

Both the past and the present affect risk-sensitive decisions of foraging rufous hummingbirds

Ida E. Bacon,^a T. Andrew Hurly,^b and Susan Healy^c

^aInstitute of Evolutionary Biology, University of Edinburgh, Kings Buildings, Edinburgh EH9 3JT, UK,

^bDepartment of Biological Sciences, University of Lethbridge, 4401 University Drive, Lethbridge, Alberta, T1K 3M4, Canada, and ^cSchool of Psychology, University of St Andrews, Saint Andrews, Fife KY16 9JP, UK

There is substantial evidence that an animal's current energy budget affects its preference for food patches that provide a constant reward relative to patches that provide a variable reward, when both patches have the same mean reward. Animals currently on a positive energy budget are expected to choose the constant option, whereas animals on a negative budget are expected to use the variable option. There is increasing evidence that prior experience can affect an animal's current decisions. We investigated choices made by rufous hummingbirds when they were tested with strong or weak sucrose solutions after several days of foraging on those strong or weak solutions. Foraging from weak concentrations prior to and during testing led to a higher preference for the variable option, whereas foraging from strong concentrations led to an increased preference for the constant option. We suggest that the energetic conditions experienced by animals prior to testing had a significant impact on the animals' risk-sensitive decisions, and their memories of those prior conditions may have played an additional role. This implies that the conditions animals are maintained under prior to testing may significantly affect the outcome of risk-sensitivity experiments. *Key words*: decisions, foraging, hummingbirds, past, risk-sensitive. [*Behav Ecol* 21:626–632 (2010)]

Given 2 food options where reward quality and mean reward amount over time are equal for both options but where the variability in reward amount differs, animals often prefer one option over the other (Logan 1965; Young 1981; Real et al. 1982; Kacelnik and Bateson 1996; Drezner-Levy and Shafir 2007; Schuck-Paim and Kacelnik 2007; Heilbronner et al. 2008). For example, blue jays (*Cyanocitta cristata*) given the option of foraging in a variable patch that provided either 2- or 4-half mealworms (a mean of 3 halves) or a constant patch that provided 3-half mealworms preferred to feed from the constant patch (ca. 70% of feeds, Clements 1990). This sensitivity to variation in reward can be explained by the energy-budget rule (Stephens 1981), which stipulates that when an animal is on a positive energy budget and is not in danger of starvation, it should choose the constant option in order to minimize the chance that it will encounter numerous small rewards and risk starvation. However, an animal in danger of starvation should choose the variable option as it increases the chance that the animal will encounter sufficiently large rewards to avoid starvation. The energy-budget rule does not fully explain risk-sensitive choice as it predicts exclusive preference for either the constant or variable option, whereas partial preferences are observed in the vast majority of cases (Kacelnik and Bateson 1996; Hurly 2003). One possible explanation for partial preferences is that animals continue sampling all options in order to enable resource tracking (Krebs et al. 1978; Schuck-Paim and Kacelnik 2007). Another possible reason for partial preferences is that animals forage

among rewards in proportion to how rewarding they find them rather than entirely avoiding less preferred options (Shapiro 2000; Schuck-Paim and Kacelnik 2007).

Manipulations of energy budgets either before or during choice trials show that an animal's sensitivity to reward variability is, indeed, state-dependant (Kacelnik and Bateson 1996). For example, dark-eyed juncos (*Junco hyemalis*) preferred the constant reward when on a positive energy budget, were indifferent when on a balanced energy budget, and preferred the variable reward when on a negative energy budget (Caraco 1981). Likewise, yellow-eyed juncos (*Junco phaeonotus*) preferred the variable option under conditions of low ambient temperature and the constant option under warmer, less energetically demanding, conditions (Caraco et al. 1990). Typically, in this kind of experiment, manipulations are designed so that animals experience a particular energy budget, which is then expected to be the main influence on their risk sensitivity. However, the duration of the energy-budget manipulations, which varies considerably among experiments, may play a significant role in the outcome of the experiments as previous foraging experiences often affect current foraging decisions. For example, young canaries fed for 8 weeks on a single seed type (hemp, niger, millet, or linseed) and then on a mixed seed diet for 15 weeks, preferred the seed type on which they were reared. Birds reared on a mix of all 4 seeds, on the other hand, preferred hemp seed (Doherty and Cowie 1994). If the context animals experienced weeks ago (such as the canaries' previous diet) can affect current preferences, then it seems likely that previous experiences may also affect an animal's sensitivity to variability. Prior knowledge of patch types and their frequency in the environment can be used by animals along side current sampling information to form an estimate/expectation of patch quality and inform, for example, patch-leaving decisions (e.g., McNamara 1982). This is

Address correspondence to I.E. Bacon. E-mail: i.e.bacon@sms.ed.ac.uk.

