Energy budgets and risk-sensitive foraging in starlings

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The effect of energy budget on risk-sensitive foraging was assessed in a laboratory experiment using starlings (Sturnus vulgaris). Subjects chose between two options offering the same mean amount of food per trial, but differing in variance: a “fixed” option gave 5 units food in every trial, and a “variable” option gave 2 or 11 units food with probabilities 2/3 and 1/3, respectively. We manipulated energy budgets by controlling the cumulative amount of food received by each bird at the end of a day. In one treatment (positive budget) individuals were allowed to eat at the level of their own ad-libitum daily consumption, while for the other (negative budget), food was rationed to provoke a steady drop in body weight during the experimental period. No subject was allowed to drop below 80% of its ad libitum body weight. Contrary to predictions from the “energy budget rule” and contrary to reported results of some other studies, starlings significantly preferred the “fixed” option irrespective of energy budget conditions. Our results support the view that persistent risk aversion for food amounts and risk proneness for food delays are the norm, and shifts in risk attitude according to energy budget are contrary to reported results of some other studies, starlings significantly preferred the “fixed” option irrespective of energy budget conditions. Several algorithms, which may have evolved to maximize energetic pay off between variable food sources, can produce this trend as a side effect. We discuss two of these algorithms: (1) maximization of local (per trial) rate as opposed to global rate of gains, with longer handling time for larger rewards, and (2) choosing larger rewards and smaller delays subject to Weber’s law in the memory for the parameters of each food supply.

Virtually all actions result in outcomes with a degree of stochasticity. As a consequence, biological decision systems are likely to have evolved under the influence of outcome variance. This is particularly prevalent in the case of foraging behavior because food sources typically have different statistics (mean and variance in prey size, intercapture interval, rate of predator attacks, etc.), so that choices between food sources are actions with stochastic outcomes. Living in a world offering statistically defined opportunities implies selection pressures on how to learn the statistics of the environment and how to use this knowledge in making choices. This last issue—namely, the choice between stochastic foraging sources differing in statistics which are known to the subject, is the target of risk sensitive foraging research and the topic of the experiment described here.

The most extensively developed theoretical framework in the functional analyses of risk is the collection of models jointly known as risk sensitive foraging theory (RSFT). The central tenet of RSFT is as follows: foraging success (rate of energy gain) results in fitness gains, but this relationship is unlikely to be linear. As a consequence, mean energetic gain from stochastic food sources is important, but not enough to rank their relative value; variances and skew also matter (Caraco and Chasin, 1984; McNamara and Houston, 1992). In a commonly considered scenario, a subject faces a single choice between two food sources that offer equal average gains but that differ in their variance. Fitness consequences are modeled as a step function resulting in death if the rate of energy gain resulting from the choice falls below a threshold and survival otherwise. The word “rate” here is used as the ratio of amount of energy gain divided by the time taken to gain it, so that prey sizes and temporal properties are both involved. This simplified scenario is encapsulated in the so-called budget rule (Stephens, 1981). Under this rule, if the average pay-off (common to both sources) is below the survival threshold, the least variable source will lead to lower fitness because it will have fewer chances of outcomes sufficiently above the mean to exceed the threshold and result in survival than the more variable alternative. The opposite will be true if the two sources have average payoffs above the survival threshold because the more variable source will have greater chances of yielding outcomes below the threshold. An animal is said to be in a positive budget if, on average, gains are above the survival threshold and on a negative budget if average gains are below that threshold. Hence, the prediction derived from the budget rule is that animals should be risk prone if they are on a negative budget and risk averse otherwise.

The budget rule poses both theoretical and experimental challenges because it is hard to determine when it should really apply. For instance, it is not obvious over which period the variance in outcome should be assessed. A simplified version of the theory refers to the outcome of a single choice, but single foraging choices rarely put animals below or above a threshold for survival. Indeed, it is virtually impossible to create this situation experimentally. Consequently, most experimental budget manipulations are based on a reasonable biological time period such as a 24-h cycle. If only one decision were to be considered, this ought to be a decision committing the animal for the full foraging day. This is, of course, hard to implement because with nonhuman subjects one cannot easily offer a choice committing the animal for such a long time and guarantee that the subject understands (is tuned to) the problem.

