

## Context-dependent decisions among options varying in a single dimension

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### ABSTRACT

Contrary to theories of rational choice, adding alternatives to a choice set can change the choices made by both humans and animals. This is usually done by adding an inferior decoy to a choice set of two favoured options that are characterized on two distinct dimensions. We presented wild, free-living rufous hummingbirds (*Selasphorus rufus*) with choices between two or three options that varied in a single dimension only. The options varied in concentration, in volume or in corolla length. When the options varied in concentration, the addition of a medium option to a choice set of a low and a high concentration caused birds to increase their preference for the high option. However, they decreased their preference for the high concentration option when a low option was added to a choice set of high and medium concentrations. When the options varied only in volume, the addition of a high volume option to a choice set of low and medium options decreased the birds' preference for the medium option. We saw no effects of adding a third option when the options varied in corolla length alone. Hummingbirds, then, make context-dependent decisions even when the options vary in only a single dimension although which effect occurs seems to depend on the dimension being manipulated. None of the current theories alone adequately explain these results.

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During its lifetime an animal has to make decisions in a range of situations, such as foraging, nesting building, mate choice and social interactions and the choices made can have dramatic effects on the fitness of that animal. Understanding decision making in animals, and how and whether context affects particular decisions, enables us to understand how animals respond to changing environments as well as helping us to examine the cognitive processes involved in the processing of information.

It has long been assumed that animal decision making is rational such that animals assign an unchanging value to each item encountered and then consistently choose the item with the highest value (Pyke et al., 1977; Schoener, 1971). A consequence of this assumption is that in any situation the animal is expected to choose consistently the option with the highest value but also to choose this option at the same frequency regardless of other, inferior options available. Each option is, therefore, independent of the other options available, both in number and type of options available. Additionally, the relative preferences between two items

should not be altered by the inclusion of an inferior option (Tversky and Simonson, 1993).

For humans, however, it has been accepted for some time that choices are often based on relative judgements (Huber et al., 1982; Tversky, 1977; Tversky and Kahneman, 1974; Zellner et al., 2003) and it is beginning to appear that using absolute currencies may also not describe all decisions that other animals make. Decisions that are not consistent with the use of absolute currencies have been recorded in mammals (Scarpi, 2011), birds (Bateson, 2002; Bateson et al., 2002, 2003; Schuck-Paim et al., 2004), eusocial insects (Edwards and Pratt, 2009; Shafir et al., 2002) and eukaryotic slime moulds (Latty and Beekman, 2011). In these experiments, organisms appear to have used relative currencies such that the decision to be made was changed by the context in which it was placed, in particular the number or kind of alternative options in the choice set.

In such context-dependent experiments, the human or animal is typically asked to choose between two favourable options, which are presented alongside one or more additional options (decoys, i.e. options that are not expected to be chosen). The effect of such a decoy may depend on its relationship to the two options of interest. For example, the inclusion of an asymmetrically dominated decoy to a choice set tends to increase the preference for the

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option by which it is dominated. Rufous hummingbirds have been presented with such a task in which the sucrose options presented to the birds varied in two dimensions, volume and concentration (Bateson et al., 2003). One option (Volume Target) had a large volume (40  $\mu$ l) coupled with a low concentration (20%) while the other option (Concentration Target) had a small volume (20  $\mu$ l) with a high concentration (40%). It was assumed that birds would see these two options as being essentially equivalent and that neither would be preferred over the other. The decoy options added to this pair of targets, in two separate treatments (i.e. the birds faced a choice between only three options, the target, competitor and a decoy but were presented with both sets of trinary choices) were both inferior to the two target options. The Volume Decoy (30  $\mu$ l, 10%) had more sucrose than the Concentration Target but was less concentrated than was the Volume Target. This decoy was, then, dominated by the Volume Target. The Concentration Decoy (10  $\mu$ l, 30%), on the other hand, was more concentrated than the Volume Target but contained less sucrose than did the Concentration Target. This decoy was, then, dominated by the Concentration Target. The addition of each of these decoys to the binary pairing of the two target options led to an increase in the number of choices the birds made to the Target by which it was dominated: addition of the Volume Decoy caused birds to increase their preference of the Volume Target, relative to the binary condition whereas the addition of the Concentration Decoy increased the birds preference for the Concentration Target, relative to the binary condition. The impacts of decoys appear to be very robust and have been observed in a range of human decision making such as in choices of management or game strategies, for products such as tapes, batteries, juice, cars, beer, films, TV's, computers and microwaves as well as for restaurants or tradespeople (Bateman et al., 2008; Colman et al., 2007; Doyle et al., 1999; Huber et al., 1982; Pettibone and Wedell, 2007).

