 2), showing that starlings peck at a higher rate when they are waiting for a fixed amount rather than a variable

Table 2

Mean pecks per 20-s delay in the last three sessions of Treatment A (144 trials of each type).

Bird	Fixed	Variable
0	28.81	28.74
1	64.85	61.54
2	48.94	48.69
3	54.27	49.06
4	46.47	43.83
5	47.88	42.74
M ± 1 *SEM*	48.54 ± 4.81	45.77 ± 4.36

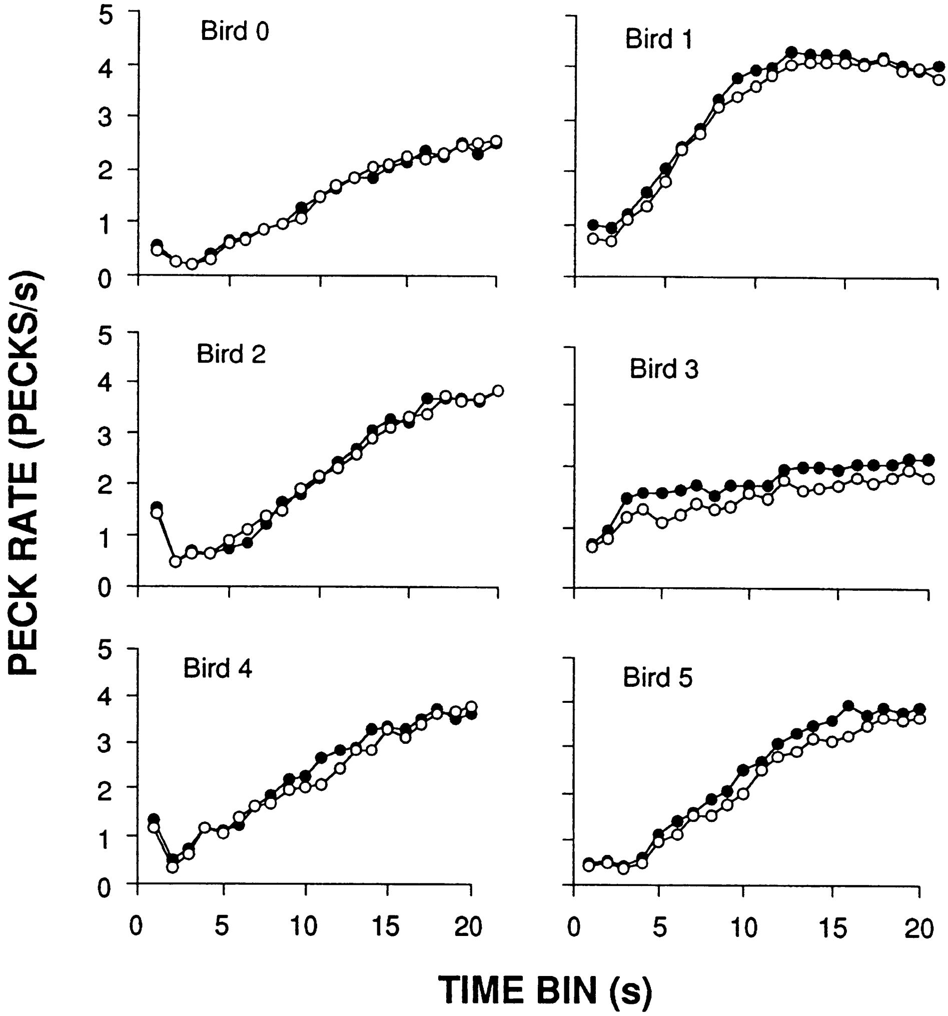

Fig. 5. Mean pecking rates in 1-s intervals in the forced trials of the last three sessions of Treatment A. Filled circles are data from fixed-amount trials, and open circles are data from variable-amount trials.

Table 3

Mean pecks in the first 2 s of the delay in the last three sessions of Treatment D (144 trials of each type).

Bird	Fixed	Variable
0	1.33	5.42
1	1.57	6.09
2	2.37	9.21
3	3.53	8.89
4	2.34	8.06
5	0.92	7.74
M ± 1 *SEM*	2.01 ± 0.38	7.57 ± 0.62

amount of food. Due to the different pattern of pecking between fixed and variable delays (see below), this analysis was not possible in Treatment D.

