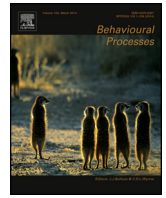




Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: [www.elsevier.com/locate/behavproc](http://www.elsevier.com/locate/behavproc)



## Individual differences in decision making by foraging hummingbirds

Kate V. Morgan<sup>a,\*</sup>, T. Andrew Hurly<sup>b</sup>, Susan D. Healy<sup>a</sup>

<sup>a</sup> School of Biology, University of St Andrews, Harold Mitchell Building, St Andrews KY16 9TH, Fife, Scotland, UK

<sup>b</sup> Department of Biological Sciences, University of Lethbridge, Lethbridge, AB, Canada AB T1K 3M4

### ARTICLE INFO

Article history:  
Available online xxx

Keywords:  
Asymmetrically dominated decoy  
Context-dependent choice  
Decision making  
Foraging  
Hummingbird  
Individual differences

### 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.

© 2014 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/3.0/>).

### 1. Introduction

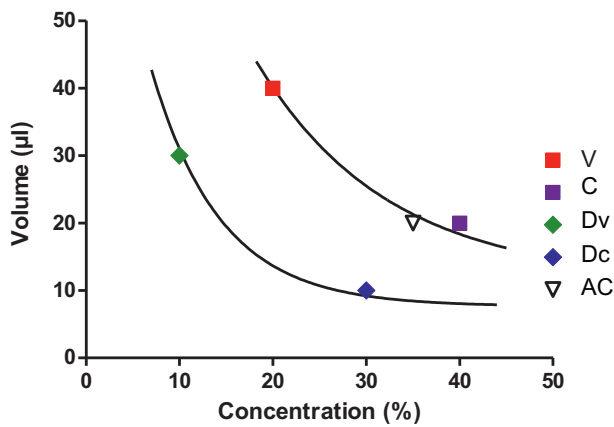
Observing the choices animals make is critical to our understanding of animal behaviour. These choices can be used both to uncover the features that animals prefer (such as sexually selected traits) and to make predictions about which options they should choose in order to maximise their fitness (such 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

\* Corresponding author. Tel.: +44 (0)7889099901.  
E-mail address: [km745@st-andrews.ac.uk](mailto:km745@st-andrews.ac.uk) (K.V. Morgan).



**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  $\mu$ l of 20% sucrose (145 J per well), the concentration option (C) 20  $\mu$ l of 40% (158 J), the volume decoy option (DV) 30  $\mu$ l of 10% (52 J), the concentration decoy option (DC) 10  $\mu$ l of 30% (58 J) and the alternative concentration option (AC) contains 20  $\mu$ l of 35% (135 J). The lines are isoclines where the energy at each point in the isocline 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  $\mu$ l of 40% sucrose solution) presented alongside a volume option (40  $\mu$ l of 20% sucrose; Fig. 1). When these two favourable options were presented alongside a decoy that was either 10  $\mu$ l of 30% sucrose (the concentration Decoy) or 30  $\mu$ 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 ( $\mu$ 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  $\mu$ 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

Download English Version:

<https://daneshyari.com/en/article/10971223>

Download Persian Version:

<https://daneshyari.com/article/10971223>

[Daneshyari.com](https://daneshyari.com)