As described above, the impact of decoys on decision making in animals has been investigated experimentally by presenting animals with options that varied in two dimensions simultaneously. However, although an impact of decoy on preferences was seen in all these tests, the interpretation of the effect was not readily interpreted (e.g. Bateson et al., 2002, 2003). One possibility was that because the options the birds had to choose between varied in two dimensions they did not perceive the options as intended. The choice of parameters for the two-dimensional (volume and concentration) options was made on the assumption that changes in concentration and in volume are perceived along an approximately similar, arithmetic scale. However, this may not be the case as although volumes may be most discriminable when they are small, changes in concentration for these hummingbirds may peak around 25% (Blem et al., 2000). As both dimensions changed with each option it is possible that the way the birds perceived the options differed from the original assumptions i.e. that the placement of decoys relative to the target and competitor was not how the birds perceived them. An alternative explanation is that the birds made their choices based on their energetic state. The clearest prediction in this case is that the inclusion of poorer options would lower the bird's energetic state, so it should increase its preference for any option that offers a better caloric return (Schuck-Paim et al., 2004). This explanation could not be entirely excluded with the data produced by those earlier experiments.

As manipulations with two dimensions resulted in a more complex outcome than expected, we attempted in this experiment to present birds with options that would allow us to determine more readily how their preferences were related to the options we provided. To do this as simply as possible, we presented rufous hummingbirds with options that varied in a single dimension only (Wedell et al., 2005; Wedell and Pettibone, 1999; Choplin and Hummel, 2005).

To manipulate choice in a single dimension we presented birds with binary and trinary comparisons in which volume, concentration or corolla length alone were varied. For each experimental treatment (volume, concentration or corolla length), birds faced three binary conditions and a single trinary condition. In this trinary condition, each option was effectively a decoy for the other two options. If the birds choose options based on energetic value, in all conditions, the birds should choose the option that provides the greatest energetic return. The inclusion of a third, poorer option may dilute the preference for the best option but should not alter that preference relative to the second-best option. This was what we expected the birds to do but with the additional effect that we would observe whether our linearly related options would be matched by linearly related preferences.

If the birds make decisions based on the absolute energetic value on the available options, we predicted that they would prefer the option that affords them the greatest energetic return, which may mean the lowest energetic expenditure, as in the case of the corolla treatment. If, however, the birds employ other comparison mechanisms to decide among options, there were a number of possible outcomes, depending on the relationship among the options.

1. The inclusion of the smallest option (longest for the Corolla Treatment) may lead the bird to increase its preference for the middle option at the expense of the largest option if the bird perceives that middle option to be better than it appeared in comparison with the largest option. This possibility is predicted by Helson's (1964) Adaptation Level Theory, in which options are judged to be good or bad relative to the average of the options in the context in which they are presented. For example, a middle option paired with a higher option will be below the average of the two options and therefore should not be often chosen often when in the presence of the higher option. If, however, a low option is added to the choice set then the middle option becomes the average and so might be chosen more frequently than it was in the binary context.
2. The inclusion of the middle option may lead the bird to increase its preference for the largest option over the smallest option because the two extreme options now appear to be more different. This outcome is suggested by Krumhansl's (1978) Distance Density Model in which it is considered to be easier to make more sensitive distinctions when the available options are more similar to one another.
3. The inclusion of the largest option might lead the bird to decrease its relative preference for the middle option. This is also suggested by Helson's (1964) Adaptation Level Theory as the middle option would go from being above average in a low/middle binary choice set to being the average option in a low/middle/high trinary choice set. As in our Volume (Ratio) Treatment the middle option would be much poorer than average in the trinary condition than it is in the low-middle binary condition, the decrease in preference for the middle option should be more pronounced than in the other Treatments.

The experiment was conducted using wild male rufous hummingbirds foraging in the field from artificial flowers. The sucrose contents of artificial flowers from which the hummingbirds were feeding were manipulated along three dimensions: volume, concentration or corolla length. These dimensions were chosen because they all affect choices made by foraging hummingbirds: they prefer shorter corollas, larger volumes and higher concentrations (Montgomerie, 1984).