Received 30 July 2009; revised 18 February 2010; accepted 20 February 2010.

referred to as Bayesian or Bayesian-like decision making and has been described in many species including: the Arizona pocket mouse, *Perognathus amplus*; Merriam's kangaroo rat, *Dipodomys merriami*; and the round-tail ground squirrel, *Spermophilus tereticaudus* (Valone and Brown 1989); Inca doves, *Columbina inca* (Valone 1991); Black-chinned hummingbirds, *Archilochus alexandri* (Valone 1992), and Bumblebees, *Bombus impatiens* Cresson (Biernaskie et al. 2009).

Expectations can be affected by experiences from throughout the animal's life (Simitzis, Bizelis, et al. 2008; Simitzis, Deligeorgis, et al. 2008). Effects of expectations about the quality of specific foraging locations on foraging behavior have been demonstrated both in vertebrates and invertebrates (Lima 1983; Schilman and Roces 2003; Gil et al. 2007): animals return more often to and invest more effort in investigating locations or food types associated with higher rewards, but if those reward values are decreased, animals continue to show more interest in those resources than their current value would predict. Thus, past experience is clearly often used in foraging decisions and to aid the assessment of current conditions. In addition, current conditions may also be assessed in terms of contrast: change relative to past conditions. Marsh and Kacelnik (2002) demonstrated that starlings foraging in a risk-sensitive task selected options according to whether the current conditions were perceived as better or worse than past conditions. In this instance, the past affected current decisions as if a change in energy budget/resource value had occurred when in fact it had not. When changes in resource value are real such contrast effects may also be at work but as they change behavior in the same way as actual changes in resource quality, they would be hard to detect.

Here, we tested whether the foraging context preceding test conditions and the foraging context during test conditions affected rufous hummingbirds' (*Selasphorus rufus*) preference for high or low variability rewards. We manipulated food concentration in the feeder (low vs. high) before testing and during testing (low vs. high) in a factorial design. As far as we are aware, this is the first time that the effects of both past and current foraging conditions on risk-sensitive foraging have been tested simultaneously. Hummingbirds are useful subjects for studies involving energy manipulations as their high metabolic rate means they must feed frequently throughout the day and balance their energy budget daily or even hourly. Their natural food (flower nectar) varies considerably in the concentration and volume within and between plants (Ornelas et al. 2007), and in experimental manipulations of reward variability hummingbirds are, indeed, sensitive to reward variability, usually avoiding flowers providing the highest variability in reward volume (Hurly and Oseen 1999; Biernaskie et al. 2002). Our hypothesis was that both past and current context would affect birds' sensitivity to variability. Assuming that higher energy budgets lead generally to risk aversion, birds should choose the constant option more often when they experienced the higher sucrose concentration both prior to and during testing. They should choose the constant option least often when they experienced the lower concentration prior to and during testing. The factorial design allowed us to determine whether the pretesting and testing influences are additive or whether they interact in a more complex fashion. There were no clear predictions as to the effects of expectations that may be carried over from the pretesting to the testing period nor with regard to the effects of contrast between the periods (e.g., the perception of the foraging situation improving from low-concentration food during the pretesting period to high-concentration food during testing or vice versa). Unlike most experiments investigating risk sensitivity, we were not concerned with

significant departures from risk neutrality but rather with how the conditions prior to and during testing influenced the relative preferences for constant and variable options.

MATERIALS AND METHODS

Subjects were 8 male rufous hummingbirds which had been defending territories for several weeks in the Westcastle River valley, Alberta, Canada (lat +49°20'56.41", long -114°24'35.08"). Each male's territory contained a 14% sucrose ad libitum feeder that he defended and from which he obtained almost all of his nectar. To allow individual identification, birds were marked with waterproof, colored, nontoxic ink on the upper breast.

Subjects were trained to feed from arrays of 20 wells and to associate the color of wells with a particular sucrose concentration and volume variability reward type. The wells (10 mm deep × 3.5 mm diameter) drilled in to a rectangular Plexiglas plate (28 × 21.5 × 1.2 cm) were arranged in a hexagonal pattern such that neighboring wells were 5.2 cm apart. The plate was attached to a stake that held it approximately 60 cm from the ground. Surrounding each well was a paper reinforcement colored pink, purple, blue, or orange, each representing a different reward type. Two of the reward types, 14% constant and 25% constant, always contained 20 μl sucrose solution, of 14% and 25% sucrose, respectively. The different concentrations were indicated by the color of paper reinforcement surrounding the wells. The other 2 reward types were 14% variable and 25% variable represented by 2 colors that differed from those used for the constant wells. Wells in the variable reward types contained either 10 or 30 μl sucrose solution in equal number giving a mean reward of 20 μl sucrose solution. The color of the reinforcement did not indicate the volume of sucrose in the variable wells. No 2 birds had the same well-color/well-type combinations.

Training consisted of presenting the bird with a board on which all 20 wells were marked with a single color, that is, all 20 wells were of the same reward type. The bird was allowed to visit and feed from the array 5 times before being presented with a board on which all the wells were of one of the other reward types. Once all 4 reward types had each been presented on 5 occasions, birds were presented with all 4 types again but with 3 successive visits for each type. The last 4 sessions of training consisted of birds visiting a board of a different reward type just once before another reward type was presented. The sequence of presentation of well types was different for each bird. Training was completed in a single day. Feeders were removed both during training and testing. Preferences do not mean exclusive use of sucrose from the feeders. However, birds obtained virtually all of their daily energy requirements from either the feeder or test arrays and were seen to visit natural flowers only on 1 or 2 occasions. Additionally, it seems likely that the birds gain at least some significant proportion of their protein from feeding on insects.

