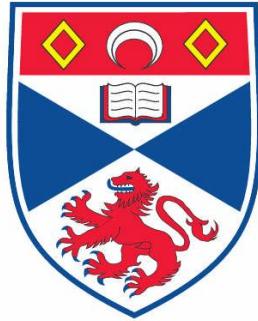


# Context-dependent decision making in wild rufous hummingbirds

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This thesis is submitted in partial fulfilment for the degree of PhD  
at the  
University of St Andrews

August 2012

**Declaration of authorship for the work contained in this thesis**

All of the experiments in chapters 2-5 were designed by me in conjunction with Sue Healy and T. Andrew Hurly. I designed the experiments in Chapters 6 and 7 were designed in conjunction with Sue Healy. I collected all of the data in Chapters 2, 4, and 7. The data in chapters 3, 5 and 6 was collected with the help of Undergraduate research assistants. The data in Chapter 3 was collected in conjunction with Jennifer Wiggins. The data contained in Chapter 5 was collected by Lauren Martin and I. I collected the data in Chapter 6 with help from Andrew Morton. All of the analyses I present here were conducted by me, and I was solely responsible for writing all of the chapters contained in this thesis as presented here, with revisions as recommended by my supervisor.

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## **Abstract**

Conventional models of decision making assume that animals and humans will evaluate available options based on the benefit that they provide and then choose the option that provides the largest benefit. However, there is evidence that the choices of both animals and humans violate this assumption as the choices that are made can be altered by the context in which decisions are presented. In this thesis I used free-living, foraging rufous hummingbirds (*Selasphorus rufus*) to investigate the effect of context on the decisions they make. Firstly, I gave birds choices between two preferred options and found that the addition of a third non-preferred option changed their preference when options varied in either two dimensions simultaneously (volume and concentration of sucrose), or in only a single dimension (volume or concentration). I also manipulated the learning context and found that hummingbirds have stronger preferences when options are learned simultaneously than when those same options are learned about sequentially. I also manipulated the experience that birds had of the options prior to the choice and found that birds with prior experience did not make different choices than hummingbirds without prior experience. In addition to work with hummingbirds, I also completed experiments with humans looking at the effect of context on decisions about health of others. I manipulated the yellowness of faces and found that when participants choose between two preferred options the addition of non-preferred options changed their preference. These data demonstrate humans and hummingbirds make irrational choices as the decision making context can change the choices that they make. Current theories of decision making are insufficient to explain context-dependent choices made by hummingbirds.

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## Introduction

In order to survive and reproduce individuals, both animal and human, may make multiple decisions every day. These decisions include what to eat, where to find food, where to sleep and who to mate with. Not only do these individuals need to make decisions they need to make good decisions, furthermore in order to maximise fitness we predict that animals will choose the best options. To do this, individuals are expected to either assess the value of each option or to behave as if they can assess the value of each option (Arrow, 1959, Berg and Gigerenzer, 2010, Gigerenzer and Goldstein, 1996, Hammerstein and Hagen, 2005, Kahneman, 2003, Luce, 1959, Luce, 1977, Luce, 1992, McFadden, 1999, Simon, 1959, Von Neumann and Morgenstern, 1944). The assumption that both animals and humans should behave as if they calculate the value of each of the options available has underpinned many of the experiments into decision making in humans and animals. For example, experiments investigating the food and mating preferences of animals and humans are implicitly assuming that these preferences are related to the value of that trait (Amundsen et al., 1997, Coetzee et al., 2009, Cotton et al., 2006, Freed, 2000, Harder and Real, 1987, Mitchell, 1989, Montgomerie, 1984, Montgomerie et al., 1984, Roberts, 1996, Ryan et al., 2007, Samson et al., 2010, Sanderson et al., 2006, Stephen et al., 2011, Summers et al., 1999, Thornhill and Gangestad, 1999). This assumption is grounded in utility theory which states that the number (or proportion) of choices made to any option is related to the value (or utility) of that option (Arrow, 1959, Luce, 1959, Von Neumann and Morgenstern, 1944).

Expected utility theory was the solution proposed by Daniel Bernoulli to the St Petersburg paradox. The St Petersburg paradox was proposed by Nicolas Bernoulli in a

letter to Pierre Raymond de Montmort in 1713. The paradox is a lottery in which the possible winnings are infinitely large. Given that the winnings are infinite, people should be willing to play at any price, however as stated by Hacking “few of us would pay even \$25” (Hacking, 1980). The solution which Daniel Bernoulli proposed to the paradox was Expected Utility Theory which formally introduced the idea of Utility (Bernoulli 1738: translated Bernoulli, 1954). Bernoulli stated that “the value of an option must not be based on its price, but rather on the utility it yields” and introduced the idea that the likelihood of an option being chosen should depend on the change in utility (the benefit or satisfaction an individual gains from a good or service), the likelihood of an event occurring and your current state. Since Bernoulli, there have been several mathematical representations for describing the predicted outcome of decisions (Arrow, 1959, Luce, 1959, Thurstone, 1927, Von Neumann and Morgenstern, 1944). Many of these representations differ only slightly in the predictions which they generate and therefore are difficult to distinguish practically (Luce, 1977). Although these representations are looking for the ‘best’ option they tend to use the idea of revealed preferences (Samuelson, 1938), so theory and practical uses of the theories are based on observations of an individual’s behaviour (their revealed preference) rather than a priori assumptions as to what the decision maker should prefer.

In Economics the utility is the satisfaction that an individual gains from a particular option and the economically rational decision maker is expected to maximise their expected utility. As the utility derived from a particular option is not the same for each decision maker, in order to predict the decisions which people make economists assume that individuals are internally consistent in their preferences, but

that all individuals might not have the same preferences. This requirement for consistency is formalised in certain axioms, if the decision maker does not violate these axioms their choices are said to be economically rational. Both Luce (1959), and Von Nuemann and Morgenstern (1944) formalised four axioms of “rationality” which are a set of mathematical formulations which choices would obey if the decision maker made choices were maximising utility and so were economically rational. The first axiom of rationality states that rational choices should obey completeness, which states that a decision maker can either be indifferent between A and B, or they can prefer A more than B or they prefer B more than A. Preferences should also be transitive such that if the decision maker likes A more than B and B more than C then they should also like A more than they like C. The third axiom is that of continuity, which states that if A is preferred to B then an option very like A will also be preferred to B. Continuity describes choice where there are not large jumps in preference. The final axiom is the independence of irrelevant alternatives which states that if A is preferred to B then the addition of a non-preferred option C should not change the proportion of choices for either of the options A and B. In other words C is irrelevant to the choice between A and B. If choices do not conform to any of these axioms then rational choice then the choices are considered economically “irrational”.

Economic rationality is not the only form of rationality, psychological rationality is different from economic rationality in that it focuses on the way on which the choice is made rather than the outcome of the choice as economic rationality does. In psychology a rational decision maker makes a decision in a way which is reasonable given the information which they have and their means of deciding, the definition of rationality is therefore a procedural one rather than the outcome as is the case with

economics. A focus on the procedure means that a decision could be objectively wrong but still be classed as a psychologically rational choice (Simon, 1986). As psychological rationality focuses on the internal thoughts and beliefs of an individual, it is not easy to demonstrate that animals can be psychologically rational or irrational. Although psychological rationality is not readily testable in animals there is another type of rationality which is readily testable- Biological rationality. Biological rationality is linked to the fitness of an individual. An individual is biologically rational if it acts to increase its inclusive fitness (Kacelnik 2006). The definition of biological rationality is similar to that of economic rationality as it can be measured according to the outcome of the choice, although with biological rationality it is a change in the fitness of the animal rather than the outcome of a particular choice. It is possible for a decision maker to be rational according to one of these definitions but irrational by another. For example, if a foraging bird were to have a strong preference for a very poor food source across different contexts and make internally consistent choices the animal would be economically rational as their choices were consistent but biologically irrational as consistently choosing the very poor food source would decrease its relative fitness. The advantage of looking at economic rationality in animals is that violations of economic rationality might shed light on the mechanisms animals may be using to make decisions. Demonstrating economically irrational choices in animals would not imply that the animal was also biologically irrational.

Some of the first examples of economically irrational choices were described by Kahneman and Tversky and were violations of transitivity (Tversky, 1969). Although perhaps their most striking example of irrational decision-making is the finding that the way a decision is framed can hugely alter the option that people choose

(Tversky and Kahneman, 1981). This was found in an experiment where participants were told that there was an outbreak of a rare Asian disease which had infected 600 people and were asked to choose between two alternative programs of treatment. In one treatment (problem 1) participants were told how many people would survive as a result of treatment and in the other treatment (problem 2) participants were told how many people would die despite treatment; the options in both treatments were the same in respect to the actual numbers of people who would die. The values in the brackets indicate the percentage of participants who choose each of the treatment options.

Problem 1-

Program A: If Program A is adopted, 200 people will be saved [72%].

Program B: If Program B is adopted, there is 1/3 probability that 600 people will be saved, and 2/3 probability that no people will be saved [28%].

Problem 2-

Program C: If Program C is adopted 400 people will die [22%].

Program D: If Program D is adopted there is 1/3 probability that nobody will die, and 2/3 probability that 600 people will die [78%].

In problem 1 72% of participants favored the certain option where 200 out of 600 people would live, whereas in problem 2 only 22% of participants said that 400 out of 600 people should die. Obviously these two options are equivalent and therefore rational decision makers should have treated them as the same thing. If people made choices consistent with utility theory, then the outcome should not have been changed

by the way that the choice was framed. These violations of economic rationality suggested that when making decisions humans treat losses differently than gains. Importantly, it also demonstrated that violations of rationality could be used to examine decision-making mechanisms. This changed the course of the way researchers thought about decision making and importantly has changed the focus of work from the examination of what people choose to the way in which choices are made.

