



Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds

T. ANDREW HURLY & MICHAEL D. OSEEN

Department of Biological Sciences, University of Lethbridge

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We tested the risk-sensitive foraging preferences of wild rufous hummingbirds, *Selasphorus rufus*, with three types of artificial flowers. All three flower types provided the same mean volume of 30 μ l of sucrose, but differed in terms of variability of the reward: constant, low variance and high variance. In trinary comparisons, subjects preferred the low-variance reward over the constant reward, and the constant reward over the high-variance reward; a result not predicted by risk-sensitive foraging theory. However, when tested with traditional binary comparisons, hummingbirds showed conventional risk-averse behaviour and selected the constant reward over the low- or high-variance rewards. This reversal of preference represents a context-dependent foraging preference. The utility of selecting intermediate levels of risk and the source of the preference reversal are discussed relative to risk-sensitive foraging theory and the effects of local context on foraging choices.

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Animals are sensitive not only to mean foraging intake or energetic return, but also to variation about this mean. Consideration of the stochastic nature of foraging success greatly increases the authenticity of foraging studies. Risk-sensitive foraging has blossomed from its theoretical origins (Caraco 1980; Real 1980), through various levels of empirical and theoretical development, to the point where symposia are dedicated to this topic (see Smallwood & Cartar 1996).

With few exceptions, experimental tests of risk-sensitive foraging have involved captive animals and manipulated food sources (see review by Kacelnik & Bateson 1996). Only Barkan's (1990) study of black-capped chickadees, *Poecile atricapillus*, used wild birds in the field. Even tests of foraging by bumble bees have employed enclosed colonies except for a single study by Cartar (1991) on free-foraging wild bumble bees, *Bombus melanopygus*, *B. mixtus*, *B. sitkensis*. Generally, experimental protocols in risk sensitivity studies require strict control of animals to ensure that they experience, and then choose between, the specific foraging options presented to them.

Most studies of risk sensitivity require animals to make a binary choice: a constant versus a variable option with identical means. The importance of variability to foraging preferences would be more convincing if animals chose between more than two foraging options, just as the

results of a pharmacological study are more convincing when a dose–response curve is presented rather than merely reporting a difference between a treatment and a control.

Here we present the results of a risk-sensitive foraging experiment with rufous hummingbirds, *Selasphorus rufus*. The study is unique in two ways. First, it involved wild, territorial birds that were free to engage in natural foraging, defensive and breeding behaviours between visits to our artificial flowers. Second, we offered hummingbirds the choice of three flower types which provided the same mean reward but differed in variation about that mean. One flower type was constant, the second offered a moderate amount of variation and the third provided substantial variation. To our knowledge this is the first risk-sensitive test consisting of trinary, rather than binary, choices.

METHODS

Subjects and Study Site

The subjects were nine adult male rufous hummingbirds observed in the wild, four in 1994 and five in 1995. The study area was the Westcastle Valley in southwestern Alberta, in the eastern range of the Rocky Mountains (49°29'N, 114°25'W). In early May, commercial hummingbird feeders containing a 14% sucrose solution were placed throughout the study area with a minimum distance of approximately 100 m between them. A male

Correspondence: T. Andrew Hurly, Department of Biological Sciences, University of Lethbridge, 4401 University Drive, Lethbridge, AB, T1K 3M4, Canada (email: hurly@uleth.ca).

defending a feeder was marked by spraying a small amount of waterproof marking ink on the white area of its breast. Different colours and differently shaped marks allowed us to identify individuals.