The training day was followed by 2–3 days (mean 2.50 ± 0.19 days) in which the bird's feeder contained either 14% or 25% sucrose. On the morning after the days of feeder access, the bird was presented with a choice test. Each choice test was followed by 2–3 days during which the birds were provided with only their feeders (mean 2.04 ± 0.04 days). Each bird experienced all 4 treatments, and the order of treatments differed across the 8 birds:

Treatment 1: (25|25): 2 days feeding from 25% sucrose in the feeder was followed by a variable/constant choice test using 25% sucrose.

Treatment 2: (25|14): 2 days feeding from 25% sucrose in the feeder was followed by a variable/constant choice test using 14% sucrose.

Treatment 3: (14|25): 2 days feeding from 14% sucrose in the feeder was followed by a variable/constant choice test using 25% sucrose.

Treatment 4: (14|14): 2 days feeding from 14% sucrose in the feeder followed by a variable/constant choice test using 14% sucrose.

During choice tests all wells on the board contained sucrose of the same concentration but half of the wells were designated variable flowers (i.e., 5 contained 10 μ l and 5 contained 30 μ l), whereas the other half of the flowers were designated constant wells (i.e., 10 flowers containing 20 μ l). Each well type was marked with the appropriate color from the training period. So that the birds did not learn the position of the wells containing 30 μ l, the location of 10 μ l and 30 μ l wells was changed every 5 feeding bouts (visits to the board). Additionally, the board was moved at least 15 cm and rotated 90 degrees between every feeding bout. The sequence of each well visited and the volume consumed from each was recorded for each feeding bout. The volume of sucrose consumed from each well was measured by collecting and measuring the volume of any residue using a microcapillary tube and then subtracting that volume from the initial volume in the well.

We recorded 56–150 feeding bouts in total for each of the 8 individuals (feeding rates were determined by the free-living birds). We used mean values for each treatment for each bird. Data were tested for normality using a Shapiro–Wilk test. The Mauchly criterion test was used to test for sphericity. If variances were nonhomogeneous, data were square-root transformed so that residuals were normally distributed.

RESULTS

Choice of constant or variable flowers—number of each type visited

Birds visited 1–16 wells per bout (mean = 5.52 ± 0.07 wells) and on average, revisited only $0.14 \pm 0.12\%$ of wells within a bout. We calculated the proportion of all wells visited that were the constant option for each bird for each treatment. We used one-sample *t*-tests to determine birds' preferences in each treatment (the proportion of constant wells chosen compared with an expected 50% if choices were random). Birds preferred the constant option in the 25|25 treatment ($t_7 = 3.72$, $P < 0.01$) but had no statistically significant preference in all other treatments ($t_7 = 1.26$ – 0.79 , $P = 0.24$ – 0.45).

The within-subject design of the experiment permits us to examine patterns of choices across the 2 treatments (feeder concentration and test concentration). In the following analyses, choices to the constant option were compared across treatments using a maximum-likelihood mixed-model in R. Model simplification based on Akaike information criterion (AIC) was used to determine the significant factors and interactions. We are aware of concerns about using model simplification but feel it was justified in these circumstances and that the *P* values are meaningful due to both the very limited number of comparisons made and only slight differences between the *P* values of factors in the full and reduced models (Mundry and Nunn 2009). The full model included: test concentration, feeder concentration, an interaction term between the 2, and bird as a random factor. The interaction term was not significant and was removed from the model ($F_{1,21} < 0.01$, $P = 0.95$). Both in the full model and model with the interaction removed, the sucrose concentration used in the choice tests had a significant effect on the birds' choices: birds chose the constant option more often when the test concentration was 25% than when it was 14% (full model: $F_{1,21} = 5.49$, $P = 0.03$; reduced model: $F_{1,22} = 5.69$, $P = 0.03$, Figure 1). Feeder concentration also played

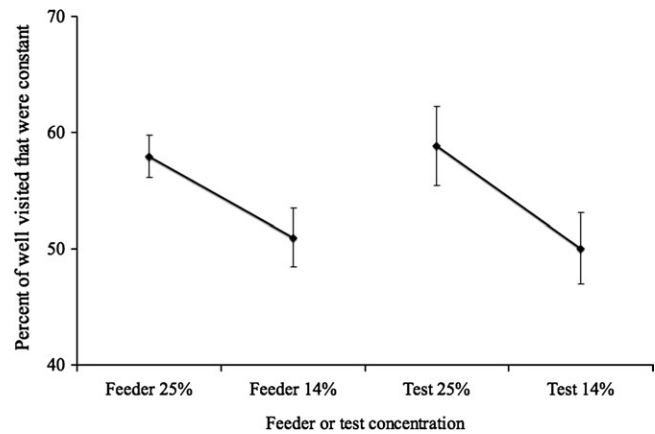


Figure 1

The proportion of the total number of wells visited that were the constant option for high and low feeder and test concentrations. Data are means and standard errors.

