

Individual differences in decision making by foraging hummingbirds



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ABSTRACT

For both humans and animals preference for one option over others can be influenced by the context in which the options occur. In animals, changes in preference could be due to comparative decision-making or to changes in the energy state of the animal when making decisions. We investigated which of these possibilities better explained the response of wild hummingbirds to the addition of a decoy option to a set of two options by presenting Rufous hummingbirds (*Selasphorus rufus*) with a foraging experiment with two treatments. In each treatment the birds were presented with a binary choice between two options and a trinary choice with three options. In treatment one the binary choice was between a volume option and a concentration option, whereas in treatment two the same volume option was presented alongside an alternative concentration option. In the trinary choice, birds were presented with the same options as in the binary choice plus one of two inferior options. Birds changed their preferences when a poorer option was added to the choice set: birds increased their preference for the same option when in the presence of either decoy. Which option differed across individuals and the changes in preference were not readily explained by either energy maximisation or the decoy effect. The consistency in response within individuals, however, would suggest that the individual itself brings an extra dimension to context-dependent decision-making. This article is part of a Special Issue entitled: Cognition in the wild.

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1. Introduction

Observing the choices animals make is critical to our understanding of animal behaviour. These choices can be used both to uncover the features that animals prefer (such as sexually selected traits) and to make predictions about which options they should choose in order to maximise their fitness (such as in optimal foraging theory). However, the mechanism(s) by which animals make these choices are still unclear.

One of the assumptions made in many animal decision-making or foraging models is that the animals have (or behave as if they have) full information about the world (Emlen, 1966; Pyke et al., 1977) and, when foraging, animals are expected to know the frequencies of different types of food sources, the energetic value of these options (Emlen, 1968; Sih and Christensen, 2001; Schaefer et al., 2003). A further assumption is that animals choose those options that return the greatest energetic value or based on the amount they contain of some crucial nutrient (Pyke et al., 1977). Two consequences of animals choosing according to the absolute value of options are that: (a) they should not choose poor options,

(b) the presence or absence of poor options should not alter the choices they make between better options. However, as there is increasing evidence that for animals (as is the case with humans) the presence of poor options can change their preferences for better options (Bateson, 2002; Bateson et al., 2002, 2003; Hurly and Oseen, 1999; Latty and Beekman, 2011; Shafir et al., 2002; Waite, 2001) it appears that animals do not necessarily make choices based on the absolute value of those options. These changes in preference in response to the addition of poor options increasingly support the suggestion that animals, like humans, might use relative decision-making strategies, such that their choices are based on the relative value of the options available rather than on their absolute value (Bateson, 2002; Bateson et al., 2003; Latty and Beekman, 2011; Morgan et al., 2012; Shafir et al., 2002).

Decisions that are altered by the addition of poorer options to choice sets are considered to be economically irrational. Economically rational choices are those that maximise the utility of the decision maker and a consequence of maximising utility is that choices of options should be independent of the addition of irrelevant or inferior alternatives (Luce, 1959). For some animals such as foraging hummingbirds, however, it is possible that the apparent violations of the independence of irrelevant alternatives are actually due to the hummingbirds compensating for the decreased intake caused by sampling the poorer option

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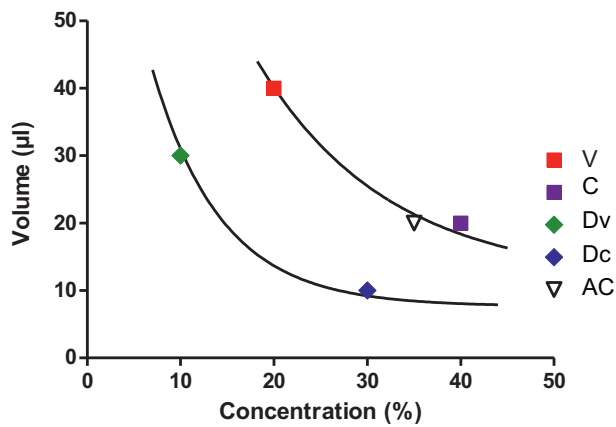


