



Context-dependent foraging choices in risk-sensitive starlings

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Existing models of risk-sensitive foraging assume that animals assign value to different options according to an absolute currency. It follows from this assumption that choices are expected to be both transitive and regular, because the value assigned to an option is independent of its context. I tested these predictions by comparing preferences obtained in binary and trinary contexts. European starlings, *Sturnus vulgaris*, were trained using an operant paradigm to forage for three options: Constant (C) that provided a fixed number of food pellets; Low variance (L) with a coefficient of variation of 71% in the number of pellets; High variance (H) with a coefficient of variation of 106%. The preferences of the birds were tested in three binary choice treatments (CL, CH, LH) and one trinary choice treatment (CLH). Overall, there was no evidence for violations of either transitivity or regularity. However, overall, a bird's relative preference for its most preferred option over its second most preferred option was significantly greater in the trinary treatment than in the comparable binary treatment. This effect of context on choice is compatible with starlings' use of comparative instead of absolute currencies in decision making.

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A large body of experimental literature has shown that foraging animals are sensitive not only to their mean rate of energy intake, but also to the variation in this rate (reviewed in Kacelnik & Bateson 1996). This phenomenon, known as risk sensitivity, has been the subject of intense theoretical interest by both behavioural ecologists and animal psychologists (reviewed in Kacelnik & Bateson 1997; Bateson & Kacelnik 1998). However, there is currently a lack of agreement over whether risk sensitivity is an adaptive response to variability in food sources, or whether it is the nonadaptive by-product of the cognitive processes that underlie decision making. In this study, I addressed the proposal that a factor in our inability to arrive at a unified explanation for risk-sensitive foraging may be our dependence on data obtained from binary choice tests, and our consequent focus on a single category of choice models.

Most data on risk-sensitive foraging have been obtained from experiments in which a forager is presented with a binary choice of two foraging options differing in the variance in rate of reward (e.g. Stephens & Paton 1986; Caraco et al. 1990; Reboresda & Kacelnik 1991; Bateson & Kacelnik 1996). However, our reliance on these findings, and hence also the models derived and discarded on the basis of them, has recently been cast into doubt by results showing that the direction of risk-sensitive preferences can depend on the context in which the foraging options

are presented. According to Hurly & Oseen (1999), rufous hummingbirds, *Selasphorus rufus*, are risk averse for variance in nectar volume when they are presented with a binary choice, either between a constant option (with zero variance) and a low-variance option, or between a constant option and a high-variance option. However, when the birds are presented simultaneously with the trinary choice of constant, low- and high-variance options, they switch to preferring the low-variance option. This result is important, because, as explained below, it implies that existing models of animal choice are based on an incorrect assumption about the basic category of choice mechanism used by foraging animals.

Existing models of risk-sensitive foraging mostly assume that animals make choices between alternative foraging options according to the value of a currency (Table 1). All of these models assume absolute currencies, meaning that the value assigned to an option corresponds to an intrinsic property of that option, and should therefore be independent of the other options present at the time of evaluation. In some cases, this focus on absolute evaluation mechanisms comes from a belief that the fitness consequences of choosing a particular option should be absolute, and, therefore, that the currencies used as short-term surrogates for fitness should also be absolute (but see Houston 1997 for an alternative view).

If animals use absolute currencies to evaluate alternative options, it follows that we expect animal choice to be rational, where rationality implies that preference between options does not depend on the presence or

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Table 1. Currencies maximized in existing risk-sensitive foraging models

Model	Currency maximized	Source
Z score Variance discounting	Probability of survival $\mu - k\sigma^2$	Stephens 1981; Stephens & Krebs 1986 Oster & Wilson 1978; Caraco 1980; Real 1980a, b
Coefficient of variation Short-term rate	μ/σ Short-term rate of food intake	Shafir 2000 Harder & Real 1987; Bateson & Kacelnik 1996
Scalar Utility Theory	Magnitude of a sample from memory	Reboreda & Kacelnik 1991; Kacelnik & Brito e Abreu 1998

μ is the mean, σ^2 is the variance and k is a constant relating to the undesirability of variance.

absence of other options. Transitivity and regularity are two of the most frequently cited properties of rational decision making, and tests of these properties are commonly used to assess rationality in humans (Tversky 1969; Huber et al. 1982; Tversky & Simonson 1993).

The property of transitivity applies to a series of binary choices. A choice is defined as transitive if, when A is preferred to B, and B is preferred to C, then A is also preferred to C. When choice is stochastic, weak stochastic transitivity is violated if C is preferred to A, and strong stochastic transitivity is violated if the preference for A over C is less than either the preference for A over B or the preference for B over C.

The property of regularity applies to choices between different numbers of options. A choice is defined as regular if the absolute preference for a particular option cannot be increased by the addition of further options to the choice set. Regularity is a special case of the principle of independence of irrelevant alternatives (Luce 1959), which states that the addition or subtraction of an option that is irrelevant to the comparison should not influence the relative preferences between the original options. The pattern of choice described by Hurly & Oseen (1999; T. A. Hurly, personal communication), whereby the addition to a set of a third, less preferred option (the high-variance option) increases the absolute preference for one of the original options (here the low-variance option), is formally a violation of regularity (Huber et al. 1982).

