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Starlings' preferences for predictable and unpredictable delays to food

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Abstract. Risk-sensitive foraging theory is based on the premise that unpredictable runs of good or bad luck can cause a variable food source to differ in fitness value from a fixed food source yielding the same average rate of gain but no unpredictability. Thus, risk-sensitive predictions are dependent on the food intake from variable sources being not only variable but also unpredictable or 'risky' in outcome. This study tested whether unpredictability is a component of the value that foraging starlings, *Sturnus vulgaris*, attribute to food sources that are variable in the delay to obtain food. Two groups of birds chose between a fixed and a variable delay option; the variable option was unpredictable in the risky group and predictable in the risk-free group in the overall rate of intake it yielded. In both groups the fixed option was adjusted by titration to quantify the magnitude of preference for predictable and unpredictable variance. On negative energy budgets both groups were significantly risk-prone, with the risky group being significantly more risk-prone than the risk-free group. Switching the birds to positive budgets by doubling the size of each food reward had no significant effect on preference, and similar trends to those found with negative budgets were observed. These results are not readily explained by risk-sensitive foraging theory, but may be explained by the algorithm used by the birds to attribute value to average expected rewards.

Environmental variance is well known to affect the foraging decisions made by animals. One manifestation of this is that two food sources with the same average long-term rate of gain but different variances in rate of gain are seldom treated as having equivalent value (for reviews see Barkan 1986; Real & Caraco 1986; Stephens & Krebs 1986; Gibbon et al. 1988; Bateson 1993). The dominant evolutionary framework for explaining why such preferences have evolved is risk-sensitive foraging theory. This comprises a number of different models capable of explaining sensitivity to variance all of which rely on the assumption that there is a non-linear relationship between rate of food intake and fitness (for a review see McNamara & Houston 1992). However, despite the fact that risk-sensitive foraging theory is one of the most sophisticated areas of modelling in behavioural ecology, and has prompted many experiments, supporting evidence for the theory remains scarce.

The daily energy budget rule is the most intuitively appealing, and as a consequence, the most often tested prediction to emerge from risk-sensitive foraging theory. This rule says that an animal choosing between food sources yielding equal average rates of gain should be risk-averse, that is prefer a low variance option, when this yields a rate of gain high enough for it to survive the night, but be risk-prone, that is prefer a high variance option, when the low variance option does not meet this requirement (Stephens 1981). Theoretically, the energy budget rule applies whether the variability is in the amount of food or in the time delay to obtain it (McNamara & Houston 1992; Zabludoff et al. 1988), but whereas a few experiments have found support for the energy budget predictions when variability is in amount of food (for the most convincing demonstration see Caraco et al. 1990), no experiment has succeeded in showing the predicted shift in preference when variability is in delay to food or in effort required per food item (for attempts see Ha et al. 1990; Ha 1991; Case et al. 1995). One possible explanation for these failures is that the experiments have tested the wrong model

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(e.g. Houston 1991), since risk-sensitive foraging theory does not constitute a single model, and not all of the available models predict a switch in preference with energy budget (McNamara & Houston 1992). While this criticism is certainly valid, it may be difficult to choose an appropriate risk-sensitive foraging model a priori since this involves having precise knowledge of the subject's biology, and moreover of whether, and if so how, this will be influenced by the artificial conditions necessary for well-controlled choice experiments.

Here we address the problem that different models make different predictions regarding the effects of energy budget, by testing a prediction of risk-sensitive foraging theory that we believe arises from all of the models so far produced. Risk-sensitive foraging theory is based on the assumption that if an animal makes a risk-prone choice it chooses an option where the outcome is not only variable from choice to choice, but also unpredictable or 'risky'. The unpredictability is crucial because the logic of the risk-sensitive foraging explanation for such a choice depends on the possibility of a run of good or back luck occurring when the high variance option is chosen. Thus, a risk-sensitive forager should be risk-prone or risk-averse only if the high variance option is also risky in its outcome; an option in which the outcome is variable in the short-term but predictable in the longer term should be treated as equivalent in value to a fixed option yielding the same mean. The experiment we present in this paper is designed to test this prediction.

We chose to examine starlings' preferences for food sources yielding either fixed or variable delays to food. In common with previous risk-sensitive foraging experiments we presented the subjects with a choice of two options, one in which the delay to food was fixed and another in which it was variable. However, rather than a choice yielding a single food item, each choice committed the subject to a chain of six delayed food items. This allowed us to create variable food sources with or without predictability. In all cases choosing the fixed option resulted in a chain of six delays with the same length within any trial, while choosing the variable option resulted in a chain of six delays, each of which could take one of two lengths (short or long). There were two experimental groups that differed in the predictability of the variable option. In the risk-free group the sequence of short and long delays in the variable option was predictable both in the order of delays and the number of short and long delays, whereas in the risky group the sequence in the variable option was unpredictable both in the order and in the number of short and long delays. The mean of the sum of the six delays in the variable option was equal in the predictable and the unpredictable groups. Since risk-sensitive foraging depends on uncertainty of outcomes, from a functional point of view the variable but risk-free option is equivalent to a fixed option, whereas the option offering a variable and risky outcome has different properties subject to the usual reasoning of risk-sensitive foraging. Thus, if the birds can learn about predictability in addition to learning about variability, then risk-sensitive foraging theory predicts that risk-sensitive preferences should be seen in the risky group but not the risk-free group. Also, if energy budget affects preference, it should do so in the riskly group but not in the risk-free group.