Fig. 1. Relative positions on the concentration and volume dimensions of the five flower types used in treatments one and two. The volume option (V) contains 40 μ l of 20% sucrose (145 J per well), the concentration option (C) 20 μ l of 40% (158 J), the volume decoy option (DV) 30 μ l of 10% (52 J), the concentration decoy option (DC) 10 μ l of 30% (58 J) and the alternative concentration option (AC) contains 20 μ l of 35% (135 J). The lines are iso-lines where the energy at each point in the iso-line is equal to either the volume option or to the volume decoy.

by choosing the option with the highest energetic content more often (Schuck-Paim et al., 2004). This could explain why foraging hummingbirds faced with three options, two favourable (one with a higher caloric value but volumetrically smaller and the other less valuable calorically but a larger quantity) and one poor (low calorically and a small volume), changed their preferences in the presence of the poor option to increasingly tending to prefer the sweeter, smaller option, which also provided a slightly higher caloric return (Bateson et al., 2002, 2003; Morgan et al., 2012). Foraging hummingbirds are useful for looking at complex decision making as they can remember the spatial location of food sources in addition to the volume, concentration and variability of sucrose provided and attend to cues pertaining to both the taste and the energetic contents of the items on which they forage (Bacon et al., 2010, 2011; Healy and Hurly, 2003, 2004).

In order to test whether the changes in the preference shown by hummingbirds are better explained by comparative decision-making mechanisms or by energy state changes, we replicated the design of the asymmetrically-dominating decoy experiment described in Bateson et al. (2003) but added a second, key treatment. In the Bateson et al. study, birds were offered a choice between two favourable options: a concentration option (20 μ l of 40% sucrose solution) presented alongside a volume option (40 μ l of 20% sucrose; Fig. 1). When these two favourable options were presented alongside a decoy that was either 10 μ l of 30% sucrose (the concentration Decoy) or 30 μ l of 10% (the volume decoy) the birds did change the choices they made in response to the addition of the decoy options but their response to the presence of the asymmetrically-dominated decoys in a way that is not consistent with economic rationality: in the presence of the concentration decoy the birds tended to increase their choices to the concentration option over the volume option while in the presence of the volume decoy they tended to increase their choices made to the volume option. The concentration option offered a caloric return of 155 J (Table 1) while the volume option offered a caloric return of 142 J per well emptied, a slightly smaller caloric return. Although in the original Bateson et al. study the birds' choices were interpreted as evidence for context-dependent decision making, it is not possible with the experimental design used to exclude the alternative possibility that the birds' choices were due to changes in energy state caused by the addition of decoy options (Schuck-Paim et al., 2004). As decoy options offered a smaller caloric return than did the target options, the hummingbirds would have had a lower

Table 1

The energetic value in Joules of the sucrose contained in one well of each option.

Option	Volume (μ l)	Concentration (% sucrose)	Joules
Concentration	20	40	158
Volume	40	20	145
Concentration decoy	10	30	58
Volume decoy	30	10	52
Alternative Concentration	20	35	135

energetic intake when foraging from the trinary choice sets than when foraging from the binary choice sets. They might, therefore, have chosen the option with the greatest caloric payoff to make up the energetic shortfall. Although this explanation would not explain why the hummingbirds increased their preference for different options in the presence of the decoys, we considered that it would be useful to test it explicitly. To test whether energetic state would explain the hummingbirds' choices in the Bateson et al. (2003) experiments, therefore, in the current experiment we presented some birds with a replica treatment as used by Bateson et al. (2003) and presented other birds with a second treatment that would allow us to examine whether the caloric return of the options could explain the hummingbirds' choices in the presence of decoy options. In this second treatment, then, we presented birds with a concentration option (now 20 μ l of 35%) that offered a smaller caloric return (133 J) than did the volume option (142 J, as in the first treatment; Fig. 1). The decoys were the same as in the first treatment with both offering a little over 50 J caloric return (Table 1). Furthermore, although it has been assumed in previous experiments that when a bird visits a well containing one of the options that he will drink the entire contents of that well but as hummingbirds do not always do this, even when the option visited is relatively good (Bacon et al., 2011), we also measured the amount of sucrose the birds actually consumed on each choice (Table 2).

Due to the difference in caloric return between the two favourable options, in our second treatment we expected the birds to prefer the volume option over the concentration (the 'alternative' concentration) option when these options were presented as a binary choice. Furthermore, if the birds base their decision on caloric intake in the presence of either of the poorer decoys, then their preference for the volume option should increase in the presence of either decoy. If, on the other hand, the birds make relative decisions consistent with asymmetrically dominated decoy effects, then any change in response to the presence of a decoy should depend on the nature of the decoy: in the presence of the volume decoy birds should increase the proportion of their choices to the volume option whereas in the presence of the concentration decoy they should increase the proportion of choices to the alternative concentration option.

