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Irrational choices in hummingbird foraging behaviour

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It is conventionally assumed that, when animals evaluate alternative options, the value assigned to an option is absolute and independent of the other options available. It follows that animal choices should exhibit the rational property of regularity whereby the proportion of choices for an option cannot be increased by the addition of further options to the choice set. However, violations of regularity occur in human decision making, suggesting that humans may use comparative evaluation mechanisms whereby the value of an option is computed relative to the other options available. For example, in the asymmetrically dominated decoy effect the preference for a target option over a competitor is altered by the addition of a decoy option that is inferior to the target and competitor on one attribute, but lies between them on a second. We tested whether foraging wild rufous hummingbirds, *Selasphorus rufus*, would demonstrate violations of regularity in response to an asymmetrically dominated decoy. Sixteen birds chose between three artificial flower types (Target: 15 μl, 40% sucrose; Competitor: 45 μl, 30%; Decoy: 10 μl, 35%) in Binary (Target versus Competitor) and Trinary (Target versus Competitor versus Decoy) treatments. We predicted higher preference for the Target in the Trinary treatment. The birds ranked the three options in the same order in the Binary and Trinary treatments (Competitor>Target>Decoy). Seven birds showed violations of regularity, six increasing their absolute preference for the Competitor in the Trinary treatment. Overall, relative preference for the Competitor over the Target was higher in the Trinary than in the Binary treatment. These changes in preference are incompatible with an absolute evaluation mechanism.

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Understanding the mechanisms animals use to make choices between alternative options is fundamental to many areas of animal behaviour such as mate choice and foraging. Most existing models of animal choice assume that animals evaluate alternative options by using a proximate currency that is assumed to correlate well with the long-term fitness consequences of decision making. Examples of such currencies are long-term net rate of energy intake (Kacelnik 1984) and risk (i.e. variance, Caraco et al. 1990) in the foraging literature, and tail length (Andersson 1982), number of eye spots (Petrie et al. 1991) or display rate (Gibson 1996) in the mate choice literature. These currencies are all absolute in nature, meaning that the value assigned to an option corresponds to intrinsic properties of that option, and is therefore independent of the other options present at the time of evaluation. This focus on absolute evaluation mechanisms, as opposed to the alternative comparative evaluation mechanisms, in which the value of an option is computed relative to the other options available at the time of choice, comes from a belief that the fitness consequences of choosing a particular option should be absolute (but see Houston 1997 for an alternative view). Models of choice based on absolute evaluation mechanisms have been extremely successful at predicting some animal behaviour, such as, for example, the quantitative details of how foraging animals choose between two options differing in the variance in delay to reward (e.g. Mazur 1984; Bateson & Kacelnik 1996). However, recent evidence suggests that in order to understand some phenomena in animal decision making we may need to acknowledge the existence of comparative evaluation mechanisms.

A corollary of assuming that animals use absolute evaluation mechanisms is that we expect animal choice to be rational, where rationality implies that preference between options does not depend on the presence or 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

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commonly used to assess rationality (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. In the context of stochastic choice, 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. In contrast, the property of regularity applies to choices between different numbers of options. A choice is defined as regular if the 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 (e.g. poorer than all the other options) should not influence the relative preferences between the original options.

The few attempts to test for rationality, as defined above, in animals, have all shown evidence of irrational behaviour (Navarick & Fantino 1972; Shafir 1994; Hurly & Oseen 1999; Waite 2000, 2001). For example, both grey jays, *Perisoreus canadensis*, and honeybees, *Apis mellifera*, show violations of strong and weak stochastic transitivity when faced with binary choices between foraging options manipulated in two attributes (Shafir 1994; Waite 2001), and rufous hummingbirds, *Selasphorus rufus*, switch from being risk averse in a binary choice between artificial flowers differing in the variance in nectar content to preferring an intermediate level of risk in a trinary choice (Hurly & Oseen 1999). This latter result represents a violation of regularity because all four birds tested in both binary and trinary contexts had higher absolute preference for the intermediate variance option in the trinary context (T. A. Hurly, unpublished data). These results are hard to reconcile with the use of absolute evaluation mechanisms, and suggest that animals may well evaluate alternative options using comparative mechanisms, whereby the value assigned to a given option is dependent on the other options available at the time the evaluation is made.

In contrast to the animal literature, reports of violations of transitivity and regularity are common in human decision making, and much theoretical and empirical research has already been dedicated to trying to understand the mechanisms underlying these effects (Tversky 1969; Shafir et al. 1993; Tversky & Simonson 1993). A phenomenon known as the asymmetrically dominated alternative effect has been particularly useful in differentiating between competing models of choice (Wedell 1991). An asymmetrically dominated alternative is an option that is dominated by at least one option in the set (designated the Target), but is not dominated by another of the options (the Competitor). An option A is defined as dominating an option B, if for every attribute of B the value for A is never less than the value for B, and if for at least one attribute, the value for A is greater than the value for B. Figure 1 shows possible values for a Target, Competitor and an asymmetrically dominated alternative (the Decoy). The asymmetrically dominated decoy effect manifests itself as a higher preference for the Target over the Competitor when subjects are given the trinary choice of the Target, Competitor and Decoy than when they are given the binary choice of the Target and Competitor.