To explain violations of transitivity and regularity it is necessary to assume that animals do not use absolute currencies to evaluate alternative options, but instead use comparative currencies, whereby the value of an option is computed relative to the other options available at the time of choice. Models of choice based on comparative currencies are capable of explaining why animals might sometimes show violations of transitivity and regularity, because they allow the relative preference for one option over another to change according to the context of the choice (Huber et al. 1982; Tversky & Simonson 1993). Such models of choice all apply to situations in which the options differ in more than one dimension, whereas in Hurly & Oseen's (1999) study, only the single dimension of risk was explicitly manipulated. However, although the options were designed to differ only in risk, it is possible that the hummingbirds in their study perceived variation in other dimensions, such as the rate of energy intake or the skew in energy intake offered by the three options.

Thus it is possible that Hurly & Oseen's results could be accommodated by existing theories of choice.

Given the potential importance of Hurly & Oseen's (1999) result for models of risk-sensitive foraging, my aim in this study was to replicate and extend their experiment in a different system. I chose to use European starlings, *Sturnus vulgaris*, foraging in Skinner boxes in the laboratory, because starlings have been the source of much of the detailed, quantitative data on risk-sensitive foraging on which mechanistic models of risk have been based (e.g. Reboreda & Kacelnik 1991; Bateson & Kacelnik 1995, 1996, 1997; Brito e Abreu & Kacelnik 1999). I tested starlings' preferences for variance in food amount in four treatments: the three possible binary combinations of constant, low variance and high variance (Hurly & Oseen omitted low versus high variance), and the trinary treatment of constant, low and high. Comparison of the preferences obtained in the three binary treatments permits analysis of whether the birds' choices are transitive, whereas comparison of the preferences obtained from the binary and trinary treatments permits analysis of whether the birds' choices are regular. Violations of either transitivity or regularity provide evidence for comparative choice mechanisms in starlings.

METHODS

Subjects

Subjects were eight European starlings, four males and four females, caught as fledglings 1 month before the study. For the period of the experiment, the birds were housed individually in wire cages 44.5 cm high \times 75 cm wide \times 45 cm deep, situated in an indoor, air-conditioned laboratory maintained at ca. 14°C. with a 12:12 h light:dark cycle. The birds were fed Purina Wild Game Starter supplemented with mynah granules, mealworms and assorted fruit. Free-feeding weights were established for each bird for 1 week before the beginning of training. Once training commenced, birds were weighed daily before training, and after training they were fed a ration that was adjusted to keep their weights at ca. 90% of their free-feeding weights. This ration had always been completely consumed before training the subsequent day. If a bird's weight fell below 85% of its free-feeding weight, training was halted, and the ration was adjusted until the bird again exceeded its 85% weight. For the purposes of

Table 2. Parameters of the three foraging options

Option	Number of pellets and probability of occurrence (P)	Mean number of pellets	Coefficient of variation (%)
Constant (C)	4 ($P=1.0$)	4	0
Low variance (L)	2 ($P=0.667$) or 8 ($P=0.333$)	4	71
High variance (H)	1 ($P=0.667$) or 10 ($P=0.333$)	4	106

One pellet=45 mg.

training, I divided the birds into two groups of four. The AM group was trained between 0900 and 1200 hours, and the PM group between 1200 and 1500 hours each day. The birds were trained 7 days a week throughout the experiment. After the experiment, the birds were retained for future use.

Apparatus

For their daily training and experimental sessions, I transferred the birds to purpose-built starling operant boxes (Campden Instruments, Loughborough, U.K.) with internal dimensions of height 26 cm, width 25 cm and depth 23 cm. Each box was lit with a central white house light that remained on throughout training and experimental sessions. The left wall of the box was equipped with a horizontal row of three 4-cm-diameter, translucent pecking keys that could be transilluminated with either red, green or amber light (adjusted to have equal luminance). Below the keys was a single food hopper connected to an external pellet dispenser; the hopper could be illuminated with white light. The middle key was 7 cm from the hopper, and the outer two were 10 cm (centre to centre). Custom-made 45-mg precision starling pellets (P. J. Noyes, Lancaster, New Hampshire, U.S.A.) were used for reinforcement throughout the experiment. A perch was situated in front of the pecking keys and food hopper, and a water bottle was located on the opposite wall of the box. The boxes were housed inside sound-attenuating chambers equipped with fans to provide continuous ventilation and masking white noise. Four identical operant boxes were connected to an Acorn Archimedes PC equipped with the Arachnid experimental control language and associated interfacing hardware (CeNeS, Cambridge, U.K.). The computer controlled the presentation of stimuli and reward contingencies and collected the data.