The patterns of pecking seen in the fixed delays of Treatment D were similar to those seen in Treatment A, with the peck rates peaking towards the end of the 20-s delay (see Figure 6). In the long delays of the variable option, pecking rate showed a first peak at 2.5 s, then dropped to almost zero before

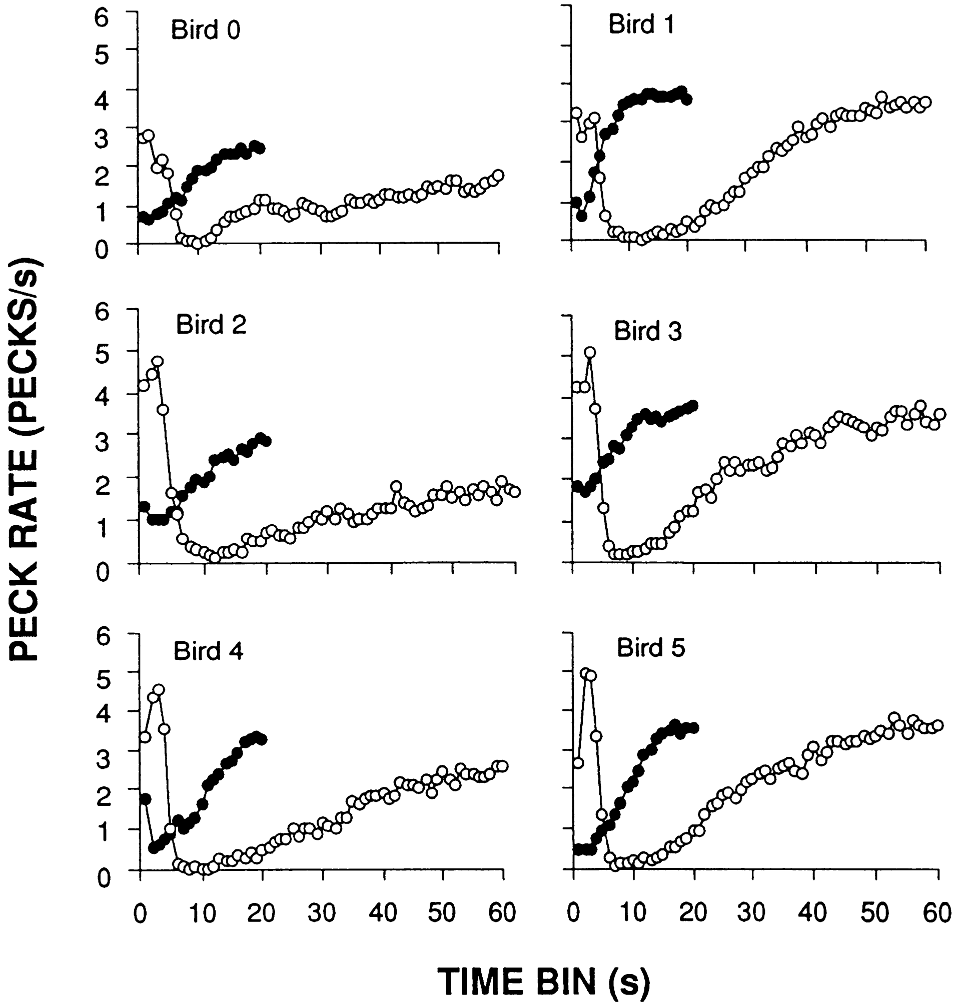

Fig. 6. Mean pecking rates in the forced trials of the last three sessions of Treatment D. Filled circles are data from fixed-delay trials, and open circles are data from variable-delay trials.

rising again toward the end of the delay at 60.5 s when the birds received food. The peak at 2.5 s corresponds to the time locus of short delays when the birds could potentially have received food on half of the variable-delay trials. The mean cumulative number of pecks made in the first 2 s of the fixed and variable delays was significantly different (sign test, $p = .0312$; see Table 3), showing that the birds could discriminate between the fixed- and variable-delay options on the basis of the length of the delays.

Comparing the three points at which the birds could receive food (20 s, 2.5 s, or 60.5 s), both the maximum peck rate and the shape of the growth in pecking rate varied with the length of the delay. In all birds (except for Bird 1), the highest peck rates and steepest rise in rate were for the peak at 2.5 s, even though these delays ended in reward 50% of the time, as opposed to 100% of the time for the peaks at 20 and 60.5 s. Similarly, the peak at 20 s was generally higher and had a steeper rise in rate than the peak at 60.5 s. These results are consistent with the assumptions of Weber's law for delay. The patterns indicate that in this experiment the birds had precise information about the different possible delays and were not constrained by perceiving the ratios of amount over delay directly.

DISCUSSION

Our aim in this paper is to ask whether the addition of psychological constraints to a simple rate-maximizing approach can generate models that are capable of explaining observed patterns in the response of animals to variability in their food sources. We presented two possible models. The first assumes that animals may be constrained to maximize the expected ratio of amount of food over time spent foraging (EoR) because they can only perceive rate of intake directly. The second is based on scalar expectancy theory, and assumes that the accuracy of perception of amounts of food and time intervals is constrained by Weber's law and that a sampling procedure governs the recall of information from memory. In an experiment designed to test both of these models, we measured preference between fixed and variable food sources. There were two treatments, one in which variability was in amount and one in which variability was in delay. The schedules were programmed so that in both treatments the expected ratio of gain over time (i.e., EoR) was equal in the fixed and variable options. Given these conditions, the model based on maximizing EoR predicts that there should be no preference for either option in either treatment, whereas the SET model predicts a preference for variability in delay and an aversion to variability in amount. In addition, the EoR model assumes that the subjects should have no knowledge of the individual amounts and delays, because they are constrained to perceive their ratio directly.