2. Materials and methods

2.1. Subjects and study site

The subjects were 11 wild male rufous hummingbirds defending feeding territories in a valley in the Eastern Range of the Rocky Mountains (49°21'N, 114°25'W, elevation 1400 m), Alberta, Canada. All of this work was approved by the University of St Andrews Ethical Committee and the University of Lethbridge Animal Welfare Committee under permits from Environment Canada and the Alberta Sustainable Resource Development Fish and Wildlife Division.

In mid-May, we placed commercial hummingbird feeders containing 14% sucrose were placed in potential territories and by late May these were defended by males. We marked these territorial

Table 2

The average energetic value in joules that birds consumed from each option in the binary condition.

Treatment	Option	Volume (μl)	Concentration (% sucrose)	Average number of Joules per well
Treatment 1	Concentration	20	40	127
Treatment 1	Volume	40	20	92
Treatment 2	Alternative concentration	20	35	142
Treatment 2	Volume	40	20	101

males for individual identification by applying a small amount of waterproof, non-toxic ink to their breasts.

2.2. Training

We trained the birds to feed from a Plexiglas board (28 cm \times 21.5 cm \times 1.2 cm) tilted at an angle of 45° mounted on a stake ca. 80 cm high at a 45° angle. The board contained 18 wells (10 mm deep, 3.5 mm in diameter) each of which could hold a maximum of 120 μl . The wells were arranged in an offset pattern with each well 5.2 cm from each of its nearest neighbours. For the duration of training all of the wells were marked with yellow reinforcements and all contained 50 μl of 25% sucrose solution. After each visit the board was rotated through 90°. Rotating the board changed the spatial arrangement of the wells so that birds could only learn the contents of the wells using the colour of the surrounding ring. Once the board had been rotated four times training was considered complete and the experiment began. Training took approximately 2 h. All birds that completed training successfully progressed to the experiment.

2.3. Experimental manipulation

We used the same apparatus for the experiment as used in training except that the colour of coloured reinforcement marking each of the wells indicated its contents. We used eight colours for the reinforcements across the experiment (blue, yellow, indigo, pink, red, green, violet and orange), using three new colours for each condition in order that birds had to relearn all of the colour associations for each condition. Each bird received a different set of eight colours such that no bird had the same colour combination as any other bird. We pseudo-randomly assigned birds to either treatment one or treatment two.

2.4. Treatment one

In this treatment (essentially a replicate of Bateson et al., 2003), we presented six birds with one binary condition and two trinary conditions. We pseudorandomised the order of presentation so we assigned the same number of birds to each order of presentation.

In the binary condition, we presented birds with a choice of two options: nine wells were randomly assigned to contain the concentration option (20 μl of 40% sucrose solution), and the remaining nine wells contained the volume option (40 μl of 20% sucrose).

In the volume decoy trinary condition, we presented birds with a choice of three options: six of the wells were randomly assigned to contain the concentration option (20 μl of 40% sucrose), six were randomly assigned to contain the volume option (40 μl of 20% sucrose), and the final six wells were assigned to contain the volume decoy (30 μl of 10% sucrose).

In the concentration decoy trinary condition, we presented birds with a choice of three options: one third of the wells were randomly assigned to contain the concentration option (20 μl of 40% sucrose), one third were randomly assigned to contain the volume option (40 μl of 20% sucrose), and the final third were assigned to contain the concentration decoy (10 μl of 30% sucrose).

2.5. Treatment two

In this treatment, we presented five new birds with one binary condition and two trinary conditions. We pseudorandomised the order of presentation so that we assigned approximately the same number of birds to each presentation order.

In the binary condition in this treatment, however, one of the two options presented to the birds differed from that presented in the first treatment: nine wells were randomly assigned to contain the 'alternative' concentration option (20 μl of 35% sucrose solution) and the remaining nine wells contained the volume option (40 μl of 20% sucrose).

In the volume decoy trinary condition, we presented birds with a choice of three options: six of the wells were randomly assigned to contain the alternative concentration option (20 μl of 35%), six were randomly assigned to contain the volume option (40 μl of 20% sucrose), and the final six were assigned to contain the volume decoy (30 μl of 10% sucrose).