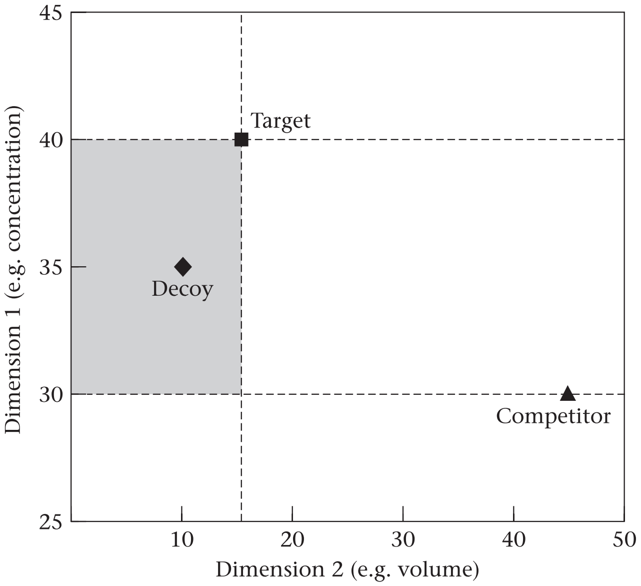

Figure 1. Diagram showing the position of an asymmetrically dominated decoy option relative to a Target and Competitor option. A decoy positioned anywhere in the shaded box is defined as asymmetrically dominated, because it is dominated by the Target on both dimensions 1 and 2, but it is dominated by the Target only on dimension 1. In human choice experiments the addition of an asymmetrically dominated Decoy enhances the relative preference for the Target over the Competitor. This graph shows the positions chosen for the three artificial flower types used in the current experiment, in which dimension 1 was concentration of nectar (% sucrose) and dimension 2 was volume of nectar (μl).

The asymmetrically dominated decoy effect should not occur if the subjects are using absolute evaluation mechanisms. It is formally a violation of regularity, because the absolute preference for the Target increases when the Decoy is added to the choice set. This effect appears to be robust, and has been reported both in humans making decisions in lotteries (Wedell 1991), between alternative consumer products such as baked bean brands, beer or batteries (Huber et al. 1982; Doyle et al. 1999) and even in partner selection (Sedikides et al. 1999). Although the majority of such experiments involve paper and pencil tasks in which the subjects are confronted with written descriptions of the alternative options, the effect of asymmetrically dominated decoys has recently also been demonstrated for real in-store purchases (Doyle et al. 1999), confirming its relevance to real decisions.

Various explanations have been proposed for the effect of asymmetrically dominated alternatives; however, the explanation best supported by the literature is that the Decoy serves to alter the relative attractiveness of the Target and Competitor by changing the dominance relationships among the options in the set (Huber & Puto 1983; Wedell 1991). In the binary context the Target and Competitor are each dominant on one dimension, and

Table 1. Relative ranks of the Target, Competitor and Decoy on dimensions 1 and 2 in Binary and Trinary contexts

	Target	Competitor	Decoy
Binary choice			
Dimension 1	1	2	—
Dimension 2	2	1	—
Sum of ranks	3	3	—
Trinary choice			
Dimension 1	1	3	2
Dimension 2	2	1	3
Sum of ranks	3	4	5

thus have equal overall ranks. However, in the trinary context, the Decoy ranks between the Target and Competitor on the dimension on which the Target is superior to the Competitor, and thus has the effect of reducing the overall ranking of the Competitor relative to the Target (see Table 1 for details). This is clearly a comparative evaluation mechanism because the rank of an option can only be defined relative to the other options present.

Since animals are frequently faced with choices between options differing in more than one dimension, it is possible that the mechanisms animals use to evaluate such options produce violations of regularity. Although the asymmetrically dominated alternative effect has been previously discussed in the context of animal decision making (Real 1996), it has not yet been empirically demonstrated in animals. We investigated whether this effect can be seen in the foraging decisions of wild rufous hummingbirds choosing between nectar rewards explicitly designed to differ in two dimensions.