To overcome this difficulty, an additional, usually implicit, assumption is often made: if a subject’s budget is manipulated over a 24-h period, its attitude toward risk will show in decision problems involving multiple, less consequential, choices. For instance, in the paradigmatic experimental tests of these ideas, Caraco and collaborators (Caraco, 1981; Caraco et al., 1980, 1990) modified the energy budget of small birds (dark-eyed and yellow-eyed juncos, Junco spp.) during experimental sessions lasting less than 4 h by appropriately setting the average size of rewards, the inter-reward interval, or the ambient temperature. This means that rate of gains during the session, if extrapolated to cover the whole day, would be below or above the average needs for survival. When the experimental sessions finished, the subjects were fed ad libitum. Birds in either a positive or a negative budget were then tested over multiple decisions within each session, by making them choose between food sources that differ in their variance (for instance, one source delivering always three seeds per choice and the other delivering one or five seeds per choice with equal probability). Because sessions involve forced trials to instruct the subjects on the statistical properties of the food sources, the overall variance in payoff among sessions is small, and it is impossible for the subject to attribute the variance in cumulative payoff over the whole session to the proportion of its choices. Predictions about risk attitude are based on assuming that the subjects extrapolate the variance in the consequences of their choices to the potential accumulated outcome over the 24-h period.

An additional problem is to guarantee that the subjects know the mean and variance of the stochastic alternative. The problem of assessing the parameters of a distribution using limited experience is a hard one in the best of cases, and much harder if the subjects do not know that they are dealing with two distributions of a given kind. Kacelnik and Bateson (1996) have shown that given the experienced sample sizes (the number of choices in a session and its consequences), good knowledge is unlikely in the case of the experimental...
juncos; the confidence interval of the subjects’ estimates must have been extremely large. Incomplete knowledge confounds the interpretation because under those conditions subjects are also expected to sample their alternatives so as to reduce uncertainty, whereas risk sensitivity predictions are developed under the assumption of full knowledge. Within the framework of these difficulties, it is, nonetheless, tantalizing that several studies have shown switches between risk aversion and risk seeking depending on energy budget (Caraco, 1981; Caraco et al., 1980, 1990). Should this result be confirmed, it may mean that animals modify risk attitude easily and generalize across time scales.

However, negative results are also often reported. In particular, risk attitude reversals have never been found in animals experiencing variance in the time or work components of foraging payoffs (see review in Kacelnik and Bateson, 1996). In a strong test of the theory, Ha et al. (1990) used gray jays (Perisoreus canadensis) that experienced variance in amount of work (and hence time) to obtain food rewards. The jays were subject to a budget that, in the negative treatment, led to their progressive weight loss over a number of days. In the positive budget condition they had enough food to hold their energetic reserves. The budget manipulation was thus stronger than in the junco tests, as the junco’s budget was only controlled during the sessions, and they were allowed to hold their weights constant even in the negative budget treatments. In spite of this, the jays were consistently risk prone. A similar result is reported by Case et al. (1995) using water rewards.

Many differences between experimental conditions might account for inconsistent results. It may be that there is a fundamental difference between variance in amount and variance in time or effort. It may also be that the size of the subjects is crucial: perhaps smaller animals do switch in risk attitude, whereas larger species are persistently risk averse because of their greater ability to buffer short-term fluctuations in intake (students of human attitudes to risk usually refer to “risk aversion” rather than risk sensitivity, implying that aversion is the predominant attitude in their subjects). This account of results on the bases of the size effect sits uncomfortably with the observation that animals of different size show the same trends when comparing between amounts and delays, and even large species are systematically risk prone for delays.

It is also possible, however, that risk attitude reversals are much rarer and hard to replicate than previously thought (or even that success in previous studies was due to chance), a hypothesis that is hard to prove because it implies accepting a null hypothesis (lack of effect of budget manipulations). Indeed, it is likely that the set of reported failures to obtain a shift is a less complete representation of the number of attempts than is the case for positive results, which are easier to publish.

**Budget-insensitive interpretations**

There are, of course, alternative budget-independent interpretations. Several models have been proposed that treat choices between variable sources of reward as cases of maximization of expected payoff in foraging, rather than reasoning about the putative nonlinearity of the gains-versus-fitness relation. All these models have in common the suggestion that something in the algorithm by which the subjects attempt to maximize feeding payoff leads to paradoxical choices (i.e., preference for submaximal average gain rate) in the presence of variance. Kacelnik and Bateson (1996, 1997) discuss these various models. These models per se do not predict any reversal in risk attitude as a function of the subject’s state, but all the models could have features added to accommodate this if evidence indicates that reversals are prevalent. These alternative models have been discussed elsewhere, so we restrict ourselves to their simple enumeration.