To assess the relative and absolute value of risk-free variable and risky variable food sources, we used a titration procedure in which the length of the delays in the fixed option (τ) was altered until the subjects showed no preference for either the fixed or variable option. When the two options are chosen equally often we refer to the length of τ as the 'indifference point'. Having this quantitative measure of preference allows us to discriminate alternative hypotheses concerning the explanation for the birds' preferences. Table I shows the indifference points predicted by risk-sensitive foraging theory and various alternatives which are explained later. In this experiment an indifference point above the arithmetic mean of the short and long delays corresponds to risk-aversion, whereas an indifference point below the arithmetic mean corresponds to risk-proneness.

METHODS

Subjects

The subjects were 12 wild-caught European starlings, *Sturnus vulgaris*, six males and six females, housed individually in cages measuring 120 × 50 × 60 cm arranged such that they were visually but not acoustically isolated. Temperature in the laboratory ranged between 13 and 15°C, and the lights were on between 0500

Table I. Indifference points (τ) predicted by the different theories and algorithms under consideration

Theory/algorithm	Risk-free group	Risky group
Risk-sensitive foraging theory	10.50 s (i.e. the arithmetic mean of 3 and 18 s)	Negative budget: <10.50 s Positive budget: >10.50 s (if energy budget rule applies)
Long-term rate (equation 2: n large, $f=n$)	10.50 s	10.50 s
EoR (equation 2: n large, $f=1$)	5.14 s (i.e. the harmonic mean of 3 and 18 s)*	5.14 s*
Equation 2: n large, $f=6$	10.50*	9.84*
Parallel discounting	5.06 s*	4.50 s*

An effect of energy budget is predicted only in the top right-hand cell of the table. See Discussion for a description of equation 2, f and n.

*These indifference points are computed taking only the programmed delays to reinforcement into account. The inter-trial interval, latency to choose and the pauses between reinforcement and the start of the next delay are not included in the calculations since previous experiments suggest that the birds may not be sensitive to these intervals (Bateson & Kacelnik 1995a, 1996).

and 1800 hours. The birds were food-deprived from 1600 hours until the start of each session at 0600 hours the following morning. During the experimental sessions the birds were rewarded with turkey starter crumbs, and in the period between the end of the session and 1600 hours the birds were given four mealworms and ad libitum turkey crumbs. The body weights of the birds remained stable over the course of the experiment. After the experiments had been completed the birds were retained for future research.

Apparatus

Each cage had an operant panel in the centre of the back wall with two response keys (3.5 cm in diameter), 6 cm on either side of a central food hopper. Coloured lights (red and green) on the pecking keys were used as the discriminative stimuli indicating the fixed and variable options. The assignment of colours to options was balanced across birds and treatment groups. Thus, for a given bird, one colour was always associated with the fixed option and the other with the variable option. The food hopper was connected to a pellet dispenser (Campden Instruments, Loughborough, U.K.) filled with turkey crumbs sieved to an even size. One unit of food averaged 0.012 g of turkey crumbs and took 1 s to deliver. An Acorn Archimedes microcomputer running Arachnid experimental control language (Paul Fray Ltd, Cambridge, U.K.) controlled the stimulus events and response contingencies and also recorded the data. The birds were already familiar with the apparatus and had previously been trained to peck at illuminated keys to obtain food using an autoshaping procedure (Bateson & Kacelnik 1995a); however, they had not been exposed to red and green lights as discriminative stimuli prior to this experiment.

Schedules

We divided the birds into two treatment groups, each consisting of three birds of each sex, which we shall refer to as the 'risk-free' and the 'risky' group. Each bird served in only one of these groups. In each of these groups the birds had two foraging options: the 'variable option' and the 'fixed option'. For both options a single trial consisted of a chain of six delayed reinforcements where each reinforcement was a single unit of turkey crumbs (in the final phase of the experiment reinforcements were doubled in size to two units of crumbs). In the fixed option the six delays to reinforcement were of identical length within any one trial but varied in length during the course of the experiment (as explained below). In the variable option each of the six delays to reinforcement was either 3 s (short) or 18 s (long) in length with the order being determined by the treatment group. In the variable option of the risk-free group the six delays alternated in length with the first always being short, that is the sequence was: 3, 18, 3, 18, 3, 18. In the variable option of the risky group the first delay in the chain was always short, a randomly chosen one of the other five delays was always long, and each

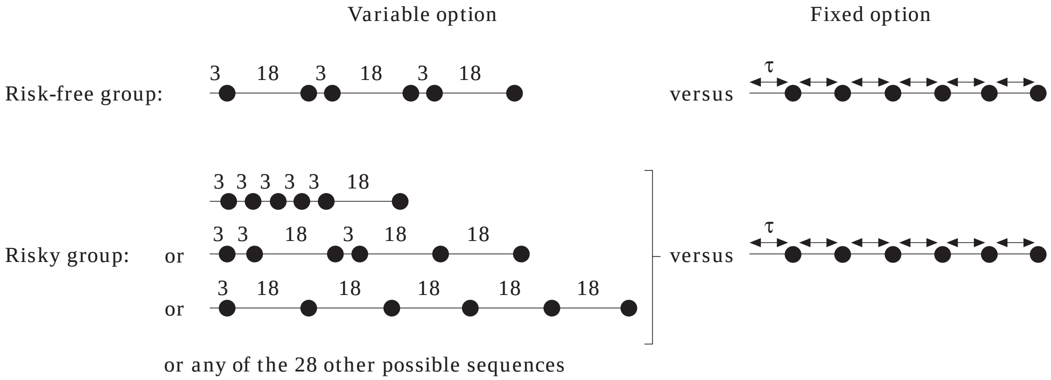

Figure 1. Schematic representation of the sequence of delays to receive reinforcement in the two options of each treatment. The arrows show the delay that was adjusted, τ, in the titration phases of the experiment. Note that only three of the 31 possible sequences are shown for the variable option in the risky group.