Since the Tversky and Kahneman (1981) experiment, economically irrational choices have been found in human decision making in a wide range of experimental situations looking at products (Ge et al., 2009, Prelec et al., 1997, Simonson, 1990, Simonson and Tversky, 1992, Tanner, 2008), services (Dato-on and Dahlstrom, 2003), voting (Callander and Wilson, 2006, Hedgcock et al., 2009), attractiveness (Geiselman et al., 1984, Kenrick and Gutierres, 1980, Kernis and Wheeler, 1981, Melamed and Moss, 1975, Wanke et al., 2001, Wedell et al., 1987, Wedell et al., 2005). In these experiments the majority of irrational choices are violations of the independence of irrelevant alternatives (Bateman et al., 2008, Choplin and Hummel, 2005, Colman et al., 2007, Doyle et al., 1999, Heath and Chatterjee, 1995, Hedgcock et al., 2009, Pechtl, 2009, Pettibone and Wedell, 2000, Pettibone and Wedell, 2007, Reaney, 2009, Slaughter et al., 2011, Tssetsos et al., 2010, Wedell, 1991, Wedell and Pettibone, 1996). These violations of rational choice have led psychologists to attempt to determine the mechanisms which may result in economically irrational choices (Choplin and Hummel, 2005, Gigerenzer and Goldstein, 1996, Gigerenzer et al., 1999, Hotaling et al., 2010, Kahneman, 2003, Kahneman and Thaler, 2006, Kahneman and Tversky, 1979, McGraw et al., 2010, Pothos and Busemeyer, 2009, Roe et al., 2001, Simonson

and Tversky, 1992, Sunstein et al., 2002, Tsetsos et al., 2010, Tversky and Kahneman, 1974, Tversky and Kahneman, 1981, Tversky and Kahneman, 1986). Economists are interested in predicting the behaviour of markets therefore the utility curves used to predict the behaviour of people in a variety of situations are altered to better describe the choices that people make. However, the underlying mechanism which may be causing irrational changes in preference is rarely considered (Berg and Gigerenzer, 2010, Kahneman and Tversky, 1979).

There are different approaches to understanding irrational choice. One such approach, frequently used by economists I am going to refer to as optimization under constraints (although is sometimes called bounded rationality). The people using this approach suggest that the decision maker is attempting to make an optimal choice but some constraints (such as constraints on the brain, perceptual system, time or memory) may prevent the decision maker from achieving economic rationality and therefore if we knew enough about the various constraints on the system we would be able to model decision making as if it were rational (Eilon, 1972, Livnat and Pippenger, 2008, Taylor, 1975, Wall, 1993). Confusingly there is another approach also termed Bounded rationality. This form of bounded rationality in the tradition of Herbert Simon is the approach most commonly taken by psychologists. Herbert Simon argued that good decisions could be made in less time and with less information if individuals exploited only certain features of their environments (Simon, 1959, Simon, 1997). Individuals could achieve this by satisficing where instead of making the best choice individuals attempt to achieve some minimum level of a particular variable (Simon, 1959, Simon, 1997). Alternatively, if one cue was a reasonable indicator of the quality of all available options then individuals could ignore other cues and make a decision

using one piece of information only. This approach suggests that in particular environments choice processes can be simplified and yet still produce good decisions (Gigerenzer and Goldstein, 1996, Gigerenzer et al., 1999, Simon, 1997) for example by using certain ‘rules of thumb’ or heuristics to aid that decision-making processes by enabling the decision maker to use less information (Hutchinson and Gigerenzer, 2005). Heuristics would be expected to work well in most situations (i.e. result in approximately the ‘right’ or most efficient outcome) but wouldn’t be expected to result in rational choices (Tversky and Kahneman, 1974). It has been suggested that if the heuristic used was appropriate for the decision making environment the choices that resulted might be better than if the individual rigidly stuck to the formal logic of economic rationality, this is termed ecological rationality (Gigerenzer et al., 1999). An example of ecological rationality in practice is the decisions about the care given to a person admitted to hospital with a suspected heart attack. The patients must be classified as high or low risk upon arrival to ensure that they receive appropriate treatment. Many measurements could be taken, all of the information could be considered together, put into a statistical package, weighted in terms of how important each measurement is to the diagnoses. However, this would be time consuming as well as requiring the patient to have a battery of tests, some of which may not even be that important in influencing the decision reached. Now consider the advantages of following a simple decision making tree such as this one (Figure 1) created by Breiman (1993), here large amounts of information do not need to be collected before a decision is reached. Instead a maximum of three yes/no questions have to be answered to decide whether the patient should be classed as high risk or not. By using a heuristic like this a decision about treatment can be made more quickly and with less

information. When the decision making tree described here is compared to a complex statistical model the simple tree performs better at categorising patients than the model taking into account all of the information (Breiman et al., 1993).

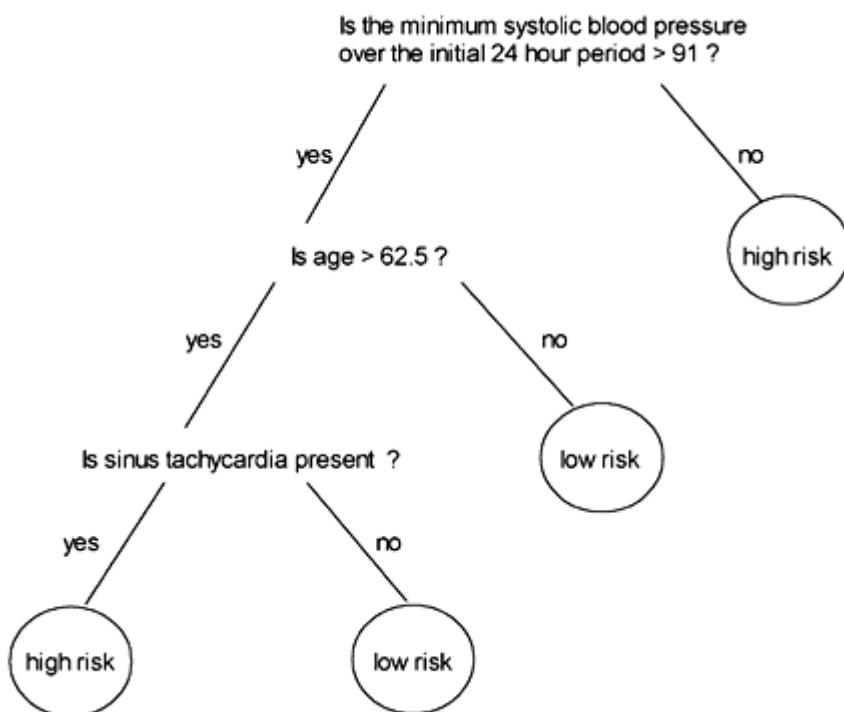


Figure 1.

A decision making tree for the categorisation of heart attack patients into high and low risk categories taken from Gigerenzer and Todd (2000).

In humans, heuristics are usually something which people spontaneously use to help make decisions rather than the formalised heuristic described in Figure 1, however the principle would remain the same and the heuristic would still be expected to enable the person to make a good choice (most of the time) and to use less information than a rational choice. An example of a heuristic working in the animal world is the oviposition decisions made by the parasitoid wasp *Trichogramma*

*minutum* instead of assessing the volume of a host using length and height, the wasp instead assesses the curvature of the host (Schmidt and Smith, 1987). The wasp makes good decisions about the size of the host and oviposits appropriately whilst needing less information.

Both the bounded rationality approach of psychologists and the optimization under constraints approach of economists have been argued to be more feasible than rationality as they take into account that the brain and perceptual systems are not unlimited in their capacities (Rabin, 1998). However, the approaches differ as optimization under constraints suggests that humans are limited in their time and information and so should use a stopping rule to determine when the benefit of collecting more information outweighs the cost of collecting that information. As a result of a stopping rule the decision maker would need to know the cost of searching, the utility they have at each point in the search and the utility that they could require if they continued to acquire information (Gigerenzer et al., 1999). Whereas boundedly rational decision makers are expected to make mostly good choices without calculating the utility of the options available. The common ground between these theories is the recognition that Expected Utility Theory is insufficient to explain many of the choices made by people.

Not only is utility theory fundamental to theories of human decision making, it has formed the backbone of key theories of animal decision making. Economic ideas of various types have been very influential in biology, for example the markets of economics are represented in biology in the form of mating “markets” (Hammerstein and Hagen, 2005) where animals are modelled as if they choose the traits of other animals just like human would be expected to choose products with animals attempting

to get the mate with the most attractive features (Noë and Hammerstein, 1994). Game theory has also been derived from economic game theory in which cooperation on tasks has been used to describe human and animal decisions (Axelrod and Hamilton, 1981, Smith, 1979). Optimal foraging theory is similar to the Expected Utility Theory of economics by assuming that the most successful animals would be those which could forage most efficiently to maximise a determinant of their fitness such as net energy gained (Charnov, 1976, Pyke, 2010, Perry and Pianka, 1997, Pyke et al., 1977, Stephens and Charnov, 1982). Animals are expected to maximise a function such as energy intake like economists expect decision makers to maximise utility. However, as rational choices which maximise expected utility do not describe the choices made by humans, rational choice theory was also investigated in animals.

As a result of these investigations it is becoming clear that animals like humans can make economically irrational decisions (Bateson et al., 2002, Latty and Beekman, 2011, Shafir, 1994, Waite, 2001b). Economically irrational choices might be favoured by natural selection if the benefits of making irrational choices (such as quicker decision-making) are greater than the costs of not consistently choosing the option with the highest energy. Therefore animals could forage optimally without needing to be economically rational. Looking at economic rationality in animals could help to establish the decision making mechanism which animals may be using. As we have a much greater understanding of the instances in which humans make irrational choices, the experimental testing of animal decision making has been heavily influenced by experimental paradigms used to examine human decision making (Bateson et al., 2002, Bateson et al., 2003, Chen et al., 2006, Latty and Beekman, 2011, Shafir, 1994, Shafir et al., 2002, Waite, 2001b). An example of an experimental paradigm used in human

decision making which was then tested in animals is the framing effect described previously in Tversky and Kahneman (1981) where there is an outbreak of a disease and the question is framed as lives saved or lives lost. A similar paradigm has been used with capuchin monkeys in a token trading game, here options were either presented as a loss or a gain. Monkeys had a choice of two options in the first option monkeys were presented with two food items and 50% of the time were given both and 50% of the time one was taken away so they were given one. In the other option they were presented with one food item and 50% of the time they got this item only and 50% of the time they had another item added and received two rewards. Despite the two options having the same average pay off the monkeys preferred the option framed as a gain (when an option was added) more than they did the option framed as a loss (Chen et al., 2006); this result is consistent with the human data (Tversky and Kahneman, 1981). When options are variable starlings also seem to be sensitive to framing effects, when options are presented as a loss (the birds get less than they expect) starlings choose variable options more frequently than options which are not variable (Marsh and Kacelnik, 2002).

As is the case with humans, probably the best investigated of the violations of rationality in animals is the independence of irrelevant alternatives. Humans violate the independence of irrelevant alternatives regularly when inferior options are added to the choice set: these options do change the participants' preference for the better, available options (Choplin and Hummel, 2005, Colman et al., 2007, Doyle Heath and Chatterjee, 1995, Hedgcock et al., 2009, Pechtl, 2009, Pettibone and Wedell, 2000, Pettibone and Wedell, 2007, Slaughter et al., 2011, Wedell, 1991, Wedell and Pettibone, 1996). The most common violation of irrelevant alternatives in human choice is the

asymmetrically dominating decoy effect (or just the decoy effect). Here an inferior option (a decoy) is added to the choice set and the addition of this decoy increases the preference for the option that it is dominated by (Bateman et al., 2008, Colman et al., 2007, Doyle et al. 1999, Heath and Chatterjee, 1995, Pechtl, 2009). An option is asymmetrically dominated when it is inferior in every dimension to one of the options and inferior to another option in at least one dimension but superior in at least one dimension. For example, in Figure 2 the decoy is inferior to the target option in both dimension 1 and 2 and therefore is dominated by the target option, the competitor however, is superior to the decoy in dimension 2 but inferior in dimension 1. As the addition of a decoy option is expected to increase the preference for the option which dominates it, the presence of the decoy option in choice sets would be expected to increase the proportion of choices for the target option compared to choice sets without the presence of the decoy option, which violates the independence of irrelevant alternatives.