We measured three indices of preference between the fixed and variable options in the two treatments. Our results can be summarized as follows:

1. For the first index, choice, the subjects were indifferent to variability in amount but strongly preferred variability in delay. This pattern was observed in both interspersed and consecutive choice trials.

2. For the second index, latency to peck, the subjects showed shorter latencies for fixed trials when variability was in amount but shorter latencies for variable trials when variability was in delay.

3. For the third index, number of pecks during the delay, the subjects pecked slightly more during the delay to fixed trials when variability was in amount. Numbers of pecks could not be compared in the treatment with variability in delay.

4. The patterns of pecking during the delays reveal that the birds possessed information about the different times at which reinforcement could be delivered in the different types of trial. This could have been anticipated from results obtained in other species and protocols (e.g., Catania & Reynolds, 1968).

All the measures of preference suggest that starlings strongly prefer variable delays to fixed delays. By comparison, the measures based on latency and number of pecks suggest that starlings have a weak aversion to variable amounts of food, although this was not borne out by the choice data that showed no preference when variability was in amount. These results are summarized in Figure 7.

The SET account is supported by the data in correctly predicting preference for variability in delay and aversion to variability in amount. Its assumption that animals have separate information about the timing of food rewards is also supported, whereas the EoR account fails in its predictions of no preference in either treatment and possession of information only on the rate of reinforcement. On first inspection these results appear to support the SET account over the EoR account. However, it would be premature to conclude that the EoR account is incorrect. Our analysis so far has been biased against EoR on two counts. The first concerns the discrepancy between the programmed and observed latencies, and the second is the issue of which time intervals the birds actually include in their assessment of the value of the two options. We will now discuss the impact of each of these points on the EoR account.

All of the predictions made so far in relation to EoR have been calculated on the basis of a latency of 1 s, but in fact the experienced latencies were always far in excess of this (see Figure 4). We use latency in forced trials as a measure of the value assigned to an option on the assumption that the longer the latency the stronger the reluctance to accept that option. This assumption is based on the observation that in forced trials the birds often spent some time moving back and forth between the illuminated key on offer and the dark key opposite as if taking some time "to

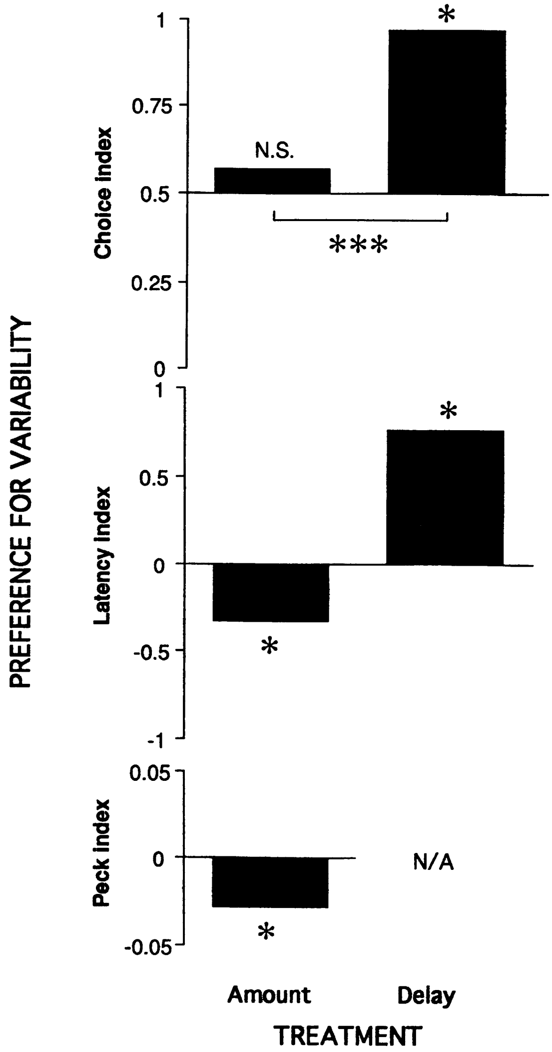

Fig. 7. Summary of results. The choice index is equal to the proportion of times the variable option was chosen. The latency index is equal to $(l_f - l_v)/(l_f + l_v)$, where l_f and l_v are the latencies to start fixed and variable trials, respectively. The peck index is equal to $(p_v - p_f)/(p_f + p_v)$, where p_f and p_v are the number of pecks made in constant and variable trials, respectively. All data are from the last three sessions of each treatment. Indices were calculated for each of the birds, and the bars represent the median of these six values. Single asterisks indicate a significant difference from the central line on each graph ($p < .05$, sign test; i.e., all 6 birds went the same direction). The three asterisks indicate a significant difference between the treatments ($p < .001$, ANOVA described in Results section).