## 1. Methods

### 1.1. Subjects and study site

The subjects were 21 wild male rufous hummingbirds defending feeding territories in a valley in the Eastern Range of the Rocky Mountains (49° 35'N, 114° 41'W, elevation 1400 m), Alberta, Canada. In mid-May commercial hummingbird feeders containing 14% sucrose were placed in potential territories and by late May most feeders were defended by males. These territorial males were individually identifiable by the application of a small amount of waterproof, non-toxic ink to the breast. No birds lost their territories as a result of the ink application and the marks had faded by the time by the birds migrated in mid-July.

### 1.2. Experimental training

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

### 1.3. Experimental procedure

The experimental apparatus consisted of a Plexiglas board (28 cm × 21.5 cm × 1.2 cm) drilled with 18 holes (3.5 mm diameter) arranged in offset rows such that nearest neighbour distances were 5.2 cm. Inserted into each well on the underside of the Plexiglas board was a length of plastic tubing with the end melted closed. The length of this tube (corolla) was determined by the experimental treatment (see below). The wells (flowers) were marked with coloured reinforcement rings that were used to indicate the length of the corolla, the volume or the concentration of sucrose (nectar) contained in the flower. The flowers were presented to the birds by mounting the board at a 45° angle on a stake approximately 80 cm high.

There were four experimental treatments. Within each of these treatments there were four conditions, three binary choice sets and one trinary choice set:

- (1) *Concentration*: Birds were presented with flowers with a corolla length of  $1.5 \pm 0.05$  cm containing 30 µl of 20%, 25% or 30% sucrose solution. The flowers were presented as choices between two types of flower or all three. Thus, the binary options for the Concentration Treatment were low/medium = 20%/25%, medium/high = 25%/30%, low/high = 20%/30% while the trinary option was 20%/25%/30%.
- (2) *Corolla*: There were three corolla lengths measured to  $\pm 0.05$  cm: short =  $1.0 \pm 0.05$  cm, medium =  $1.5 \pm 0.05$  cm and long =  $2.0 \pm 0.05$  cm. The binary options presented were short/medium, medium/long, short/long and all three, short/medium/long, were presented in the trinary condition. The volume of sucrose was 30 µl and the sucrose concentration was 25% for all the options in this Treatment.

- (3) *Volume (Interval)*: We presented the Volume Treatments in two different ways. In the first, the values for the three types were at constant intervals: 20 µl, 30 µl and 40 µl. The binary options in this Volume (Interval) Treatment were low/medium (20 µl/30 µl), medium/high (30 µl/40 µl) and low/high (20 µl/40 µl), and the trinary consisted of all three types. The corolla length was  $1.5 \pm 0.05$  cm and the sucrose concentration was 25% in all of the options.
- (4) *Volume (Ratio)*: In the Volume (Ratio) Treatment the values for the three types of flower were chosen to be at a constant ratio (*R*) to each other: 10 µl, 20 µl and 40 µl. The binary options in this Treatment were wee/low (10 µl/20 µl), low/high (20 µl/40 µl) and wee/high (10 µl/40 µl), and the trinary was all three types. The corolla length was  $1.5 \pm 0.05$  cm and the sucrose concentration was 25% in all of the options.

For each of the four Experimental Treatments, each bird was tested in three binary and one trinary condition. The order of presentation was randomly chosen from an unbiased schedule such that no order was over-represented in any of the Treatments. Birds that were presented with the Volume Treatment were presented with both Interval and Ratio Treatments, with half of the birds doing the Interval Treatment first and the other half the birds doing the Ratio Treatment first.

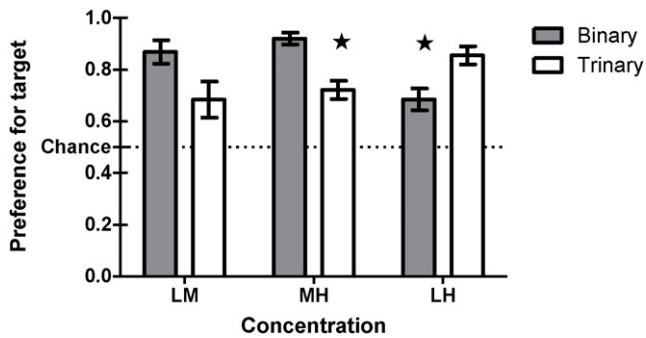
Eight birds completed the Concentration Treatment and six different birds completed the Corolla Treatment. Five different birds completed the Volume (Interval) Treatment and all of these birds also completed the Volume (Ratio) Treatment. One further bird completed the Volume (Ratio) Treatment only.