In the concentration decoy trinary condition, we presented birds with a choice of three options: six of the wells were randomly assigned to contain the alternative concentration option (20 μl of 35%), six were randomly assigned to contain the volume option (40 μl of 20% sucrose), and the final six were assigned to contain the concentration decoy (10 μl of 30% sucrose). For the number of joules of energy per well contained in each option, see Table 1.

During each visit to the board (a bout), the bird was allowed to feed from as many wells as he wished. For each bout, we recorded the number and type of wells from which the bird fed in addition to the time the bout began. A bout ended once the bird had finished feeding and flown away. After a bout was finished, we emptied all wells from which he had appeared to feed using a capillary tube to determine the amount of sucrose remaining. Birds never emptied all of the wells in a single bout. The emptied wells were then refilled and the board rotated 90°. After four bouts, the board was replaced with another board with a different random pattern of coloured wells. A bird was allowed to visit 150 wells in each treatment.

3. Analysis

So as to reduce the effects on preference of learning the contents of the wells we included only the last 75 well visits for each condition in the analyses.

As we wanted to determine which options the hummingbirds chose as well as the energetic content of those options, we measured preference in two ways. The first measure was the proportion of choices birds made to the most concentrated option. In the first treatment this was the concentration option and in the second treatment it was the alternative concentration option. In the second measure for each bird we determined the option that had provided the most energy in the binary choice (using the volumes taken) and we looked at the change in preference for the option that was most rewarding for each bird. In both measures, we excluded the choices to the decoy options. We also excluded the data from any bird that took more than an average of six wells (the number of wells per option) per bout so that we could detect exclusive preference for a single option.

Prior to analysis, these proportional data were transformed using an arcsine square root transformation. We tested whether birds preferred one option over another in the binary choices using a one-sample *t*-test. All the differences between conditions were tested using repeated measures ANOVAs.

To determine whether individual birds changed their preference when a decoy option was added, we used Fisher's exact tests to analyse their last 75 well visits of each choice set. In both treatments the number of well visits to the concentration/alternative concentration and volume options in the binary choice sets was the expected number of well visits and the number of well visits to these same options in the trinary choice sets were the observed number of well visits. If birds did not make visits to both concentration/alternative concentration and volume options in the last 75 well visits then their data could not be analysed in a Chi-Squared test as this test requires choices to be made to each option.

We calculated the energy contained in each well using the following equation:

$$\text{Joules} = \left((\text{volume } (\mu\text{l}) \times (\text{moles of solute per litre}/100,000)) \right. \\ \left. \times \text{grams of sucrose per mole} \right) \times \text{Joules per gram sucrose}$$

where volume is the amount of sucrose solution in each well, a mole is made up of 342 g of sucrose and a gram of sucrose contains 16,800 J.

4. Results

4.1. Group data

4.1.1. Treatment one

As a group, the birds preferred neither option in the binary choice ($t(5)=1.805$, $p=0.131$) and their preference did not change after the addition of either the volume decoy (Dv) or the concentration decoy (Dc: $F(2,10)=0.411$, $p=0.870$; Dc: $F(2,10)=0.411$, $p=0.402$; Figure 2a and 4a).

4.2. Treatment two

As a group, the birds preferred the alternative concentration option in the binary choice ($t(4)=4.571$, $p=0.010$) and the addition of neither the volume decoy (Dv) nor the concentration decoy (Dc) changed their preference (Dv: $F(2,8)=0.204$, $p=0.878$; Dc: $F(2,8)=0.204$, $p=0.776$; Figure 2b and 4b).

4.3. Individual data

4.3.1. Treatment one

When the volume decoy was added to the choice set, two birds decreased (Fisher's exact test; bird 2: $p<0.001$; bird 6: $p=0.022$) and two birds increased their preference for the concentration option (bird 1: $p<0.001$; bird 4: $p<0.001$), while the preferences of two birds did not change (bird 3: $p=0.367$; bird 5: $p>0.99$; Fig. 3a).

Fig. 4

When the concentration decoy was added to the choice set, two birds decreased and two birds increased their preference for the concentration option (bird 4: $p<0.001$; bird 6: $p<0.001$; bird 1: $p<0.001$; bird 2: $p=0.008$) while two birds did not change their preference (bird 3: $p=0.689$; bird 5: $p=0.111$; Fig. 3a).