Training

The first phase of training involved acclimating the birds to the operant boxes and training them to eat food from the hoppers. Next, the birds were trained to peck at illuminated keys to obtain food using a standard autoshaping procedure (e.g. Bateson & Kacelnik 1995) in which one of the keys was illuminated for 10 s followed by the delivery of food to the hopper. Trials were separated by a 100-s intertrial interval. Birds were reinforced

for pecking at the illuminated key by immediate delivery of food (two pellets). All three key positions (left, centre and right) and all three key colours (red, green and amber) were used during autoshaping to ensure equal familiarity with these alternatives before the experiment.

Choice Experiment

The experiment involved the comparison of three foraging options differing in the variance in the number of pellets delivered on a given trial. The options were designated Constant (C), Low variance (L) and High variance (H) (Table 2). The coefficient of variation of L was chosen to be similar to the variable option in a previous risk-sensitivity experiment with starlings that found clear risk-aversion for variance in food amount (Brito e Abreu & Kacelnik 1999). Skewed distributions were used in L and H to increase the coefficient of variation for a given mean number of pellets; this was important since the maximum number of 45-mg pellets a starling will eat in a single trial is limited.

Comparisons were made in four treatments. Three treatments involved binary comparisons between two of the options: C versus L, C versus H and L versus H. The fourth was a trinary comparison between all three options: C versus L versus H. Each bird experienced the four experimental treatments in a different order, chosen such that, overall, there was no correlation between a treatment and the position in which it was received: overall, each option appeared twice in position 1, twice in position 2, twice in position 3 and twice in position 4. A different-coloured light (red, amber or green) indicated each option. The assignment of colours to options was constant for a given bird throughout the experiment, but counterbalanced across birds such that there was no overall association between colour and option.

Within each treatment, a bird received daily sessions composed of 18 training trials followed by 18 choice trials. Training trials allowed the birds to learn the association between a given colour and option with which it was associated, and choice trials measured the birds' preferences for the options. In each training trial, only a single option was presented to the bird. The training trials for each treatment were arranged such that the bird experienced the different options (two for binary treatments and three for the trinary treatment) an equal number of times (nine each for binary treatments and six each for the trinary treatment) in a random order. The

number of pellets delivered in the L and H options was also chosen such that over the 18 training trials the probabilities programmed (Table 2) were actually experienced by the birds. The key used in each trial was chosen randomly to discourage the development of position biases.

A training trial started with one of the keys beginning to flash (on 0.7 s, off 0.3 s). The bird had to peck the flashing key once to initiate the trial. The first peck caused the key light to illuminate solidly, and started a 5-s fixed interval. The first peck after this 5 s had elapsed caused the key light to extinguish and the appropriate number of pellets to be delivered to the hopper. Food delivery was indicated by the hopper light coming on for the duration of pellet delivery, and was followed by a fixed intertrial interval (ITI) of 240 s, during which only the house light was illuminated. A long ITI was used to allow the birds the chance to consume the large 8- and 10-pellet rewards before the start of the next trial.

In each choice trial, either two (binary treatments) or three (trinary treatment) options were presented simultaneously, and the bird had to choose between them. In these trials, the position in which each option was presented was chosen randomly. The number of pellets delivered in the L and H options was chosen randomly according to the probabilities given in Table 2. Choice trials were programmed identically to training trials, except that a trial started with two (binary treatments) or three (trinary treatment) keys flashing. The first peck made by the bird caused the chosen key light to cease flashing and illuminate solidly, as in the training trials, and the other light (binary treatments) or lights (trinary treatment) to extinguish for the remainder of the trial.

A session was terminated either after the 36 programmed trials had been completed or after 3 h, whichever came sooner. Birds received one session daily. For each bird, a treatment continued until 10 'good' sessions had been obtained, where I defined a good session as one in which the bird completed 90% (i.e. 16 or more) of the 18 possible choice trials, and no more than 10% (i.e. 14) of the average of 144 pellets delivered remained on the floor or in the hopper at the end of the session.

Analysis

The birds that developed significant preferences varied in the number of sessions it took for their preferences to emerge; the maximum number of sessions required for asymptotic preference was five. I therefore discarded the choice data from the first five sessions of each treatment and based the analyses on the data from the last five good sessions obtained from each bird in each treatment. This equates to 90 choice trials in 30 cases and 89 in the remaining two, where a bird failed to complete the final choice trial within the 3 h allocated for a session.

To quantify the difference in the birds' preferences between the binary and trinary treatments, I computed two measures of preference. The first measure of preference was the absolute proportion of choices for each option in each treatment. A violation of regularity is defined as occurring if the absolute proportion of choices

allocated to an option is higher in the trinary treatment than in any of the binary treatments. The second measure of preference I computed was relative preference, where the relative preference for option A over option B is defined as:

$$\text{Relative preference} = \frac{\text{proportion A} - \text{proportion B}}{\text{proportion A} + \text{proportion B}} \quad (1)$$

This relative preference score ranges between -1 and $+1$. A score of -1 corresponds to zero choices for A, a score of $+1$ corresponds to zero choices for B, and a score of 0 corresponds to an equal number of choices to options A and B. Luce's (1959) choice axiom predicts that if a new option is added to the choice set, it should take its share of choices from the pre-existing options in proportion to their original shares, and therefore that relative preference should be unaffected by context (see Bateson et al. 2002 for a proof of this).