In each Treatment the flower types were indicated to the bird by the colour of the ring surrounding the well of sucrose. Colours were randomly assigned to treatments and for each bird the colours were randomly assigned to flower types within a treatment. We used a total of eighteen colours, two for each Binary treatment and three for each trinary treatment, such that each bird had to learn completely new colour associations in each treatment it received. We designed the experiment this way in order to prevent the carry-over of strong preferences that were developed in one condition into the subsequent conditions. In both binary and trinary conditions, the flowers for each type were randomly allocated to the 18 holes in a board: nine of each type in the binary conditions and six of each type in the trinary condition.

Birds visited the boards of flowers approximately every 10 min throughout the day. On a feeding bout, a bird was allowed to feed from as many holes as he wished and the colour of each hole from which he fed was recorded. Once a feeding bout had finished and the bird had flown away, the corollas from which he had fed were cleaned and refilled with the appropriate volume and concentration of nectar. The board was rotated through 90° between visits. Every four visits a new board was used with a different random pattern of flowers and the board was moved approximately 1 m in order 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 at least two of the available flower types in the course of its first ten flower visits (binary) or the first 15 flower visits (trinary), we forced him to visit at least 10 flowers of the under-visited colour or colours by presenting him with boards with flowers of only that type. Following this correction procedure the choice experiment was restarted and birds had to make 150 well visits. Flower visits made before and in the course of the correction procedure were not included in the data set.

Both binary and trinary treatments were continued until a bird had made a total of at least 150 choices of the flowers presented. A single treatment typically took between one and three days to



**Fig. 1. Concentration Treatment:** Proportions of choices to the target in binary and trinary conditions in the last 15 bouts.  $H=40\%$  sucrose,  $M=30\%$ ,  $L=20\%$ . The shaded bars represent the preference for the target (always the higher of the two concentrations) in the binary condition and the white bars represent the preference for that same target relative to the same competitor, both now in the presence of the third option e.g. LM represents the choices to  $M$  (target) when it is paired with  $L$  (shaded bars) and LM in the presence of  $H$  (white bars). Indifference between the two options is 50%. The data are means  $\pm$  s.e. ( $N=8$ ). The stars indicate which options differed significantly with the addition of a trinary option.

complete. Breaks for the night, lunch or rain were ignored since they did not appear to have any effect on preference.

#### 1.4. Data analysis

We looked at the data in two ways. We analysed all of the data from well visits made during the last 15 bouts completed by each bird and we redid all the analyses using only the first visit of each of these 15 bouts. In each set of analyses, the birds' well visits were used to calculate the proportion of choices made to each option. For each condition in each Treatment, one of the options was designated the 'target' and the other was the 'competitor'. For the Concentration Treatment the higher concentration in each pair was the target and the lower was the competitor. Similarly for the Volume Treatment, the target was the larger volume and the competitor the smaller volume. For the Corolla Length Treatment, the shorter corolla was the target and the longer corolla the competitor. For all Treatments, then, the target is the option we expected to be most preferred and the competitor the less preferred.

The preferences were calculated using the following equation:

$$\frac{\text{Proportion of choices for target}}{\text{Proportion of choices for target} + \text{proportion of choices for competitor}}$$

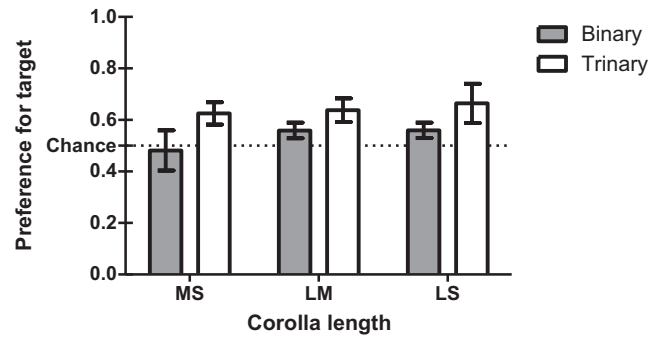
All analyses were carried out using PASW for Windows version 18. We used paired  $t$ -tests to compare the preference between the binary and trinary conditions using a significance level of 0.0166 to correct for multiple tests. Chi-squared tests were used to confirm that birds' choices of the two or three available options differed from each other.