**Associative learning**

Risk attitude could be a consequence of training. Because experimental animals are trained to choose among pecking keys, hopping perches, color lids, levers, etc., they must be exposed repeatedly to these manipulanda and their consequences to learn what they mean. Training efficiency is a function of both reward size and temporal contiguity between onset of the opportunity and outcome, and neither of these effects is linear. If the positive effect of reward size on the strength of the association between a manipulandum and food is concave, and the negative effect of delay is convex (as normally observed; see Tarpy, 1997) then one expects a lower subjective value for a manipulandum, leading to variable rather than to fixed outcomes when variance is in amount and the opposite when variance is in delay. Quantitative predictions based on this idea are hard to formulate because they depend on the precise form of the curves describing amount and delay dependency, including estimates of asymptotic associative value. This requires full parametric studies of the acquisition process under various sizes of reward or delays, and this information is not available within the foraging literature. Indeed, we do not have this information for the experiment reported here.

**Rate computations**

If subjects base their choices on an algorithm that computes mean rate as the average of amounts and times taken per event, rather than over a continuous period (that is, they commit the fallacy of averages), then one should expect risk proneness for variance in delay and risk neutrality in variance for amount (Bateson and Kacelnik, 1996; Gilliam et al., 1982; Templeton and Lawlor, 1981). This risk neutrality turns into risk aversion if, while delays to food are constant, handling time is proportional to reward size. In this case, amount variance may produce risk sensitivity piggybacking on the temporal effects (Caraco et al., 1992).

**Weber’s law**

Risk attitude can also derive from the processing of information about amounts and times (Bateson and Kacelnik, 1995b; Kacelnik and Brito e Abreu, 1998; Reboreda and Kacelnik, 1991). The idea here is that subjects choose the food source that they recall as yielding a bigger reward or a shorter delay, but stimuli (e.g., prey size or interprey intervals) are remembered with confidence intervals proportional to their magnitude. This psychophysical effect (a form of Weber’s law) causes subjects to remember the probability distribution of outcomes of a variable food source with greater positive skew than the objective (experienced) distribution. For instance, if two food sources yield normally distributed outcomes with equal mean but different variance, the subject will represent them internally as distributions with equal mean, but with a smaller median for the more variable one. Choice criteria that are sensitive to skew (e.g., if choices are based on the medians rather than on the means of internal representations) produce risk aversion for variability in amount (or any positive dimension of reward) and risk proneness for variability in time (or any aversive dimension of reward).

The goal of this paper is to reexamine the contrast between the reversal in risk attitude observed for amounts in juncos and the picture of weak risk aversion for amounts and strong risk proneness for delays emerging from other cases. We did not investigate delay variance here, as this is sufficiently well established, but we used a strong budget manipulation similar
to that used by Ha et al. (1990), exposing starlings to a choice between food sources that differ in variance in reward size as in the junco experiments. We also relate our results to budget-insensitive models.

**METHODS**

**Subjects**
The subjects were eight naive, wild-caught European starlings (*Sturnus vulgaris*). After capture the subjects were kept together for approximately 6 weeks in an outdoor aviary with free access to water and food, a mixture of turkey starter crumbs, Orlux pellets, and mealworms (*Tenebrio* sp.). One week before the beginning of the experiment, we moved the birds to an indoor laboratory and housed them in individual cages measuring 77 cm × 50 cm × 53 cm.

**Apparatus**
The experiments were conducted in the birds’ home cages. Each cage had a removable panel with a centrally mounted food hopper (4 cm × 3.5 cm) and three response keys with 3 cm diameter (one at the center above the hopper, 23 cm from the floor, and the other two at 20 cm from the floor and 8 cm to the left and right of the hopper). The keys could be illuminated with either orange, green, or red lights. In front of the panel, at 20 cm from the floor, there was a perch from which the birds could access the hopper and the keys. This perch was mounted on a digital balance (Mettler 601), so that the bird’s weight could be recorded without disturbance. An Acorn Risc PC 600 microcomputer programmed with Arachnid experimental control language (Paul Fray Ltd., Cambridge, UK) controlled the stimulus events and the response contingencies and recorded the data (including the readings from the balances). Birds’ responses were reinforced with turkey starter crumbs delivered in the food hopper by pellet dispensers (Campden Instruments). Units of crumbs delivered from these dispensers had a mean ± SD weight of 0.017 ± 0.0048 g, and food rewards consisted of multiple units that were delivered at a rate of 1 unit/s.

Temperature in the laboratory ranged from 9°C to 15°C, and the lights were on between 0700 h and 1700 h. During the experiment the birds were visually but not acoustically isolated.