a role. Although preference for the constant option did not quite change significantly with feeder concentration (full model: $F_{1,21} = 3.44$, $P = 0.08$; reduced model: $F_{1,22} = 3.56$, $P = 0.07$), removal of feeder concentration from the model increased AIC, and the resulting model explained the variation significantly more poorly than did the model including feeder concentration (analysis of variance comparison of the model including feeder concentration with the model excluding feeder concentration: $L_{ratio_{2,4}} = 3.70$, $P = 0.05$). We conclude, therefore, that the concentration of sucrose in birds' feeders for the 2 days preceding tests did have a significant effect on the choices they made during tests about which wells to visit. Specifically, when birds had fed for 2 days from a feeder containing 25% sucrose, they were more likely to choose the constant option in the choice tests (Figure 1).

Choice of constant or variable flowers—volume of sucrose consumed

An alternative way to quantify preference is to measure the volume of sucrose consumed from each flower type because birds did not necessarily consume all the nectar from each flower they visited. We used one-sample *t*-tests to determine the birds' preferences in each treatment (the proportion of sucrose drunk per feeding bout from constant wells compared with an expected 50% if choices were random). Birds drank more from the constant option in the 25|25 treatment ($t_7 = 3.61$, $P < 0.01$) but showed no preference in all other treatments ($t_7 = 1.71$ – 0.58 , $P = 0.93$ – 0.28).

The influence of treatments (feeder and test concentrations) on how much birds chose to drink from each flower type was then modeled (as above for total number of wells). Data were means of the total proportion of sucrose consumed from constant wells within feeding bouts, for each bird/treatment ($N = 8$). The full model included: test concentration, feeder concentration, an interaction term between the 2, and bird as a random factor. The interaction was not significant ($F_{1,21} < 0.01$, $P = 0.99$) and was removed from the model. Both in the full model and model with the interaction removed, the sucrose concentration used in the choice tests had a significant effect on the birds' choices: birds drank more from constant wells than from variable wells when the test concentration was 25% (full model: $F_{1,21} = 6.14$, $P = 0.02$; reduced model: $F_{1,22} = 6.36$, $P = 0.02$). Feeder concentration also had a significant effect (full model: $F_{1,21} = 4.13$, $P = 0.06$; reduced model: $F_{1,22} = 4.27$, $P = 0.05$) such that when birds had fed for 2 days

from a feeder containing 25% sucrose they drank more from constant wells during the subsequent choice tests.

Choices of the variable option

To ensure that the constant/variable tests were not biased by birds learning which specific variable wells held 30 μl of sucrose, we calculated the total number of 10 μl and 30 μl wells visited by each bird in the variable option. Birds did not visit more of either sort of well, indicating they did not learn the position of the 30 μl wells (paired t -test: $t_7 = 1.06$, $P = 0.32$).

Role of increasing experience within and among bouts

We assessed the role of experience on decision-making during the test trials in 3 ways. First, we compared preferences for the constant option within feeding bouts. We calculated the percentage of first well choices that were to the constant option for each visit to the board and compared this value with the average value across all subsequent wells visited within the feeding bout. Choices made to the first wells visited during feeding bouts and the mean choice across all later wells in feeding bouts did not differ ($F_{1,50} = 2.16$, $P = 0.15$), indicating that birds' preferences at the beginning of a feeding bout did not change. The main effects of test concentration ($F_{1,50} = 15.65$, $P < 0.01$) and of feeder concentration ($F_{1,50} = 7.47$, $P < 0.01$) remained. There were no significant interactions ($F_{1,50} = 0.53$ to 0.03, $P = 0.87$ to 0.47).

Second, we compared choices to the constant option in the first feeding bout with choices in all subsequent feeding bouts. Choices made during the first bout were similar to those made during later bouts ($F_{1,50} = 0.06$, $P = 0.80$), indicating that birds' preferences did not change systematically between the first bout and later bouts. Again, the main effects of test concentration ($F_{1,50} = 5.33$, $P = 0.03$) and of feeder concentration ($F_{1,50} = 3.65$, $P = 0.06$) remained. There were no significant interactions between the feeder concentration or test concentration and bouts ($F_{1,50} = 0.80$ and 0.789, $P = 0.36$ and 0.38, respectively). The interaction between feeder and test concentration was nearly but not quite significant ($F_{1,50} = 3.79$, $P = 0.06$).

Third, we tested whether preferences changed progressively across the course of each treatment. We split the data into 3 blocks of 5 feeding bouts within each treatment (bouts 1–5, 9–14, and 18–22). For each block, we calculated the mean proportion of wells visited that were to the constant option (Figure 2). There was no effect of feeding block ($F_{2,46} = 0.79$, $P = 0.46$). Birds did not systematically change their preferences with increasing experience within test days.