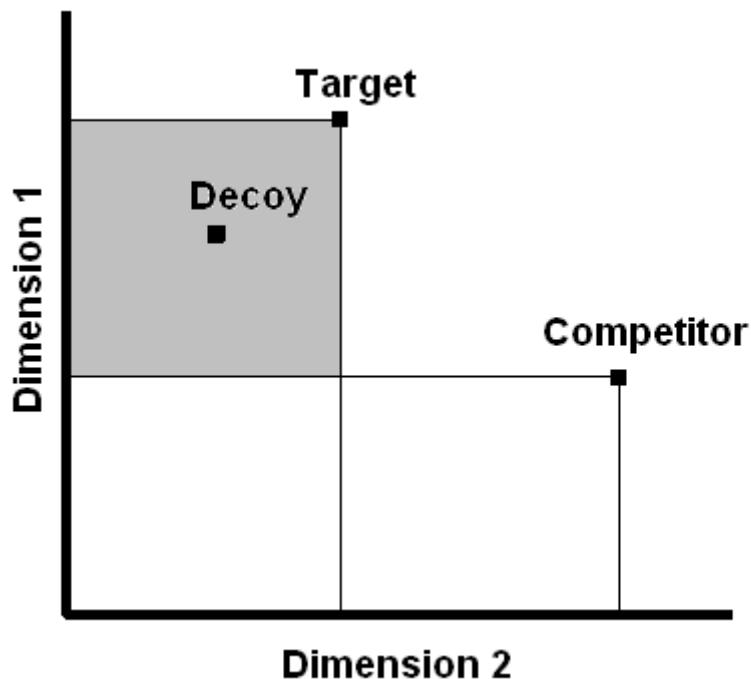


Figure 2.

An example of a decoy being asymmetrically dominated, in this case the decoy is dominated by the target but not by the competitor. The grey area indicates all of the possible positions in which the decoy could be in order to be asymmetrically dominated by the target.

Violations of the independence of irrelevant alternatives have been reported in the choices made by birds, fish, mammals, and invertebrates (Bateson et al., 2002, Bateson et al., 2003, Hurly and Oseen, 1999, Morgan et al., 2012, Royle et al., 2008, Sasaki and Pratt, 2011, Scarpi, 2011, Shafir et al., 2002). As the asymmetrically dominating decoy effect has been one of the most robust violations of rationality in humans, therefore, it is perhaps unsurprising that experiments trying to recreate the effect have also been carried out in animals (Bateson et al., 2002, Bateson et al., 2003, Latty and Beekman, 2011, Royle et al., 2008, Sasaki and Pratt, 2011, Shafir et al.,

2002). However, sometimes in animal experiments the addition of these decoy options do not increase the preference for the option which they are dominated by (as in humans), instead the addition of these decoy options increase the preference for the options which they are not dominated by (Bateson et al., 2003, Morgan et al., 2012, Royle et al., 2008, Shafir et al., 2002). The majority of animal experiments looking at irrationality have to date replicated the design of experiments with humans (Bateson et al., 2002, Bateson et al., 2003a, Royle et al., 2008, Sasaki and Pratt, 2011, Scarpi, 2011, Shafir, 1994, Shafir et al., 2002, Waite, 2001a, Waite, 2001b), this is because there is a relative wealth of studies in human decision making which have provided possible circumstances where irrational choice might be likely to occur. However, when a robust human paradigm such as the decoy effect is replicated in animals and does not generate similar choices, the assumption that the processes underlying these changes in preference are similar may need to be questioned. An investigation into the similarities and differences between the choices made by humans and animals would be worthwhile to establish if these systems are similar enough for the choices made by humans to continue to be worthwhile, as a starting point for experiments with animals.

Currently experiments looking at irrational choice in animals are mostly focused on the addition of inferior options to choices amongst options which vary in two dimensions (Bateson et al., 2002, Bateson et al., 2003, Latty and Beekman, 2011, Royle et al., 2008, Sasaki and Pratt, 2011, Scarpi, 2011, Shafir et al., 2002). However, the addition of inferior asymmetrically dominating decoy options is not the only way in which context could influence the choices which animals make. Background context in terms of previous experience of the options has been shown to change the choices made to options by gray jays (Waite, 2001a, Waite and Passino, 2006), violations of

the independence of irrelevant alternatives has also been shown in options which only vary in a single dimension (Bateson, 2002, Hurly and Oseen, 1999, Morgan et al., 2012). As context-dependent decisions seem to be made by animals in a variety of circumstances, future experiments looking at the effect of context on choice could look at manipulating other types of context, such as context whilst learning, at what stage in the experiments is the decoy presented as well as previous experience; may well find that these types of context also change the choices made.

In this thesis I attempted to address the similarities or differences in the irrational decision making behaviour of humans and animals. In addition I also investigated the variety of instances in which context might change the choices made by animals. To do this I conducted a series of foraging experiments using wild free-living rufous hummingbirds in addition to experiments using human subjects.

The rufous hummingbird *Selasphorus rufus* is a small (around three grams) hummingbird that migrates from its overwintering sites in Mexico to its breeding grounds in the United States (as far north as Alaska) and Canada. These birds are suitable for research in the effects of context on decision making for a number of biological and logistical reasons. Firstly, the nectar provided by the flowers on which the birds feed can vary in a number of ways, including the concentration and volume of the nectar provided, the nectar refill rate and the length of a flower's corolla. Not only do the flowers vary in these ways, it is clear that hummingbirds can detect and respond to many aspects of the reward provided, including changes in the concentration, volume, variability and refill schedule of the flowers from which they forage, generally preferring higher concentration, larger volumes, less variability and adjusting their return rates to approximate the refill schedules of flowers (Blem et al.,

2000, Henderson et al., 2006, Hurly and Oseen, 1999, Montgomerie, 1984, Tamm and Gass, 1986). Therefore, there are many possible aspects of flowers which can be manipulated experimentally and that we know hummingbirds will respond to.

In addition to the complexity of its natural food resources, the rufous hummingbird migrates vast distances and will encounter a wide range of habitats and feeding environments. Therefore, the options that the birds encounter are expected to be quickly learned and the birds' preference for these options should be flexible and dependent on the other options available in order for birds to be able to take advantage of a variety of different environments. As birds are expected to be aware of other options in order to respond to changing environmental conditions, context in terms of the other options available may be affecting the choices that they make.

During experiments a territorial male Rufous hummingbird will feed approximately every 10 minutes throughout the day (Bacon et al., 2010, Hixon and Carpenter, 1988). As a result they make many choices in a day so the cost of making one poor choice for hummingbirds is likely to be low. It is assumed that decision making is time consuming and expensive (either due to brain activation or due to missed opportunities) (Gigerenzer and Goldstein, 1996, Gigerenzer et al., 1999, Simon, 1959, Simon, 1997). In animals we know that decision making is time consuming as animals show a speed accuracy trade off where faster decisions are less accurate (Chittka et al., 2009). Decision-making in hummingbirds is also assumed to be costly or time consuming and as hummingbirds make many choices in a day these costs would be expected to add up. As a result a bird that could minimise the costs of making decisions would have a selective advantage over other birds. Therefore we

might expect that hummingbirds are a very plausible animal to make short cuts in their decision making.

Looking at decision making in the field has biological advantages. The advantage to testing context-dependent decision-making in wild, free-living animals is that their decisions are made in a ‘real-life’ situation, i.e. the birds make foraging decisions in our experiments whilst they continue to display to, and mate with, females, as well as defending their territory from intruding males. Therefore the choices which are made have real fitness consequences and if bird fails to make good choices then they may not survive or may not be able to defend their territory and reproduce. In contrast animals in laboratory situations which are receiving supplementary feeding may become indifferent to options over time as there are no fitness consequences of the choices that they make. The choices made by hummingbirds in the wild may, then, be more likely to represent decisions that are made under the time constraints and competition this species would experience in its daily life. However, laboratory experiments do have several advantages over field experiments as the age, experience, nutritional state or body condition of animals can be controlled. As a result if there are individual differences in decision making these might be able to be explained.

Hummingbirds are considered to be net rate maximisers (Hixon, 1982, DeBenedictis et al., 1978). So when making decisions birds would be predicted to take almost exclusively from the option with the highest caloric pay off. The option with the highest caloric pay off would be the option with the largest number of calories given for the cost taken to acquire it. As viscosity of sucrose increases with concentration, handling times may be higher with more concentrated sucrose as the

time taken to load the sucrose onto the tongue via capillary action will be longer (Kingsolver and Daniel, 1983). However, larger volumes will incur greater flight costs and so birds should not fill their crops with sucrose (DeBenedictis et al., 1978). As the viscosity of sucrose will change with temperature it will not always be possible to predict the option that a net rate maximising hummingbird would choose in the field. However, in the same environmental conditions it would be expected that the same option would be preferred in each choice set. As such the prediction would be that the proportion of choices to the best option (whichever that may be) would be the same in each choice set.

In addition to being a biologically plausible candidate, there are also a number of logistical benefits to using rufous hummingbirds for examining context-dependent decision-making. On arrival at their breeding grounds, rufous hummingbird males establish and strongly defend a feeding territory. At the site in the eastern Canadian Rockies where I conducted my research, the territories are established around artificial feeders containing sucrose solution, which are hung between trees along the length of the Westcastle valley in early May. The birds are caught and marked with an application of ink to the breast feathers allowing the birds to be identified within a breeding season without the need for recapture. As the territorial males vigorously exclude other males from their breeding territory I can reliably train and test individuals.

As the hummingbirds are free-living they can feed from flowers growing in the environment if they wish. However, they do not. The birds participating in our experiments feed almost exclusively from the feeder placed in their territory and then

from the sucrose provided in the experiment(s). As a result I can monitor the energetic intake of the hummingbirds through the amount of sucrose that they drink in the experiment, although I am not able to measure energy expenditure, which may vary considerably across the course of the experiments as a result of differences in temperature and activity. Rufous hummingbirds birds can be trained to experimental apparatus within an hour or two and not only do birds learn to feed from a variety of artificial feeders or ‘flowers’, they will also readily learn associations between the colour and the contents of those feeders. Furthermore, territorial male will feed around once every 10 minutes which means a fairly large amount of data can be collected in the space of a field season.