**Training**
After 1 week of adaptation to the cages, the birds were induced to peck the response keys by a standard autoshaping procedure. Starlings initially experienced the delivery of standard rewards (5 units of food) preceded by 8 s of an orange light on the center key, with an intertrial interval (ITI) of 60 s. They were then gradually shifted to an operant schedule where rewards were delivered conditional on key pecking at the central key. During training subjects experienced 2 or 3 sessions per day of 100 trials each, and we provided ad libitum food after the last session.

**Energy budgets**

*Ad libitum consumption*
We measured the daily ad libitum food consumption of each individual subject in our apparatus using a schedule in which birds had to peck once at an illuminated key to access food. A session of 450 trials began every day at 0700 h (lights on). In each trial an orange light illuminated the center key for up to 8 s, and pecking would cause the light to go off and the delivery of a standard reward (5 units) followed by an ITI of 60 s. If no peck occurred in the 8-s interval, the light was turned off and the ITI started. Therefore, our subjects had a chance to feed every 68 s, during the first 8.5 h of the 10-h day. This schedule allowed the birds to obtain a theoretical maximum of 38 g of food per day (450 trials × 5 units × 0.017 g), considerably more than their normal consumption of about 20 g (see Table 1).

Birds were kept on this schedule for 9 days, and they stabilized their daily intake after 3 days (stability was judged by visual observation). We estimated each bird’s daily consumption using the records from the last 6 days. Also, during this stage we measured the body weight of the subjects on every trial and used these readings to estimate their average free-feeding weights.

**Budget manipulations**
The total food received by the subjects during the choice experiment (explained in next section) was not enough to satisfy their daily needs, and supplementary food had to be delivered after the experimental sessions. We manipulated energy budgets by controlling the amount of supplementary food given to each subject. Birds on treatment N (negative budget) received an amount of supplementary food so that the total amount of food received by the end of the day (food delivered in the experimental sessions + supplementary food) would add up to half of their daily individual ad libitum intake, while birds on treatment P (positive budget) were given their full daily ad libitum consumption. The decision on halving their ad libitum intake was made after pilot experiments showed that less drastic reductions did not cause reliable weight loss. Starlings have the ability to change food utilization and reduce expenditure so as to compensate for imposed variations in intake (Bautista et al., 1998).

During the choice experiment we regularly monitored the subjects’ body weight. This was particularly important in the negative budget treatment because it was crucial to observe a steady decrease in the bird’s body weight while avoiding a weight loss beyond the boundaries of natural variation in the wild (no bird was allowed to fall below 80% of its free feeding body weight).

Supplementary food was delivered in two parts: one-third after the first session and two-thirds after the end of the second session. This ensured that the birds were not satiated when the second session began (1400 h) and that they had time to eat the supplementary food delivered after the second session, before the lights were turned off in the laboratory (1700 h).

**Table 1**

<table>
<thead>
<tr>
<th>Bird</th>
<th>Sex</th>
<th>Daily food intake (g) (mean ± SD)</th>
<th>Free-feeding weight (g) (mean ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Male</td>
<td>22.0 ± 0.96</td>
<td>73.5 ± 2.36</td>
</tr>
<tr>
<td>1</td>
<td>Female</td>
<td>18.5 ± 0.97</td>
<td>91.0 ± 4.69</td>
</tr>
<tr>
<td>2</td>
<td>Male</td>
<td>23.0 ± 2.15</td>
<td>79.5 ± 2.95</td>
</tr>
<tr>
<td>3</td>
<td>Female</td>
<td>18.5 ± 1.54</td>
<td>93.0 ± 1.86</td>
</tr>
<tr>
<td>4</td>
<td>Female</td>
<td>22.5 ± 1.18</td>
<td>75.5 ± 0.85</td>
</tr>
<tr>
<td>5</td>
<td>Female</td>
<td>21.0 ± 1.45</td>
<td>89.0 ± 3.19</td>
</tr>
<tr>
<td>6</td>
<td>Male</td>
<td>18.0 ± 0.87</td>
<td>81.5 ± 2.85</td>
</tr>
<tr>
<td>7</td>
<td>Male</td>
<td>23.5 ± 2.05</td>
<td>90.5 ± 2.09</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>20.88 ± 0.79</td>
<td>84.19 ± 2.69</td>
<td></td>
</tr>
</tbody>
</table>
Choice experiment

In the main phase of the experiment, the birds faced a choice between two options: a fixed option which always delivered 5 units of food, and a variable option that offered either 2 units of food (with 0.66 probability) or 11 units (with 0.33 probability). Therefore, both options offered the same mean reward (5 units), but one had no variance and the other had a coefficient of variation between trials of 0.86. The fixed and variable options were signaled by different colors on the lateral keys (red and green, balanced between subjects).