## 2. Results

### 2.1. Concentration Treatment

Using all the visits from the last 15 bouts, in the Concentration Treatment, the addition of  $M$  (25%) to a choice set of  $L$  (20%) and  $H$  (30%), resulted in birds choosing  $H$  more frequently ( $L:H+M$ :  $t(7)=7.313$ ,  $p<0.001$ ). When  $L$  was added to a choice set of  $M$  and  $H$ ,  $H$  was chosen less often ( $M:H+L$ :  $t(7)=3.316$ ,  $p=0.013$ ; Fig. 1). There was no significant change in preference when  $H$  was added to a choice set of  $L$  and  $M$  ( $L:M+H$ :  $t(7)=2.723$ ,  $p=0.030$ ;  $p$ -value set at 0.0166 due to Bonferroni correction). The mean number of well visits = 66.6 (95% C.I. 59.5–73.7).

Using only the first well visit from the final 15 bouts, when  $M$  (25%) was added to a choice set of  $L$  (20%) and  $H$  (30%), birds



**Fig. 2. Corolla Treatment:** Proportions of choices to the target in binary and trinary conditions in the last 15 bouts.  $S=0.5$  cm corolla length,  $M=1$  cm,  $L=1.5$  cm. The shaded bars represent the preference for the target (always the shorter of the two lengths) in the binary condition and the white bars represent the preference for that same target relative to the same competitor, both now in the presence of the third option. Indifference between the two options is 50%. The data are means  $\pm$  s.e. ( $N=7$ ).

chose  $H$  more frequently ( $L:H+M$ :  $t(7)=3.442$ ,  $p=0.011$ ). When  $L$  was added to a choice set of  $M$  and  $H$ ,  $H$  was chosen less often ( $M:H+L$ :  $t(7)=4.135$ ,  $p=0.004$ ). There was no significant change in preference when  $H$  was added to a choice set of  $L$  and  $M$  ( $L:M+H$ :  $t(7)=2.190$ ,  $p=0.065$ ).

Both measures of performance lead to the same conclusion: when  $M$  was added to the choice set the birds chose  $H$  more often and when  $L$  was added to the choice set of  $M$  and  $H$  then,  $H$  was chosen less frequently.

### 2.2. Corolla Treatment

When we included all of the data from the last 15 bouts in the analysis, in the Corolla Treatment, there were no significant changes in preference from the binary to the trinary condition for any of the options ( $S(1\text{ cm}):M(1.5\text{ cm})+L(2\text{ cm})$ :  $t(5)=2.082$ ,  $p=0.092$ ;  $S:L+M$ :  $t(5)=1.504$ ,  $p=0.293$ ;  $M:L+S$ :  $t(5)=1.663$ ,  $p=0.157$ ; Fig. 2). The mean number of well visits = 75.5 (95% C.I. 63.9–87.2).

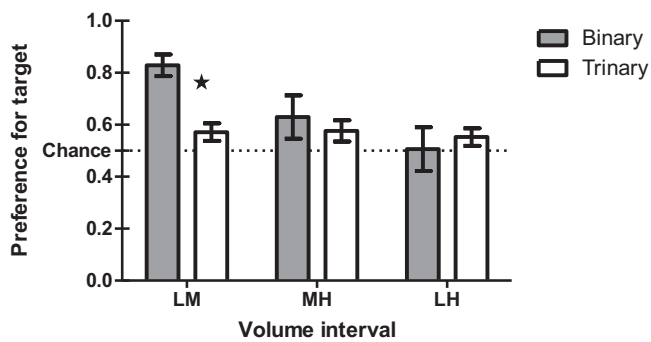
When we included only the data for the first well visits from the final 15 bouts, the outcome was the same: there was no significant change in preference from the binary to the trinary condition for any of the options ( $S(1\text{ cm}):M(1.5\text{ cm})+L(2\text{ cm})$ :  $t(5)=3.222$ ,  $p=0.023$ ;  $S:L+M$ :  $t(5)=1.271$ ,  $p=0.260$ ;  $M:L+S$ :  $t(5)=0.907$ ,  $p=0.406$ ).

In sum, using either measure, the birds' preferences for corolla length did not change with the addition of a third option to any of the binary choice sets.

### 2.3. Volume (Interval) Treatment

When we included all of the well visits from the last 15 bouts, in the Volume (Interval) Treatment (LMH), the inclusion of  $H$  ( $40\mu\text{l}$ ) to the choice set of  $L$  ( $20\mu\text{l}$ ) and  $M$  ( $30\mu\text{l}$ ) decreased the birds' preference for  $M$  ( $t(4)=4.387$ ,  $p=0.012$ ; Fig. 3). The inclusion of a third option to the other binary choice sets had no effect ( $L:H+M$ :  $t(4)=0.875$ ,  $p=0.431$ ;  $M:H+L$ :  $t(4)=0.593$ ,  $p=0.585$ ). The mean number of wells visits in the final 15 bouts = 65.4 (95% C.I. 57.8–73.0).