In addition to experiments using hummingbirds, this thesis also contains experiments using human participants. Experiments with humans are often not directly comparable to those with animals as animals do not have language. This is important as generally humans are told about the options whereas animals have to experience each of the options repeatedly to learn about them. Therefore, to compare human decision making with that of animals, I conducted experiments which shared a key feature with animals, namely that humans had to assess the value of the options themselves.

In the research described in this thesis I had two main aims.

- (1) To determine how context affects the choices that hummingbirds make when foraging. To do this, I designed experiments in which different types of context

were manipulated. This included the types of options presented as well as the impact of current or previous context on the choices made.

- (2) To determine how similar hummingbird decision-making is to decision-making by humans. To do this, I gave humans and hummingbirds comparable experiments in which decoy options were added to choice sets.

## **Chapter 2: Context-dependent decision-making in hummingbirds: the role of decoys and energetic state on preference**

### **Introduction**

Economists and ethologists alike are interested in the choices a human or an animal should make in order to maximise their fitness. Neoclassical economists (the dominant school of economics today) predict what humans will choose by assuming that humans should maximise the utility acquired for their given budget (Kahneman and Thaler, 2006). In economics, utility is the satisfaction that the individual derives from each option while for animals, utility is equivalent to the currency the animal is expected to maximise in a specific choice situation. For example, when foraging, animals are expected to attempt to maximise energy intake but when choosing a mate, animals are expected to try to choose the partner that will maximise their own fitness (Pyke et al., 1977). When predicting the choices that an individual should make, both optimal foraging theory and economics models make the same assumptions: that the individual uses all the information that they have available, individuals should choose the best option.

In economics, rational choice theory describes the decision making behaviour of an individual that is consistent choosing options which maximise the utility they acquire. Rational choice theory is based on the use of simple axioms of choice to predict the preference for different options. One such axiom is Luce's choice axiom (Luce, 1959), which states that the probability of choosing an option is the value (or utility) of that option divided by the sum of all the utilities of all options in the choice set. A consequence of defining an economically rational choice in this way is that the

choice of an option is expected to be independent of irrelevant alternatives, such that the probability of an individual choosing A from a choice set of A and B should not be influenced by the addition of an inferior option C. The reason for this independence is that the presence of an inferior option should not change the ratio of the utilities of A and B.

The independence of irrelevant alternatives is frequently violated when humans make decisions across a variety of different domains, including elections (Hedcock et al., 2009), employment decisions (Slaughter et al., 2011), as well as consumer purchasing (Bateman et al., 2008, Doyle et al., 1999, Heath and Chatterjee, 1995, Simonson, 1989). When choices are susceptible to changes in context (in this case, the addition of inferior options to a choice set), humans are not making economically rational decisions: instead of assigning each option a fixed value depending on its utility and so making an ‘absolute’ choice, people are judging options relative to the other options in the choice set. A result of not assigning each option a fixed value is that the addition of irrelevant alternatives can change the preferences between options.

The most well-studied violation of irrelevant alternatives is the asymmetrically dominating decoy effect, in which typically an inferior option (decoy) is added to a choice set of two options that vary in two dimensions. An asymmetrically dominating decoy is inferior to both of the original options but is similar to one of the options in one or more dimensions. The presence of an asymmetrically dominating decoy causes an increase in preference for the option to which it is most similar (Bateman et al., 2008, Colman et al., 2007, Huber et al., 1982, Krumhansl, 1978). .

Like human decision-making, animal decision-making does not seem to be independent of the effects of irrelevant alternatives. When asymmetrically dominating decoys are added to choice sets, animals change their preferences (Bateson, 2002, Bateson et al., 2002, Bateson et al., 2003, Hurly and Oseen, 1999, Latty and Beekman, 2011, Shafir et al., 2002, Waite, 2001b). These changes in preference in response to the addition of decoys suggest that animals, like humans, might be using relative decision-making strategies (Bateson, 2002, Bateson et al., 2003, Latty and Beekman, 2011, Morgan et al., 2012, Shafir et al., 2002). However, for foraging hummingbirds, at least, it is possible that the violations of the independence of irrelevant alternatives are due to the lower energy return offered by the inferior decoy options changing the state of the animal (Schuck-Paim et al., 2004). Hummingbirds foraging on the inferior decoy as they learn about the decoy could cause the animal to select more of the option with the highest energetic content to compensate for the decreased intake caused by sampling the poorer option. This could explain why foraging hummingbirds faced with three options, two favourable (one sweeter but smaller and the other less sweet but larger) and one poor changed their preferences in the presence of the poor option as they tended to prefer the sweeter, smaller option, which also provided a slightly higher caloric return (Bateson et al. 2002, Bateson et al. 2003, Morgan et al. 2012). It still remains plausible, then, that economically irrational choices in foraging animals are due to changes in energetic state rather than to a comparative choice mechanism.

Hummingbirds are thought to be net energy rate maximisers (Hixon and Carpenter, 1988, Houston and Krakauer, 1993). The reproductive success of an energy maximiser is an increasing function of its net energy intake (Hixon, 1982). The net

energy intake of the birds would be the amount of energy consumed minus the cost of acquisition and processing then divided by the length of time. In experiments offering options which vary in both the concentration and volume of sucrose all of the options will have different amounts of energy but they will also have different costs. There are two separate costs which might be incurred differentially by the options provided. The first is the time it takes to extract the sucrose from each option. Increasing the concentration of sucrose also increases its viscosity. Hummingbirds feed by using the tubes in the tongue to suck up sucrose via capillary action (Kingsolver and Daniel, 1983). If birds use the capillary action to drink sucrose, then more concentrated solutions of sucrose would incur a greater cost as they would be taken up more slowly by the birds. However, there is recent evidence that the tongue of the hummingbird acts as a fluid trap rather than a capillary tube (Rico-Guevara and Rubega, 2011) and therefore higher viscosities should not carry a much higher time cost. The second cost which may occur differentially over the options is the cost of transporting the sucrose. Drinking a large volume of sucrose will result in increasing flight costs (DeBenedictis et al., 1978) therefore to reduce flight costs hummingbirds should try to take in a lower volume of higher concentration sucrose. Given that both the viscosity of sucrose and the energy required by hummingbirds will change with temperature it is unlikely that we would be able to calculate all of the costs and benefits that each option may bring to hummingbirds in the wild. However, the advantage of looking at economic rationality to examine decision making mechanisms in hummingbirds is that we do not need to complete these calculations. Instead it is assumed that the costs and benefits of choosing an option with a particular volume and concentration should be the same in each choice.

In this experiment, I attempted to use asymmetrically dominating decoys to see if hummingbirds made economically irrational decisions and if so, whether these changes were more consistent with comparative decision-making mechanisms or context-dependent utility caused by energy state changes. To do this, for the first treatment, I repeated the design of part of the asymmetrically dominating decoy experiment described in Bateson et al. (2003) but I added a second, key treatment. In the first treatment, birds were offered a choice between two favourable options: a Concentration option ( $20\mu\text{l}$  of 40% sucrose solution) presented alongside a Volume option ( $40\mu\text{l}$  of 20% sucrose; Figure 1a). I then presented these two favourable options alongside a decoy that was either  $10\mu\text{l}$  of 30% sucrose (the Concentration Decoy) or  $30\mu\text{l}$  of 10% (the Volume Decoy). If the birds respond to asymmetrically-dominated decoys in a way similar to the ways humans respond, then the addition of the Concentration Decoy should increase the birds' preference for the Concentration option over the Volume option and the Volume Decoy should produce the reverse response. However, as Bateson et al. (2003) found that the hummingbirds tended to prefer the Concentration option, which offered a slightly greater caloric return (155 kJ; Table 1) over the Volume option (142 KJ), we ran a second treatment in which the Concentration option (now  $20\mu\text{l}$  of 35%) offered slightly less in calories (132 kJ) than did the Volume option (as in the first treatment) (Figure 1b). The decoys remained the same as in the first treatment and both offered a little over 50kJ caloric return. In the second treatment, the birds should prefer the Volume option over the Concentration (the 'Alternative' Concentration) option in the binary choice and if they base their decision on caloric intake, then preference for the Volume option should increase in the presence of either decoy. Importantly, and unlike Bateson et al. (2003), I also

measured the amount of sucrose the birds actually consumed on each choice. In the previous experiments, visits to options were assumed to result in the entire contents of the well being consumed but it is increasingly obvious that hummingbird do not do this, even when the option visited is relatively good (Bacon, 2011). If, on the other hand, the birds make relative decisions, then their choice should change in response to the presence of a decoy and be different for each decoy.

Figure 1a.

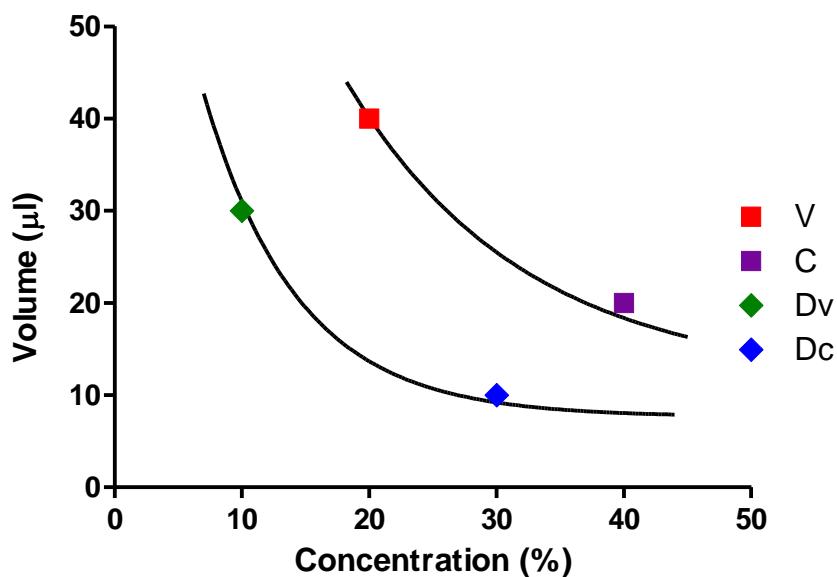


Figure 1a. Relative positions on the concentration and volume dimensions of the four flower types used in the Concentration Treatment. The Volume option (V) contains 40  $\mu\text{l}$  of 20% sucrose (142 joules per well), the Concentration option (C) 20  $\mu\text{l}$  of 40% (155 joules), the Volume Decoy option (DV) 30  $\mu\text{l}$  of 10% (51 joules) and the Concentration decoy option (DC) 10  $\mu\text{l}$  of 30% (55 joules). The lines are isoclines where the energy at each point in the isocline is equal.

Figure 1b.