Amount of sucrose consumed per well

We calculated the mean reward volume consumed from variable and constant wells for each bird for each treatment. Birds drank a mean of $17.9 \pm 0.18 \mu\text{l}$ (mean \pm standard error) from each constant well and $17.23 \pm 0.52 \mu\text{l}$ from each variable well, taking more ($0.62 \pm 0.31 \mu\text{l}$) from constants well than from variable wells ($F_{1,50} = 4.84$, $P = 0.03$). There was no effect of feeder concentration ($F_{1,50} = 1.74$, $P = 0.19$) or of test concentration ($F_{1,50} = 0.78$, $P = 0.38$). There was a significant interaction between the feeder concentration and test concentration such that birds drank more ($0.81 \pm 0.34 \mu\text{l}$) per well in the 25|25 treatment than they took in the other treatments ($F_{1,50} = 4.56$, $P = 0.04$). There were no significant interactions between well type (constant or variable) and either feeder concentration ($F_{1,50} = 0.27$, $P = 0.60$) or test concentration ($F_{1,50} = 1.07$, $P = 0.31$).

The amount of sucrose the birds left behind in the wells was dependent on the initial volume of sucrose in the wells ($F_{2,79} = 116.88$, $P < 0.01$). This was unaffected by either the test concentration ($F_{1,79} = 0.903$, $P = 0.34$) or the feeder concentration ($F_{1,79} = 0.29$, $P = 0.59$). Birds left significantly more sucrose in 30 μl than in 20 μl wells ($4.95 \pm 0.65 \mu\text{l}$ vs. $2.08 \pm 0.25 \mu\text{l}$; post hoc paired t -test: $t_7 = 5.92$, $P < 0.01$) and significantly more in 20 μl wells than in 10 μl wells ($2.08 \pm 0.25 \mu\text{l}$ vs. $0.62 \pm 0.12 \mu\text{l}$; $t_7 = 8.21$, $P < 0.01$). The volume left was not an equal proportion of the 3 well volumes ($6.24 \pm 1.17\%$ of 10 μl wells, $10.38 \pm 1.23\%$ of 20 μl wells, and $16.49 \pm 2.15\%$ of 30 μl wells; $F_{1,22,8.57} = 23.96$, $P < 0.01$; degrees of freedom corrected for violation of sphericity).

Energy availability per minute

We calculated the mean energy available to the birds per minute from what they consumed from our experimental apparatus:

$$\begin{aligned} & \text{Joules/per minute} \\ &= (\text{mean meal size(liters)}/\text{mean interbout interval(min)}) \\ & \quad \times (\text{mols sucrose/litre}(14\% \text{ sucrose} \\ & \quad = 0.431\text{mol/l and } 25\% \text{ sucrose} = 0.806\text{mol/l})) \\ & \quad \times \text{mass of 1 mol of sucrose} = 342 \text{ g} \\ & \quad \times \text{joules/g sucrose} = 16480 \text{ J} \end{aligned}$$

Birds consumed more energy when the test concentration was 25% than when the test concentration was 14% (mean energy available per minute; 25% = $29.81 \pm 0.97 \text{ J}$, 14% = $23.14 \pm 1.34 \text{ J}$; $F_{1,16} = 40.57$, $P < 0.01$), but there was no effect of feeder concentration ($F_{1,16} = 1.77$, $P = 0.20$) and

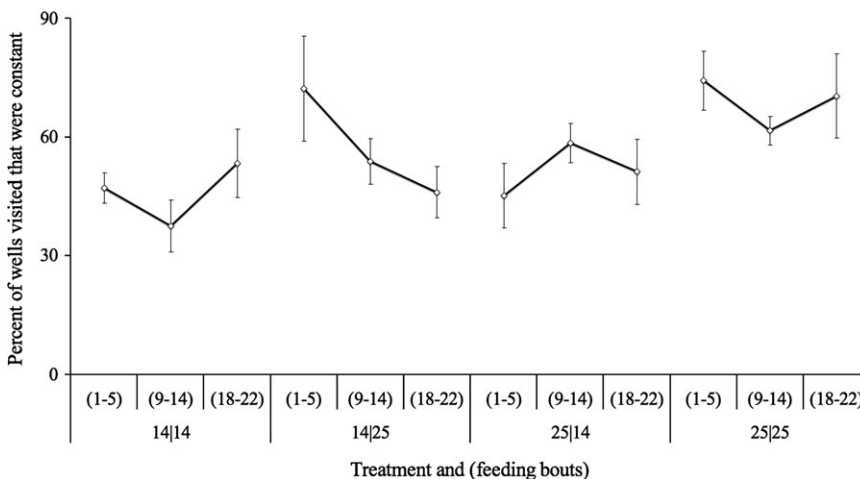


Figure 2

The proportion of the total number of wells visited that were the constant flower type for 3 equally spaced blocks of 5 feeding bouts (bouts 1–5, 9–14, and 18–22) throughout the day of each treatment. Data are means and standard errors.

no interaction between the feeder and test concentrations ($F_{1,16} < 0.01$, $P = 0.97$).