Energetics

To determine the relationship between rate of net energy intake (E) and flower volume, each subject was trained to drink 20% sucrose (nectar) from 20 wells drilled in a Plexiglas plate ($28 \times 21.5 \times 1.2$ cm). The wells (10 mm deep \times 3.5 mm diameter) could hold up to 120 μ l and were arranged in a hexagonal pattern such that all nearest neighbour distances were 5.2 cm. Each well was marked with a white reinforcement ring. A repeating syringe dispenser was used to dispense sucrose volumes of 10, 20, 30, 40 or 50 μ l. The wells in a plate were filled with the same volume of solution and visits were recorded with a Hi-8 video camera. Wells were cleaned and replenished between feeding bouts. When a subject had visited at least 21 flowers of a certain volume (across several bouts), another volume was tested until the subject had experienced all five volumes in random order. Probe times (T_p) and interfloral travel times (T_t) were measured by video analysis to the nearest 1/30 s. Data were collected from five subjects in 1995. We calculated the rate of net energy return for each flower volume using an equation modified from Harder & Real (1987):

$$E = \frac{(VepS - (T_p + T_t)(C_p + C_{p(ws)}/2))}{(T_p + T_t)}$$

The net rate of energy intake is a function of the amount of nectar consumed minus the costs of flight while probing a flower and while travelling between flowers. For energy intake, V is the volume of nectar (μ l), e is the energy content of sucrose (16 500 J/g); p is the nectar density (1005.4 kg/m³); and S is the concentration of sucrose (20%). We calculated costs of flight following Tamm (1989). We calculated timing and costs from the midpoint of the flight between flower _{x} and flower _{$x+1$} to the midpoint of the flight between flower _{$x+1$} and flower _{$x+2$} . Thus, the cost of flight is influenced by the cost of moving the average mass of the bird (3.5 g, $C_p=0.7734$ J/g \times s), plus the additional cost of moving the mass of the nectar it drank at flower _{$x+1$} ($C_{p(ws)}$). Similarly, the cost of flight during probing is influenced by the bird's mass and the additional mass it accumulated while drinking nectar. Division of $C_{p(ws)}$ by a factor of 2 accounts for the gradual increase in mass while probing and obtaining this mass in the middle of the foraging flight. Because the flowers were closely spaced (5.2 cm), the birds maintained the same orientation while probing and travelling between flowers; thus, we used the same costs for probing and travelling.

Results from the energetic analysis indicated that the relation between rate of net energy intake and flower volume was approximately linear (Fig. 1). Thus, risk sensitivity could be tested by manipulating nectar volumes without the confounding effects of a strong non-linear relationship between rate of net energy intake