Nonparametric statistics were used throughout the analysis because the data were not normally distributed, and this problem was not corrected by any standard transformation. I used two-tailed tests with $\alpha=0.05$.

RESULTS

Binary Treatments

Overall results

Figure 1a shows the median proportion of choices made by the eight birds to the less variable option (i.e. C in treatments CL and CH, and L in treatment LH) in the three binary treatments. In the CL and CH treatments, preference was not significantly different from random (single-sample Wilcoxon signed-ranks tests against a random expectation of 0.5: $T+=12.5$ and 24.5 , respectively, $N=8$, NS), but in the LH treatment the birds were significantly risk averse ($T+=36.0$, $N=8$, $P=0.014$).

Comparing the three binary treatments, the median proportion of choices for the less variable option differed significantly between treatments (Friedman test: $F_{2,2}=6.25$, $N=8$, $P=0.05$), and post hoc multiple comparisons (Siegel & Castellan 1988, pp. 180–181) show that this effect comes from the difference between the CL and LH treatments, with the birds significantly more risk averse in LH than in CL (critical difference = 6.771, $|R_{CL} - R_{CH}|=5$, $|R_{CL} - R_{LH}|=10$, $|R_{CH} - R_{LH}|=5$; therefore, only the comparison of CL and LH exceeds the critical difference). These overall results are consistent with the following ranking of the three options: $L > C > H$, where ' $>$ ' indicates 'is preferred to'. Since the two adjacent preferences between L and C, and C and H, were not great enough to be significant, but the preference between L and H was great enough to be significant, these results conform with both weak and strong forms of stochastic transitivity.

Behaviour of individual birds

In each of the binary treatments, the significance of individual birds' preferences was established using chi-square goodness-of-fit tests, for which the expected values

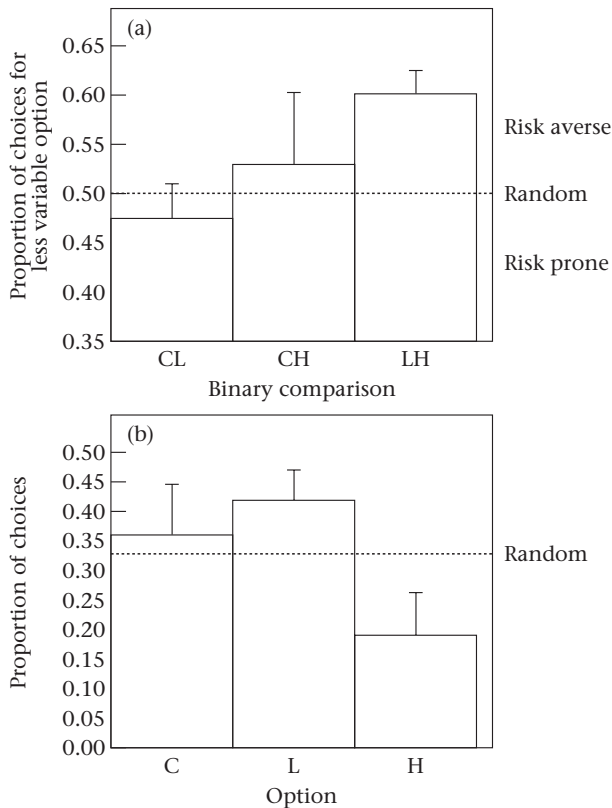


Figure 1. Birds' preferences in the binary (a) and trinary (b) treatments. Both (a) and (b) show the median of the eight birds' preferences+semi-interquartile ranges. The expectation of random choice is indicated by the dotted line. C=constant option, L=low-variance option, H=high-variance option.

Table 3. Significant preferences from individual birds in the three treatments

Bird	Binary			Trinary
	CL	CH	LH	
1	—	C>H*	L>H†	L>C>H**
2	—	C>H***	—	C>L>H***
3	L>C***	H>C***	L>H*	L>H>C***
4	—	—	L>H†	L>H>C*
5	—	—	L>H†	—
7	—	—	L>H***	C>L>H***
8	—	—	L>H†	L>C>H**
9	—	C>H**	L>H***	C>L>H***

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; chi-square tests; dashes indicate no significant preference.

were equal to half the total number of choices (i.e. 45 in 22 comparisons, and 44.5 in the remaining two). Of the total of 24 comparisons, only eight produced preferences that were significantly different from random ($\chi^2_1 = 4.44-30.04$, $P < 0.05$), and four more comparisons produced preferences marginally significantly different from random ($\chi^2_1 = 2.84-3.60$, $P < 0.1$; Table 3). Only one subject (Bird 3) had significant preferences in all three binary

treatments. Three subjects (Birds 4, 5, 8) had no significant preferences in the binary treatments. Of the five birds with one or more significant preferences, three ranked L highest, and four ranked H lowest. No bird ranked H highest or L lowest.