DISCUSSION

The concentration of sucrose used for testing and that in birds' feeders prior to testing had a significant effect on the degree to which they were risk sensitive. The birds' preference for the constant option over the variable option was relatively lower when faced with 14% sucrose in the test than it was when they were presented with 25% sucrose in the test. Their preference for the constant option was also relatively lower when their feeder had contained 14% sucrose rather than 25% sucrose prior to testing, irrespective of the concentration used during testing. This effect was seen both in the number of each well type from which the bird chose to drink during testing as well as in the total volume they drank from each well type. The effects of test concentration and the context of prior feeder contents on choices were not due to birds drinking different amounts of sucrose from one or other well type nor because risk sensitivity changed systematically within the day (they did not).

The effects of feeder concentration and test concentration were consistent with each other and seemed to operate independently and additively. This implies that the risk-sensitive choices exhibited in past experiments may have been influenced not just by the energy-budget manipulations but also by the difference between the pretest and test conditions. For example, all the birds tested in the Caraco (1981) experiment were not deprived of food for the first hour and a half of each day of testing. Based on our results, we contend that the food available early in the day may have caused these birds to be more risk averse than if the energy-manipulation period had been maintained consistently throughout the day. Similarly, our results suggest that hummingbirds in previous studies provided with 14% sucrose and tested with 20% were more risk averse than they would have been if they had been tested with 14% sucrose (Hurly and Oseen 1999; Biernaskie et al. 2002). It is possible that past experiments in which no effect of energy-budget manipulation was seen may have been affected by energy-budget conditions during the pretesting period (e.g., Clements 1990; Wu and Giraldeau 2004; de Jonge et al. 2008).

The probability of the past affecting the experimental data is reduced in laboratory studies of risk sensitivity in which the experimental energy-budget manipulation is extended for several weeks prior to testing (e.g., Caraco et al. 1990) or when testing occurs regularly within a prolonged energy-budget manipulation (e.g., Hamm and Shettleworth 1987; Ha et al. 1990; e Abreu and Kacelnik 1999). In the present study, birds had been using 14% sucrose feeders since their arrival on the feeding grounds several weeks prior to testing and only rarely visited wildflowers, preferring to use the feeders. Thus, their energy budgets were likely to have been positive and stable for a prolonged period prior to our manipulations. Here, we are interested in situations in which animals are tested under conditions different from those on which they were maintained. In addition to effects of past energy budgets, animals' expectations/estimates of the present conditions formed using past experiences are violated when a resource changes, creating a contrast between the expectation and actual conditions. This contrast can affect behavior even in the absence of a change in resource quality. For example, starlings trained for 10–14 days to expect either 1 or 7 food pellets after pecking reward keys were then tested for risk sensitivity using a constant reward of 4 pellets and a variable reward of 2 or 6 pellets. If expectations were based on a contrast effect, starlings trained to expect 7 pellets might view the mean reward of 4

pellets as a loss, whereas starlings trained with a single pellet might regard 4 pellets as a gain, even though energy obtained over time was kept equal for both groups. Indeed, significantly more starlings were risk prone in the "loss" treatment than in the "gain" treatment (Marsh and Kacelnik 2002). Behavioral responses to perceived changes in resource value (contrast) may have been favored by selection so as to allow animals to anticipate energy-budget changes and to adjust behavior appropriately in a timely fashion. Thus, perception of changes in resource value may be a mechanism by which behavior is adjusted although the energy-budget rule may be the ultimate reason why different behaviors are more appropriate under different conditions.

If expectations about the quality of a known patch carry over from the past based on a certain memory window (Shettleworth and Plowright 1992), then hummingbirds' responses to new conditions (14|25 or 25|14) and current sampling information may be mediated by this carryover. For example, conditions that currently provide a poor reward but recently provided a high reward may appear better than when both past and present conditions were poor. Bumblebees foraging in a Bayesian-like way (using prior knowledge of food distributions alongside current information) continue to use prior information about resource distributions to inform patch-leaving decisions even when tested in an environment with a very different resource distribution (Biernaskie et al. 2009). Bees used to relatively poor patches leave high-quality patches after finding fewer rewards than do bees with prior experience of high-quality patches. It is not yet clear how long such cognitive effects commonly persist, but there is evidence that some types of effect can be very long lived (Simitzis, Bizelis, et al. 2008; Simitzis, Deligeorgis, et al. 2008). In some cases, using a period of acclimatization with the aim of allowing restabilization of an animal's energy balance prior to an experiment may not sufficiently reduce the influence of past experience on the experimental data. Alternatively, the contrast effect may be a short-lived cognitive rule of thumb that allows animals to adjust their behavior to changes in reward quality before sufficient postingestive feedback is available for them to assess more accurately how the change has affected their energy budget.

Although we present convincing evidence that both past and current conditions influence risk-sensitive choices in hummingbirds, the design of our experiment cannot easily provide insight into the influence of contrast versus carryover effects. When test and feeder concentrations differ, the same response is predicted both by the energy-budget rule and the contrast effect. In both cases, birds should be less risk averse if they think conditions have got worse, or if they really have got worse, and vice versa. Thus, on top of the energy-budget rule, the contrast effect would cause the lines in Figure 1 to be steeper, whereas the carryover effect would cause the lines to be shallower. Distinguishing between these different expectation effects would require multiple manipulations of exposure time and food quality.