4.4. Treatment two: Alternative concentration

The addition of the volume decoy caused one bird to increase its preference for the volume option (bird 8: $p<0.001$), two birds decreased their preference for the volume option (bird 9: $p<0.001$;

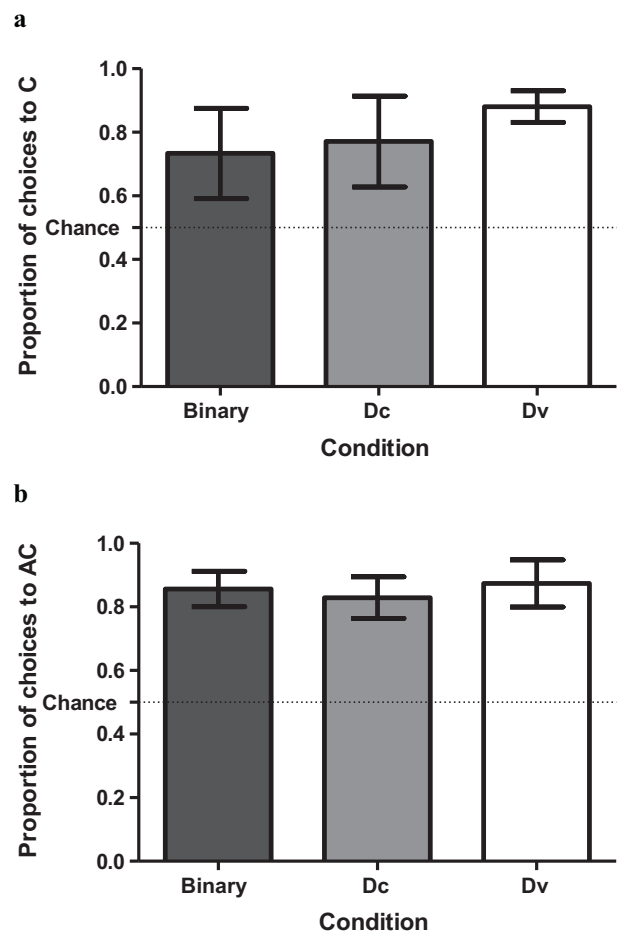


Fig. 2. (a) Treatment one. Proportion of choices made to the concentration option in the binary and the two decoy choice sets. Data are taken from the last 75 well visits and use choices to the concentration and volume options. The data are means \pm s.e. ($N=6$). (b) Treatment two. Proportion of choices made to the alternative concentration options in the binary and the two decoy choice sets. Data are taken from the last 75 well visits and only use choices to the alternative concentration and volume options. The data are means \pm s.e. ($N=5$).

bird 10: $p=0.005$) and two birds did not change their preference (bird 7: $p=0.396$; bird 11: $p=1.000$; Fig. 3b).

When the concentration decoy was added, two birds increased their preference for the volume option (bird 7: $p=0.001$; bird 8: $p=0.005$), one bird reduced his preference for the volume option (bird 9: $p<0.001$) and the preferences of two birds did not change (bird 10: $p=0.627$; bird 11: $p>0.99$; Fig. 3b).

4.5. Preference for the option with the largest experienced energy

If the birds had drunk all of the contents of each well, the concentration option would have provided the highest energetic return in treatment one while in the treatment two the volume option would have been the most rewarding. As each bird varied in the amount of sucrose he removed from each well type, we redid the analyses above using the preference for the option from which each bird acquired the most joules. For each bird, the most profitable option was taken to be the option from which the birds removed the highest number of joules per well in the binary choice set.