The preferences of Bird 3 were consistent with both weak and strong forms of stochastic transitivity in that $L > H$, $H > C$ and $L > C$, and in the LC comparison the preference was greater than in either of the adjacent comparisons (LH and HC).

Trinary Treatment

Figure 1b shows the median proportion of choices made by the eight birds to each option in the trinary treatment. The proportion of choices made to both the C and L options was not significantly different from random (single-sample Wilcoxon signed-ranks tests against a random expectation of 0.33: $T_+ = 24$ and 31, respectively, $N = 8$, NS). However, the birds chose option H significantly less than predicted ($T_+ = 3$, $N = 8$, $P = 0.042$), although the overall effect of option was not significant (Friedman test: $F_{2,2} = 3.25$, $N = 8$, NS). The results of the trinary treatment are broadly consistent with those from the binary treatments, in that option L was ranked highest and option H was ranked lowest in both treatments.

As for the binary treatments, the significance of preference in individual birds in the trinary treatment was established using chi-square goodness-of-fit tests. However, in this case, expected values were equal to one-third of the total number of choices (i.e. 30 in all birds). Bird 5 had no significant preferences (as in the binary treatments), but the remaining seven birds all had choices that departed from random ($\chi^2_2 = 7.40-38.06$, $P < 0.05$). Four of seven birds ranked L highest, and the other three ranked C highest. Five of seven birds ranked H lowest, and the other two ranked C lowest. Therefore, as observed in the binary treatments, no bird ranked H highest or L lowest. Table 3 gives the individual birds' rankings of the three options in the trinary treatment.

Comparison of Binary and Trinary Results

Since Bird 5 showed no significant preferences in either the binary or trinary treatments, I excluded it from further analyses on the grounds that there is no evidence that it learned anything in the experiment. In the remaining seven birds, any significant preferences recorded in the binary treatments were in the same direction as the ranking of options an individual bird displayed in the trinary treatment; in no case was there a significant reversal of preference between the binary and trinary treatments (Table 3). There was also no overall evidence for a violation of regularity. In all cases, the absolute proportion of choices made to a particular option was lower in the trinary treatment than in the binary treatments (Table 4).

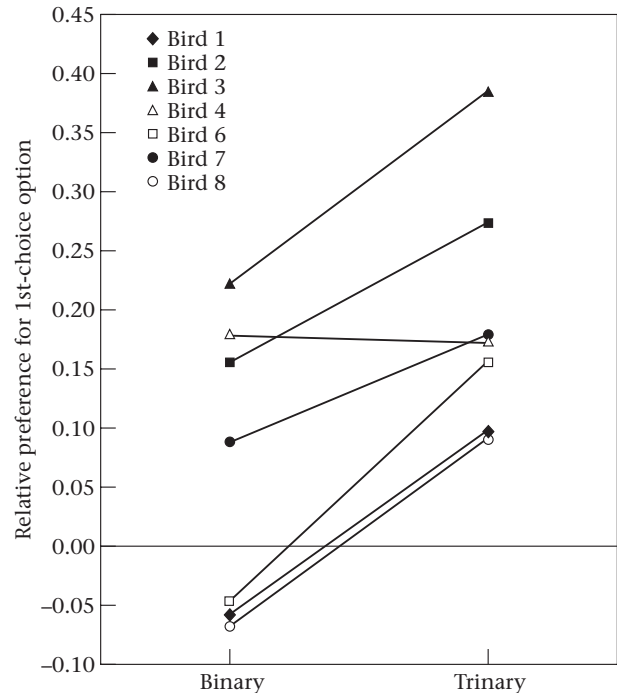
Despite the regular nature of the group data, two birds (Birds 3, 7) showed violations of regularity. In these birds,

Table 4. Median absolute proportions of choices for each option in the binary and trinary treatments showing no violations of regularity

Option	Binary			Trinary
	CL	CH	LH	
C	0.472	0.528	—	0.361
L	0.528	—	0.600	0.417
H	—	0.472	0.400	0.189

the absolute preference for one of the options was more extreme in the trinary treatment than in one or more of the binary treatments: Bird 3 had a stronger absolute preference for its most preferred option, L, in the trinary treatment than in the LH binary treatment, and Bird 7 had a stronger absolute preference for its most preferred option, C, in the trinary treatment than in either the CL or CH binary treatments ($p(C)=0.50$ in trinary versus 0.48 and 0.49 in CL and CH, respectively). Although it is not possible to establish the significance of these increases in preference because of a lack of replication, a violation of regularity is an unlikely result. According to Luce's choice axiom, the addition of a third option to the choice set would be expected to take choices proportionately from each of the other two options, leading to a reduction in all absolute preferences in the trinary treatment. Since the minimum proportion of choices allocated to the least preferred option in the trinary treatment is 10% (median 16.67%), Luce's choice axiom predicts a minimum of a 10% reduction in the absolute proportion of choices to the most preferred two options in the trinary treatments, compared to the proportion of choices received by these options in the binary treatments.