Our birds' choices are consistent with predictions from the energy-budget rule: Birds were more risk averse when they were or had been foraging on 25% sucrose than when they were or had been foraging on 14%. Our data are also consistent with predictions that come from a contrast expectation model. That is, animals perceiving a decrease in sucrose concentration would be expected to be more risk prone, even if their energy budget was unaffected (Kahneman and Tversky 1984; Kuhberger 1998; Marsh and Kacelnik 2002). Territorial hummingbirds' mass gain during the day is limited to 1–2% to reduce flight costs (as opposed to 35–40% increase mass in 20 min before dark), intake rate tends to be fairly constant across the day even following periods of fast and compensatory feeding is limited

(Tooze and Gass 1985; Calder 1991). Major adjustments of energy budgets occur via manipulations of metabolic costs during the night (Tooze and Gass 1985). As birds fed from their feeders for several hours in the morning before testing, birds feeding from a 25% feeder would have accumulated more energy than when feeding from a 14% feeder by the time the testing began, even if they started the day on fairly equal energy budgets. If they were then tested using 14% sucrose, their highest energy budget during recording should have been during the first few test feeding bouts. Therefore, if the birds' decisions were entirely governed by an energy-budget rule, we would have expected that birds that had had a feeder containing 14% sucrose would have been least risk averse during the first few test feeding bouts when tested with 25% sucrose. Conversely, we would have expected that birds that had had a feeder containing 25% sucrose would have been most risk averse during the first few test feeding bouts when tested with 14% sucrose, unless any difference in intake rate between 14% and 25% sucrose were compensated for by changes in behavior, for example, reducing flying time. We found no evidence, however, that the birds changed their preferences across a test day. We cannot, therefore, rule out that at least in the 14|25 and 25|14 treatments, contrast expectation may have played a role in the birds' decision making.

One unexpected result was that when birds did not empty wells, they neither left the same amount per well nor did they leave an amount proportionate to the well's contents. If birds were trying to maximize foraging efficiency, then they would be expected to empty 30 μ l wells, but they did not. A plausible explanation for this result is that the birds were constantly updating their estimate of the number and location of the different well types, as they took the same total volume and were not volume limited, in all the test conditions. As wells were not completely emptied, it seems unlikely that birds were attempting to get a better estimate of the actual well volume. The situations in which animals continue to sample a patch that is consistently poorer than another is known as contrafreeloading (Damato 1974; Osborne 1977). Information gathering of this kind appears to occur only when the resource or patch contents cannot readily be assessed visually (Bean et al. 1999), as is the case for the sucrose-containing wells we presented to our hummingbirds.

In summary, we show that prior experience can significantly impact current preference for variability although we were not able to distinguish between the effects due to the animal's energy budget and the animal's expectations. As prior experience is gathered throughout an animal's life, we predict that, in addition to effects due to differences in animals energy budgets, prior experience and expectations may well have a more substantial effect on risk-sensitive preferences than is often considered.

FUNDING

Natural Environment Research Council (UK); Natural Sciences and Engineering Research Council of Canada.

We thank Anjie Harris and Arild Husby for statistical advice, Christine Michell, Sandeep Mishra, and 2 anonymous reviewers for providing comments on an earlier version of the manuscript, and Sandra Goded and Emma Rosenfeld for their assistance in collecting data.

REFERENCES

Abreu FB, Kacelnik A. 1999. Energy budgets and risk-sensitive foraging in starlings. *Behav Ecol*. 10:338–350.
 Bean D, Mason GJ, Bateson M. 1999. Contrafreeloading in starlings: testing the information hypothesis. *Behaviour*. 136:1267–1282.