Table II. Statistics on the foraging options available

	Variable option		Fixed option
	Risk-free group	Risky group	Both groups
Expected reward (units)	6	6	6
Variance in reward (units^2)	0	0	0
Expected total delay (s)	63	63	6τ
Variance in total delay (s^2)	0	225	0
Range of possible delays (s)	0	60 (33–93)	0

Each group chose between a variable and a fixed option, and τ was the adjusting dependent variable used to compare the value of the variable options between the two groups.

of the remaining four delays was randomly assigned to be either short or long with equal probability. Thus 31 different (not equally probable) sequences of short and long delays were possible. Figure 1 shows the options presented to the birds and Table II shows the summary statistics of the different options in the risk-free and risky treatments.

We used a discrete-trials procedure with a fixed inter-trial interval of 40 s. There were two types of trials, ‘forced’ trials and ‘choice’ trials. The forced trials allowed the birds to experience the two options and showed the extent to which they had learned their characteristics. The choice trials tested the birds’ preferences. A forced trial began with one of the key lights flashing (on for 0.7 s and off for 0.3 s). When the bird pecked the key the light changed from flashing to being continuously illuminated, and a delay to receive the first reinforcement in the chain began to elapse. The first peck after the first programmed delay had elapsed extinguished the key light and caused the delivery of one unit of food to the hopper. Next followed a 6-s pause for the bird to consume the food after which the same key light re-illuminated and the second delay of the sequence began to elapse. The first peck after the second delay had elapsed extinguished the key light and caused delivery of food to the hopper. The sequence of events from the beginning of the 6-s pause was repeated four more times. After the sixth reinforcement of the chain the inter-trial interval began. Choice trials were identical to the forced trials with the exception that a choice trial began with both keys flashing (on for 0.7 s and off for 0.3 s), one in each colour, and as soon as the bird pecked one of the keys this was illuminated continuously and the other was extinguished. Thus a bird chose one of the options with its first peck. Trials were arranged in blocks of three consisting of two forced trials, one of each option with both the order and the sides of presentation being randomly chosen in each block, followed by one choice trial, in which the sides of presentation of the two options were again randomly chosen in each block. This sequence of trials ensured that the birds had equal experience with each option before having to choose between them. This pattern of blocks of three trials was maintained throughout the experiment. Each session consisted of 30 blocks (i.e. 90 trials) with two 30-min breaks following blocks 10 and 20, respectively, to reduce the effects of satiation. The birds were given one session per day. Sessions were run daily without breaks either within or between the different phases of the experiment.

Experiment

During the first phase of the experiment the value τ was fixed at 18 s. The birds were trained in this condition for a minimum of 15 sessions (some had up to 22). This training had two goals: first, to confirm that the birds had a preference for the variable option under conditions where such a preference is predicted by all of the theories under consideration in order to validate the use of red and green lights as discriminative stimuli for the two options, and second, to allow the birds to learn the sequences of delays associated with the variable options before titration commenced.

In the second phase, the value of τ started at 18 s, but was subsequently changed after each choice trial according to the following rule. If the bird chose the variable option then τ was decreased by 1 s, whereas if a bird chose the fixed option the value of τ was increased by 1 s. The value of τ could not drop below zero seconds, but had no upper limit. Therefore while the delay in the 'fixed' option was fixed within any trial it could adjust between trials in this phase of the experiment. Each new session began with τ set at the value at which it finished in the previous session. This titration was continued for 10 sessions after which the mean value of τ in the last nine sessions was calculated for each bird. We have previously confirmed that a similar titration procedure produces valid indifference points in starlings (Bateson & Kacelnik 1995b, 1996).

In the third phase τ was fixed at the average value calculated from the previous phase (rounded to the nearest second) and thenceforth was altered at the end of each session only if either of the following criteria was satisfied. If the bird had chosen the variable option significantly (two-tailed binomial test, $P<0.05$) more often than the fixed option in that session (=30 choices) then τ was decreased by 1 s, whereas if a bird had chosen the fixed option significantly more often than the variable option then τ was increased by 1 s. Again, the value of τ could not drop below zero seconds, but had no upper limit. The rationale of this phase was to examine whether the indifference points obtained in the previous phase would be maintained when the value of τ was stable for an entire session. This is an important check, since the indifference points obtained in the previous phase could be affected by the between-trial variation in the value of τ introduced by the titration procedure. This phase of the experiment was continued for 10 sessions.

The fourth phase was a continuation of the previous phase with the exception that the number of units of food delivered at each reinforcement was increased from one to two in all options. This change was estimated to result in the birds being switched from negative to positive energy budgets (see Results for calculations). This phase of the experiment ran for a further 10 sessions.

Data Collection and Analysis

Throughout the experiments we collected the following data. In the forced trials the number of pecks made during each second of each of the six delays was recorded. This gave information on what the birds had learnt about the predictability of the time of occurrence of the rewards. In the choice trials the choice made was recorded to give some indication of current preference between the two options. During phases 2–4 the current value of τ was recorded as a quantitative measure of the value a bird attributed to the variable option. The final indifference points in the risk-free and risky groups were estimated from the values of τ in phases 3 and 4. All of the P-values reported for Wilcoxon and Mann–Whitney tests are two-tailed.