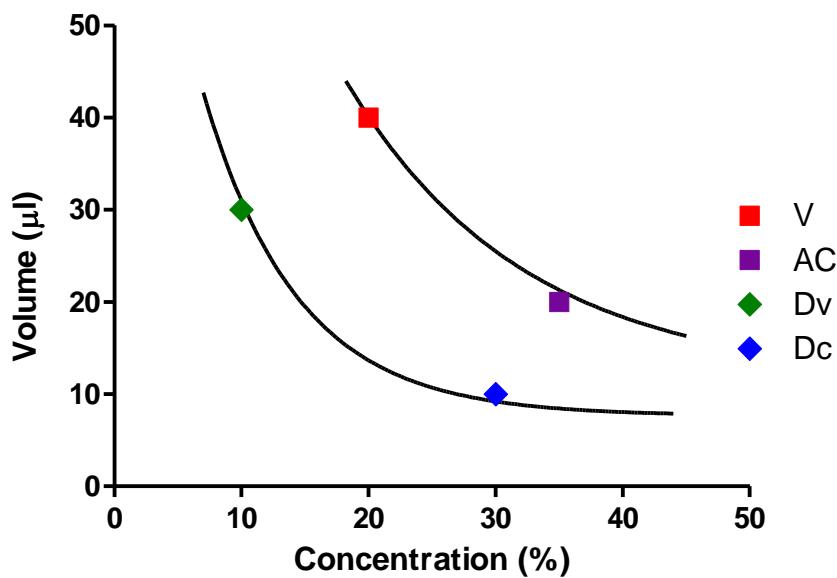


Figure 1b. Relative positions on the concentration and volume dimensions of the four flower types used in the Volume Treatment. The Volume option (V) contains 40  $\mu\text{l}$  of 20% sucrose (142 joules per well), the Alternative Concentration option (AC) contains 20  $\mu\text{l}$  of 35%, the Volume Decoy option (DV) 30  $\mu\text{l}$  of 10% (51 joules) and the Concentration decoy option (DC) 10  $\mu\text{l}$  of 30% (55 joules). Lines are isoclines of equal energy.

Table 1.

Option	Volume ( $\mu\text{l}$ )	Concentration (% sucrose brix)	Joules
Concentration	20	40	154.99
Volume	40	20	142.48
Concentration decoy	10	30	55.69
Volume decoy	30	10	51.23
Alternative Concentration	20	35	132.79

Table 1. The energetic value in joules of the sucrose contained in one well of each option.

## Materials and Methods

### *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 1400m), Alberta, Canada. All work was approved by the University of St Andrews Ethical Committee, conducted according to the requirements of the Canadian

Council on Animal Care and under permits from Environment Canada and the Alberta Sustainable Resource Development Fish and Wildlife division.

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 marked by applying a small amount of waterproof, non-toxic ink to their breasts. The data were collected in May-July 2009 between 8:00 and 19:00 hours Mountain Standard Time.

### *Training*

The subjects were initially trained to feed from a small Plexiglas board containing three wells (10 mm deep, 3.5 mm in diameter) in a triangular formation set on a stake 80cm tall. The edge of each well was marked with a yellow paper reinforcement ring. The wells were filled with 25% sucrose, a concentration that was not used again in this experiment. Once the bird had fed from any of the wells in the board the feeder was removed. After each visit made by the bird to the board, the board was rotated 90° and the volume of sucrose in each well was lowered until the wells all contained 50 $\mu$ l. Once the bird had fed from each of the wells, this stage of the training was complete.

The small Plexiglas was then replaced with a larger Plexiglas board (28 cm x 21.5 cm x 1.2 cm) containing 18 wells (10 mm deep, 3.5 mm in diameter) that could hold a maximum of 120 $\mu$ l. These wells were arranged in an offset pattern with each well 5.2cm from each of its nearest neighbours. All of the wells were marked with yellow reinforcements and all contained 50 $\mu$ l of 25% sucrose solution (see appendix

figures 1 and 2). The board was initially parallel to the ground but each time the bird fed from the board the angle of the board was tilted by approximately 10° until it reached an angle of 45°. After each visit the board was rotated through 90°. Rotating the board changes the spatial arrangement of the wells, which means that birds can only learn the contents of the wells by the colour of the ring rather than the spatial location of the wells. Once the board had been rotated four times training was considered complete and the experiment proper began. Training took approximately two hours. All birds that completed training successfully progressed to the experiment.

### *Experimental manipulation*

For the experiment, we used the larger Plexiglas boards described above. The wells were marked with coloured reinforcement rings to indicate the contents of the well. The board was mounted on a stake *ca.* 80 cm high at a 45° angle. Birds were pseudo randomly assigned to either the Treatment One or Treatment Two.

### *Treatment One*

In this treatment (essentially a replicate of Bateson et al. 2003), six birds were presented with one binary condition and two trinary conditions. The order of presentation was pseudo-randomised so that each order of presentation had approximately the same number of birds assigned to it.

In the Binary condition, we presented birds with a choice of two options: nine wells were randomly assigned to contain the Concentration option ( $20\mu\text{l}$  of 40% sucrose solution), and the remaining nine wells contained the Volume option ( $40\mu\text{l}$  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 ( $20\mu\text{l}$  of 40% sucrose), six were randomly assigned to contain the Volume option ( $40\mu\text{l}$  of 20% sucrose), and the final six wells were assigned to contain the Volume decoy ( $30\mu\text{l}$  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 ( $20\mu\text{l}$  of 40% sucrose), one third were randomly assigned to contain the Volume option ( $40\mu\text{l}$  of 20% sucrose), and the final third were assigned to contain the Concentration decoy ( $10\mu\text{l}$  of 30% sucrose).

### *Treatment Two*

In this treatment, five birds were also presented with one binary condition and two trinary conditions. The order of presentation was pseudo-randomised so that each order of presentation had approximately the same number of birds assigned to it.

In the Binary condition, 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 $\mu$ l of 35% sucrose solution) and the remaining nine wells contained the Volume option (40 $\mu$ l of 20% sucrose).

In the Volume decoy trinary condition, birds were presented with a choice of three options: one third of the wells were randomly assigned to contain the Alternative Concentration option (20 $\mu$ l of 40%), one third were randomly assigned to contain the Volume option (40 $\mu$ l of 20% sucrose), and the final third were assigned to contain the Volume decoy (30 $\mu$ l of 10% sucrose).

In the Concentration decoy trinary condition, birds were presented with a choice of three options: one third of the wells were randomly assigned to contain the Alternative Concentration option (20 $\mu$ l of 35%), one third were randomly assigned to contain the Volume option (40 $\mu$ l of 20% sucrose), and the final third were assigned to contain the Concentration decoy (10 $\mu$ l of 30% sucrose). For the number of joules of energy per well contained in each option, see Table 1.

Each of the wells was marked with a coloured reinforcement indicating its contents. We used eight colours (blue, yellow, indigo, pink, red, green, violet and orange), using three new colours for each condition such that birds were required to relearn all of the colour associations for each condition.

During each visit to the board (a bout), the bird was allowed to feed from as many wells as he wished. For each bout, the number and type of wells that the bird fed from was recorded in addition to the time that the bout began. Once the bird had finished feeding and flown away, we emptied all wells from which he had fed using a capillary tube to determine the amount of sucrose remaining. 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.

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 option that offered the highest amount of energy per well (Equation 1; Appendix). In the first treatment this was the Concentration option and in the second treatment it was the Volume option (Equation 2; Appendix). 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 which was most rewarding for each bird (Equation 3; Appendix).

## Analysis

So as to diminish 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. Prior to analysis, these proportional data were transformed using an arcsine square root transformation. Preference for option in the binary choices was with a one sample T. All the differences between conditions were calculated using repeated measures ANOVAs.

I also looked at the choices made by individual birds. To determine whether individual birds changed their preference when a decoy option was added, we used Chi-Squared 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. 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. A sample of ten choice sets from ten different birds was analysed to look at the rate of revisiting. Of the ten conditions sampled, five birds revisited one well and one further bird revisited two wells

## Results

### *Treatment One*

There was a trend for birds to prefer (unless otherwise stated preference refers to the proportion of choices) the Concentration option in the binary choice ( $t(5) = 1.805$ ,  $p = 0.131$ ) and their preference for this option was not different after the addition of either the Volume Decoy (Dv) or the Concentration decoy (Dc) than it was in the binary choice set (Dv:  $F(2,10) = 0.411$ ,  $p = 0.870$ ; Dc:  $F(2,10) = 0.411$ ,  $p = 0.402$ ; Figure 2).

Figure 2.

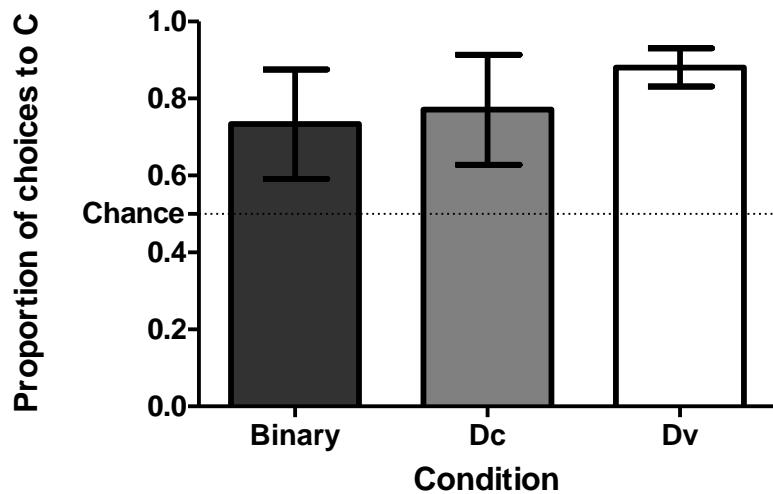


Figure 2. Concentration Treatment: Proportion of choices made to the Concentration option in the Binary, and the Concentration and Volume decoy added choices. Data are taken from the last 75 well visits and use choices to the Concentration and Volume options. The data are means  $\pm$  s.e. (N=6).

#### *Treatment Two*

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:  $F(2,8) = 0.2035$ ,  $p = 0.878$ ; Dc:  $F(2,8) = 0.2035$ ,  $p = 0.776$ ; Figure 3).

Figure 3.