When we used only the data for the first visit in those last 15 bouts, the inclusion of  $H$  ( $40\mu\text{l}$ ) to the choice set of  $L$  ( $20\mu\text{l}$ ) and  $M$  ( $30\mu\text{l}$ ) decreased the preference for  $M$  ( $t(4)=6.724$ ,  $p=0.003$ ). The inclusion of a third option to the other binary choice sets had no effect ( $L:H+M$ :  $t(4)=0.634$ ,  $p=0.561$ ;  $M:H+L$ :  $t(4)=1.105$ ,  $p=0.331$ ).



**Fig. 3.** Volume (Interval) Treatment: Proportions of choices to the target in binary and trinary conditions in the last 15 bouts.  $H=40\ \mu\text{l}$  sucrose,  $M=30\ \mu\text{l}$ ,  $L=20\ \mu\text{l}$ . The shaded bars represent the preference for the target (always the larger volume) in the binary condition and the white bars represent the preference for that same target relative to the same competitor, both now in the presence of the third option. Indifference between the two options is 50%. The data are means  $\pm$  s.e. ( $N=5$ ). The star indicates which options differed significantly with the addition of a trinary option.

Using either measure of performance, when  $H$  was included to a choice set of  $L$  and  $M$  there was a decrease in preference for  $M$ .

#### 2.4. Volume (Ratio) Treatment

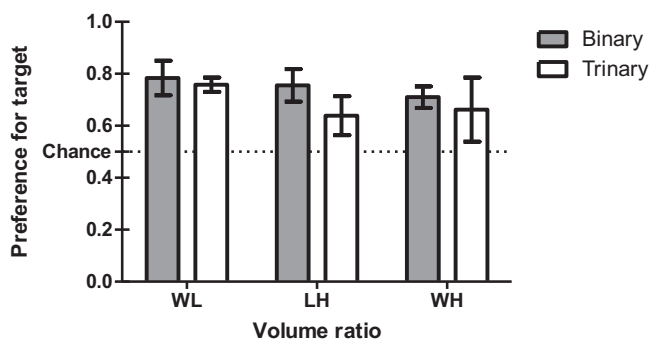
Using all of the data from the last 15 bouts in the Volume (Ratio) Treatment, we found no effect of the inclusion of a third option to the binary choices on preference for any of the options ( $W(10\ \mu\text{l}):L(20\ \mu\text{l})+H(40\ \mu\text{l})$ :  $t(5)=0.591$ ,  $p=0.580$ ;  $W:H+L$ :  $t(5)=0.966$ ,  $p=0.379$ ;  $L:H+W$ :  $t(5)=0.359$ ,  $p=0.734$ ; Fig. 4). The mean number of wells visits in the final 15 bouts = 63.4 (95% C.I. 56.4–70.4) well visits.

When we included only the first choice of the last 15 bouts in the analysis the inclusion of a third option to the binary choices in the Volume (Ratio) Treatment had no effect on preference for any of the options ( $W(10\ \mu\text{l}):L(20\ \mu\text{l})+H(40\ \mu\text{l})$ :  $t(5)=0.476$ ,  $p=0.654$ ;  $W:H+L$ :  $t(5)=0.243$ ,  $p=0.817$ ;  $L:H+W$ :  $t(5)=0.106$ ,  $p=0.920$ ).

Using either measure, the addition of a third option to any of the binary choice sets had no discernable effect.

### 3. Discussion

The inclusion of a third option to binary choices where all three options varied along a single dimension did not lead to a clear pattern of effect on the decisions made in the presence of that



**Fig. 4.** Volume (Ratio) Treatment: Proportions of choices to the target in binary and trinary conditions in the last 15 bouts.  $H=40\ \mu\text{l}$  sucrose,  $L=20\ \mu\text{l}$ ,  $W=10\ \mu\text{l}$ . The shaded bars represent the preference for the target (always the larger volume) in the binary condition and the white bars represent the preference for that same target relative to the same competitor, both now in the presence of the third option. Indifference between the two options is 50%. The data are means  $\pm$  s.e. ( $N=5$ ).

third option. In most instances, preferences seen in the binary choices were not significantly altered by the inclusion of the third option. However, for two of the four treatments (Concentration and Volume (Interval)), the birds' preferences were affected by that inclusion. In the Concentration Treatment the addition of the medium option to the low and high options lead to an increased preference for the high option while the addition of a low option to the medium and high options decreased the preference for the high option (Fig. 1). In the Volume (Interval) Treatment, the addition of a high option to the medium and low options led to a decreased preference for the medium option (Fig. 3). These effects were observed both when the data we included in the analyses were all the choices from the last 15 bouts or only the first choices from the last 15 bouts.