RESULTS

Energy Budgets

In phases 1, 2 and 3 the birds received 6.48 g of turkey crumbs per session (0.012 g × 6 rewards per trial × 90 trials). Given that the birds finished each session in a mean of 6.5 h this equates to a mean hourly intake rate of 0.997 g/h. Assuming a daily requirement of approximately 18 g of turkey crumbs (unpublished data), the required hourly intake rate during the 13 h of light in our experiment is 1.38 g/h. Therefore during an experimental session the birds would on average be subject to a negative energy budget. When the reward was increased to two units of turkey crumbs in phase 4 the amount received per session doubled to 12.96 g and the mean session length increased to 8.5 h giving a mean hourly intake rate of 1.52 g/h. Therefore in this phase of the experiment the birds were on average subject to a positive energy budget.

Phase 1: Learning

By the end of training, before the titration commenced the birds strongly preferred the variable option. In the 30 choice trials of the last session of this phase the proportion of choices for the variable option was 0.98 ± 0.022 ($\bar{X} \pm$ SEM) for the risk-free group and 0.96 ± 0.021 for the risky group. This shows that the birds had learnt that on average rewards in the variable option could arrive sooner than in the fixed option. There was no significant difference in the level of preference seen in the two groups (Mann–Whitney test: $U=43.5$, $N_1=6$, $N_2=6$, $P=0.44$).

Figure 2 shows the mean patterns of pecking in the 60 forced trials of this same session. In the fixed option all birds showed their highest rate of pecking in the 18th 1-s time bin consistent with the fact that the first peck after 18 s was always followed by food in this option. The patterns of pecking in the variable option were different for the risk-free and risky groups. In the risky group the birds showed a peak of pecking at 3 s, then if food was not delivered, as is the case when the delay was 18 s, the birds slowed their pecking rate and showed another peak at 18 s when food occurred with certainty. This pattern is seen in all of the delays of the sequence, except the first when food was always delivered after 3 s. In the risk-free group the patterns of pecking seen in the first, third and fifth delays are different from those seen in the second, fourth and sixth delays. In odd-numbered delays food occurred after 3 s, as reflected in the peak of pecking at this time, whereas in the even-numbered delays food occurred after 18 s, and the pecking patterns are similar to those seen in the fixed option.

To quantify the extent to which each of the birds in the risk-free group had learnt the predictability of the sequence of delays the following index was devised:

$$\text{predictability}=(S_3-L_3)/(S_3-F_3) \qquad (1)$$

where S_3, L_3 and F_3 correspond to the mean number of pecks in the third 1-s bin of the 3-s delay in the variable option, of the 18-s delay in the variable option and of the fixed option, respectively (Fig. 3). When a subject has not learnt about the predictability, as is the case for the risky group where there is none to learn, S_3 and L_3 will be equal and the index will therefore be equal to zero. However, if a bird has learnt the predictability perfectly L_3 will approach F_3 and the index will therefore be close to one. We calculated the index for each bird using the data from the second to the sixth delays of all the forced trials in the last session of training. The predictability index was 0.77 ± 0.046 ($\bar{X} \pm$ SEM) for the risk-free group and 0.031 ± 0.021 for the risky group. The indices for the risk-free group are significantly larger than those for the risky group (Mann–Whitney test: $U=57$, $N_1=6$, $N_2=6$, $P=0.0051$).

Phase 2: Titration

If the choices made by the birds are unaffected by the value of τ then a random walk should be observed in the titrations. Given that all of the birds started the titration with τ equal to 18 s, the mean indifference point expected from random behaviour is 18 s. However, in the first session of titration the value of τ fell for all birds and thereafter settled into a pattern of stable fluctuation around a mean value below 18 s (see Table III for statistics). In the final nine sessions of this phase none of the birds had a significant preference for either option (normal approximation to the binomial distribution with $N=270$, $P>0.05$ for all birds). Indifference points for each bird were calculated as the mean value of τ in the