Table 4

The observed latencies and the resulting changes in the rates of food intake experienced by the birds.

Trial type	Mean observed latency (s)	Experienced RoE (units per second)	Experienced EoR (units per second)
Fixed in Treatment A	17.2	0.061	0.061
Variable in Treatment A	29.15	0.053	0.053
Fixed in Treatment D	24.7	0.056	0.056
Variable in Treatment D	4.67	0.062	0.071

make up their minds" that there was no alternative on offer. This behavior is easily explained, because it is unlikely that the birds were able to learn that they only had a choice after every eight forced trials. If this explanation for the latencies is correct, then we would predict no difference in the latencies to start the chosen fixed or variable trials in the interspersed choice trials. We tested this prediction by comparing the mean latencies to start fixed and variable trials in the last three sessions of Treatment A. A sign test showed no significant difference ($p = .2187$) between the means. A comparable analysis was not possible for Treatment D, because the birds rarely chose the fixed option in the choice trials.

To give some idea of the effect of the discrepancy between the latencies that the birds experienced and those that we programmed, we recalculated RoE and EoR using the mean experienced latencies in place of the previous estimate of 1 s. The results are shown in Table 4. Table 4 shows that the birds succeeded in altering our carefully planned design so that in both treatments neither RoE nor EoR was equal in the fixed and variable options. The figures for experienced RoE and EoR now agree with the observed preferences. Both currencies suggest that given the experienced latencies there was a small advantage to preferring fixed amounts over variable amounts of 0.008 units per second. Both RoE and EoR also suggest an advantage to preferring variable delays over fixed delays, but the advantage was more than double for EoR (0.015 units per second) what it is for RoE (0.006 units per second). Thus, to conclude, maximization of experienced RoE and EoR were qualitatively compatible with the observed results, although EoR looks marginally better because it correctly predicts a larger difference when variability is in delay than when it is in amount. In agreement with this, a reanalysis of Reboreda and Kacelnik's (1991) data shows that maximization of EoR can also explain their results if the experienced rather than the programmed latencies are used. We are not the first to report an effect of this type. Killeen, Smith, and Hanson (1981) found that some elements of rats' foraging behavior were "irrational" (as are the latencies in this experiment), but that other elements of the rats' decision making was rational given these aspects of their own behavior. However, there are still reasons for objecting to the EoR account. First, as it stands the argument is circular: The latencies are explained by the values the birds attribute to the two options, and the values are calculated using the latencies. Second, the pecking patterns provide independent evidence that at least one explanation for the use of EoR (the constraint of perceiving amount over delay directly) is incorrect.

We now discuss the second problem of which time intervals actually enter the birds' assessment of value. Psychologists and ecologists agree that, all else being equal, earlier rewards should be preferred to more delayed alternatives. It may not be obvious to all psychologists that the reason delay is important in foraging theory is that future delays are deemed to compete for the opportunity to seek other rewards, and not because of the effects of previously experienced delays on the strength of reinforcement of earlier responses. This is the so-called principle of lost opportunity (PLO) that underlies rate-maximizing optimality predictions. When deciding whether to commit itself to pursuing a given reward, a rate-maximizing forager evaluates the average time that will be used obtaining it (this time will not be available to pursue other rewards) and the value of the alternative foraging opportunities lost during this period of time. Because the ITI affects the average foraging payoff, it contributes to the opportunity lost when a particular foraging option is chosen, and should thus appear in the rate calculations. We included the ITI in our calculations because our theoretical views are based on optimality principles, and because many studies of patch exploitation have shown that animals are sensitive to the travel time between patches (e.g., Kacelnik's 1984 field experiment with starlings or its laboratory analogues, e.g., Kacelnik & Todd, 1992). Travel times are often regarded as analogous to intertrial intervals because both subtract from active foraging time, but this analogy may be purely formal. It is probable that the birds do not attribute equal cost to the different time periods that make up the foraging cycle, and differences between travel and ITI can be justified from both psychological and functional perspectives. From the psychological viewpoint, during travel the subject's attention may be focused on signals associated with the forthcoming reward, whereas during an ITI there are no such external signals. Functionally, the ITI may not present a lost opportunity because the bird may use the waiting time to perform other valuable behavior (e.g., drinking, preening, or singing; indeed, our birds were observed to do all of these things). An argument similar to that outlined above for the ITI could also be made for the latencies.