METHODS

Experimental Design

We designed three artificial flower types corresponding to a Target, a Competitor and a Decoy that differed in two dimensions, the volume of nectar (μl) and its concentration (% sucrose solution). Nectar volume and nectar concentration have both independently been shown to be important in explaining hummingbird flower preferences, with birds preferring higher volumes (Gass & Sutherland 1985) and higher concentrations (Roberts 1996) within a given range. We chose the volumes and concentrations in the Target and Competitor flowers to give similar net rates of energy intake, on the supposition that if birds are maximizing net energy intake they should not have a strong preference for either flower type. This was necessary since we did not have any prior data to suggest how the hummingbirds might trade off volume against concentration, and the human literature suggests that the effects of adding an asymmetrically dominated decoy option may be greatest when the Target and Competitor are initially similar in value. Table 2 shows the parameters of the three flowers, and Fig. 1 their relative positions.

Table 2. Characteristics of the three flower types

	Target	Competitor	Decoy
Volume (μl)	15	45	10
Concentration (%)	40	30	35
Net rate of energy intake (J/s)	81.9	92.0	59.5

Net rates of energy intake were calculated as described in the Appendix.

We tested the birds' preferences for the three flower types in two treatments, a Binary treatment in which the bird was presented with a choice between Target and Competitor flowers and a Trinary treatment with a choice between Target, Competitor and Decoy flowers. On the assumption that hummingbirds will respond similarly to humans to an asymmetrically dominated decoy, we predicted that the birds' preference for the Target should be higher in the Trinary treatment. We chose the values of volume and concentration such that the Competitor was calculated to offer a slightly higher net rate of energy intake than the Target, in the hope that the birds might show a preference for the Competitor in the Binary treatment, but switch to preferring the Target in the Trinary treatment.

Subjects and Study Site

The subjects were 16 wild rufous hummingbirds observed in the Westcastle Valley in southwestern Alberta, Canada, in the eastern range of the Rocky Mountains (49°29′N; 114°25′W, elevation 1400 m). During mid-May, we placed commercial hummingbird feeders containing 14% sucrose solution in potential territories, and by late May the majority of feeders were successfully defended by males. We individually marked males defending feeders by spraying their breast feathers with a small amount of coloured, waterproof, nontoxic ink. These ink marks had faded by the time the birds migrated in July, and no birds lost their territories as a result of marking during this study. We collected data between 0800 and 1930 hours Mountain Standard Time during May and June 2000 and 2001.

Initial Training

We removed a male's feeder and trained the bird to drink 20% sucrose solution from two wells drilled in a Plexiglas plate (5.5 × 4.8 × 1.2 cm), mounted at an angle of ca. 45° on a metal stake 80 cm high. The wells (10 mm deep × 3.5 mm diameter) could hold a volume of 120 μl, were 5.2 cm apart and were each marked by a yellow reinforcement ring that was chosen to resemble the yellow plastic flower on the commercial hummingbird feeders. Initially the wells were completely filled with sucrose, but as the birds learnt to feed from the wells we reduced the volume in each well towards those used in the experiment. The birds could drink from either one or both wells on a given bout; however, the volume of sucrose present was always sufficient that a bird could not completely empty both wells on a single feeding bout. We moved the plate at least 40 cm between each feeding bout and replenished the wells. When the bird was judged to be feeding readily from the wells, we replaced the training plate by the larger plate described below and began the experiment proper.

Experimental Procedure

The experimental apparatus consisted of a Plexiglas plate (28 × 21.5 × 1.2 cm) drilled with 18 wells (10 mm deep × 3.5 mm diameter) arranged in a hexagonal pattern such that nearest-neighbour distances were 5.2 cm. We marked the wells (flowers) with coloured reinforcement rings to indicate the volume and concentration of sucrose (nectar) contained in the flower. We presented the flowers to the birds by mounting the plate at a 45° angle on a stake ca. 80 cm high. Each bird was tested in both the Binary and Trinary treatments. (We assumed we worked on different birds in the 2 years, as the population is large and longevity low.) The birds did both treatments in immediate succession, with half of the birds receiving the Binary treatment first and the other half the Trinary treatment first.

In each treatment the flower types were indicated to the bird by the colour of the ring surrounding the well of nectar. In each year, we randomly assigned colours to treatments, and for each bird the colours were randomly assigned to flower types within a treatment. We used a total of five colours, two for the Binary treatment and three for the Trinary treatment, such that each bird had to learn completely new colour associations in the second treatment it received. We designed the experiment this way to prevent the carry-over of strong preferences that were developed in one treatment into the subsequent treatment. In 2000, red and lilac were used in the Binary treatments and orange, green and blue in the Trinary treatments, and in 2001, lilac and blue were used in the Binary treatments and red, orange and green in the Trinary treatments. In the Binary treatments nine of the 18 wells on a plate were randomly chosen as Target Flowers and the remaining nine as Competitors, whereas in the Trinary treatment six of the wells were randomly chosen as Target flowers, six as Competitors and six as Decoys.