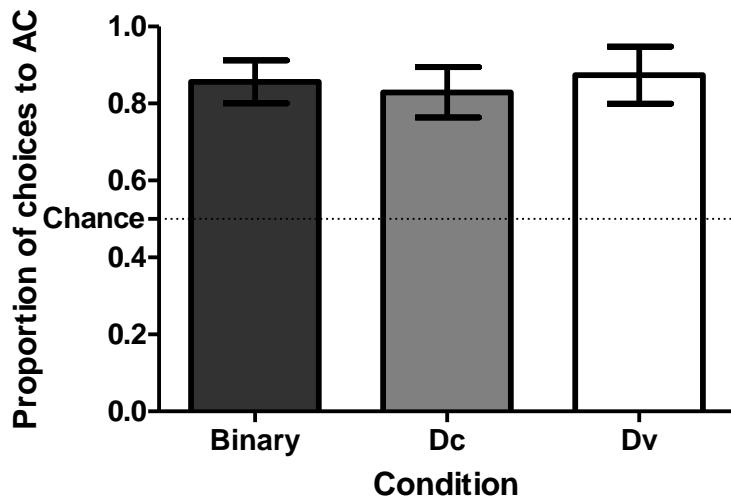


Figure 3. Volume Treatment: Proportion of choices made to the Alternative Concentration options in the Binary, and the Concentration decoy and volume decoy added choices. Data are taken from the last 75 well visits and only use choices to the Alternative Concentration and Volume options. The data are means  $\pm$  s.e. ( $N=5$ ).

#### *Sucrose consumed*

In the binary condition of Treatment One, birds consumed, on average, the same amount of energy per well from the Concentration option as from the Volume option ( $t(5) = 1.989$ ,  $p = 0.103$ ). In the binary condition of Treatment Two in the, there was a trend for birds to gain more energy per well when drinking from the Alternative Concentration wells than when drinking from the Volume wells ( $t(4) = 2.371$ ,  $p = 0.076$ ) (for Joules acquired from each option see Table 2).

Table 1.

Treatment	Option	Volume ( $\mu$ l)	Concentration (% BRIX)	Average number of joules per well
Concentration	Concentration	20	40	127.18
Concentration	Volume	40	20	92.07
Volume	Alternative concentration	20	35	142.48
Volume	Volume	40	20	100.96

Table 1. The average energetic value in joules that birds consumed from each option in the binary condition.

#### *Data from individuals*

#### *Treatment One*

When the Volume decoy was added to the choice set of the Concentration option and the Volume option, one bird decreased and three birds increased their preference for the Concentration Option (bird 5:  $c^2 (1) = 16.448$ ,  $p < 0.001$ ; bird 1:  $c^2 (1) = 45.512$ ,  $p < 0.001$ ; bird 3:  $c^2 (1) = 341.479$ ,  $p < 0.001$ ; bird 6:  $c^2 (1) = 341.479$ ,  $p < 0.001$ ), while

two birds did not change their preference (bird 2:  $c^2 (1) = 2.377$ ,  $p = 0.123$ ; bird 4:  $c^2 (1) = 1.014$ ,  $p = 0.314$ ; Figure 4).

When the Concentration decoy was added to the choice set of the Volume and Concentration options, two birds decreased and three birds increased their preference for the Concentration option (bird 4:  $c^2 (1) = 17.231$ ,  $p < 0.001$ ; bird 5:  $c^2 (1) = 390.507$ ,  $p < 0.001$ ; bird 1:  $c^2 (1) = 48.429$ ,  $p < 0.001$ ; bird 8:  $c^2 (1) = 221.110$ ,  $p < 0.001$ ; bird 6:  $c^2 (1) = 174.866$ ,  $p < 0.001$ ) while one bird did not change his preference (bird 2:  $c^2 (1) = 0.430$ ,  $p = 0.512$ ; Figure 4).

Figure 4.

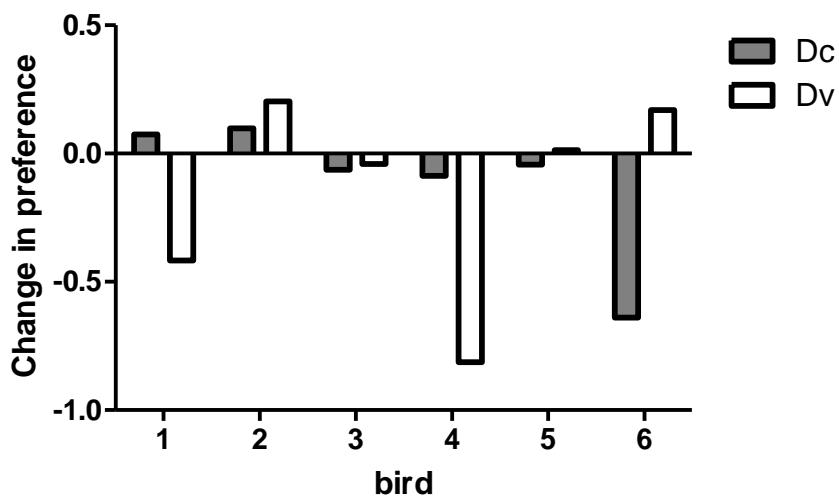


Figure 4. Treatment One: Change in the proportion of choices to the Concentration option. A positive number indicates an increase in the preference for the Concentration option and a negative number indicates an increase in preference for the Volume option. Data are the final 75 well visits ( $N=6$ ).

In sum, one bird (bird 5) decreased and three birds (birds 1, 3 and 6) increased their preference for the Concentration option when either the Volume or Concentration decoy was added to the choice set. One bird made no change in response to the inclusion of either decoy.

### *Treatment Two*

The addition of the Volume decoy caused one bird to increase its preference for the Volume option (bird 8:  $c^2(1) = 154.854$ ,  $p < 0.001$ ), two birds decreased their preference for the Volume option (bird 9:  $c^2(1) = 34.560$ ,  $p < 0.001$ ; bird 10:  $c^2(1) = 11.259$ ,  $p = 0.001$ ), one bird did not change his preference (bird 7:  $c^2(1) = 2.663$ ,  $p = 0.103$ ) and the fifth bird (bird 11) failed to sample one of the options at all in the last 75 choices so we did not analyse his data (Figure 5).

When the Concentration decoy was added, two birds increased their preference for the Volume option (bird 7:  $c^2(1) = 32.244$ ,  $p < 0.001$ ; bird 8:  $c^2(1) = 32.426$ ,  $p < 0.001$ ), one bird reduced his preference for the Volume option (bird 9:  $c^2(1) = 21.607$ ,  $p < 0.001$ ) and two birds did not change preference (bird 10:  $c^2(1) = 0.544$ ,  $p = 0.461$ ; bird 5:  $c^2(1) = 0.414$ ,  $p = 0.520$ ; Figure 5).

Figure 5.

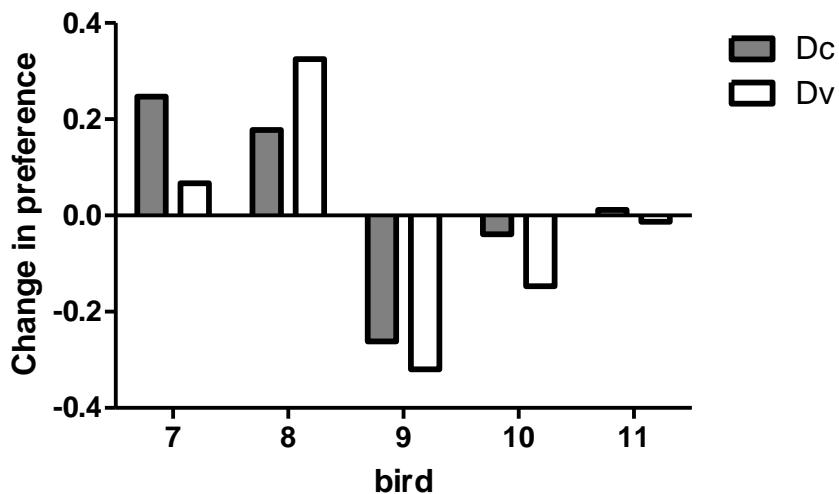


Figure 5. Treatment Two: Change in the proportion of choices to the Alternative Concentration option. A positive number indicates an increase in the preference for the Alternative Concentration option and a negative number indicates an increase in preference for the Volume option. Data are the final 75 well visits (N=5).

The preference changes of two of the birds were independent of the kind of decoy: bird 8 increased his preference for the Volume wells irrespective of decoy type while bird 9 decreased its preference for the Volume option irrespective of decoy type. Birds 7 and 10 responded to only one decoy (Volume and Concentration, respectively) while bird 11 responded to the inclusion of neither decoy.

*Preference for the option with the largest experienced energy*

If the birds drank all of the contents of each well, the Volume Option provided the highest energetic return in the Volume Treatment while in the Concentration Treatment the Concentration option should 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 (Equation 3, Appendix). 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 two birds gained the most energy per well from the Volume option (birds 1 and 4). In response to the addition of either the Concentration or Volume Decoy to the choice set two birds increased their preference for the option from which they had gained the highest energetic return (bird 3: Dv:  $c^2(1) = 341.479$ ,  $p < 0.001$ ; Dc:  $c^2(1) = 221.110$ ,  $p < 0.001$ ; bird 6 Dv:  $c^2(1) = 341.479$ ,  $p < 0.001$ ; Dc:  $c^2(1) = 174.866$ ,  $p < 0.001$ ) while two birds decreased their preference for that option (bird 5: Dv:  $c^2(1) = 16.448$ ,  $p < 0.001$ ; Dc:  $c^2(1) = 390.507$ ,  $p < 0.001$ ; bird 1: Dv:  $c^2(1) = 45.512$ ,  $p < 0.001$ ; Dc:  $c^2(1) = 48.429$ ,  $p < 0.001$ ). One bird decreased its preference for the option with the most energy only when the Concentration decoy was added (bird 4: Dcc $c^2(1) = 17.231$ ,  $p < 0.001$ ; Dv  $c^2(1) = 1.014$ ,  $p = 0.314$ ). The sixth bird (bird 2) did not respond to the

addition of either the Volume or Concentration decoy to the choice set (Dv:  $c^2(1) = 2.377$ ,  $p = 0.123$ ; Dc:  $c^2(1) 0.430$ ,  $p = 0.512$ ).

In Treatment Two, all birds gained the largest volume of energy per well from the Alternative Concentration option. One bird increased his preference from which he had gained most energy (the Alternative concentration option) in response to the addition of either the Volume or Concentration decoy to the choice set (bird 9: Dv:  $c^2(1) = 34.560$ ,  $p < 0.001$ ; Dc:  $c^2(1) = 21.607$ ,  $p < 0.001$ ) while another bird (bird 10) increased his preference for the option with the highest energy only in response to the addition of the Volume decoy (bird 10: Dv:  $c^2(1) = 11.259$ ,  $p = 0.001$ ; Dc:  $c^2(1) = 0.544$ ,  $p = 0.461$ ). Bird 8 decreased its preference for the option with the most energy in response to either the Concentration or Volume decoy being added to the choice set (bird 8 Dc:  $c^2(1) = 32.426$ ,  $p < 0.001$ ) while bird 1 only did so in response to the Concentration Decoy being added to the choice set (bird 7: Dc:  $c^2(1) = 32.244$ ,  $p < 0.001$ ; Dv:  $c^2(1) = 2.663$ ,  $p = 0.103$ ). Bird 11 did not respond to the addition of the Concentration decoy to the choice set (bird 11 Dc:  $c^2(1) = 0.414$ ,  $p = 0.520$ ). His choice for the options when the Volume decoy was added could not be analysed as this bird failed to sample one of the options at all in the last 75 choices.