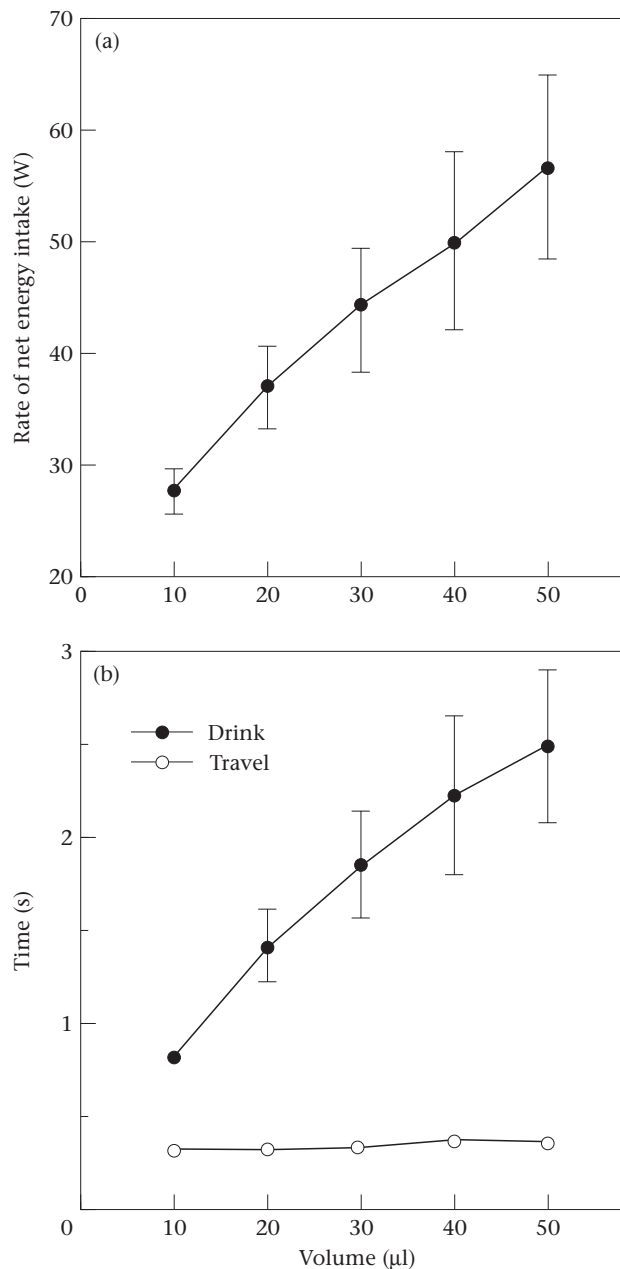


Figure 1. (a) Calculated mean (\pm SE) rate of net energy intake for hummingbirds foraging on different volumes of 20% sucrose solution (interfloral distances 5.2 cm). Energetics were calculated from Tamm (1989) and from measures of drink times and interfloral travel times (b) for different sucrose volumes (Harder & Real 1987). Standard error bars for interfloral travel times were negligible.

and nectar volume as has been observed for bumble bees (Harder & Real 1987; Cartar & Dill 1990).

Colour Preferences

To ensure that subjects choose flowers based on nectar rewards rather than on inherent colour preferences we conducted the following test. We presented each subject (1994: $N=2$; 1995: $N=5$) with three small Plexiglas blocks,

each containing three 120- μ l wells that were marked with red, yellow or pink rings and filled with 20% sucrose solution. Initially, we allowed each subject to forage repeatedly from these wells; each well was refilled between bouts. We used a chi-square test for 10–14 feeding bouts (50–60 colour choices) to determine whether a subject chose one colour more or less often than expected by chance. If a subject showed a colour preference, then the wells marked with that colour were left empty for several (four or five) bouts, after which the subject was again tested for colour preference over 10–14 bouts. Only one subject required the elimination of an initial colour preference.

Tests of Risk Sensitivity

To assess risk sensitivity, we presented all rewards together on a single Plexiglas plate that contained 18 wells (5.2-cm spacing), six of each colour (red, yellow and pink). Colour assignment to each well was randomized. For a particular subject, colours represented a specific variance regime, but colour–reward associations differed across subjects. The variance regimes were: constant: six wells contained 30 μ l of sucrose solution; low: three wells contained 20 μ l and three contained 40 μ l of sucrose; high: three wells contained 10 μ l and three contained 50 μ l of sucrose. Thus, the mean volume of nectar for wells of each type was 30 μ l, but variance was either negligible (0) in the constant volume flowers, low (10.95) or high (21.91).

Plates were presented at an angle of 45° to the horizontal. After each foraging bout at a plate, we cleaned and dried the wells before refilling them with sucrose. To ensure that subjects did not learn site or flower preferences on the plates, we used different plates with randomized patterns and we used each plate only four times, each time in a different rotational orientation. Thus, subjects could not learn that a specific flower contained a specific volume of nectar, and they could only learn that a certain level of nectar variation was associated with each colour. Trials ended when a subject completed approximately 300 drinks.

After the trinary tests were completed, we again eliminated colour preferences as described above, and then tested subjects with binary tests to compare the trinary preferences with conventional binary choice results. In 1994, two new subjects were presented with binary tests ($N=2$). In 1995, four of the five subjects tested earlier were available to be presented with binary tests ($N=4$). Plates containing 20 wells were used, with 10 wells marked yellow and 10 marked red. Positional assignment of these colours was randomized. Colours were assigned to treatments at random, with the restriction that a subject did not experience any of the same colour–treatment combinations as in its previous trinary tests. The two subjects in 1994 were tested with constant versus high-variance options and the four subjects in 1995 were tested with constant versus low-variance options.

Revisits to wells a subject had already emptied during a foraging bout were rare ($\leq 1\%$) and thus were ignored.

RESULTS

Subjects visited the foraging plates every 10–30 min throughout the day (0600–1800 hours). During each bout or visit they drank from a mean (\pm SE) of 5.1 ± 0.2 wells, consuming a total volume of 154.6 ± 6.0 μ l of nectar per bout ($N=7$ subjects). The volume consumed per bout represented a small fraction of the total volume available (trinary tests, 540 μ l; binary tests, 600 μ l).