We used a discrete trials procedure with a variable ITI generated by a truncated geometric distribution with a mean of 57.5 s (minimum = 45 s, maximum = 105 s). There were two types of trials: forced trials and choice trials. Forced trials started with the illumination of the center key with an orange light and, after the bird pecked, this light extinguished and one of the side keys (randomly chosen) was illuminated by either a red or a green light (signaling either the fixed or the variable option). When the bird first pecked the illuminated side key, a 5-s delay started, and the number of pecks during this interval was counted. The first peck after the 5-s delay extinguished the light and caused the delivery of the reward (corresponding to the presented option), which was followed by a new ITI. The purpose of the forced trials was to provide the subjects with information on the two options, forcing them to sample both options the same number of times before the choice trials. It also helped to prevent side biases because both options were presented the same number of times on each side. Some costs of this procedure are that it reduces the effect of the birds’ preferences on its experienced long-term outcomes and that it reduces the variance in total payoff across sessions.

Choice trials also started with an orange light in the center key, but after the bird pecked at it, the two side keys were illuminated, one with a green light and the other with a red light (sides randomly chosen for each trial). When the subject pecked one of the side keys, the other light was turned off and a 5-s delay was timed. The first peck after the 5 s elapsed caused the delivery of a reward.

In addition to proportion of choices for each option in the choice trials, we recorded two other measures of motivation from the data collected on forced trials: the latency to accept the presented option and the number of pecks during the 5-s delay to reward. Relative motivation gives an indication of preference.

During the experiment there were two sessions per day, each consisting of 36 trials (the first session started at 0700 h and the second at 1400 h). Each session consisted of 3 consecutive blocks of 12 trials, in which the first 6 were forced trials and the last 6 were choice trials. Each option (fixed or variable) was always presented three times in the six forced trials of each block.

Subjects were divided in two groups of four, which were tested under both positive and negative energy budgets (treatments P and N). The experiment consisted of three stages, with one group following a N-P-N sequence of treatments and the other a P-N-P sequence. We interrupted each stage for all birds in both groups whenever the first of the birds on the negative budget treatment reached 80% of its free-feeding weight (the first, second, and third stages lasted 6, 11, and 6 days, respectively). Between stages, birds were given 3 days of ad libitum food, during which no tests were run.

RESULTS

Energy budgets

Table 1 shows the estimated daily food intake and free-feeding weight of each subject. We calculated the ad libitum food intake (in grams of turkey crumbs) and the reference free-feeding weights by averaging the daily values recorded after day 3 of the energy budgets’ assessment phase.

Figure 1 shows the effects of the two energy budget treatments on body weight in the last 5 days of each treatment. Birds in the negative budget treatment lost weight significantly (simple regression; $R^2 = .24, F_{1,58} = 12.2, p = .001, n = 8$ birds), and under the positive budget conditions they kept their body weights stable (simple regression; $R^2 = .004, F_{1,58} = 0.2, p = .7, n = 8$ birds).

Risk preferences as expressed in choice trials

Figure 2 shows the proportion of choices for the variable option made by each subject under the two energy budget conditions. We calculated these values using all the choice trials of each individual, except those for the first 3 days of each stage. Data from the first 3 days were excluded to guarantee that enough time had elapsed for the energy budget treatment to have an effect.

In general, birds were risk averse (Figure 2): four of them (birds 0, 2, 3, and 7) showed weaker risk aversion under the negative than under the positive energy budget; the opposite was observed in the remaining four. In treatment P all eight birds were significantly risk averse (binomial tests, $p < .01$), whereas in treatment N risk aversion was significant only in four of the birds (binomial tests, $p < .01$).

Fit to theoretical models

To simplify the comparisons with predictions from various theories, we now examine population averages. We consider the predictive performance of four models, none of which, as we will show, resulted in a perfect fit. The comparison between average data and the predictions of the models is shown in Figure 3.

The budget rule

As a group, the subjects where risk averse (one-group $t$ tests, two-tailed, $t > 3.1, p < .02, n = 8$ birds) under both energy budget conditions (Figure 3). Our manipulation of energy budget did not affect starlings’ preferences reliably because the difference between average percent of choice for the var-
variable option between treatments was not significant (paired t test, two-tailed, \( t = 0.9, p > 0.4, n = 8 \) birds).

