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 energy 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.

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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 through-out 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 (Hurdy and Osecan 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 μl and 5 contained 30 μl), whereas the other half of the flowers were designated constant wells (i.e., 10 flowers containing 20 μl). 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 μl, the location of 10 μl and 30 μl 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 ± 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 (t7 = 3.72, P < 0.01) but had no statistically significant preference in all other treatments (t7 = 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 (F1,21 < 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: F1,21 = 5.49, P = 0.03; reduced model: F1,22 = 5.69, P = 0.03, Figure 1). Feeder concentration also played a role. Although preference for the constant option did not quite change significantly with feeder concentration (full model: F2,21 = 3.44, P = 0.08; reduced model: F2,22 = 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: Ratio2,4 = 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 (t7 = 3.61, P < 0.01) but showed no preference in all other treatments (t7 = 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 (F1,21 < 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: F1,21 = 6.14, P = 0.02; reduced model: F1,22 = 6.36, P = 0.02). Feeder concentration also had a significant effect (full model: F1,21 = 4.13, P = 0.06; reduced model: F1,22 = 4.27, P = 0.05) such that when birds had fed for 2 days

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.
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 = 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 (F1,50 = 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 (F1,50 = 15.65, P < 0.01) and of feeder concentration (F1,50 = 7.47, P < 0.01) remained. There were no significant interactions (F1,50 = 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 (F1,50 = 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 (F1,50 = 5.33, P = 0.03) and of feeder concentration (F1,50 = 3.65, P = 0.06) remained. There were no significant interactions between the feeder concentration or test concentration and bouts (F1,50 = 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 (F1,50 = 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 (F2,46 = 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 ± 0.18 μl (mean ± standard error) from each constant well and 17.31 ± 0.52 μl from each variable well, taking more (0.62 ± 0.31 μl) from constants well than from variable wells (F1,50 = 4.84, P = 0.03). There was no effect of feeder concentration (F1,50 = 1.74, P = 0.19) or of test concentration (F1,50 = 0.78, P = 0.38). There was a significant interaction between the feeder concentration and test concentration such that birds drank more (0.81 ± 0.34 μl) per well in the 25/25 treatment than they took in the other treatments (F1,50 = 4.56, P = 0.04). There were no significant interactions between well type (constant or variable) and either feeder concentration (F1,50 = 0.27, P = 0.60) or test concentration (F1,50 = 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 (F2,79 = 116.88, P < 0.01). This was unaffected by either the test concentration (F1,79 = 0.903, P = 0.34) or the feeder concentration (F1,79 = 0.29, P = 0.59). Birds left significantly more sucrose in 30 μl than in 20 μl wells (4.95 ± 0.65 μl vs. 2.08 ± 0.25 μl; post hoc paired t-test: t = 5.92, P < 0.01) and significantly more in 20 μl wells than in 10 μl wells (2.08 ± 0.25 μl vs. 0.62 ± 0.12 μl; t = 8.21, P < 0.01). The volume left was not an equal proportion of the 5 well volumes (6.24 ± 1.17% of 10 μl wells, 10.38 ± 1.23% of 20 μl wells, and 16.49 ± 2.15% of 30 μl wells; F1,22,57 = 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:

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

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 ± 0.97 J; 14% = 23.14 ± 1.34 J; F1,16 = 40.57, P < 0.01), but there was no effect of feeder concentration (F1,16 = 1.77, P = 0.20) and
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 (Hurlé 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 postigestive 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.


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REFERENCES


Beehler BM, Meier JD. 1987. Risk sensitivity in the hummingbird Sela