## Discussion

Overall, the birds' preferences for one 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 although those changes were not consistent across birds within a treatment or dependent on the value of the decoy.

I 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 several 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). While a few of the birds did make changes that were somewhat consistent with this possibility, energy return does not explain most of the changes in the birds' preferences in response to the decoys. This variability in response was seen also when we measured, not the promise of energy return, but what the birds actually gained: this measure shows that most birds responded to the decoys but not in a way that is explained by energetic intake. Hummingbirds are considered to be net rate maximisers (Hixon, 1982, DeBenedictis et al., 1978) so an alternative energetic explanation is that the birds were acting to maximise their net rate of energy intake. If this were the case birds would be predicted to take almost exclusively from the option with the highest caloric pay off (which may be different for each bird). In addition once learning has occurred birds would be expected to choose that option only. However, birds do not exclusively choose one of the options even though they were able to as the average number of wells visited was lower than the amount of wells of each type in the trinary choice sets.

However, the alternative explanation for a response to the addition of decoys to the choice set was that if the birds were using a comparative choice mechanism their preferences should have changed in response to the inclusion of an asymmetrically dominating decoy (in this case the Concentration and Volume decoys) 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 there were birds that did respond in this way, they were not the majority.

The lack of systematic results in this experiment points to another possibility, that the decoy effect does not produce systematic changes in the preference of hummingbirds. Instead their changes in preference could be seen as mistakes rather than the systematic changes in preference which would be predicted from a shared decision making mechanism. If this were the case then the hummingbirds would be economically rational and further experiments looking at the decoy effect would be unlikely to lead to a greater understanding of their decision making. It is also plausible that rather than mistakes the problem lies with our simplistic assumption that birds use the cues offered by the options in equal measure. If, for example, the hummingbirds do not pay equal attention to both the concentration and volume of the option and birds differ in the weight they give to different components of an option (e.g. preferring concentration over volume), we would expect that individual birds would change their preferences in response to the addition of decoys but not in the same way. One way to simplify the examination of the effects of poor decoys on choice is to use options that vary in a single dimension only (Morgan et al. 2012). However, even this methodological change is not, in itself, sufficient as shown by the lack of reliable

response to the inclusion of poorer decoys to choice sets in the single-dimension experiment carried out by Morgan et al. (2012). In order to see whether there are situations in which hummingbirds are making consistent economically irrational choices or if the choices they make are more consistent with rationality, more tests of the effects of poorer options on preference for favourable options are needed.

**Chapter 3: Context-dependent decision making in a single dimension: inferior options make a difference****Introduction**

Animals should make choices which maximise their fitness. One possible way of achieving this would be by assigning all options a value based on the benefit conveyed to the animal and then choosing the option with the highest value independent of the poorer options available. However we know this is sometimes not the case as some animals change their preference upon the addition of inferior options to a choice set (Bateson et al., 2003, Latty and Beekman, 2011, Morgan et al., 2012, Scarpi, 2011, Shafir et al., 2002, Stroeymeyt et al., 2011). However, as discussed in Chapter 2, in order to determine what mechanism is causing these changes in preference, it is necessary that preferences can consistently and reliably be obtained, both within and among individuals, which they are often not (Bateson et al., 2002, Bateson et al., 2003, Shafir, 1994, Waite, 2001b).

One explanation for the differences in the way animals respond to the addition of inferior options to a choice sets may be, in part, due to the nature of the options the animals are offered. In the experiments with animals, options typically vary in more than one dimension (Bateson et al., 2002, Bateson et al., 2003, Latty and Beekman, 2011, Shafir, 1994, Shafir et al., 2002, Waite, 2001b). If the animals pay attention to or prefer one dimension over another but do not all prefer the same dimension, this could lead to variation in their responses to inferior options. In order to develop an appropriate experimental paradigm for examining these possibilities, we presented

wild, free-ranging foraging hummingbirds with a choice set in which the options varied in a single dimension only.

Birds were presented with two favourable options with values of 20 & 30, which differed in either concentration (%) or in volume ( $\mu\text{l}$ ). To these binary choice sets, we added either an option that was slightly poorer (15  $\mu\text{l}$  or %) or an option that was much poorer (5  $\mu\text{l}$  or %). If the birds make economically rational decisions, their choice of the more favourable option should not change in response to the addition of either poorer option. However, there are two ways in which the birds' choices may change in response to the presence of an inferior option. The first is based on energetic intake. Drinking from either of the poorer options would be expected to lead to the birds increasing their intake of the 30 option relative to the 20 option in order to take in the same amount of energy. If this was the case, then we would expect the inclusion of the 15 option to increase preference for the 30 over the 20 option relative to the preference for 30 seen in the binary choice set, and for the inclusion of the 5 option to increase that preference for 30 even more. The second possibility is that the birds make their choices based on the relative difference among the options. In this case, the 15 option is more similar to the 20 than the 30. Therefore the 30 option appears to be better relative to the 20 option than when the birds had had only the 20 and 30 options to choose between. The birds would, then, be expected to take more of the 30 option in the presence of the 15 option than in the binary choice. The addition of the 5 option, on the other hand, would cause the 20 and 30 options to appear more similar to each other than in the binary choice. In this context, we would expect the birds to decrease their preference for the 30 option in the presence of the 5 option relative to their preference for the 30 option in the binary context.

## Materials and Methods

### *Subjects and study site*

The subjects were five wild male rufous hummingbirds defending territories in the Westcastle Valley in the eastern range of the Rocky Mountains ( $49^{\circ} 21'N$ ,  $114^{\circ} 25'W$ , elevation 1400m), Alberta, Canada. Territorial males were individually marked by a small application of non-toxic, waterproof ink to the breast feathers. The experiment was conducted from 7:00 to 20:00 hours Mountain Standard Time between May-July in 2010.

This work was approved by the University of St Andrews Ethical Committee, conducted according to the requirements of the Canadian Council on Animal Care and was carried out under permits from Environment Canada and the Alberta Sustainable Resource Development Fish and Wildlife Division.

### *Experimental procedure*

#### *Training*

The subjects were initially trained to feed from a small Plexiglas board containing three wells (10 mm deep, 3.5 mm in diameter) in a triangular formation set on a stake 80cm tall. The edge of each well was marked with a yellow paper reinforcement ring. The wells were filled with 25% sucrose, a concentration that was not used again in this experiment. Once the bird had fed from any of the wells in the board the feeder was removed. After each visit made by the bird to the board, the board was rotated  $90^{\circ}$  and

the volume of sucrose in each well was lowered until the wells all contained 50 $\mu$ l. Once the bird had fed from each of the wells, this stage of the training was complete.

The small Plexiglas was then replaced with a larger Plexiglas board (28 cm x 21.5 cm x 1.2 cm) containing 18 wells (10 mm deep, 3.5 mm in diameter) that could hold a maximum of 120 $\mu$ l. These wells were arranged in an offset pattern with each well 5.2cm from each of its nearest neighbours. All of the wells were marked with yellow reinforcements and all contained 50 $\mu$ l of 25% sucrose solution. The board was initially parallel to the ground but each time the bird fed from the board the angle of the board was tilted by approximately 10° until it reached an angle of 45°. After each visit the board was rotated through 90°. Rotating the board changes the spatial arrangement of the wells, which means that birds can only learn the contents of the wells by the colour of the ring rather than the spatial location of the wells. Once the board had been rotated four times training was considered complete and the experiment proper began. Training took approximately two hours.

### *Experimental manipulation*

For the experiment, we used the larger Plexiglas boards described above. The wells were marked with coloured reinforcement rings to indicate the contents of the well. The board was mounted on a stake *ca.* 80 cm high at a 45° angle.

There were two treatments, in the Volume Treatment options varied only in volume and in the Concentration Treatment options varied only in concentration. Each bird completed both the Volume and Concentration Treatments. Two birds completed

the Concentration Treatment first and three birds completed the Volume treatment first. In both the Volume and Concentration Treatments birds had a binary choice set and two trinary choice sets. In binary choice sets half of the wells were randomly assigned to contain each option and in trinary choice sets a third of the wells were randomly assigned to contain each option.

In both the Concentration and the Volume Treatments the binary choice set consisted of options with values of 20 and 30. For the Concentration Treatment, birds were presented with options of 20% and 30% sucrose and in the Volume Treatment, the choice was between 20 $\mu$ l and 30 $\mu$ l. There were also two trinary choice sets: one consisted of 15, 20 and 30 (% in the Concentration Treatment and  $\mu$ l in the Volume treatment), while the other consisted of 5, 20 and 30 options (% in the Concentration Treatment and  $\mu$ l in the Volume treatment; Figure 1). The order of presentation was counterbalanced across the five birds. In the Concentration Treatment, all of the options had a volume of 30 $\mu$ l. In the Volume Treatment all of the options had a concentration of 20%.

Figure 1.

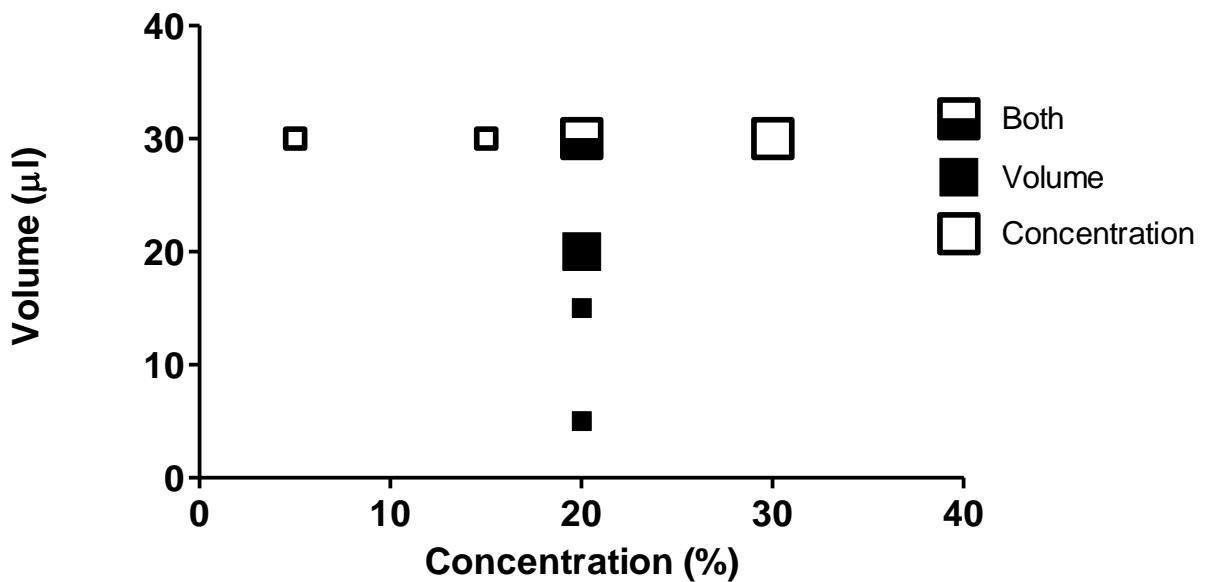


Figure 1.