Given the uncertainty as to the nature of the effect of ITIs and latencies, we reexamined the rate-maximizing predictions with and without the inclusion of the various time components of the schedule. Table 5 shows the predictions of the six currencies that are derived from the RoE and EoR algorithms combined with three alternative hypotheses about which time periods are included in the calculations. The only currency that is ruled out entirely on the basis of the qualitative direction of its predictions is RoE calculated with the delay and feeding time (the bottom left currency in Table 5). Also, neither of the other RoE currencies fits quantitatively well with our observations, because both predict stronger preferences in Treatment A than in Treatment D. All of the EoR currencies correctly predict a bias towards the variable option in Treatment D, either indifference or a bias toward the fixed option in Treatment A, and that stronger preferences should occur in D than A. The data do not allow us to discriminate confidently between the EoR currencies. However, the EoR currency that includes latency, delay, and feeding time looks quantitatively the best because it correctly predicts a modest preference for the fixed

Table 5

Summary of the predictions made by different rate currencies with the entry in each cell indicating the highest yielding option. The first of the numbers in parentheses is the absolute difference between the rates available in the two options, and the second number expresses this difference as a percentage of the smaller of the two rates available, to give some indication of how discriminable the two options are. In all of these calculations, the observed rather than the programmed latencies were used.

	Ratio of expectations (RoE)		Expectation of ratios (EoR)	
Time included	Treatment A	Treatment D	Treatment A	Treatment D
All time (i.e., latency, delay, feeding, and ITI)	Fixed (0.008 = 15%)	Variable (0.006 = 11%)	Fixed (0.008 = 15%)	Variable (0.015 = 27%)
Latency, delay, and feeding only	Fixed (0.026 = 28%)	Variable (0.02 = 20%)	Fixed (0.027 = 28%)	Variable (0.14 = 139%)
Delay and feeding only	Indifferent (0 = 0%)	Fixed (0.063 = 46%)	Indifferent (0 = 0%)	Variable (0.172 = 86%)

option in Treatment A and a strong preference for the variable option in Treatment D.

To conclude this section, there are theoretical reasons to believe that the birds may not include all of the time periods in their calculations of the value of the options. When the predictions of RoE and EoR maximizing are calculated without the ITI or the latency, the RoE currencies fare worse and the EoR currencies fare better at predicting our results. Maximization of EoR is compatible with our results, especially if the observed latencies are included and the ITI is excluded. The explanation we gave for the use of EoR must be rejected on the basis of the pecking patterns. However, other suggestions have been put forward (Real, 1991), and these should now be investigated.

We turn now to a discussion of the SET model. The predictions of SET are not affected by the experienced latencies or by the uncertainty over which time intervals should be included, because only the delays to reward or the amounts enter this model. The model correctly predicts a preference for variable delays in Treatment D and for fixed amounts in Treatment A. According to the SET model, the strength of these preferences will depend on the variance in the variable option. This prediction can be understood from a consideration of Figure 1. Predicted preference for or against variability arises from the skew in the memory distributions. When the variance in the true value of a stimulus is zero (i.e., a fixed option), the skew in memory is also zero, but as the variance is increased, the skew increases until a maximum point is reached. Because skew translates into preference, the model predicts effects of magnitude of variance on degree of preference (Bateson, 1993). In the experiment the programmed coefficient of variation in delay (1.3) was greater than the programmed coefficient of variation in amount (0.57). Therefore SET could potentially explain the difference in magnitude of the birds' preferences for variability in amount and delay as well as the direction of these preferences. The model also accommodates the observed pecking patterns, because it assumes that the subject has information about the duration of the different delays and, in accordance with Weber's law, that this information is less accurate for longer delays (this is demonstrated in Figures 5 and 6). The model fails, however, in one important respect. The predicted preference for fixed amounts is problematic, because we found clear preferences expressed in latencies and pecking rates but not in the proportion of choices made for the fixed option. We have no explanation for this observation other than that the former two indices are continuous and consequently may be more sensitive measures of underlying preference.

One of the attractions of the SET model is that the assumptions on which it is based are open to independent testing, and some are already well established. Of particular relevance, recent work on starlings has shown that accuracy in memory for both time intervals (Brunner, Kacelnik, & Gibbon, 1992) and amounts of food (Bateson & Kacelnik, in press) is compatible with Weber's law as assumed in Reboreda and Kacelnik's (1991) version of SET. Probably the least well-supported assumption is that each choice is based on only a single sample from the memory for each alternative, and some recent work suggests that this assumption may need to be modified in the future (Brunner et al., 1994). Because SET uses the simple decision criterion, "sample your memory and choose the option providing the most favorable sample," it has been possible to adapt it to a range of different foraging paradigms. When applied to decisions involving time, the model reliably predicts many experimental results (Brunner et al., 1992; Shettleworth, Krebs, Stephens, & Gibbon, 1988; Todd & Kacelnik, 1993).