In treatment one, in the binary choice, four birds gained the largest number of joules per well from the concentration option (birds 2, 3, 5 and 6) and so for these birds we looked for a change in preference for the concentration option. The other two birds gained the most energy per well from the volume option (birds 1 and 4)

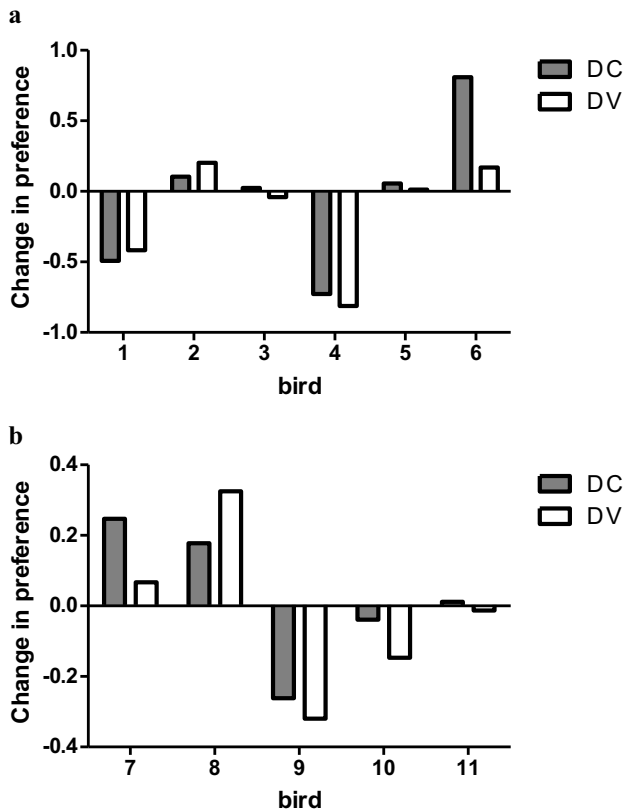


Fig. 3. (a) Treatment one: change in the proportion of choices made by individual birds to the concentration option relative to the volume option in the presence of the decoy options (Dc and Dv). This proportion includes only choices to the volume and concentration options. A positive number indicates an increase in the preference for the concentration option and a negative number indicates an increase in preference for the volume option. The data represent the final 75 well visits. (b) Treatment two: change in the proportion of choices made by individual birds to the alternative concentration option relative to the volume option in the presence of the decoy options (Dc and Dv). This proportion includes only choices to the volume and concentration options. A positive number indicates an increase in the preference for the alternative concentration option and a negative number indicates an increase in preference for the volume option. The data are the final 75 well visits.

and so we looked for the change in preference of those birds for the volume option.

In response to the addition of either the concentration or volume decoy to the choice set four birds decreased their preference for the option from which they had gained the highest energetic return (birds 1, 2, 4 and 6). Two birds did not respond to the addition of either the volume or concentration decoy to the choice set (birds 3 and 5).

In treatment two, all birds gained the largest volume of energy per well from the Alternative concentration option but four of the five birds changed their preference in the presence of a decoy option. One bird increased his preference for the option that he found the most energetically rewarding (the Alternative concentration option) in response to the addition of either the volume or concentration decoy to the choice set (bird 9) while another bird (bird 10) increased his preference for the option with the highest energy return only in response to the addition of the volume decoy. Bird 8 decreased his preference for the option with the highest energy return in response to either the concentration or volume decoy being added to the choice set while bird 7 only did so in response to the concentration decoy being added to the choice set. Bird 11 did not respond to the addition of either decoy to the choice set.