**Budget-insensitive models**

**Weber's law.** In Figure 3, the shaded area represents the predictions of the model of risky choice based on Weber’s law with single sampling of the memory distributions (see Introduction and, for a detailed description, Kacelnik and Brito e Abreu, 1998). This model has one parameter that is assumed to be idiosyncratic among individuals, representing the coefficient of variation of the memory for each fixed percept. We calculated the predictions of this model using coefficients of variation ranging from 0.35 to 0.65, because these values cover the individual variation observed in starlings' coefficients of variation when assessing amounts of food in a similar set up (Bateson and Kacelnik, 1995a). The model predicts a percent of choices for the variable option between 34.5% and 38.9%, a range that is inside the 95% confidence interval of our results (Figure 3). In spite of this remarkable fit, this must be seen with caution, as Figure 3 shows averaged data. Individual results showed considerable variation around the group’s mean, as can be seen in Figure 2.

**Expectation of the ratios.** The dotted line marked with “EoR” in Figure 3 is the prediction of a variation of the local rate maximization model (Mazur, 1984; see further explanations in Bateson and Kacelnik, 1996). This model is based on assuming that subjects choose alternatives by computing rate of energy gain and choosing the highest score but that they compute rates with an algorithm that yields rate averages per trial rather than per session.

We implemented this model’s predictions assuming that birds attribute an expected rate of gain to each option using only the time elapsed between their choice (pecking at the colored light) and the outcome. The two alternatives are valued according to the following equations:

\[
V_i = \frac{F}{D + T_i}, \quad V_v = \frac{\left(\frac{2S}{D + T_5} + \frac{L}{D + T_1}\right)}{2} \tag{3}
\]

where \( V_i \) is the value attributed to the feeding option \( i \) (fixed or variable), \( F \) is the amount delivered in the fixed option (5 units), \( S \) and \( L \) are, respectively, the small and large amounts of the variable option (2 and 11 units), \( D \) is the delay between choice and reward (5 s), and \( T_i \) is the time required to deliver \( i \) units of food (1 s per unit). This computation excludes the times between each stimulus onset and choice. We analyze these latencies in forced trials in the next section, but we exclude them for the analysis of preference in choice trials because of the confounding factor that the latencies are chosen by the birds themselves. The local rate values according to these equations are 0.5 units/s for the fixed option, and 0.42 units/s for the variable option, and therefore according to this model one should expect exclusive preference for the fixed option. However, if the probability of a bird choosing an option is proportional to its attributed value (i.e., if starlings follow something close to the so-called matching law; Davison and McCarthy, 1988; Herrnstein, 1970), this algorithm can be used to predict partial preferences. The matching version of this model still predicts risk aversion, but it
for both the fixed and variable options, under the two energy budget treatments.

during the 5-s delay before the delivery of food (b) in forced trials

Figure 4
Mean \( \pm \) SE (\( n = 8 \) birds) latency to peck (a) and number of pecks during the 5-s delay before the delivery of food (b) in forced trials for both the fixed and variable options, under the two energy budget treatments.

expects birds to choose the variable option in 45.7% of the trials [0.42/(0.42+0.5)]. Our results were clearly more extreme than this value in treatment P (i.e., risk aversion was stronger than predicted), but in treatment N the model’s prediction falls within the 95% confidence interval of the mean percentage of choices for each option (Figure 3). Inclusion of the latencies would shift the model’s prediction closer to risk neutrality (away from the data). In matching literature nomenclature, the subjects were “overmatching”.

**Associative learning.** We referred in the Introduction to the idea that risk preferences may be due to the strength of association between stimulus and reward during training. We do not have sufficient information about the precise pattern of acquisition and asymptotic associative strength to make quantitative predictions on this basis, but the idea certainly applies to our experiment and is consistent with our results.

**Risk preferences using latencies and number of pecks in forced trials**

Figure 4 shows the average latency to peck and number of pecks during the 5-s delay to reward in the forced trials. Using the Box and Cox (1964) procedure, we estimated the best power transformation to normality (\( \lambda = -0.5 \) for latencies, \( \lambda = 0.23 \) for number of pecks) and performed a two-way repeated-measures ANOVA (treatment and option) on the transformed data. There was no significant interaction between treatment and option in the number of pecks; in both treatments birds pecked more when the fixed option was presented relative to the variable option (\( F_{1,7} = 10.76, p = .001 \)). However, there was a significant interaction between treatment and option in the latency to peck (\( F_{1,7} = 3.94, p = .047 \)). In treatment N latency to peck was shorter for the variable option than for the fixed option, whereas the opposite was true in treatment P. This interaction is the only aspect of our data showing motivational shifts in agreement with the budget rule.