We are aware that our discussion is already rather involved because of our attempt to consider both functional and mechanistic implications of our data. Regrettably, we are also aware that we have not exhausted all possible theoretical approaches. In particular, we have not considered the matching law (Herrnstein, 1970), which is relevant here given that our protocol has elements in common with schedules of reinforcement such as discrete-trials concurrent chains. However, the predictions of matching for our protocol are not straightforward, because matching predicts equality between molar time allocation and molar experienced reward rates. In our experiment the subjects had no choice in eight of every nine trials and had long ITIs that may or may not be included in the calculation of the rates. Matching or its molecular relatives (e.g., melioration) may be able to account for our results, but we have chosen to restrict our discussion to explanations based on optimality considerations.

Our thesis in this paper has been that choices that initially appear to be nonadaptive may turn out to be optimal in some restricted sense, given the constraints of the information-processing machinery of the species. This approach makes the reasons for the widespread existence of these constraints an external, independent problem and ensures that the postulated models used to account for behavior remain testable. We tested two such accounts of animals' responses to variability, with the result that both appear to be tenable, although neither explains every detail of our data. We surmise that it is through the development of theories that combine psychological and evolutionarily rational thinking that most progress can be expected in this field.

REFERENCES

Ahearn, W., & Hineline, P. N. (1992). Relative preferences for various bivalued ratio schedules. *Animal Learning & Behavior, 20,* 407–415.

Barkan, C. P. L. (1990). A field test of risk-sensitive foraging in black-capped chickadees (*Parus atricapillus*). *Ecology, 71,* 391–400.

Bateson, M. (1993). *Currencies for decision making: the foraging starling as a model animal.* Unpublished doctoral dissertation, Oxford University.

Bateson, M., & Kacelnik, A. (in press). Accuracy of memory for amount in the foraging starling (*Sturnus vulgaris*). *Animal Behaviour.*

Brunner, D., Gibbon, J., & Fairhurst, S. (1994). Choice between fixed and variable delays with different reward amounts. *Journal of Experimental Psychology: Animal Behavior Processes, 20,* 331–346.

Brunner, D., Kacelnik, A., & Gibbon, J. (1992). Optimal foraging and timing processes in the starling, *Sturnus vulgaris*: Effect of inter-capture interval. *Animal Behaviour, 44,* 597–613.

Caraco, T., Blanckenhorn, W. U., Gregory, G. M., Newman, J. A., Recer, G. M., & Zwicker, S. M. (1990). Risk-sensitivity: Ambient temperature affects foraging choice. *Animal Behaviour, 39,* 338–345.

Caraco, T., Kacelnik, A., Mesnik, N., & Smulewitz, M. (1992). Short-term rate maximization when rewards and delays covary. *Animal Behaviour, 44,* 441–447.

Catania, A. C., & Reynolds, G. S. (1968). A quantitative analysis of the responding maintained by interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior, 11,* 327–385.

Cicerone, R. A. (1976). Preference for mixed versus constant delay of reinforcement. *Journal of the Experimental Analysis of Behavior, 25,* 257–261.

Clements, K. C. (1990). Risk-aversion in the foraging blue jay, *Cyanocitta cristata. Animal Behaviour, 40,* 182–195.

Cuthill, I., & Kacelnik, A. (1990). Central place foraging: A reappraisal of the "loading effect." *Animal Behaviour, 40,* 1087–1101.

Cuthill, I. C., Kacelnik, A., Krebs, J. R., Haccou, P., & Iwasa, Y. (1990). Starlings exploiting patches: The effect of recent experience on foraging decisions. *Animal Behaviour, 40,* 625–640.

Davison, M. C. (1969). Preference for mixed-interval versus fixed-interval schedules. *Journal of the Experimental Analysis of Behavior, 12,* 247–252.

Davison, M. C. (1972). Preference for mixed-interval versus fixed-interval schedules: Number of component intervals. *Journal of the Experimental Analysis of Behavior, 17,* 169–176.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review, 84,* 279–325.

Gibbon, J., Church, R. M., Fairhurst, S., & Kacelnik, A.

(1988). Scalar expectancy theory and choice between delayed rewards. *Psychological Review, 95,* 102–114.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In J. Gibbon & L. Allan (Eds.), *Timing and time perception* (pp. 52–77). New York: New York Academy of Sciences.

Gilliam, J. F., Green, R. F., & Pearson, N. E. (1982). The fallacy of the traffic policeman: A response to Templeton and Lawlor. *American Naturalist, 119,* 875–878.

Ha, J. C. (1991). Risk-sensitive foraging: The role of ambient temperature and foraging time. *Animal Behaviour, 41,* 528–529.

Ha, J. C., Lehner, P. N., & Farley, S. D. (1990). Risk-prone foraging behaviour in captive grey jays *Perisoreus canadensis. Animal Behaviour, 39,* 91–96.