Birds visited the plates of flowers approximately every 10 min throughout the day. On a feeding bout, a bird was allowed to feed from as many wells as he wished ($\bar{X} \pm \mathrm{SD}=3.53 \pm 0.694$ flowers, $N=16$), and we recorded the colour of the wells from which he fed. Once a feeding bout had finished and the bird had flown away, we cleaned the wells from which he had fed and refilled them with the appropriate volume and concentration of nectar. We rotated the plate through 90° between visits. Every four visits we used a new board with a different random pattern of flowers, and moved the plate ca. 1 m to encourage the bird to learn the association between the colour of a flower and its contents, as opposed to learning the spatial locations of preferred flower types.

In the event that a bird failed to sample all the available flower types in the course of its first 10 flower visits, we forced the bird to visit 10 flowers of the nonchosen colour or colours by presenting it with plates with flowers of only a single type. After this correction procedure we restarted the choice experiment. Flower visits made before and in the course of the correction procedure were not included in the data set. Four birds required this correction procedure in one or both treatments (the Trinary treatment for birds 00/PL01, 00/PK03 and 00/RD12 and both treatments for bird 01/GR02). Thus, the minimum number of times a bird was required to sample a flower type was one; however, none of the birds had absolute preferences, and the minimum number of times a flower type was actually sampled by a bird in the course of the experiment was 10 (Bird 00/BL06 Decoy option).

We continued both Binary and Trinary treatments until a bird had made a total of at least 150 choices of the Target and Competitor. A single treatment typically took between 1 and 3 days to complete, with Trinary treatments taking longer than Binary treatments because the birds allocated some of their choices to the Decoy flowers. Breaks for the night, lunch or rain were ignored since they did not appear to have any effect on preference.

Analysis

For each bird we computed the proportion of choices made to the Target, Competitor and Decoy options in the final 100 choices of each treatment. We discarded the first choices in each treatment from the analysis because it took the birds an average of 31 flower visits to begin showing a preference. We assumed preference began when the cumulative number of choices to the Target and Competitor permanently diverged.

To compare the preference for the Competitor over the Target in the Binary and Trinary treatments we computed two measures of preference: (1) the absolute preference (the proportion of flowers visited) for the Competitor and Target in the two treatments, and (2) the relative preference for the Competitor over the Target in the two treatments,

$$\text{Relative preference} = \frac{\text{proportion of choices for Competitor} - \text{proportion of choices for Target}}{\text{proportion of choices for Competitor} + \text{proportion of choices for Target}} \qquad (1)$$

We chose this relative measure because in situations in which the decoy option is chosen in some proportion of choices, it offers a more sensitive measure than change in absolute preference. Models of choice typically make the assumption that relative preference is independent of context, and that if a new option is added to the choice set, it should take its share of choices from the preexisting options in proportion to their original shares. This prediction is clearly demonstrated by considering how preferences predicted by the ratio rule behave in binary and trinary contexts. The ratio rule, also known as

Luce's choice axiom (Luce 1959), is a standard assumption underlying most models of choice (e.g. McNamara & Houston 1987; Wills et al. 2000). It is a rule for converting the value assigned to different options into the probability of choosing an option given a choice. It says simply 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:

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

where V_j is the value assigned to the jth option. For example, consider three options, A, B and C, with values V_{A}, V_{B} and V_{C}. In a binary context the probability of choosing A from A and B can be written:

$$\mathrm{P(A{:}\ A, B)}=\frac{V_{\mathrm{A}}}{V_{\mathrm{A}}+V_{\mathrm{B}}}, \tag{3}$$

and the probability of choosing B from A and B can be written:

$$\mathrm{P(B{:}\ A, B)}=\frac{V_{\mathrm{B}}}{V_{\mathrm{A}}+V_{\mathrm{B}}}, \tag{4}$$

Similarly, in a trinary context the probability of choosing A from A, B and C can be written:

$$\mathrm{P(A{:}\ A, B, C)}=\frac{V_{\mathrm{A}}}{V_{\mathrm{A}}+V_{\mathrm{B}}+V_{\mathrm{C}}}, \tag{5}$$

and the probability of choosing B from A, B and C can be written:

$$\mathrm{P(B{:}\ A, B, C)}=\frac{V_{\mathrm{B}}}{V_{\mathrm{A}}+V_{\mathrm{B}}+V_{\mathrm{C}}}. \tag{6}$$

The relative preference for A over B can be expressed as:

$$\text{Relative preference for A over B}=\frac{\mathrm{P(A)}-\mathrm{P(B)}}{\mathrm{P(A)}+\mathrm{P(B)}}. \tag{7}$$

In the binary context, the relative preference is found by substituting equations (3) and (4) into equation (7), and in the trinary context relative preference is found by substituting equations (5) and (6) into equation (7). In both cases the relative preference for A over B reduces to the expression:

$$\text{Relative preference for A}=\frac{V_{\mathrm{A}}-V_{\mathrm{B}}}{V_{\mathrm{A}}+V_{\mathrm{B}}}. \tag{8}$$

Therefore, if we assume that V_{A}, V_{B} and V_{C} are constant, as is the case in all absolute choice models, then the relative preference for A over B should be constant, and independent of the presence of other options.