As expected, energy budget affected subjects’ motivation; latencies to peck were shorter and subjects pecked more times in treatment N than in treatment P. The effect on pecking rate is statistically reliable (\( F_{1,7} = 78.16, p < .001 \)), but the effect on latencies cannot be reported because of the significant interaction between treatment and option.

**DISCUSSION**

Our primary aim was to assess the effects of energy budget on starlings’ preferences for variability in amount of food. We tested our subjects’ preferences between a fixed feeding option (5 units of food) versus a variable option (2 or 11 units with probabilities 2/3 and 1/3, respectively), under both positive and negative energy budgets. The experiment was designed as a direct test of the budget rule (Stephens, 1981), which states that animals should be risk averse on positive energy budgets and risk prone on negative energy budgets. Contrary to these predictions, our subjects were significantly risk averse irrespective of energy budget conditions.

Starlings’ risk-sensitive preferences have been tested before (Bateson and Kacelnik, 1995b; Bateson and Kacelnik, 1997; Reboreda and Kacelnik, 1991), and the usual result has been a strong tendency toward risk proneness when variability was caused by delay to food and weak risk aversion when variability was caused by amounts of food. A direct test of the energy budget rule, however, was unavailable.

In a related study, Koops and Giraldeau (1996) compared the use of two foraging tactics—“producer” (search for food) and “scrounger” (exploit food discovered by producers)—by starlings under conditions that differed in food availability (patch food density). These authors reported that, when food density was high, starlings increased the proportional use of scrounger, which is assumed to be a risk-averse tactic (because it decreases intake variance as well as intake rate), a result consistent with the general predictions of RSFT models. This study is hard to relate to ours because starlings may have responded to social rather than to energetic aspects of the situation. Social and energetic dimensions do interact in this species, to the extent that starlings do incur energetic losses in exchange for proximity to conspecifics (Vásquez, 1995).

One observation by Reboreda and Kacelnik (1991) suggested that there could be some effect of energy budget on starlings’ preferences for risk. They tested starlings under two different treatments. In both treatments the birds faced a choice between a fixed food source and a food source with variable outcomes. They did not manipulate the energy budget directly, as their main goal was to compare risk preferences between amount and time variability. Their results confirmed the trend toward weak risk aversion for amount (which we now reaffirm) and strong risk proneness for delay. However, due to the way food was delivered, (reward amounts were controlled by time of access to a food hopper), some of the birds experienced higher rates of intake during the experiment than others because they were more efficient at scooping food. Using these interindividual differences, Reboreda...
There was a significant correlation between intake rate and risk aversion, as predicted by the energy budget rule (Stephens, 1981), both for variability in amount ($r = .64, p < .05$) and in delays ($r = .61, p < .05$).

Although the budget effect was only a correlational observation, it suggested that energy budget could have an effect on starlings’ risk preferences. However, under the more controlled conditions of the present test, the choice results failed to confirm this effect. We examined motivation toward fixed and variable rewards by looking at the delay in accepting rewards of either kind in forced trials. These latencies showed a significant interaction between variance and budget, in agreement with the budget rule.

In a recent study designed to separate the effects of variance from that of unpredictability in outcomes, Bateson and Kacelnik (1997) tested starlings’ preferences for fixed versus variable delays to reward using a protocol that included a weak manipulation of energy budget (within-session budget was affected, but there was no loss of body weight during the experimental period). They found no effect of energy budget on preference, and, as in all the studies where risk is introduced by variability in delay, their subjects were strongly risk prone.

It is tempting to argue that failures of the budget rule may have been due to limitations of experimental design, such as insufficiently strong budget manipulations or insufficient difference in variance between alternatives. We do not think this line of thinking is promising, though. First, exactly the same caveats should apply to the experiments using juncos, where significant reversal of risk preferences were obtained in spite of a positive overall budget. Second, in Bateson and Kacelnik’s (1997) study the starlings were consistently risk prone, as it is always found with respect to delay, so that in any case risk bias was against the prediction of the budget rule for birds in a positive budget.

Because budget considerations fail to account for our results, we focus on how alternative, budget insensitive, interpretations relate to the data. Two aspects need to be examined. (1) Why is it that in spite of the strong logic of the energy budget rule, most animals seem not to have developed behavioral mechanisms that comply with it? (2) If RSFT were to be abandoned, are there other theoretical accounts of how decision-making under uncertainty may have evolved?