Trinary Tests

Examination of cumulative choices of constant, low- and high-variance rewards across all bouts revealed that all seven subjects showed distinct preferences for flower type (Fig. 2). All preferred low-variance flowers to constant flowers, and constant flowers to high-variance flowers. These preferences became evident after approximately 15–20 foraging bouts. The relatively straight lines in Fig. 2 indicate that preferences were stable and changed little in magnitude until trials terminated at 300 probes (70–90 bouts). At the time of termination, chi-square tests for each of the seven subjects indicated significant differences in the total number of each flower type chosen ($\chi^2_2 > 9.3$, $P < 0.01$).

To compare subjects' preferences quantitatively, we calculated the slopes of the cumulative choice lines (Fig. 2) across the last 30 bouts for each subject. Examining these slopes across reward types within subjects (repeated measures ANOVA) revealed significant heterogeneity ($F_{2,12}=35.23$, $P < 0.0001$). The slope for low-variance flowers was steeper than the slope for constant flowers, which was steeper than the slope for high-variance flowers (Figs 2, 3a). Thus, there was significant agreement across subjects in the order and extent of preferences. These slopes also permitted us to test whether colour itself influenced choice. When slopes were classified by flower colour, independent of reward variance, there was no significant preference ($F_{2,12}=0.093$, $P=0.91$); thus, potential colour preferences were eclipsed by the variance treatments.

On what basis did the hummingbirds prefer low-variance flowers to constant flowers, and constant flowers to high-variance flowers? The subjects usually visited more than one flower type within a foraging bout. On average, all three flower types should provide the same mean reward. Repeated measures ANOVA confirmed a lack of heterogeneity in volume per flower per bout ($F_{2,12}=2.024$, $P=0.175$; Fig. 3b), but high-variance flowers provided slightly more nectar than low-variance or constant flowers. We assume that this trend was due to chance. If birds could distinguish volumes of flowers visually, they should have chosen more 50- μ l flowers than 10- μ l flowers. A paired t test indicated that birds did not discriminate between volumes within the high-variance flowers ($t_6=2.143$, $P=0.274$).

It appears that hummingbirds chose flower types based on information integrated across bouts, rather than within bouts. If birds chose the next flower based solely on the volume of sucrose in the most recently visited flower, then one would expect them to shift flower type