Hamm, S. L., & Shettleworth, S. J. (1987). Risk aversion in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 13,* 376–383.

Harder, L., & Real, L. A. (1987). Why are bumble bees risk-averse? *Ecology, 68,* 1104–1108.

Herrnstein, R. J. (1970). On the law of effect. *Journal of the Experimental Analysis of Behavior, 13,* 243–266.

Kacelnik, A. (1984). Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *Journal of Animal Ecology, 53,* 283–299.

Kacelnik, A., & Todd, I. A. (1992). Psychological mechanisms and the marginal value theorem: Effect of variability in travel time on patch exploitation. *Animal Behviour, 43,* 313–322.

Killeen, P. R., Smith, J. P., & Hanson, S. J. (1981). Central place foraging in *Rattus norvegicus. Animal Behaviour, 29,* 64–70.

Logan, F. A. (1965). Decision making by rats: Uncertain outcome choices. *Journal of Comparative and Physiological Psychology, 59,* 246–251.

Mazur, J. E. (1984). Tests of an equivalence rule for fixed and variable reinforcer delays. *Journal of Experimental Psychology: Animal Behavior Processes, 10,* 426–436.

Mazur, J. E. (1986). Fixed and variable ratios and delays: Further tests of an equivalence rule. *Journal of Experimental Psychology: Animal Behavior Processes, 12,* 116–124.

Mazur, J. E. (1987). An adjusting procedure for studying delayed reinforcement. In M. L. Commons, J. E. Mazur, J. A. Nevin, & H. Rachlin (Eds.), *Quantitative analyses of behavior: The effect of delay and of intervening events on reinforcement value* (pp. 55–73). Hillsdale, NJ: Erlbaum.

McNamara, J. M., & Houston, A. I. (1992). Risk-sensitive foraging: A review of the theory. *Bulletin of Mathematical Biology, 54,* 355–378.

Morris, C. J. (1986). The effects of occasional short (FR1) reinforcement ratios on choice behavior. *The Psychological Record, 36,* 63–68.

Possingham, H. P., Houston, A. I. & McNamara, J. M. (1990). Risk-averse foraging in bees: A comment on the model of Harder and Real. *Ecology, 71,* 1622–1624.

Real, L. A. (1981). Uncertainty and pollinator-plant interactions: The foraging behavior of bees and wasps on artificial flowers. *Ecology, 62,* 20–26.

Real, L. A. (1991). Animal choice behavior and the evolution of cognitive architecture. *Science, 253,* 980–986.

Reboreda, J. C., & Kacelnik, A. (1991). Risk sensitivity in starlings: Variability in food amount and food delay. *Behavioral Ecology, 2,* 301–308.

Schmid-Hempel, P., Kacelnik, A., & Houston, A. I. (1985). Honeybees maximize efficiency by not filling their crop. *Behavioural Ecology and Sociobiology, 17,* 61–66.

Shettleworth, S. J., Krebs, J. R., Stephens, D. W., & Gibbon, J. (1988). Tracking a fluctuating environment: A study of sampling. *Animal Behaviour, 36,* 87–105.

Staddon, J. E. R., & Innis, N. K. (1966). Preference for fixed vs. variable amounts of reward. *Psychonomic Science, 4,* 193–194.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory.* Princeton, NJ: Princeton University Press.

Templeton, A. R., & Lawlor, L. R. (1981). The fallacy of the averages in ecological optimization theory. *American Naturalist, 117,* 390–393.

Todd, I. A., & Kacelnik, A. (1993). Psychological mechanisms and the marginal value theorem: Dynamics of scalar memory for travel time. *Animal Behaviour, 46,* 765–775.

Turelli, M., Gillespie, J. H., & Shoener, T. W. (1982). The fallacy of the fallacy of the averages in ecological optimization theory. *American Naturalist, 119,* 879–884.

Tuttle, E. M., Wulfson, L., & Caraco, T. (1990). Risk-aversion, relative abundance of resources and foraging preferences. *Behavioural Ecology and Sociobiology, 26,* 165–171.

Waddington, K. D., Allen, T., & Heinrich, B. (1981). Floral preferences of bumblebees (*Bombus edwardsii*) in relation to intermittent versus continuous rewards. *Animal Behaviour, 29,* 779–784.

Wunderle, J. M., Santa-Castro, M., & Fletcher, N. (1987). Risk-averse foraging by bananaquits on negative energy budgets. *Behavioural Ecology and Sociobiology, 21,* 249–255.

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APPENDIX

Here we derive the value of a fixed delay or amount that is subjectively equal to a variable option consisting of two equiprobable delays or amounts.