The answer to the first question might be found in the analysis provided by McNamara (1996). He considered the relative performance of three strategies: optimal risk sensitive behavior (choose between fixed and variable options according to optimal state-dependency), rigid risk aversion (always prefer the fixed option), and rigid risk proneness (always prefer the more variable food supply). He performed his analysis only for variability in amount, but because this is the variable controlled in the present experiment, the results should apply. McNamara’s fundamental finding is that although flexibility in risk attitude leads to higher fitness, under the majority of scenarios implemented in his simulations, rigid risk aversion led to a very small fitness loss, while rigid risk proneness would lead to large loss of fitness. This is mainly because the conditions favoring risk proneness are rare and normally extreme, and mortality in those cases would be high whatever the subjects choose to do. In addition, optimal implementation of flexible risk attitude assumes good knowledge of the statistical parameters of the food supply, but this assumption is rarely justified and perhaps almost unachievable in nature. With hindsight, it seems likely that the pressure to develop mechanisms for a change in risk bias according to budget may have been too weak to result in observable behavioral consequences, and what is puzzling is the fact that these reversals were often reported.

In an extensive review of studies on risk sensitivity, Kacelnik and Bateson (1996) point out that the experiments that reported a switch in preference as predicted by the energy budget rule were all on insects or relatively small fish, birds, and mammals (see also Hamm and Shettleworth, 1987). Studies on larger species such as rats, pigeons, starlings, and gray jays failed to find a shift in preference with the manipulation of energy budget. Kacelnik and Bateson suggest that body mass could be an important variable affecting risk sensitivity because smaller species with less reserves are more likely to have been subject to strong selection for short-fall minimization. Larger animals can keep a permanently higher relative level of body reserves, and therefore only rarely reach states in which a budget-dependent shift in risk sensitivity would affect their survival probability. This hypothesis can only be tested with a proper comparative study, which has not been done yet.

Second, if RSFT were to be left out, is there any other functional perspective that does a better predictive job? One possible answer is that choices between variable food sources may be better understood when looked from the perspective of maximization of rate of energetic payoff, rather than when examined from the point of view of strategic responses to variability per se. To accommodate the data, however, additional assumptions about the constraints faced by animals in computing average rates are necessary because typically they do not always choose so as to maximize long-term average rate of gain.

We compared our results against the predictions of two such models. In one of them, EoR (“expectation of the ratios”, see Bateson and Kacelnik, 1996), subjects compute reward rate in both options and choose the better alternative, but their computation of rate is based on averaging the ratio of gain to time on a per-trial basis rather than on a per-time basis, and this leads to deviations from overall rate maximization. We took into account that larger rewards take longer to consume. This was certainly true in our set up because food units were delivered at 1-s intervals. This model admits various implementations, and although it correctly predicts risk aversion for our experiment, it requires ad-hoc modifications to deal with partial preferences.

The other model in this category (Weber’s law and single
sampling) is based on considering the information-processing mechanisms involved in choice. The subjects remember the properties of each food supply with a degree of uncertainty and then make choices between samples taken from their memory for each source of reward, choosing always the sample that appears to lead to a better reward. The way uncertainty is included derives from what is known of perception of food amounts and time intervals. This model (Gibbon et al., 1988; Reboreda and Kacelnik, 1991) is described in full as applied to the present experiment and extended to more general cases by Kacelnik and Brito e Abreu (1998). It predicts risk aversion for desirable outcomes such as food amounts and risk proneness for aversive outcomes such as food delays. It also predicts partial preferences because in different trials sampling from memory yields different values for the two food supplies. We found a remarkable fit between the predictions of this model and the average results of our group of animals, but the fit is weaker when applied to each individual subject. In conclusion, we found that starlings are persistently risk averse when amount variability is involved and that this is unaltered by energy-budget manipulations. These results, together with those of other studies showing that risk attitude for delays has the opposite sign and is equally resistant to budget manipulations, are consistent with the hypothesis that in natural environments maximization of mean rate of gain may be paramount, but that the mechanisms by which mean rates are computed may lead to paradigmatic (not rate-maximizing) choices under experimental circumstances.

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REFERENCES


Stress, testosterone, and the immunoredistribution hypothesis

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Recent interest in parasites and sexual selection has focused attention on the paradox that the sexual displays which indicate parasite resistance in male vertebrates are triggered by testosterone, an apparently immunosuppressive hormone. We question the underlying assumption that testosterone is immunosuppressive and offer here the alternative of immunoredistribution to explain the changes in circulating leukocytes associated with male displays and elevated testosterone. First, we briefly examine three hypotheses that have attempted to resolve the testosterone immunosuppression paradox (Fostad and Karter, 1992; Hillgart et al., 1997; Wedekind and Fostad, 1994). Although the immunoredistribution hypothesis under-