Biernaskie JM, Cartar RV, Hurlly TA. 2002. Risk-averse inflorescence departure in hummingbirds and bumble bees: could plants benefit from variable nectar volumes? *Oikos*. 98:98–104.
 Biernaskie JM, Walker SC, Gegeer RJ. 2009. Bumblebees learn to forage like bayesians. *Am Nat*. 174:413–423.
 Calder WA. 1991. Territorial hummingbirds. *Nat Geog Res*. 7:56–69.
 Caraco T. 1981. Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behav Ecol Sociobiol*. 8:213–217.
 Caraco T, Blanckenhorn WU, Gregory GM, Newman JA, Recer GM, Zwicker SM. 1990. Risk-sensitivity—ambient-temperature affects foraging choice. *Anim Behav*. 39:338–345.
 Clements KC. 1990. Risk-aversion in the foraging blue jay, *Cyanocitta cristata*. *Anim Behav*. 40:182–183.
 Damato MR. 1974. Derived motives. *Ann Rev Psychol*. 25:83–106.
 Doherty S, Cowie RJ. 1994. Effects of early feeding experience on long-term seed choice by canaries (*Serinus canaria*). *Ethology*. 97:177–189.
 Drezner-Levy T, Shafir S. 2007. Parameters of variable reward distributions that affect risk sensitivity of honey bees. *J Exp Biol*. 210:269–277.
 Gil M, De Marco RJ, Menzel R. 2007. Learning reward expectations in honeybees. *Learn Mem*. 14:491–496.
 Ha JC, Lehner PN, Farley SD. 1990. Risk-prone foraging behaviour in captive grey jays, *Perisoreus canadensis*. *Anim Behav*. 39:91–96.
 Hamm SL, Shettleworth SJ. 1987. Risk aversion in pigeons. *J Exp Psychol Anim Behav Process*. 13:376–383.
 Heilbronner SR, Rosati AG, Stevens JR, Hare B, Hauser MD. 2008. A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biol Lett*. 4:246–249.
 Hurlly TA. 2003. The twin threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. *Anim Behav*. 66:751–761.
 Hurlly TA, Oseen MD. 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Anim Behav*. 58:59–66.
 de Jonge FH, Ooms M, Kuurman WW, Maes HR, Spruijt BM. 2008. Are pigs sensitive to variability in food rewards? *Appl Anim Behav Sci*. 114:93–104.
 Kacelnik A, Bateson M. 1996. Risky theories—the effects of variance on foraging decisions. *Am Zool*. 36:402–434.
 Kahneman D, Tversky A. 1984. Choices, values, and frames. *Am Psychol*. 39:341–350.
 Krebs JR, Kacelnik A, Taylor P. 1978. Test of optimal sampling by foraging great tits. *Nature*. 275:27–31.
 Kuhberger A. 1998. The influence of framing on risky decisions: a meta-analysis. *Organ Behav Hum Decis Process*. 75:23–55.
 Lima SL. 1983. Downy woodpecker foraging behavior: foraging by expectation and energy-intake rate. *Oecologia*. 58:232–237.
 Logan FA. 1965. Decision making by rats—uncertain outcome choices. *J Comp Physiol Psychol*. 59:246–251.
 Marsh B, Kacelnik A. 2002. Framing effects and risky decisions in starlings. *Proc Natl Acad Sci U S A*. 99:3352–3355.
 McNamara JM. 1982. Optimal patch use in a stochastic environment. *Theor Popul Biol*. 21:269–288.
 Mundry R, Nunn CL. 2009. Stepwise model fitting and statistical inference: turning noise into signal pollution. *Am Nat*. 173:119–123.
 Ornelas JF, Ordano M, De-Nova AJ, Quintero ME, Garland T. 2007. Phylogenetic analysis of interspecific variation in nectar of hummingbird-visited plants. *J Evol Biol*. 20:1904–1917.
 Osborne SR. 1977. Free food (contrafreeloading) phenomenon—review and analysis. *Anim Learn Behav*. 5:221–235.
 Real L, Ott J, Silverfine E. 1982. On the tradeoff between the mean and the variance in foraging—effect of spatial-distribution and color preference. *Ecology*. 63:1617–1623.
 Schilman PE, Roces F. 2003. Assessment of nectar flow rate and memory for patch quality in the ant *Camponotus rufipes*. *Anim Behav*. 66:687–693.
 Schuck-Paim C, Kacelnik A. 2007. Choice processes in multialternative decision making. *Behav Ecol*. 18:541–550.
 Shapiro MS. 2000. Quantitative analysis of risk sensitivity in honeybees (*Apis mellifera*) with variability in concentration and amount of reward. *J Exp Psychol Anim Behav Process*. 26:196–205.
 Shettleworth SJ, Plowright CMS. 1992. How pigeons estimate rates of prey encounter. *J Exp Psychol Anim Behav Process*. 18:219–235.

- Simitzis PE, Bizelis JA, Deligeorgis SG, Feggeros K. 2008. Effect of early dietary experiences on the development of feeding preferences in semi-intensive sheep farming systems—a brief note. *Appl Anim Behav Sci.* 111:391–395.
- Simitzis PE, Deligeorgis SG, Bizelis JA, Fegeros K. 2008. Feeding preferences in lambs influenced by prenatal flavour exposure. *Physiol Behav.* 93:529–536.
- Stephens DW. 1981. The logic of risk-sensitive foraging preferences. *Anim Behav.* 29:628–629.
- Tooze ZJ, Gass CL. 1985. Responses of rufous hummingbirds to mid-day fasts. *Can J Zool.* 63:2249–2253.
- Valone TJ. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. *Anim Behav.* 41:569–577.
- Valone TJ. 1992. Information for patch assessment: a field investigation with black-chinned hummingbirds. *Behav Ecol.* 3:211–222.
- Valone TJ, Brown JS. 1989. Measuring patch assessment abilities of desert granivores. *Ecology.* 70:1800–1810.
- Wu GM, Giraldeau LA. 2004. Risky decisions: a test of risk sensitivity in socially foraging flocks of *Lonchura punctulata*. *Behav Ecol.* 16:8–14.
- Young JS. 1981. Discrete-trial choice in pigeons—effects of reinforcer magnitude. *J Exp Anal Behav.* 35:23–29.