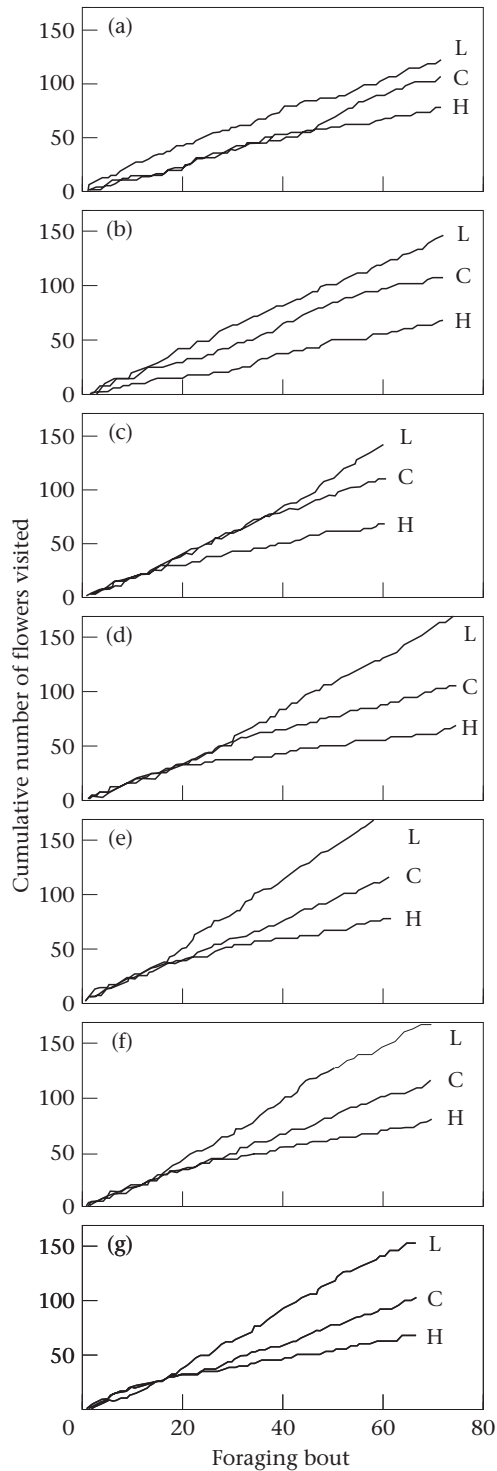


Figure 2. The cumulative number of drinks from flowers of each type versus foraging bout for the seven subjects (1994: $N=2$; 1995: $N=5$) tested in trinary choice experiments. C: Constant volume; L: low variance; H: high variance.

after experiencing a 10- μ l flower, but stay with that flower type following a 50- μ l flower. This was not observed. The probability of staying with high-variance flowers following a 50- μ l reward (0.218 ± 0.021) was no different from

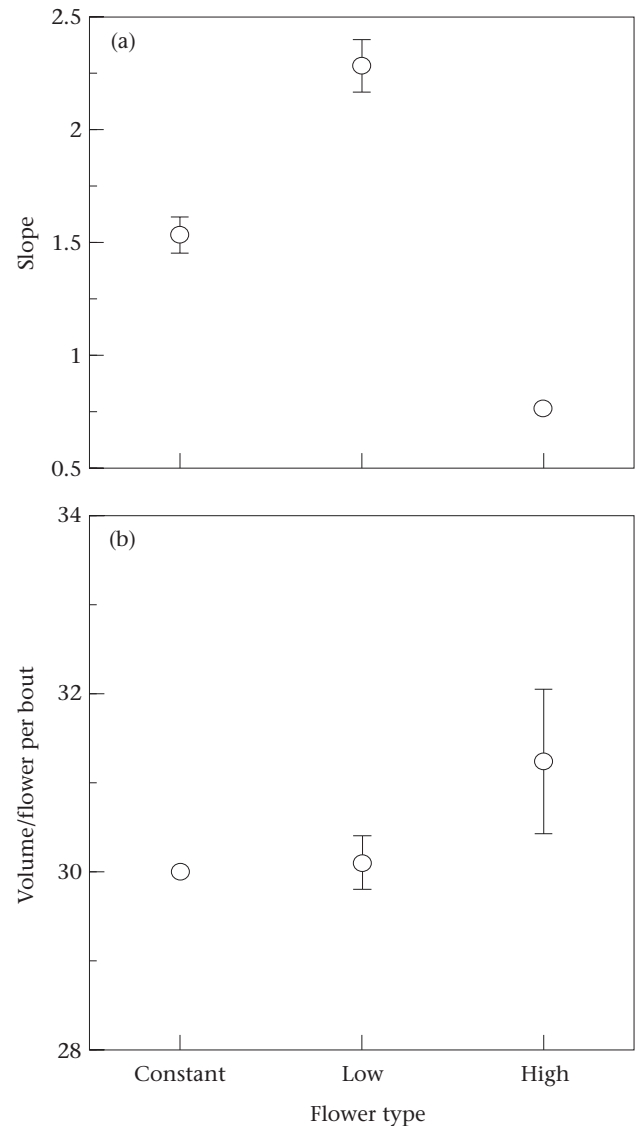


Figure 3. Preference data for trinary choice trials. (a) The mean slope of the cumulative drink lines (Fig. 2) averaged across the last 30 foraging bouts for each of seven subjects. (b) Mean volume of sucrose obtained from each flower type for each foraging bout. Mean volume must be 30 μ l for constant flowers, and should average 30 μ l for the other two flower types.

the probability of staying following a 10- μ l reward (0.227 ± 0.023) (paired t test on arcsine square-root transformed data; $t_6=0.245$, $P=0.8$). Again there was no evidence that subjects could discriminate volumes of nectar visually.