Relative preference as defined in equation (1) ranges between −1, which corresponds to zero choices for the Competitor, and +1, which corresponds to zero choices for the Target. A value of zero corresponds to an equal number of choices for the Target and Competitor. The null hypothesis in this experiment is that relative preference for the Competitor over the Target should be equal in the Binary and Trinary treatments.

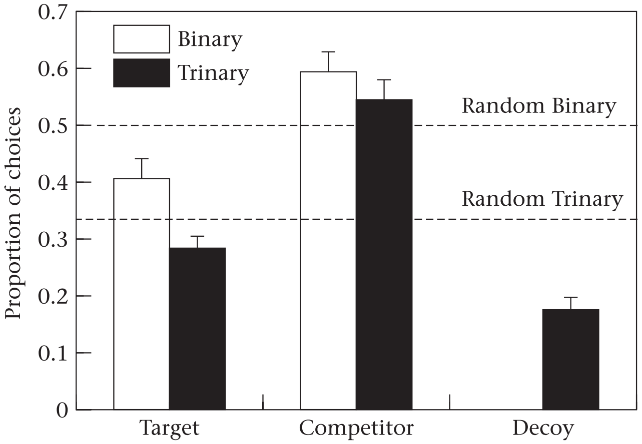

Figure 2. Mean proportion +1 SE of each option chosen in the final 100 choices of the Binary (□) and Trinary (■) treatments. The two dashed lines show the random expectations for the Binary (upper line=0.5) and Trinary (lower line=0.33) treatments.

None of the data were transformed prior to statistical analysis because visual inspection of either the data (t tests) or the residuals (ANOVA) revealed that distributions were approximately normal and variance was homogeneous.

RESULTS

Group Results

Figure 2 shows the proportions of choices to each of the options in the Binary and Trinary treatments. In the Binary treatment the birds chose the Competitor option significantly more than the Target option (one-sample t test against a random expectation of 0.5: $t_{15}=2.84$, $P=0.012$). In the Trinary treatment the birds also chose the Competitor option significantly more than random (one-sample t test against a random expectation of 0.333: $t_{15}=6.50$, $P<0.0001$) and the Decoy option significantly less than random (one-sample t test against a random expectation of 0.333: $t_{15}=-7.45$, $P<0.0001$).

Overall there was no violation of regularity: the mean absolute proportion of choices to the Competitor in the Binary treatment was 0.59 compared with the slightly smaller mean of 0.54 in the Trinary treatment. However, Fig. 2 suggests a violation of the principle of independence of irrelevant alternatives in that the drop in preference for the Target and Competitor in the Trinary treatment is more extreme for the Target than the Competitor. A direct test of this violation using repeated measures ANOVA with factors bird ($N=16$, random), order (Binary first or Trinary first) and treatment (Binary or Trinary) showed that the relative preference (as computed in equation 1) for the Competitor over the Target

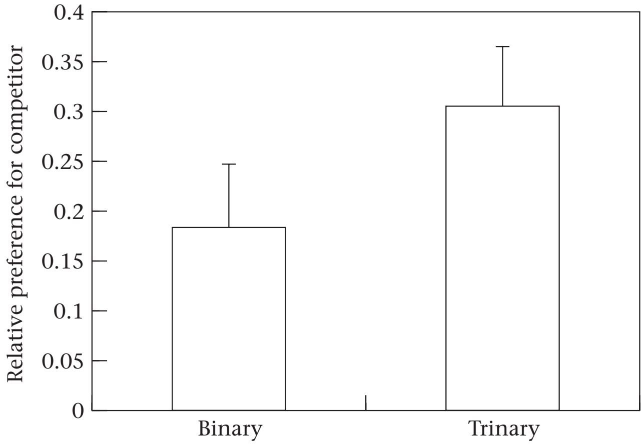

Figure 3. Mean relative preference +1 SE for the Competitor over the Target in the Binary and Trinary treatments.

was significantly higher in the Trinary treatment than in the Binary treatment ($F_{1,14}$=5.17, P=0.039; Fig. 3). There was no effect of order ($F_{1,14}$=0.32, P=0.579), and no treatment × order interaction ($F_{1,14}$<0.01, P=0.953).

Individual Birds

In the Binary treatment 11 birds had significant preferences (chi-square tests: χ^2_1=4.84–27.04, P<0.05), with 10 preferring the Competitor and one the Target. In the Trinary treatment 14 birds had significant preferences (chi-square tests: χ^2_2=6.98–111.02, P<0.05), with 11 birds having the ranking C>T>D, two the ranking C>D>T and one the ranking T>C>D.