Let μ_{fixed}, μ_{short}, and μ_{long} be the means and σ^2_{fixed}, σ^2_{short}, and σ^2_{long} be the variances of the distributions in memory representing the fixed option, short alternative of the variable option, and long alternative of the variable option, respectively. According to SET, the fixed and variable options will be equally likely to be chosen when the probability of a random sample from the distribution representing the variable option, X_{variable}, being less than a random sample from the distribution representing the fixed option, X_{fixed}, is equal to one half, that is,

$$\text{prob}(X_{\text{variable}} < X_{\text{fixed}}) = \frac{1}{2}. \quad \text{(A1)}$$

When the variable option consists of two equally likely alternatives (short and long), the left side of Equation A1 can be expressed as the sum of two probabilities:

$$\frac{1}{2}\text{prob}(X_{\text{short}} < X_{\text{fixed}}) + \frac{1}{2}\text{prob}(X_{\text{long}} < X_{\text{fixed}}) = \frac{1}{2} \quad \text{(A2)}$$

that can be rearranged to give

$$\text{prob}(X_{\text{short}} - X_{\text{fixed}} < 0) + \text{prob}(X_{\text{long}} - X_{\text{fixed}} < 0) = 1, \quad \text{(A3)}$$

where X_{short} is a random sample from the distribution representing the short alternative of variable option and X_{long} is a random sample from the distribution representing the long alternative. To calculate the above probabilities, we use the result that because X_{fixed}, X_{short}, and X_{long} are all normal, with means μ_{fixed}, μ_{short}, and μ_{long} and variances σ^2_{fixed}, σ^2_{short}, and σ^2_{long}, respectively, the differences $(X_{\text{fixed}} - X_{\text{short}})$ and $(X_{\text{fixed}} - X_{\text{long}})$ will also be normally distributed with means $(\mu_{\text{fixed}} - \mu_{\text{short}})$ and $(\mu_{\text{fixed}} - \mu_{\text{long}})$ and variances $(\sigma^2_{\text{fixed}} + \sigma^2_{\text{short}})$ and $(\sigma^2_{\text{fixed}} + \sigma^2_{\text{long}})$, respectively. Therefore Equation A3 can be rewritten:

$$\Phi\left(\frac{\mu_{\text{fixed}} - \mu_{\text{short}}}{\sqrt{\sigma^2_{\text{fixed}} + \sigma^2_{\text{short}}}}\right) + \Phi\left(\frac{\mu_{\text{fixed}} - \mu_{\text{long}}}{\sqrt{\sigma^2_{\text{fixed}} + \sigma^2_{\text{long}}}}\right) = 1, \quad \text{(A4)}$$

where $\Phi[z(x)]$ is the cumulative distribution function of a normally distributed variable, where $z(x)$ is of the form $(x - \mu)/\sigma$. Because the normal distribution is symmetrical, $1 - \Phi[z(x)] = \Phi[z(-x)]$, and Equation A4 can be rewritten

$$\Phi\left(\frac{-(\mu_{\text{fixed}} - \mu_{\text{short}})}{\sqrt{\sigma^2_{\text{fixed}} + \sigma^2_{\text{short}}}}\right) = \Phi\left(\frac{\mu_{\text{fixed}} - \mu_{\text{long}}}{\sqrt{\sigma^2_{\text{fixed}} + \sigma^2_{\text{long}}}}\right). \quad \text{(A5)}$$

Because if $\Phi[z_1(x)] = \Phi[z_2(x)]$ then $z_1(x) = z_2(x)$, Equation A5 simplifies to

$$\frac{\mu_{\text{short}} - \mu_{\text{fixed}}}{\sqrt{\sigma^2_{\text{fixed}} + \sigma^2_{\text{short}}}} = \frac{\mu_{\text{fixed}} - \mu_{\text{long}}}{\sqrt{\sigma^2_{\text{fixed}} + \sigma^2_{\text{long}}}}. \quad \text{(A6)}$$

SET assumes that the coefficient of variation, γ, is constant for all the distributions in memory in a given animal, therefore, $\sigma_{\text{fixed}} = \gamma\mu_{\text{fixed}}$, $\sigma_{\text{short}} = \gamma\mu_{\text{short}}$, and $\sigma_{\text{long}} = \gamma\mu_{\text{long}}$. Substituting the above into Equation A6 and cancelling the γs, we obtain

$$\frac{\mu_{\text{short}} - \mu_{\text{fixed}}}{\sqrt{\mu^2_{\text{fixed}} + \mu^2_{\text{short}}}} = \frac{\mu_{\text{fixed}} - \mu_{\text{long}}}{\sqrt{\mu^2_{\text{fixed}} + \mu^2_{\text{long}}}}. \quad \text{(A7)}$$

Solving for μ_{fixed} gives

$$\mu_{\text{fixed}} = \sqrt{\mu_{\text{short}}\mu_{\text{long}}}. \quad \text{(A8)}$$

Thus, indifference between fixed and variable options will occur when the fixed option has a value equal to the geometric mean (i.e., the square root of the product) of the two alternatives of the variable option. This result is independent of the value of γ.