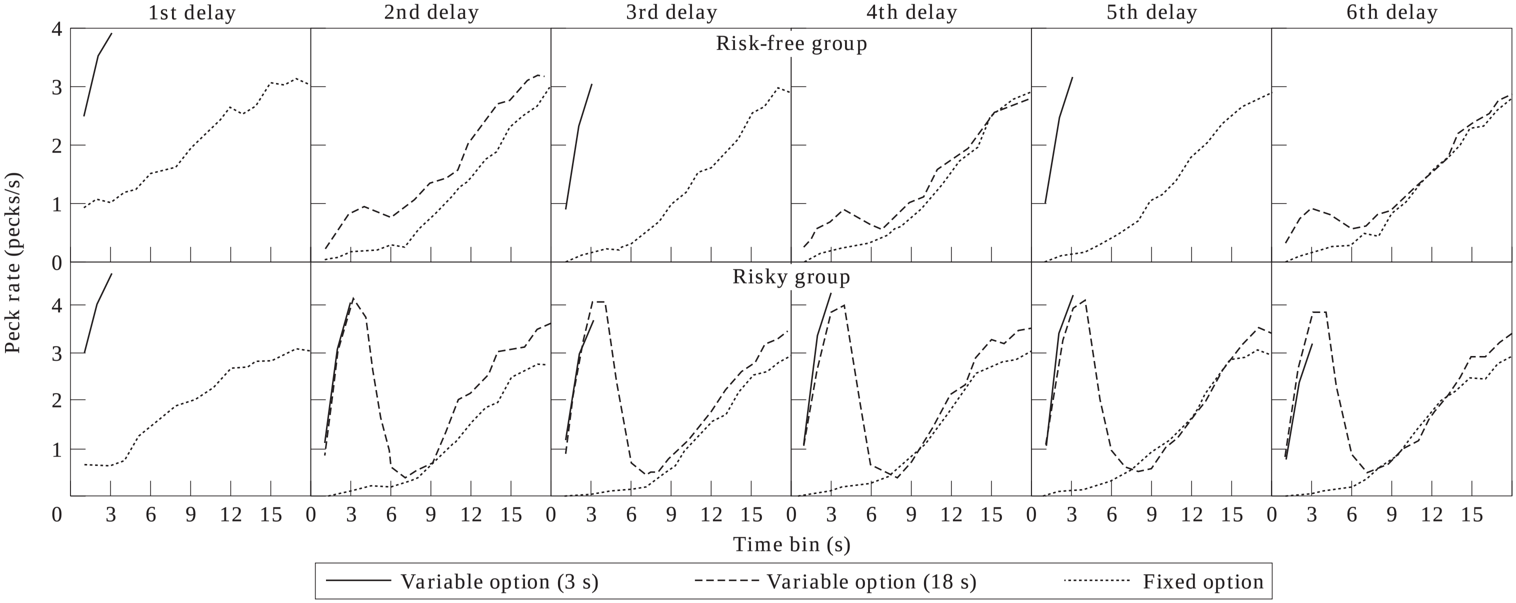

Figure 2. Mean peck rates for the risk-free (upper sequence) and risky (lower sequence) groups. Data are from the forced trials of the last session of training. See text for details.

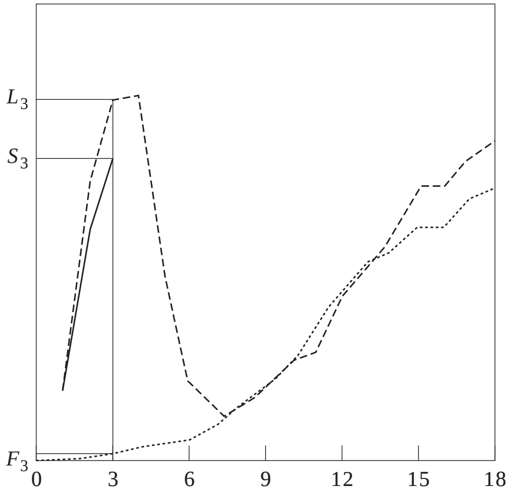

Figure 3. Pecking rates from the risky option showing the values of S_3, L_3 and F_3, where S_3, L_3 and F_3 correspond to the mean number of pecks in the third 1-s bin of the 3-s delay in the variable option, of the 18-s delay in the variable option and of the fixed option, respectively. In this example the predictability index is low. Key as for Fig. 2.

last nine sessions of this phase (see Table III). All the birds were risk-prone, that is τ was less than 10.5, with the exception of bird 7. Rounded to the nearest second the mean values of τ provided the starting values of τ in the next phase.

Phase 3: Indifference Points under Negative Budgets

To investigate whether the values of τ showed any change during this phase we computed the slope of the regression of τ on session number for each bird and tested the six slopes in each experimental group against an estimated median of zero. Since there was no systematic trend in the value of τ (Wilcoxon one-sample tests: risk-free group, $T=3.0$, $N=4$, $P=0.584$ and risky group, $T=1.0$, $N=5$, $P=0.106$; the values of N are less than 6 because some slopes were 0), we used the mean of the values taken by τ in all 10 sessions as our estimate of the indifference point for each bird in this phase. The indifference points obtained did not differ significantly from those obtained in the previous phase (Wilcoxon paired-sample test: $T=25.0$, $N=12$, $P=0.290$), and they were significantly higher in the risk-free group than in the risky group (Mann–Whitney test: $U=54.5$, $N_1=6$, $N_2=6$, $P=0.0161$). Thus on average the birds were risk-prone with the birds in the risky group being significantly more risk-prone than the birds in the risk-free group. We then compared the indifference points with the predictions given in Table I. All statistics reported are from one-sample Wilcoxon tests against a median equal to the value under test. In all cases $N=6$. In the risk-free group the indifference points were significantly different from 10.50 s ($T=1.0$, $P=0.059$), 5.14 s ($T=0.0$,

Table III. Statistics describing the value of τ in phase 2 of the titrations

Group	Bird	Mean (s)	Median (s)	SD (s)	Period*
Risk-free	0	4.59	5	3.18	10.38
Risk-free	1	7.63	8	3.00	6.67
Risk-free	2	7.49	8	2.56	5.51
Risk-free	6	8.76	9	3.57	8.43
Risk-free	7	12.66	12	3.83	11.68
Risk-free	8	7.05	7	3.29	7.71
Risky	3	6.28	6	3.32	8.44
Risky	4	4.94	5	2.57	9.64
Risky	5	6.40	6	2.62	6.59
Risky	9	6.56	7	2.81	8.71
Risky	10	1.93	1	1.84	4.29
Risky	11	6.59	6	2.66	6.00

The data used are from the final nine sessions of phase 2 (i.e. $N=270$ for each bird).

*The ‘period’ is defined as the total number of choices (=270) divided by the number of choices for which τ is equal to the median value of τ for that bird.

†A value of τ below 10.5 indicates risk-proneness and a value above 10.5 risk-aversion.

$P = 0.036$) and 5.06 s ($T = 0.0$, $P = 0.036$), although this difference was only borderline in significance in the first case, whereas in the risky group the indifference points were significantly different from 10.50 s and 9.84 s ($T = 0.0$, $P = 0.036$ in both cases) but not from 5.14 s ($T = 11.0$, $P = 1.00$) or 4.50 s ($T = 7.0$, $P = 0.529$).

To examine whether any of the variance between subjects in the indifference points in the risk-free group was attributable to the extent to which the individual birds had learnt the predictability of the variable option, we computed predictability indices for the birds in the risk-free group in this phase of the experiment. However, since the delay in the fixed option was not set at 18 s as before, the pecking in this option could not be used as a baseline for F_3. In equation 1 F_3 was therefore given the value of zero making the index to be computed $(S_3 - L_3)/(S_3)$. As before, an index of 0 indicates that the bird had not learnt the predictability, and an index of 1 that it had learnt it perfectly. For each of the six birds an index was computed for each of the 10 sessions and the values obtained averaged to obtain a single index for each bird. A regression of the indifference points on these average predictability indices shows no evidence for any positive correlation ($F_{1,4} = 0.24$, $P = 0.653$).