The same pattern described for Birds 3 and 7 appeared in a more subtle form in all seven of the birds with significant preferences when I compared their relative as opposed to absolute preferences. For each bird, I calculated the relative preference (equation 1) for its most preferred option (henceforth referred to as 'first choice') over its second most preferred option (henceforth referred to as 'second choice') in the trinary treatment. I also calculated the relative preference for these same two options in the binary treatment in which these two options were compared. The critical test then involved comparing the relative preference for the first-choice option in the binary and trinary treatments. Thus, for example, if the first- and second-choice options in the trinary treatment were L and C, respectively (as was the case for Birds 1 and 8, Table 3), I compared the relative preference for L over C in the trinary treatment with the relative preference for L over C in the CL binary treatment. Similarly, if the first- and second-choice options in the trinary treatment were L and H, respectively (as was the case for Birds 3 and 4), I compared the relative preference for L over H in the trinary treatment with the relative preference for L over H in the LH binary treatment. Overall, the relative preference for the first-choice option was significantly higher in the trinary treatment than in the binary treatment (Wilcoxon signed-ranks test:

**Figure 2.** The relative preference each bird had for its most preferred (first choice) option over its second most preferred (second choice) option in both the binary and trinary treatments. Most and second-most preferred options were defined according to the order in which each bird ranked the three options in the trinary treatment (Table 2).

$T+=1$, $N=7$, $P<0.05$; Fig. 2). This increase in relative preference observed in the trinary treatment violates the principle of independence of irrelevant alternatives.

Effects of Temperature

In an attempt to explain the variation in how individual birds ranked the three options in the trinary comparison, I looked for differences between the conditions under which the trinary choices sessions were run. Since the birds experienced the four treatments in different orders, and each bird took a different amount of time to reach its criterion number of 'good' sessions within a treatment, the five sessions providing the results for the trinary treatment occurred on different days for each bird. Throughout the experiment, the temperature in the laboratory was recorded at the same time each morning. Although the temperature was thermostatically controlled, daily fluctuations in temperature did occur owing to variation in the external temperature. Given that previous experiments have suggested that ambient temperature could affect the direction of risk-sensitive preferences (Caraco et al. 1990), I examined the effect of temperature on preference in the trinary treatment. For each bird, I computed the mean measured temperature on the 5 days on which the last five 'good' sessions of the trinary treatment occurred, and plotted against these mean temperatures the proportion of choices for options C, L (Fig. 3a and b, respectively) and H for the seven birds with significant preferences. Linear regression shows that

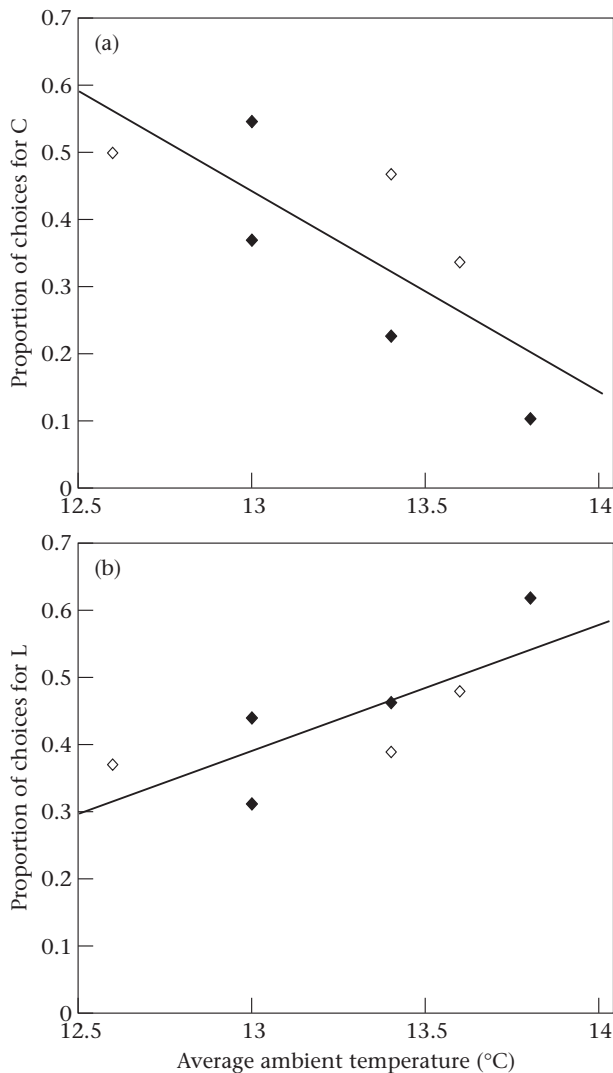


Figure 3. Absolute proportion of choices for (a) option C and (b) option L from the trinary treatment, plotted against the average morning temperature on the 5 days of the final five good sessions of the trinary treatment. ◆: Birds trained in the morning (AM group); ◇: birds trained in the afternoon (PM group). The timing of the temperature recordings corresponds with the start of the AM group. However, since the two sessions (AM and PM) were separated by only ca. 3 h, the temperature is likely to be strongly correlated with that experienced by the PM group. The solid lines result from the linear regressions described in the text: proportion of choices for C = $4.23 - 0.292 \times \text{temperature}$; proportion of choices for L = $-1.99 + 0.183 \times \text{temperature}$. There were insufficient data to evaluate whether the temperature effects were equally strong in the AM and PM groups.