Although these changes were not seen in every treatment, each of these changes in preference is consistent with our initial predictions. Helson's (1964) Adaptation Level Theory predicts two of the effects: that the inclusion of the lowest concentration led birds to increase their preference for the medium concentration and that the inclusion of the largest volume leads bird to decrease their preference for the medium option. Krumhansl's (1978) Distance Density Model predicted the third effect we observed, which was that in the Concentration Treatment birds increased their preference for the high concentration over the low option when the medium concentration was added. Our results do not favour one of these hypotheses over the other. Additionally, we had two volume treatments in an attempt to distinguish experimentally between the Adaptation Level Theory (ALT) and the Distance Density Model (DDM): the ALT would have predicted that the addition of the medium option to the low and high options in the Volume (Interval) Treatment would lead to an increased preference for the high option, which it did. However, we would have expected this effect to have been even greater in the Volume (Ratio) Treatment and this was not the case (we saw no effect of adding the high option). The DDM predicted an increased preference for the high option when presented with the wee and low options and we did not see this effect.

In addition to the inconsistency in the explanation of the observed effects, the pattern of effects was not consistent across the three dimensions we tested. This may be because the birds differ in their abilities to discriminate the values of the options with which we presented them, depending on the dimension. If this was the case, variation in discriminability across the dimensions should not alter the direction of preference: birds are always expected to prefer high volumes, high concentrations and small corolla lengths. However, this variation could affect the strength of preference: the lack of a change in preference might simply be due to poor discriminability of the options rather than to a lack of context effects. However, as we chose values for volumes, concentrations and corolla lengths that we know these birds can discriminate among the particular options, this seems an unlikely explanation (Blem et al., 2000; Montgomerie, 1984; Montgomerie et al., 1984).

Although we cannot readily provide a single explanation to encompass all of the effects of adding a third option, these hummingbirds do appear to have made context-dependent decisions, even though the options to choose among varied in a single dimension only. Furthermore, they do so not only in the dimensions we manipulated here as both hummingbirds (Hurly and Oseen, 1999; Hurly, 2003) and starlings (Bateson, 2002) also alter their choices between binary and trinary contexts when tested with rewards that differ only in the degree of variation. Comparative decision-making strategies are thought to be used because they make decision making easier and quicker. One might think that choosing among options varying in a single dimension would already be easy and thus not susceptible to comparative effects. These animal data, along with data from humans making single dimension choices,

would suggest that context affects even these apparently simple decisions.

It has been argued that context-dependent decision making in animals can be explained by changes in energy state (Schuck-Paim et al., 2004). The options added to a choice set are often inferior and increasing preferences for the higher energetic option can be readily explained by considerations of energetic state. This is because the decisions are usually set in a foraging context and the animal needs to sample all of the options to learn about them. Simply by sampling the poorer option the animal will change its energetic state. If the animal is in different energy states in the different conditions we might expect that the animal will make different choices and specifically that when its energy state has been lowered due to the inclusion of an inferior option that the animal would select more of the better option to balance its energy requirements. In our experiment, it is not possible to explain the changes in preference with changes to the bird's energetic state through sampling the new, lower option as in the Concentration Treatment the addition of an energetically poorer option actually decreased the preference for an energetically richer option.

The main aim of this experiment was to determine whether the linearly related options with which we presented the birds would be matched with linearly related preferences. If this had been the outcome, we could return to examination of context-dependent decision making using a two (or more) dimensional set of options, which is more closely related to the variation in real foraging options faced by these birds in the wild. However, this was not the case. It appears that context is affecting these birds' decisions but we cannot yet explain how, certainly not well enough to allow us to predict how any one extra option (decoy or not) would affect preferences between two relatively favourable alternatives. It would seem that further experimentation in single dimensions may provide some useful insight into this problem.