Phase 4: Indifference Points under Positive Energy Budgets

Again we computed the slope of the regression of τ on session number for each bird and tested the six slopes in each experimental group against an estimated median of zero. Since there was no systematic trend in the value of τ (Wilcoxon one-sample tests: risk-free group, $T = 10.0$, $N = 6$, $P = 1.000$ and risky group, $T = 0.0$, $N = 4$, $P = 0.100$), we used the mean of the values taken by τ in all 10 sessions as our estimate of the indifference point for each bird in this phase. No significant difference was found between the indifference points obtained in phases 3 and 4 when all 12 birds were analysed together (Wilcoxon paired-sample test: $T = 20.0$, $N = 12$, $P = 0.147$). The result was the same when the risk-free and risky groups were analysed separately (Wilcoxon paired-sample tests: both with $N = 6$, risk-free group, $T = 7.0$, $P = 0.529$ and risky group, $T = 2.0$, $P = 0.093$). In both groups the variance in the indifference points is greater in phase 4 than phase 3 (see inter-quartile ranges in Fig. 4) resulting in reduced statistical power in the following tests. The indifference points were now not statistically different between the risk-free and risky groups (Mann–Whitney test: $U = 50.0$, $N_1 = 6$, $N_2 = 6$, $P = 0.0927$). Comparing the observed indifference points against the predictions in Table I using the same methods as for phase 3, the values in the risk-free group were not significantly different from 10.50 s ($T = 3.0$, $P = 0.142$), 5.14 s ($T = 2.0$, $P = 0.093$) or 5.06 s ($T = 1.5$, $P = 0.075$), whereas in the risky group the values were significantly different from 10.50 s and 9.84 s ($T = 0.0$, $P = 0.036$ in both cases) but not from 5.14 s ($T = 8.0$, $P = 0.675$) or 4.50 s ($T = 10.5$, $P = 1.00$). Figure 4 shows the indifference points from the last two phases of the experiment and Table IV shows the results of our comparisons with the various predictions.

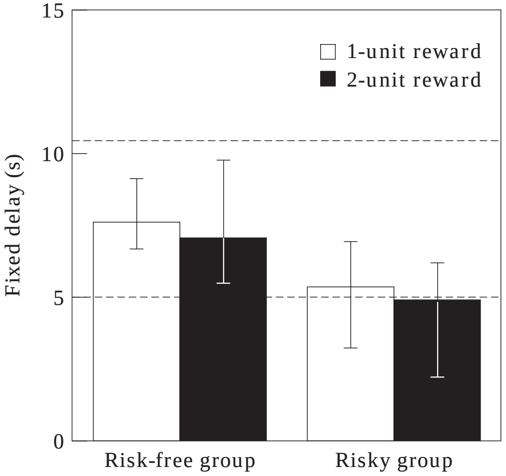

Figure 4. Indifference points in the two treatments. Data are the median indifference points from phases 3 and 4. Error bars show the inter-quartile ranges. Each bar is based on values from six birds. The dotted lines show the arithmetic mean of 3 and 18 s at 10.50 s and the harmonic mean at 5.14 s.

DISCUSSION

Our aim in this experiment was to ascertain whether the unpredictability of the variable food source is important in determining preferences between fixed and variable food sources. We compared the preference of starlings choosing between fixed and variable options where the

Table IV. Summary of how the observed indifference points compare with the predictions in Table I

	Negative budgets (phase 3)		Positive budgets (phase 4)	
	Risk-free group	Risky group	Risk-free group	Risky group
Risk-sensitive foraging theory (energy budget rule)	†	NS	NS	*
Long-term rate	†	*	NS	*
EoR	*	NS	†	NS
Equation 2: *n* large and $f=6$	†	*	NS	*
Parallel discounting	*	NS	†	NS

NS ($P \geqslant 0.1$) indicates that the results support the prediction.
†$P<0.1$; *$P<0.05$.

variable option was either predictable (risk-free) or unpredictable (risky) in the total time taken to deliver six food rewards. According to a strict interpretation of risk-sensitive foraging theory, preferences for one or the other option should be observed only in the risky treatment where the variability also involves unpredictability. The data did not provide strong support for this prediction, since both the risky and risk-free groups were significantly risk-prone on negative energy budgets, and a similar trend was observed when the birds were switched to positive budgets, although some support for the prediction was provided under the negative budget condition where the risky group was significantly more risk-prone than the risk-free group. Counter to the predictions of a number of risk-sensitive foraging models there was also no effect of energy budget on preference in either the risky or risk-free groups. The reduction in the significance of the preferences when the birds were switched from negative to positive budgets is due to increased individual variation in this phase of the experiment probably brought about by the birds being less hungry and therefore less motivated to discriminate the options.

A justified objection to falsifications of evolutionarily based theories using laboratory data on behaviour is that the subjects may be insensitive to the experimental manipulations performed. We shall discuss whether this objection applies to our data, dealing first with the manipulation of energy budget and second with the manipulation of the riskiness of the variable option.