temperature had a significant negative effect on the proportion of choices for C ($R^2=0.583$, $N=7$, $P=0.046$), but a significant positive effect on the proportion of choices for L ($R^2=0.568$, $N=7$, $P=0.05$); the effect on the proportion of choices for H was not significant ($R^2=0.377$, $N=7$, $P=0.143$). The two significant relationships are theoretically independent, because the birds had a third (H) option available to them, meaning that a

significant positive correlation between temperature and proportion of choices for L does not require an associated negative correlation between temperature and the proportion of choices for C. Thus the morning temperature in the laboratory correlated with whether the birds favoured option C or L in the trinary treatment, with birds being more risk averse at lower temperatures.

DISCUSSION

My aim in this study was to look for evidence that starlings use comparative instead of absolute currencies when evaluating foraging options differing in riskiness. Specifically, I looked for violations of transitivity and regularity, which are generally regarded as hallmarks of comparative choice currencies. The group results from the binary treatments showed no evidence for violations of either weak or strong stochastic transitivity, and are compatible with the birds ranking the low-variance option highest and the high-variance option lowest (Fig. 1a). This group result is also reflected in the behaviour of individual birds: although the birds varied in their rank order for the three options, no bird showed any evidence of violating transitivity (Table 3). The group results from the trinary treatment are also compatible with the results from the binary treatments, where the birds ranked the low-variance option highest and the high-variance option lowest (Fig. 1b). Overall, there was no violation of regularity, because the absolute proportions of choices to each option in the trinary treatment were lower than the same proportions in the binary treatments (Table 4). However, two individual birds did show violations of regularity, meaning that their absolute proportion of choices for one of the options in the trinary treatment was higher than their proportion of choices for the same option in one or more of the binary treatments. Overall, relative preferences (as defined in equation 1) were exaggerated in the trinary treatment relative to the binary treatment, with individual birds showing an enhanced relative preference for their most preferred option (either C or L) when it was presented in the trinary context (Fig. 2).

Do these results provide evidence that starlings evaluate foraging options using comparative instead of absolute currencies? Overall, the choices made by the birds were both transitive and regular and provide no evidence against the initial assumption that animals should use absolute currencies. These results agree with those of another recent study on starlings choosing between foraging options differing in the riskiness in delay to food (Schuck-Paim & Kacelnik, in press), which showed no evidence for violations of transitivity or regularity. Two birds showed violations of regularity, however, and I argue below that the overall increase in relative preference for the most preferred option in the trinary treatment may constitute evidence for contextual effects on choice.

Relative preference (equation 1) is a more sensitive measure of the effects of context than absolute preference, because it can detect changes in preference even

when the third option is chosen in a significant proportion of trials in the trinary treatment. Thus in an experiment such as this, in which the least preferred option was chosen on a substantial proportion (median 16.67%) of trials in the trinary treatment, contextual effects on preference are more likely to show up as shifts in relative preference than as violations of regularity. However, the crucial question for this paper is what a change in relative preference implies about the mechanisms of choice. Does a change in relative preference constitute unique proof of the birds' use of comparative currencies, whereby the value assigned to a given option is dependent on the other options available at the time the evaluation is made (Huber et al. 1982; Tversky & Simonson 1993), or are there other explanations for the observed change in relative preference?

Models of choice based on absolute currencies typically make the prediction that relative preference should be independent of context, and that, if a new option is added to the choice set, it should take its share of choices from the pre-existing options in proportion to their original shares. This 'constant ratio rule' follows directly from the fact that most models of choice assume Luce's (1959) choice axiom which states that the probability of choosing a given option, i , from n alternatives is the ratio of the value assigned to this option, V_i , to the sum of the values assigned to all the options on offer:

$$P(i) = \frac{V_i}{\sum_{j=1}^n V_j}, \quad (2)$$

where V_j is the value assigned to the j th option (see Bateson et al. 2002 for a proof of this). It follows therefore, that a change in relative preference can mean one of two things: first, that Luce's choice axiom is true, but that the value of an option can change depending on its context (i.e. that the currencies used in choice are comparative), or second, that Luce's choice axiom is false. Thus, although my finding of a change in relative preference is compatible with the birds' use of comparative currencies, it does not prove this, unless Luce's choice axiom can be shown to hold.