Seven birds showed violations of regularity, meaning that the absolute proportion of choices to a particular option was higher in the Trinary treatment than in the Binary treatment (see Table 3 for individual data). Of these birds, six had a higher proportion of choices for the Competitor in the Trinary treatment than the Binary treatment, and one had a higher proportion of choices for the Target in the Trinary treatment than in the Binary treatment. These birds provide particularly strong evidence for a change in preference, because in the Trinary treatment a mean ± SD of 14.9 ± 7.98% of their choices were lost to the Decoy. Thus, increased absolute preference for another option represents a dramatic shift of preference between the Target and Competitor. To examine whether these violations of regularity were significant we conducted contingency table analysis of the number of choices made to the Target and Competitor in the Binary and Trinary treatments. These analyses showed that four birds' preferences differed significantly between treatments (chi-square tests: 1 *df*, $P \leq 0.05$, see Table 3 for details). An additional four birds had P values ≤ 0.1 in this same analysis. The probability of obtaining eight or more birds out of 16 by chance with a difference in preference between treatments significant at at least the P=0.1 level is equal to 0.0001 (binomial probability).

DISCUSSION

Our results provide compelling evidence that the presence of the Decoy option caused a change in preference for the Target and Competitor. Violations of regularity occurred in seven birds, but, contrary to our predictions, in six of 16 birds the absolute preference for the Competitor was higher in the Trinary treatment than in the Binary

Table 3. The number of visits to each flower type in the last 100 visits of each treatment for individual birds

	Number of choices						
	Binary		Trinary				
Bird	Target	Competitor	Target	Competitor	Decoy	χ^2_1	P
00/RD05	55	**45**	21	**54**	25	12.72	<0.01
00/PL01	69	31	35	29	36	3.45	0.06
00/BL06	39	**61**	36	**62**	2	0.11	0.74
00/PK03	24	76	21	67	12	0.00	0.98
00/BK04	37	63	36	56	8	0.09	0.76
00/GR02	36	64	35	53	12	0.28	0.59
00/RD12	32	**68**	18	**70**	12	3.20	0.07
00/GR13	45	55	36	50	14	0.19	0.67
01/RD10	27	73	20	56	24	0.01	0.92
01/GR08	55	**45**	35	**48**	17	2.99	0.08
01/GR02	**34**	66	**41**	38	21	5.81	0.02
01/BK45	39	61	29	44	27	0.01	0.92
01/PK03	24	**76**	9	**83**	8	6.80	0.01
01/PK12	43	57	24	53	23	2.59	0.10
01/BL04	59	**41**	36	**45**	19	3.80	0.05
01/BL165	35	65	20	62	18	2.41	0.12

The χ^2 values come from the 2×2 contingency tables comparing the number of choices for the Target and Competitor in the Binary and Trinary treatments. Preference reversals are indicated with underlining, and violations of regularity with bold.

treatment. Overall, the birds ranked the three flowers in the same order in both the Binary and Trinary treatments, preferring the Competitor to the Target and the Target to the Decoy. However, the relative preference for the Competitor over the Target was higher in the Trinary treatment than in the Binary treatment, a violation of the principle of independence of irrelevant alternatives. This behaviour can be described as irrational in the sense that the hummingbirds did not appear to make choices using an absolute evaluation mechanism.

The order in which the birds ranked the three flowers can be explained by the net rate of energy intake that the three flower types were estimated to provide (Table 2). In this respect the behaviour of the birds accords well with the predictions of classical optimal foraging theory. However, neither maximization of net rate, nor any absolute currency, can currently explain the difference in preference observed between the Binary and Trinary treatments. According to the principle of independence of irrelevant alternatives, if the birds are using an absolute currency, then their preference for the Competitor over the Target should be unaffected by the addition of further options to the choice set. A new option added to the choice set should take its share of choices from the pre-existing options in proportion to their original shares (Luce 1959, 1977). The expectation was, therefore, that the addition of the Decoy to the choice set should decrease the absolute preferences for both the Target and Competitor, and leave their relative preferences unchanged. Although the group data do show the expected drop in absolute preference for the Target and Competitor, the relative preference for the Competitor over the Target is significantly higher when the Decoy is added to the choice set. At the level of individual birds, seven birds showed an increase in absolute preference for either the Target or Competitor when the decoy was added to the choice set. Our results therefore provide evidence against both of the predictions arising from rational choice theory, and suggest that the birds did not use an absolute currency to evaluate the options. Our results therefore agree with the findings of Hurly & Oseen (1999) in suggesting a role for comparative choice mechanisms in hummingbird decision making.

Although our results show that the addition of asymmetrically dominated decoy options can produce violations of regularity, the direction of our effect is in the opposite direction to that predicted. In the human literature, asymmetrically dominated decoys act to shift preference towards the Target option, where the Target is defined as the option that dominates the Decoy on both dimensions (Huber & Puto 1983), whereas we report a shift away from the Target towards the Competitor. Our result therefore cannot be explained using the dominance relationship rationale presented in Table 1.