Binary Tests

Given the preference of low-variance over constant reward, but aversion to high variance, we have to ask whether there is something unusual about hummingbird foraging preferences and sensitivity to risk. Following the trinary tests, we presented our birds with binary tests. In

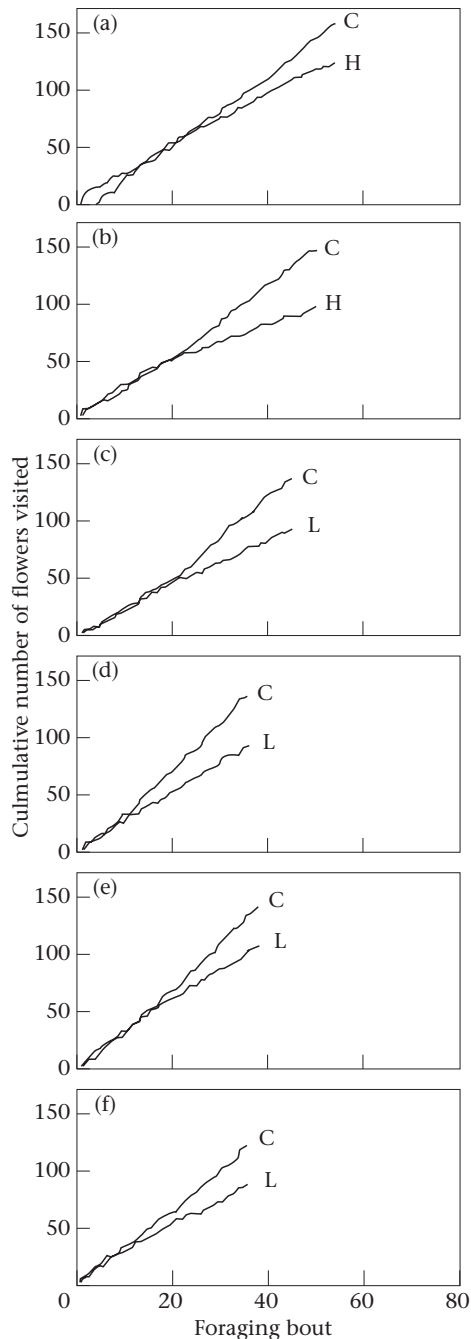


Figure 4. The cumulative number of drinks from flowers of each type versus foraging bout for the six subjects (a, b: 1994: $N=2$; c, d, e, f: 1995: $N=4$) tested in binary choice experiments. C: constant volume; L: low variance; H: high variance.

1994, two out of two new birds chose constant reward over high-variance reward, as one might predict based on the three-choice trials. However, in 1995, four birds tested (8.8 ± 2.4 days) previously with trinary choices were tested with constant versus low-variance rewards, and they too preferred the constant reward (Fig. 4). Thus, hummingbirds showed the same types of risk aversion we see in other species when presented with binary choices.

Analyses of the slopes of lines over the last 30 bouts revealed a significant preference for constant over variable (high or low) rewards ($F_{1,5}=163.0$, $P<0.0001$) when subjects from 1994 and 1995 were combined. Restricting analyses to 1995 data on constant versus low rewards again indicated a preference for the constant reward ($F_{1,3}=168.9$, $P=0.001$). As in the three-choice tests, classification of flowers by colour, independent of variance treatment, revealed no colour preference ($F_{1,5}=1.23$, $P=0.3$).

DISCUSSION

Rufous hummingbirds foraging on artificial flowers showed two unusual and unanticipated behaviours. First, they demonstrated intermediate risk preference through their disposition for the low-variance foraging option over the no-variance and high-variance options. Second, this preference in the trinary tests was context specific. The strong preference for the low-variance reward over the constant reward in trinary tests was reversed in binary tests.