In a review of experimental tests of the choice axiom, Laming (1973) concluded that, in general, the choice axiom appears to hold for both human and animal choices between sets of heterogeneous alternatives, but starts to fail when the set has some natural structuring (Debreu 1960). For example, the choice axiom breaks down when sets of options are structured such that two or more of the options are regarded as equivalents (e.g. Rumelhart & Greeno 1971). In the context of the current experiment, it is possible that some structuring in the choice set could cause the change in relative preference observed between the binary and trinary treatments. However, there is no obvious reason why the birds should regard any two of the options as functionally equivalent.

A second case in which the choice axiom can fail occurs when the subject allocates some proportion of their choices at random between the options. For example,

consider the situation in which a subject allocates 50% of its choices between options A and B according to a fixed probabilistic bias of, say, 6/10 to A and 4/10 to B, but the remaining 50% of choices are allocated at random between the options. Thus, the relative preference for A over B, as calculated from equation 1, is 0.1. Now consider what happens when option C is added to the choice set. If we assume that the subject maintains its bias for A over B, and the only choices allocated to C are one-third of the 50% of choices allocated at random, then the relative preference for A over B increases to 0.12, despite the fact that the bias for A over B is unchanged. This increase in relative preference occurs because, by absorbing one-third of the choices allocated at random, option C dilutes the masking effect of these random choices on the true bias for A over B. Henceforth I refer to this phenomenon as the 'random dilution' effect. This effect cannot produce increases in absolute preference, however, and therefore is not an alternative explanation for violations of regularity.

The random dilution effect could occur in an animal choice experiment of the type reported in this paper. Animals often have strong positional biases preferring one side of the box or one pecking key to another, independently of which stimuli are presented. To guard against such positional biases resulting in spurious choice results, choice experiments are usually designed so that the position in which the different options are presented is either randomized or balanced. The result of this procedure is that, if the animal shows a bias for a particular pecking key, this bias will merely contribute random noise to the data. However, this random noise could result in an enhancement in relative preference in a trinary context via the random dilution effect described above.

Changes in relative preference have thus far been regarded as evidence for comparative choice currencies in the animal behaviour literature (Bateson et al. 2002; Shafir et al. 2002). However, the above description of the random dilution effect shows that there may be an alternative explanation for these findings. If side biases are responsible for the enhancement in relative preference seen in the current experiment, there should be a positive correlation between the strength of the side bias shown by an individual bird and the enhancement in relative preference seen in the trinary treatment. Unfortunately, data on which side the options were presented were not recorded in this experiment, but this prediction could be tested in a future experiment. A second prediction arising from the description of the random dilution effect above is that the nature of the least-preferred third option should not affect the enhancement in relative preference observed. Against this prediction, Shafir et al. (2002) presented evidence from honeybees, *Apis mellifera*, that the nature of the least preferred option is important in determining its effect on the preference between the two other options. However, a test of the prediction in starlings will require a further experiment.

This is not the first study claiming evidence that foraging animals may use comparative currencies when

making choices. Three studies have compared the preferences of foragers in binary and trinary contexts, and all showed evidence for contextual effects on choice. In Hurly & Oseen's (1999) study of risk-sensitive preferences in wild rufous hummingbirds, all four birds tested in both binary and trinary contexts showed higher absolute preference for the intermediate variance option in the trinary context (T. A. Hurly, personal communication), and thus violated regularity. Similarly, Shafir et al. (2002) reported violations of regularity in grey jays, *Perisoreus canadensis*, choosing between foraging options differing in the distance to food (length of a tube) and the number of raisins. Significant shifts in relative preference (as I report here) between binary and trinary contexts have been shown in both honeybees (Shafir et al. 2002) and rufous hummingbirds (Bateson et al. 2002) choosing between artificial flowers differing in two attributes (corolla length and volume of sucrose in the case of the bees; volume and concentration of sucrose in the case of the hummingbirds). Two other studies (Shafir 1994; Waite 2001) on bees and grey jays, respectively, have reported violations of transitivity in foraging animals. Thus, my results add to a growing body of evidence that suggests that, like humans, foraging animals may use comparative currencies to evaluate alternative options.

In addition to the evidence provided by my study for comparative choice mechanisms, two aspects of the starlings' behaviour deserve comment. First, although the group results from the binary treatments showed either indifference to risk (CL and CH) or risk aversion (LH), and thus replicate previous studies of sensitivity to variance in amount of food in starlings and other species (Reboreda & Kacelnik 1991; Bateson & Kacelnik 1995; Kacelnik & Bateson 1996; Brito e Abreu & Kacelnik 1999), in the trinary treatment, four of the seven birds with significant preferences ranked the low-variance option (L) highest of the three options. Preference for an intermediate level of variance is unusual, and has previously been reported only by Hurly & Oseen (1999) in rufous hummingbirds tested in a trinary context. Second, the finding of increased risk aversion with decreased temperature is also in direct opposition to previous results on the effects of temperature on risk-sensitive foraging decisions that show increased risk proneness with decreasing temperature (Caraco et al. 1990). These latter two results are not explained by any existing mechanistic or functional model of risk-sensitive foraging. Further experiments, including explicit temperature manipulations, will be necessary to explore their importance.

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