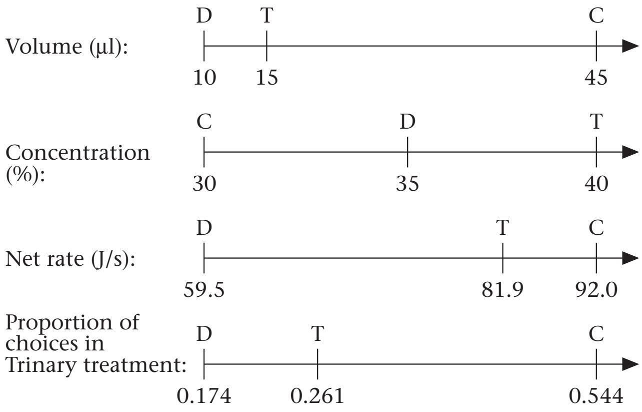

Figure 4. Relative distributions of the Target (T), Competitor (C) and Decoy (D) options along the three dimensions volume, concentration and net rate of energy intake. For comparison, the mean proportions of choices of the options selected during the trinary treatment are also presented.

One possible solution to the discrepancy between the human and hummingbird results lies in the way the hummingbirds perceived the options. Although there is independent evidence that hummingbirds prefer flowers with larger nectar volumes and higher nectar concentrations (Gass & Sutherland 1985; Roberts 1996), it is not necessarily the case that the birds perceive these two attributes as independent dimensions. Instead, the birds might perceive the flowers as varying along just a single dimension such as volume, concentration or net rate of energy intake. Figure 4 shows the relative positions of the three options along these three possible dimensions. Both the net rate of energy intake and the volume of nectar in the flowers correlate with the overall ranking of the options, but volume correlates best with the relative preferences for the three options in the Trinary treatment.

It seems intuitively plausible that the variance in a particular attribute might affect the salience of that attribute to a forager, because the higher the variance, the higher the cost of making an incorrect decision. As a consequence of choosing combinations of concentration and volume that provided similar rates of net energy intake in the Target and Competitor options, we inadvertently picked values that resulted in far higher variance in the volume dimension than in the concentration dimension. The coefficient of variation of the three values of volume we used is 66%, compared with only 12 and 17% in the concentration and rate dimensions, respectively. Thus it is possible that the birds were attending only to the volume dimension. If this were the case, then the Target and Competitor would not asymmetrically dominate the Decoy, since asymmetric domination requires two dimensions. In unidimensional human decisions the similarity of a new option to existing options is found to be important in determining choice. In general, a new alternative will take choices disproportionately from the existing option to which it is most similar (Rumelhart & Greeno 1971), a phenomenon that is also not predicted by rational choice theory. In the case of our flowers, the Decoy is most similar to the Target on the volume dimension, and should therefore take choices disproportionately from the Target option in the Trinary treatment. This prediction accords with our results, suggesting a possible explanation for the overall increase in relative preference for the Competitor in the presence of the Decoy option. However, this explanation is unable to account for the increases in absolute preferences seen in the Trinary treatment by seven birds.

If the above interpretation is correct then we would predict that if we replicated the experiment with equivalent coefficients of variation in the volume and concentration dimensions, the birds might attend to both dimensions, and show the predicted effect of an asymmetrically dominated alternative. Clearly further experiments are needed to unravel the precise mechanisms by which context affects choice in hummingbirds.

Our results raise a number of theoretical and practical issues that deserve discussion. We start by considering the generality of our results. So far, only a few studies have tested for regularity in animal decision making, and the other studies (Hurly & Oseen 1999; M. Bateson, unpublished data; T. A. Hurly, unpublished data), such as this one, also focus on foraging decisions in birds. However, if we put these studies together with those showing violations of transitivity (Navarick & Fantino 1972; Shafir 1994; Waite 2001b) and a recent study showing effects of background context (Waite 2001a), we have a growing body of evidence suggesting that comparative currencies may be more common than has previously been assumed. Previous studies of animal choice are unlikely to have detected violations of regularity: first, because they have not compared preferences in a binary context with those obtained in a trinary context, and second, because in well-controlled choice experiments it is usual not to vary more than one attribute of the options simultaneously. However, there are many situations in the natural environment where animals are faced with more than two options simultaneously, and where the options differ in more than one important attribute, suggesting that comparative currencies deserve widespread consideration. For example, mate choice on leks offers a clear case where comparative choice might be detected if the appropriate experiments were performed.