The preferences shown by these hummingbirds were not likely experimental artefacts. There was complete concordance among the subjects across 2 years. Similar results were found in related experiments across an additional 2 years in which binary choices were offered before trinary choices (T. A. Hurly, unpublished data). Thus, an order or seasonal artefact is unlikely. The preferences in both binary and trinary tests were strong and stable over time (Figs 2, 4). These stable preferences occurred even though the subjects were free to choose any flower type at any time with equal cost. Many examples of risk-prone foraging have generally forced subjects to choose between two alternatives with no option of reversing choices within a foraging bout (e.g. Caraco 1981; Barnard et al. 1985). Finally, the rewards offered during the experiment ($10\text{--}50\ \mu\text{l}$, 20% concentration) were larger, but on a similar order of magnitude, to volumes found in plants frequented by hummingbirds. Mean concentration of nectar in 202 plants known or presumed to be pollinated by hummingbirds is 25.4% (Pyke & Wasser 1981). Mean volumes of nectar for plants used by rufous hummingbirds, such as *Ipomopsis*, *Castilleja* and *Penstemon*, range from 1.4 to 3.3 μl , with maximum volumes as high as 10 or 20 μl (Kodric-Brown & Brown 1978; Pyke 1978; Zimmerman 1988; Gass & Roberts 1992).

Can we explain the risk-intermediate choices hummingbirds made when presented with the three foraging options? Conventional models of risk sensitivity predict risk-prone choices only when subjects perceive that they are on negative energy budgets (Caraco 1981; Stephens 1981). In contrast, our hummingbirds must have been on positive energy budgets. Our study site supports healthy hummingbird populations and thus subjects were unlikely to approach a critical starvation threshold frequently. Furthermore, subjects were free to forage from surrounding flowers if they wished. The fact that they returned consistently to our experimental patch suggests that these represented foraging options that were better

than those available in natural patches of flowers. Finally, subjects often delayed return to our experimental patch and engaged in other behaviours such as chasing, vigilance and preening, and thus did not appear to be stressed energetically.

Traditional models of risk-sensitive foraging postulate a critical starvation threshold that an animal must exceed daily, or even hourly, for survival. Foraging policies that maximize such short-term survival map onto long-term survival and thus fitness (McNamara & Houston 1992). Theoretically, risk-prone behaviour may be favoured if additional thresholds beyond the starvation threshold are considered. McNamara *et al.* (1991) developed a model of risk-sensitive foraging for an animal that engages in reproduction (see also Caraco & Gillespie 1986). Inclusion of an energetic threshold for reproduction reveals advantages for risk-prone behaviour when mean energy intake is relatively low and when current energetic reserves are relatively high. Bednekoff (1996) too modelled the influence of risk on reproduction and showed that nonlinearity in the fitness function may select for risk-prone foraging. Essentially, fitness advantages of reproduction increase beyond a threshold of energy acquisition, but all foragers pay the same price for falling below this reproductive threshold, termed the bankruptcy effect.

The reproduction models of McNamara *et al.* (1991) and Bednekoff (1996) identify some conditions under which variable foraging options may be preferred over constant foraging options. Our experiments occurred during the breeding season and thus it is possible that preference for the low-variance option in trinary choices was related to an attempt to maximize fitness relative to both starvation and reproduction. However, the subjects did not choose the most variable option, but instead chose the low-variance option, an intermediate level of variation. Are there conditions under which intermediate levels of risk are optimal? Trinary choices have not been considered previously in models of risk sensitivity. The only way in which intermediate levels of risk have been considered is in models in which the forager can switch freely between constant and variable options (e.g. McNamara *et al.* 1990). It is not clear that such a blended tactic is similar to choosing a pure intermediate level of variance.

Why were hummingbird foraging preferences in this experiment context specific? Regularity of choices is a fundamental assumption of consumer choices in both economics and psychology. Specifically, regularity states that the addition of a new option to a set cannot increase the proportional choice of one of the original options (Huber *et al.* 1982). More generally, the preference between two options should not be influenced by the consideration of other options (Tversky & Simonson 1993). A preference for constant over low-variance options in binary comparisons, but a preference for low-variance options over constant in trinary comparisons suggests that the addition of high variance to the option set changed the perception of values or utilities of the low and constant options.