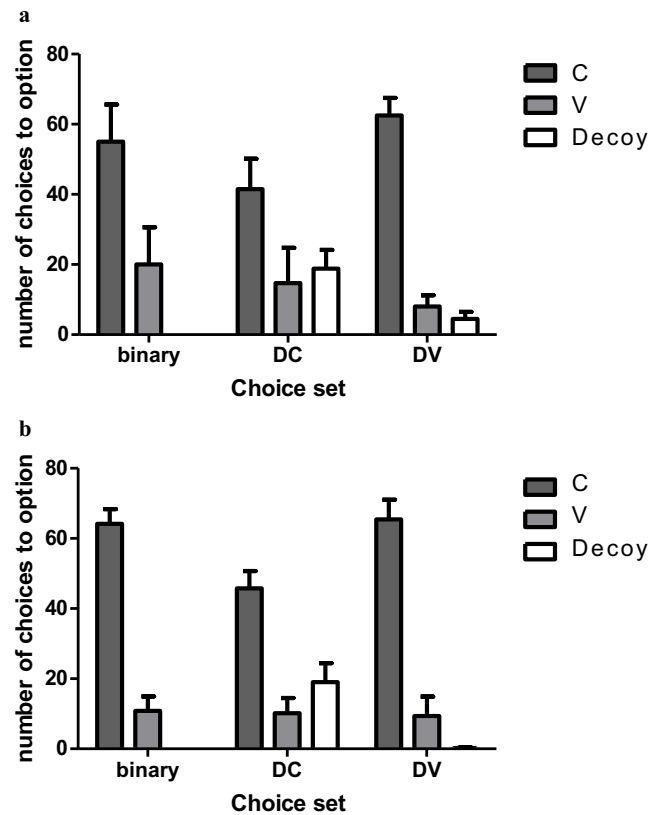


Fig. 4. (a) Number of choices made to each of the options. The volume option (V) contains 40 μ l of 20% sucrose, the concentration option (C) 20 μ l of 40%. In the Dv choice set the decoy is the volume decoy option (Dv), which contains 30 μ l of 10%. In the Dc choice set the decoy option is the concentration decoy option (Dc; 10 μ l of 30%). (b) Number of choices made to each of the options. The volume option (V) contains 40 μ l of 20% sucrose, the alternative concentration option (AC) 20 μ l of 35%. In the Dv choice set the decoy is the volume decoy option (Dv), which contains 30 μ l of 10%. In the Dc choice set the decoy option is the concentration decoy option (Dc; 10 μ l of 30%).

5. Discussion

When we assessed the birds' preference as a group, their preferences for one good option over another in the binary choice set did not change when an inferior decoy option was added to that choice set. Individually, however, birds' preferences did change and those changes were dependent on the type or value of the decoy.

We conducted this experiment to distinguish between two possible explanations for the responses made by foraging hummingbirds to the inclusion of poorer decoy options to a choice set observed in previous experiments (Bateson et al., 2002, 2003; Morgan et al., 2012). If hummingbirds make decisions based on their energetic state, in the presence of either inferior decoy option the birds should have increased their preference for the option from which they would gain the largest energetic return (Schuck-Paim et al., 2004). As a group, we saw no response by the birds to the inclusion of the inferior alternative, an outcome that is consistent with birds ignoring the poorer alternative. Individually, however, all but two of the 11 birds changed their preference for one or other of the good options in the presence of an inferior decoy. Each bird had two opportunities to change their preference one for each decoy (a total of 12 in treatment one, 10 in treatment two). Of those 22 opportunities, 3 of the changes we observed were consistent with the birds increasing their energy intake in response to the consumption of a poorer decoy. Energy return did not, however, explain the

changes in preferences of the remaining opportunities: the birds either increased their choices to the option with a lower energy value (11 opportunities) or did not change their preference (8 opportunities). We also saw this variability in response when we measured, not the promise of energy return, but what the birds actually gained: their consumption shows that most birds responded to the decoys but not in a way that is explained by energetic intake.

The comparative choice mechanism proposed by Bateson et al. (2003) does just as poorly in explaining the birds' individual responses to the presence of the decoys. If the birds were using a comparative choice mechanism their preferences should have changed in response to the inclusion of an asymmetrically dominating decoy by increasing their preference for the option to which that decoy is most similar (Bateman et al., 2008; Colman et al., 2007; Doyle et al., 1999). Although some of those changes in preference were consistent with this (6 opportunities), they were not the majority.

Although neither of the proposed explanations fit the observed data, the changes in preference that the birds expressed are consistent within individuals as the each bird changed his preference in the same way in response to either decoy. For some birds this led to an increased preference for the concentration option in response to both of the decoys, whereas for other birds this led to increased preference for the volume option. Similar across-individual variation in response to the addition of poorer alternatives to choice sets has been often been observed, suggesting that these individual differences might be widespread in animal decision making experiments (Bateson, 2002; Bateson et al., 2002, 2003; Shafir, 1994; Waite, 2001). While it could be that this variation is essentially experimental 'noise' due to a lack of experimental control, another possibility is that previous variation in experience of the animals leads to individuals weighting the difference components of each option differently. If, for example, hummingbirds differ in the weight they give to concentration over volume, individual birds would be expected to change their preferences in response to the addition of decoys but not in the same way: a bird that attends more to the volume of solution might increase its preference for the volume option in response to the addition of either decoy whereas a bird attending mainly to the concentration of the solution might increase the number of choices it makes to the concentration option. This possibility requires experimental testing.

In sum, our data suggest that there is considerable variation in individuals' decision making and that they add a further layer of 'context' to experiments in which we attempt to investigate the mechanisms underpinning context-dependent decision making.

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