The possibility that comparative choice might be widespread in the animal kingdom has implications for both models of choice and the design of choice experiments. So far, the majority of models of animal choice have assumed absolute currencies, and this assumption vastly simplifies the experimental study of choice. If choices are independent of the range and number of alternatives available, then the relative ranking of options, and hence the precise currencies used for decision making, can easily be established from a limited number of choice tests. For example, in the quantitative study of risk-sensitive foraging, models are currently entirely based on the outcomes of binary choices (Reboreda & Kacelnik 1991; Bateson & Kacelnik 1996; Brito-e-Abreu & Kacelnik 1999). Although the currencies derived from this approach are successful at predicting the outcome of simplified binary choice tests, our results suggest that these currencies may fail in situations where animals are faced with several options simultaneously. Similarly, in the laboratory study of mate choice, conclusions about the phenotypic features that make individuals attractive are drawn on the basis of experiments in which the number of stimulus animals is not manipulated, but varies from two upward, depending on the laboratory doing the research. Our results suggest that the number of stimulus animals may be an important factor in determining the relative attractiveness of individuals, and may thus help to explain discrepancies in the findings of different laboratories (e.g. see review by Collins & ten Cate 1996).

The final issue we need to address is that of why comparative evaluation mechanisms have evolved. A common resort when faced with seemingly imperfect behaviour in animals is to evoke an evolutionary trade-off between the costs of producing the perfect mechanism, and the costs of sometimes making choices that are suboptimal (e.g. Shafir 1994; Bateson & Whitehead 1996). If comparative evaluation mechanisms were found to consume fewer computational resources than absolute mechanisms, yet produce behaviour that is usually close to optimal, then it is easy to see that comparative evaluation mechanisms might be favoured by natural selection. In this vein, Tversky (1969) has argued that certain forms of comparative evaluation mechanisms may be more efficient than absolute evaluation mechanisms because it is easier to form comparisons within dimensions than across dimensions, and comparative mechanisms require fewer interdimensional evaluations than absolute mechanisms. To pursue this idea, we need more information on the exact comparative mechanisms animals use to assess options, and also more information on the potential fitness costs of using these mechanisms in natural contexts. It is important to note that in the current experiment, although the overall change in relative preference between the Binary and Trinary treatments was significant, it was not a large effect, and in both treatments the birds ranked the three options in terms of the net rates of intake they provided. Thus although the behaviour of the birds was irrational in the limited sense defined in the Introduction, we are not suggesting that the use of comparative choice mechanisms implies that the birds were behaving maladaptively.

Behavioural ecologists have focused on absolute currencies because it has been widely assumed that the fitness consequences of choosing a given option are absolute. However, Houston (1997) has recently argued that this view is erroneous. He showed that a rate-maximizing model of simultaneous choice with error can result in violations of strong stochastic transitivity. This occurs because the probability of choosing an option depends on the future rate of gain, which in turn depends on the probability of choosing the option. This dependency results in the value of an option being determined by the energy payoffs and the handling times of both the options the forager is choosing between. Houston used this result to argue that comparative evaluation of options is likely to have been favoured by natural selection. This is clearly an important result, but further theoretical work is needed to establish whether similar lines of argument can be used to explain violations of weak stochastic transitivity, regularity and the more subtle changes in relative preference reported in this paper.

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Appendix

To estimate the net rate of energy intake provided by each of the three flower types we used the equation given in Hurly & Oseen (1999):

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

where: V=volume of sucrose (μl), e=energy content of sucrose (16.5 J/mg), p=density of sucrose (1.0807 mg/μl), S=concentration of sucrose (% weight), T_p=probe time (s), T_f=interflower travel time (s), C_p=cost of hovering flight (0.7734 J/g × s), $C_{p(ws)}$=additional cost of moving the mass of nectar imbibed at the previous flower.

Note that although only V and S were explicity manipulated, T_p depends on V, and $C_{p(ws)}$ on both V and S. T_p and T_f were estimated from Hurly & Oseen (1999, Fig. 1b). Concentration of sucrose was not assumed to affect T_p and the probe times recorded for 20% sucrose by

Hurly & Oseen (1999) were assumed throughout. Since the flowers were closely spaced (5.2 cm) and the birds hovered, maintaining the same orientation, while probing and travelling between flowers we assumed the same costs for both probing and travelling between flowers. C_p was estimated from the equation provided by Montgomerie (1979) and cited in (Tamm 1989):

$$\text{Cost of hovering} = \frac{1}{0.168}\left[\frac{6.13\times10^{-3}W^{1.5}}{b\rho^{0.5}} + 6.28\times10^{-7}s^{0.7}b^{0.3}f^{2.7}c^{2.7}\rho\right]$$

where: W=body mass (average 3.5 g for *S. rufus*), b=wing spread (10.23 cm for a wing chord length of 4.03 cm), ρ=air density (0.00107274 g/cm^3 at 1400 m), s=wing area (10.64 cm^2 for a wing chord length of 4.03 cm), f=wing beat frequency (48.71 Hz for a hovering *S. rufus*), c=wing chord length (average 4.03 cm for *S. rufus*).

$C_{p(ws)}$ was also calculated from the above equation using the mass of nectar imbibed.