Despite our claim that we switched the birds from negative to positive budgets, it is possible that the birds did not experience a change in energy budget. Our calculations were based on the rate of intake during the experimental sessions. However, it could be argued that the birds were able to learn that they received ad libitum food at the end of each daily session, and that as a consequence their daily budgets were always positive. Against this criticism, other studies using open economy designs similar to ours (e.g. Caraco et al. 1990) have generated switches in preference by manipulating budget within experimental sessions. Even if we accept that the birds did experience a change in energy budget, our result that the change had no effect on preference does not allow us to reject risk-sensitive foraging theory since energy budget effects are not predicted by all of the models or under all sets of parameter values.

The pecking patterns show that the birds learnt when rewards were due. They convincingly show that within a chain of rewards the birds were uncertain of the delay to the next food item only in the variable option of the risky group, and in all other cases there was no unpredictability. However, this does not demonstrate that the birds knew the expected length of an entire chain, since it is possible that they never learnt that each chain consisted of six delayed rewards. This is an important point, since our predictions from risk-sensitive foraging theory arise from the difference between the risky and risk-free group in the variance in the total duration of a chain. While we have no direct evidence for this, we have two pieces of data that relate to the aspects of the variable option that influenced choice. First, the indifference points were longer than the value of the short delay with which both variable options always began. Second, on negative budgets the indifference points were significantly different in the risky and risk-free groups. These two results show that the birds' preferences at the point of choice were influenced by the structure of the variable option beyond just the first delay of the chain. Later we present a more detailed discussion of this point, but here we elaborate further on the possible effect of incomplete learning of the schedule characteristics.

We claim to have shown that unpredictability per se is not the only cause of preferences for variable over fixed food sources, since risk-free variability produced preferences by itself. The role of predictable variability could be questioned by arguing that lack of indifference in the risk-free group is due to the birds having learnt the predictability imperfectly. In this situation, then as with our data, a risk-sensitive forager would not be indifferent between the fixed and variable options in the risk-free group because the risk-free variable option is still perceived as somewhat risky. If this is the case then we might expect a positive correlation between the predictability index and the indifference point obtained across the birds in the risk-free group. However, despite considerable variation in the predictability index no such relationship was observed.

This experiment does not justify a rejection of risk-sensitive foraging as an explanation for the evolutionary causes of preferences for variability in delay because natural selection might have driven the evolution of a mechanism for measuring the riskiness of foraging sources by measuring their variance. Such a mechanism would be functionally indistinguishable from a mechanism that detected true unpredictability in a world in which all variable food sources were also risky. In such a world natural selection would be blind to the possible advantages of a true risk detection mechanism over a variance detection mechanism. Unfortunately not all possibilities can be examined because although it is possible to look at variance without risk, it is not possible to devise situations with risk but no variance. What our experiment demonstrates is that at a mechanistic level preference for variability in delay does not require uncertainty and does not follow changes in budget as expected from risk-sensitive foraging. Since ours is the first report in which variance and uncertainty are experimentally distinguished, the strength of previous evidence for risk-sensitive foraging needs to be questioned. A logical sequitur of weakening the available functional interpretations of preference is to seek alternatives. We devote the remainder of this discussion to this search.

We shall concentrate on whether any particular algorithm for rate-maximizing can explain our data, since the use of specific rate-computing algorithms has previously been suggested as an alternative explanation for the effects of variability on foraging decisions (Real et al. 1990; Real 1991; Bateson & Kacelnik 1995a, 1996). One major difference between these theories and risk-sensitive foraging is that rate-computing algorithms do not predict any effects of energy budget. However, since we found no evidence of a budget effect, there is no a priori reason to reject this kind of explanation.

Consider a predator that obtains prey from a single food source. Each prey may have a different energy content and take different time to find and consume. Given that a forager remembers having acquired n prey items each with associated energetic content (G) and foraging time (T) there are a range of ways in which it can compute its rate of intake. Many of these alternatives are particular cases of the following equation (Bateson & Kacelnik 1996; Bateson & Whitehead 1996):

$$\text{Rate} = \frac{\sum_{j=1}^{n/f} \left(\frac{\sum_{i=1}^{f} G_i}{\sum_{i=1}^{f} T_i} \right)}{n/f} \tag{2}$$

where G_i is the energy gained from the ith food item, T_i is the time taken to acquire this item, n is the number of events remembered and f is the frame ($f \leq n$) over which the forager computes the rate. When n is large and $f=n$ this converges on the true long-term rate of energy gain in the environment, which is the rate currency assumed in the majority of classical optimal foraging models (for examples see Stephens & Krebs 1986). This currency is not sensitive to variance in either G or T, and thus predicts no preferences in either of the treatment groups in our experiment (i.e. at indifference the value of τ in the fixed option should be the arithmetic mean of 3 and 18 s: see Table I). Therefore this algorithm is incompatible with our data (Table IV) in agreement with previous failures of long-term rate as the currency

	Trial 1						Trial 2					
Item	1	2	3	4	5	6	1	2	3	4	5	6
G (units)	1	1	1	1	1	1	1	1	1	1	1	1
T (s)	3	18	3	18	18	3	3	3	18	3	3	3

Algorithm													Mean rate
$f=n=12$	$\frac{1+1+1+1+1+1+1+1+1+1+1+1}{3+18+3+18+18+3+3+3+18+3+3+3}=\frac{12}{96}$												= 0.125
$f=6$, $n=12$	$\frac{1+1+1+1+1+1}{3+18+3+18+18+3}=\frac{6}{63}$						$\frac{1+1+1+1+1+1}{3+3+18+3+3+3}=\frac{6}{33}$						= 0.139
$f=1$, $n=12$	$\frac{1}{3}$	$\frac{1}{18}$	$\frac{1}{3}$	$\frac{1}{18}$	$\frac{1}{18}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{18}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	= 0.241
Parallel discounting	$\frac{1}{3}+\frac{1}{3+18}+\frac{1}{3+18+3}+\frac{1}{3+18+3+18}+\frac{1}{3+18+3+18+18}+\frac{1}{3+18+3+18+18+3}$						$\frac{1}{3}+\frac{1}{3+3}+\frac{1}{3+3+18}+\frac{1}{3+3+18+3}+\frac{1}{3+3+18+3+3}+\frac{1}{3+3+18+3+3+3}$						= 0.562

Figure 5. An example illustrating how the four different algorithms we have considered would value the risky variable option on the basis of the experience of the two example trials given at the top of the figure.

maximized by foraging starlings (Bateson & Kacelnik 1995a, 1996). Long-term rate was supported by some experimental evidence but only in cases when, owing to lack of any variance in T, equation 2 did not differentiate between currencies with alternative values of f (e.g. Kacelnik 1984).