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### References

- Bateman, I.J., Munro, A., Poe, G.L., 2008. Decoy effects in choice experiments and contingent valuation: asymmetric dominance. *Land Economics* 84, 115–127.
- Bateson, M., 2002. Context-dependent foraging choices in risk-sensitive starlings. *Animal Behaviour* 64, 251–260.

- Bateson, M., Healy, S.D., Hurly, T.A., 2002. Irrational choices in hummingbird foraging behaviour. *Animal Behaviour* 63, 587–596.
- Bateson, M., Healy, S.D., Hurly, T.A., 2003. Context-dependent foraging decisions in rufous hummingbirds. *Proceedings of the Royal Society of London B* 270, 1271–1276.
- Blem, C.R., Blem, L.B., Felix, J., van Gelder, J., 2000. Rufous hummingbird sucrose preference: precision of selection varies with concentration. *Condor* 102, 235–238.
- Choplin, J.M., Hummel, J.E., 2005. Comparison-induced decoy effects. *Memory & Cognition* 33, 332–343.
- Colman, A.M., Pulford, B.D., Bolger, F., 2007. Asymmetric dominance and phantom decoy effects in games. *Organizational Behavior and Human Decision Processes* 104, 193–206.
- Doyle, J.R., O'Connor, D.J., Reynolds, G.N., Bottomley, P.A., 1999. The robustness of the asymmetrically dominated effect: buying frames, phantom alternatives, and in-store purchases. *Psychology and Marketing* 16, 225–243.
- Edwards, S.C., Pratt, S.C., 2009. Rationality in collective decision-making by ant colonies. *Proceedings of the Royal Society B* 276, 3655–3661.
- Helson, H., 1964. *Adaptation Level Theory: An Experimental and Systematic Approach to Behaviour*. Harper and Row, New York.
- Huber, J., Payne, J.W., Puto, C., 1982. Adding asymmetrically dominated alternatives-violations of regularity and the similarity hypothesis. *Journal of Consumer Research* 9, 90–98.
- Hurly, T.A., 2003. The twin threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. *Animal Behaviour* 66, 751–761.
- Hurly, T.A., Oseen, M.D., 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Animal Behaviour* 58, 59–66.
- Krumhansl, C.L., 1978. Concerning applicability of geometric models to similarity data-interrelationship between similarity and spatial density. *Psychological Review* 85, 445–463.
- Latty, T., Beekman, M., 2011. Irrational decision-making in an amoeboid organism: transitivity and context-dependent preferences. *Proceedings of the Royal Society B* 278, 307–312.
- Montgomerie, R.D., 1984. Nectar extraction by hummingbirds—response to different floral characters. *Oecologia* 63, 229–236.
- Montgomerie, R.D., Eadie, M., Harder, L.D., 1984. What do foraging hummingbirds maximise? *Oecologia* 63, 357–363.
- Pettibone, J.C., Wedell, D.H., 2007. Testing alternative explanations of phantom decoy effects. *Journal of Behavioral Decision Making* 20, 323–341.
- Pyke, G.H., Pulliam, H.R., Charnov, E.L., 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* 52, 137–154.
- Scarpi, D., 2011. The impact of phantom decoys on choices in cats. *Animal Cognition* 14, 127–136.
- Schoener, T.W., 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2, 364–404.
- Schuck-Paim, C., Pompilio, L., Kacelnik, A., 2004. State-dependent decisions cause apparent violations of rationality in animal choice. *PloS Biology* 2, 2305–2315.
- Shafir, S., Waite, T.A., Smith, B.H., 2002. Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behavioral Ecology and Sociobiology* 51, 180–187.
- Tversky, A., 1977. Features of similarity. *Psychological Review* 84, 327–352.
- Tversky, A., Kahneman, D., 1974. Judgment under uncertainty: heuristics and biases. *Science* 185, 1124–1131.
- Tversky, A., Simonson, I., 1993. Context-dependent preferences. *Management Science* 39, 1179–1189.
- Wedell, D.H., Pettibone, J.C., 1999. Preference and the contextual basis of ideals in judgment and choice. *Journal of Experimental Psychology: General* 128, 346–361.
- Wedell, D.H., Santoyo, E.M., Pettibone, J.C., 2005. The thick and the thin of it: contextual effects in body perception. *Basic and Applied Social Psychology* 27, 213–228.
- Zellner, D.A., Rohm, E.A., Bassetti, T.L., Parker, S., 2003. Compared to what? Effects of categorization on hedonic contrast. *Psychonomic Bulletin & Review* 10, 468–473.