Regularity is required when choices are made on an 'absolute' basis (see Tversky 1969; Navarick & Fantino 1974). That is, each option is assessed according to its many possible dimensions and assigned a subjective utility that is absolute or independent of other options (McCleery 1978; Caraco 1981; Harder & Real 1987). The option with the highest utility is preferred. A 'comparative' method of choice assesses options differently. Here, options are compared across each separate dimension, and then the differences along each dimension are summed to assess the best overall option. Different dimensions may carry different weights in the final decision. Thus, the attributes of one option may influence the perceived utility of another.

These two models of choice were presented and tested in humans by Tversky (1969) and more recently by Shafir (1994) in honeybees. Shafir (1994) constructed artificial flowers that differed in both volume of nectar reward and length of corolla. Flowers with larger rewards had longer corollas, which increased the cost of handling. Bees were presented with pairs of flowers and their choices recorded. Twelve of 15 bees made choices that were consistent with both the absolute and comparative choice models. However, three bees displayed distinct intransitive choices that were consistent only with the comparative choice model. Shafir concluded that the comparative model requires additional consideration in foraging theory.

Human choices may sometimes depend on local context. Consumers preferred A to B, but reversed their preference in the context of a third, less attractive option, C (Simonson & Tversky 1992; Tversky & Simonson 1993). Whereas initially this behaviour appears similar to that displayed by the hummingbirds in this study, it differs because each option was described by at least three dimensions: price, quality and discount. Similarly, the intransitive choices reported by Tversky (1969) and Shafir (1994) rely on the careful construction of options with two or three dimensions (see also Wedell 1991). In general, comparative models of choice appear limited in their ability to explain our hummingbird preferences because they depend upon options being defined with multiple attributes or dimensions. In the present experiment there was only a single experimental dimension, that of variance. Mean reward did not vary significantly in the manipulation or due to chance in the actual foraging of the hummingbirds (Fig. 3b). Thus, the preference reversal we observed is not explained in an obvious way by the comparative choice model through the evaluation of multiple dimensions.

It is possible to consider multiple energetic thresholds equivalent to multiple dimensions. That is, our three foraging options may have offered different fitness consequences relative to a starvation threshold and relative to a separate and higher reproductive threshold. Comparing the three foraging options relative to a starvation threshold and a reproductive threshold separately, and then summing the results may produce different preferences than assessing the utility of each of the options independently and then comparing them (Tversky 1969; Shafir 1994). Thus, the perceived value of low variance

under the trinary choice when the full range of options was immediately available, may have differed from its perceived value when compared only with a constant option (see *Tversky & Simonson 1993*). The ability of a third option to change the context of choice, and thus preference between the two options, has been attributed to three possible models as reviewed by *Wedell (1991)*. The new option, or 'decoy' may change the weighting of multiple dimensions; it may alter the subjective value of an option along some dimensions; or the decoy may alter dominance relationships between options in an asymmetric way.

The final and critical issue involves the ultimate effects of the reversing choices made by the hummingbirds. That is, does the local knowledge of all three foraging options available during the trinary choices confer a fitness advantage to choosing the low-variance option over the constant option? Alternatively, we can postulate that the cognitive system that governs risk-sensitive choices, and which has evolved under natural selection, has malfunctioned under the specific conditions presented in this experiment. The malfunction alternative seems unlikely. Our trinary choices were likely to be more similar to the natural range of nectar variability than were binary choices in that natural nectar sources show a relatively broad range of variation (*Zimmerman 1988*). Furthermore, the strengths of preferences and the concordance between subjects suggest that the observed preferences were not likely to be cognitive artefacts of unusual experimental conditions. To our knowledge, this is the first experiment that has presented animals with three levels of variance simultaneously. For generality, it is important to explore this paradigm with other species. Our results suggest that hummingbirds may not assign an absolute utility to foraging options according to their variance. That is, the assignment of utility may be influenced by other options available at the same time. This context-specific preference reversal is the type of paradox (*Real 1996*) that may provide new insights into our understanding of risk-sensitive foraging.

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