An alternative rate currency for combining G and T supported by work on starlings (Bateson & Kacelnik 1996) and bumblebees (Real et al. 1990; Real 1991) is the expected ratio of G over T, or EoR (for Expectation of Ratios). EoR appeared in the foraging literature in the context of the ‘fallacy of the averages’ controversy, and amounts to computing the ratio G/T each time a prey item is encountered and then averaging these ratios (see Fig. 5). Equation 2 converges on the true EoR for the environment when n is large and $f=1$. Unlike long-term rate this currency is sensitive to variance in T and predicts that a fixed and a variable food source will be subjectively equivalent in rate when the long-term rate of the fixed option is higher than that in the variable option, that is, preference will show the same bias as risk-prone behaviour. This algorithm is not sensitive to the order of the food items and gives the same rates in the variable option of both the risk-free and risky treatment groups of our experiment (the predicted indifference point is at the harmonic mean of 3 and 18 s: see Table I). Therefore, while maximization of this currency predicts the preference for variability that we find (Table IV), it cannot explain why the birds in the risky group had significantly stronger preferences than the birds in the risk-free group.

A third potential rate algorithm is suggested by the structuring of the trials in this experiment. It is possible that the birds computed the long-term rate for each trial (six prey items), but then averaged the rates experienced across trials to arrive at an estimate of rate for the option (see Fig. 5). Equation 2 describes this algorithm when n is large, $f=6$ and the beginning of each frame corresponds to the beginning of each successive trial. This rate algorithm predicts indifference in the risk-free group, but a slight preference for the variable option is the risky group (see Table I). Therefore while this currency predicts the difference we observed between the two treatment groups it does not accurately predict the level of preference in either group (Table IV).

The final algorithm we consider is not described by equation 2 and was named parallel hyperbolic discounting by Brunner & Gibbon (1995). This currency most accurately described rats' choices for different sequences of food items when compared with other forms of hyperbolic discounting and long-term rate maximization (Brunner & Gibbon 1995). The cumulative reward experienced in a single trial is computed by summing the *G/T* for each item of the sequence, timing the delays from the point of choice at the beginning of the trial rather than timing each delay from the delivery of the previous food item. For example, the value of one trial of the risk-free variable option is computed as:

$$\text{Value} = \frac{1}{3} + \frac{1}{3+18} + \frac{1}{3+18+3} + \frac{1}{3+18+3+18} + \frac{1}{3+18+3+18+3} + \frac{1}{3+18+3+18+3+18}$$

The value for an option is then estimated by averaging the estimates obtained from each trial of the option (for further clarification see Fig. 5). This has the effect of making the value of an option sensitive both to variance in T and to the order of delays experienced, since, owing to their larger T, food items later in the sequence add progressively less value. This algorithm is not exactly an estimate of rate but an index of value of the expected cumulative reward in a full trial, which could be used to establish preference. In our experiment parallel discounting predicts a strong preference for the variable option in both treatment groups with the risky group having a stronger preference than the risk-free group (the indifference points are both close to the harmonic mean of 3 and 18 s and are shown in Table I). The difference between the treatment groups arises because in the risk-free variable option the second delay of a trial is always long, whereas in the risky variable option the second delay is short on 50% of trials resulting in this option having a higher value. The above predictions are qualitatively similar to what we observed, the main discrepancy being in the risk-free group where the indifference point is significantly higher than predicted (Table IV). The parallel discounting algorithm predicts preference for the variable option because in both the risky and risk-free variable groups the variable option began with a short, 3-s delay to reinforcement, and, as explained above, the first interval has a strong impact on value. If, alternatively, the variable options had been programmed to begin with a long 18-s delay the prediction of parallel discounting (but not of the other examples) should switch to preference for the fixed option. Thus parallel discounting could very easily be tested by beginning the variable options with a long rather than short delay. We should point out that other forms of parallel discounting, such as for example exponential discounting, would produce qualitatively similar predictions. We have not considered such models here since many other experiments have suggested that exponential discounting rarely provides an accurate description of choice data (for recent examples see Myerson & Green 1995; Green & Myerson, in press).

Parallel discounting may provide an accurate description of the starlings' behaviour; however, at present we do not make any claims as to why such an algorithm has evolved. Whereas both risk-sensitive foraging and long-term rate maximization have a clear evolutionary rationale, maximization of EoR and parallel discounting do not. A partial explanation is that parallel discounting may be a by-product of the mechanisms of associative learning that have evolved for the function of detecting causal relationships in the environment. In the context of some foraging decisions these learning mechanisms may act as constraints on animals' abilities to acquire and process the information that controls their choices (see Kacelnik & Bateson 1996 for a fuller explanation).

In conclusion, we have shown that risk-sensitive foraging does not provide an adequate picture of the proximate control of preferences for variability in delay to reward, and suggest that the explanation for animals' preferences for variable delays may well lie in the algorithm that they use to value average expected reward from foraging options.

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