Volumes and concentrations of the options we presented to the birds. The open squares indicate options presented in the Concentration Treatment: a binary choice between the 20% and 30% options, as well as two trinary options in which the birds were presented with a choice set of 5%, 20% and 30% as well as the choice set of 15%, 20% and 30%. The black squares indicate options that birds were presented with in the Volume Treatment: a binary choice between the 20 $\mu$ l and 30 $\mu$ l options, as well as two trinary options where birds had a choice set of 5 $\mu$ l, 20 $\mu$ l and 30 $\mu$ l and 15 $\mu$ l, 20 $\mu$ l and 30 $\mu$ l. There is one option in each of the treatments with the same volume and concentration; which is indicated by a half black square. For both Volume and Concentration treatments options which are present in all the choices in that treatment are indicated by larger squares than options which are only present in a trinary choice.

Each option was indicated to the bird by the colour of paper reinforcement ring placed around the well. Eight colours were used green, navy, purple, sky blue, pink,

red, yellow and orange. Within each treatment a bird had one binary choice set and two trinary choice sets. For each of these choice sets there was a new set of colours so that the birds had to relearn all the colour associations afresh in each choice set.

When a bird visited the board he was allowed to feed from as many wells as he wished. Once he had left the board any sucrose remaining in the wells was measured using a 20 $\mu$ l pipette. The empty wells were then refilled and the board was rotated through 90°. After four visits, the board was replaced with another board on which a different set of wells were randomly assigned to contain each option. Moving the board and changing the spatial arrangement of the wells' contents was to ensure that the birds learned the contents of the wells by the colour of the assigned ring rather than by the spatial location of the wells.

On two occasions a bird failed to sample every flower type within the first 10 visits to the board. When this occurred we forced him to drink the missed option by presenting him with a board containing only the unsampled option.

Each choice set was considered complete when a bird had visited 100 wells. Birds usually took less than a day to visit 100 wells.

### *Data Analysis*

To determine whether there were changes in the preference for the 20% and 30% options in the Concentration Treatment and the 20 $\mu$ l and 30 $\mu$ l options in the Volume Treatment I looked at the proportion of choices that birds made to their preferred option in the binary choice set and then compared that preference to the choices to that

option in the two trinary choice sets. I calculated the birds' preferences in all choice sets across both the Volume and the Concentration Treatments by dividing the number of choices to the preferred option by the total number of choices to both the 20 and 30 options.

As some of the early visits to the wells were likely to be when the birds were learning about options, we analysed only the final 50 well visits for each condition. We calculated the choices to the preferred option in two ways: (1) by using all of the choices that the bird made in the final 50 well visits; and (2) by using only the data for the first three well visits in each bout. Taking the first three well visits allows us to assess preference before the number of wells of each option becomes limited (in the trinary choice sets there were only six wells for each option). Only 2 birds made any revisits to a well they had already emptied. These revisits were not counted and occurred twice or less per condition. As the data were not normally distributed, all proportions were transformed using an arcsine-square-root transformation. I used paired T-Tests to compare preferences in each of the trinary conditions to the preference in the binary condition and repeated-measures ANOVAs to look at the volume of sucrose birds consumed in each choice set. All statistics were calculated in PASW statistics version 18.

## Results

### *Concentration Treatment*

Using all of the data from the last 50 choices, when the 5% option was added to the choice set of 20% and 30% options, birds chose the 30% option less frequently than they had chosen it in the binary choice context ( $t(4) = 3.260$ ,  $p = 0.031$ ; Figure 2). When a 15% option was added to the choice set of 20% and 30% birds did not change their preference ( $t(4) = -0.563$ ,  $p = 0.604$ ). We saw similar effects when we used only the data from the first three well visits that birds made in each bout (5%:  $t(4) = -2.933$ ,  $p = 0.043$ ; 15%:  $t(4) = -0.487$ ,  $p = 0.652$ ). For number of each option selected in each choice set see Figure 1; appendix.

Figure 2.

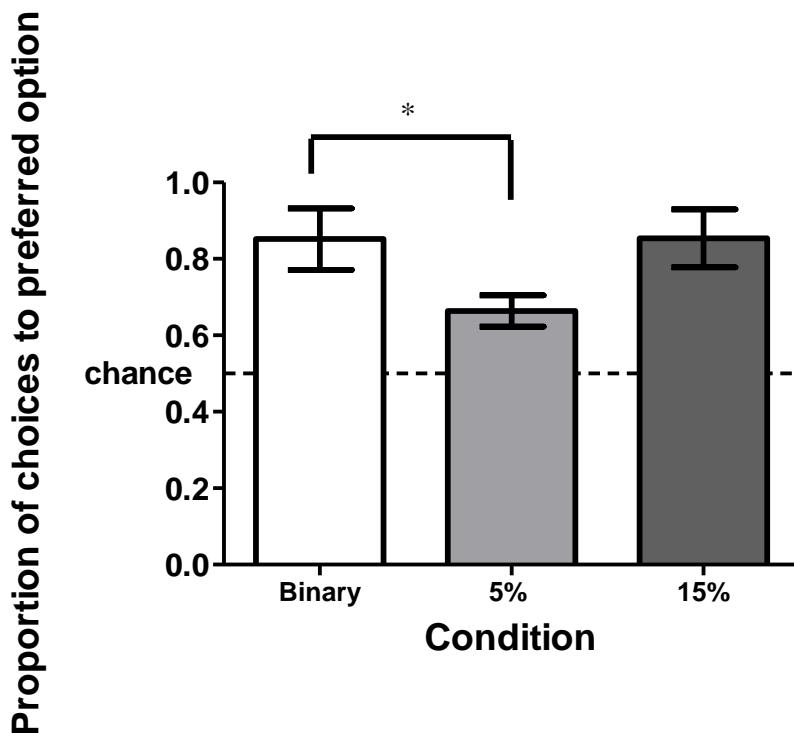


Figure 2. The mean ( $\pm$  s.e.) proportion of choices which birds made to their preferred option in the trinary and binary choices of the Concentration treatment. For each bird the preferred option was the option which they chose most in the binary choice. All birds preferred the 30% option in the binary choice set. The data are means  $\pm$  s.e. ( $N = 5$ ) from the last 50 well visits. The asterisk indicates significance at  $p \leq 0.05$ .

### *Volume Treatment*

Using all of the data from the last 50 choices, when the 5 $\mu$ l decoy was added to the choice set of 20 $\mu$ l and 30 $\mu$ l, birds decreased the number of choices made to their preferred option from the binary choice set ( $t(4) = -4.530$ ,  $p = 0.011$ ; Figure 3). Birds did not change their preference in response to the addition of the 15 $\mu$ l decoy to the choice set of 20 $\mu$ l and 30 $\mu$ l ( $t(4) = -0.541$ ,  $p = 0.617$ ). We saw similar effects when only the data for the first three choices of each bout were analysed (5 $\mu$ l:  $t(4) = -2.725$ ,  $p = 0.053$ ; 15 $\mu$ l:  $t(4) = 0.791$ ,  $p = 0.473$ ). For number of choices birds made to each option in each of the choices sets see Figure 2; appendix.

Figure 3.

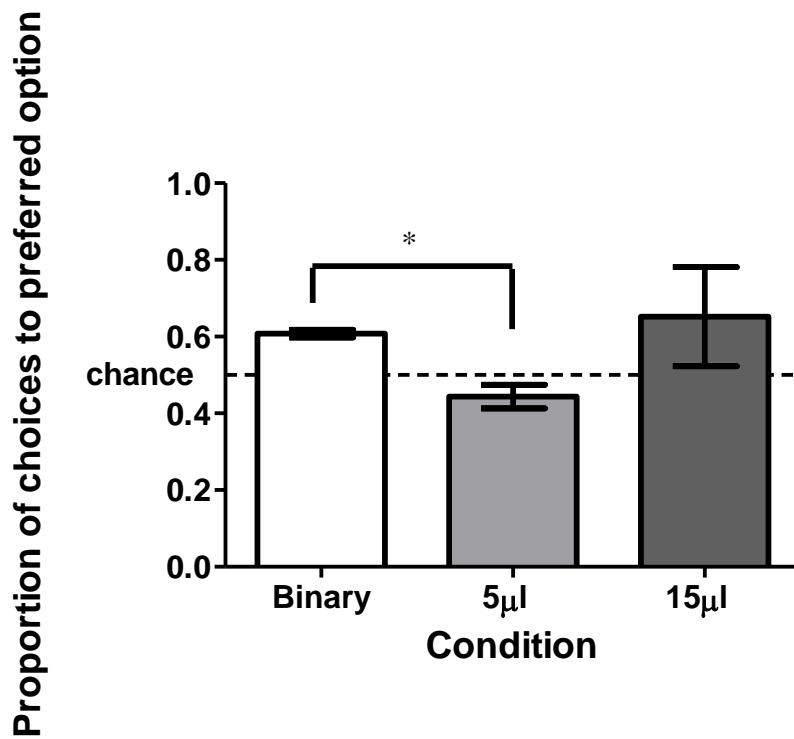


Figure 3. The mean ( $\pm$  s.e.) proportion of choices which birds made to their preferred option in the trinary and binary choices of the Volume Treatment. For each bird the preferred option was the option which they chose most in the binary choice. For four birds this preferred option was the 20 $\mu$ l option and for one bird the preferred option was the 30 $\mu$ l option. The data are means  $\pm$  s.e. ( $N = 5$ ) for the final 50 well visits. The asterisk indicates significance at  $p \leq 0.05$ .

#### *Volume of sucrose remaining*

I also measured the volume of sucrose remaining in the wells after birds had visited them. In the Concentration Treatment, the birds drank a similar volume of sucrose

from the 30% wells in all of the binary and trinary choice sets ( $F(2,8) = 1.601$ ,  $p = 0.260$ ). Birds also consumed a similar volume of sucrose from each of the 20% wells in all of the choice set ( $F(2,8) = 0.868$ ,  $p = 0.456$ ; Figure 3, appendix). Birds did not visit a different number of wells per bout in the binary and trinary choice sets of the concentration treatment ( $F(2,8) = 2.930$ ,  $p = 0.111$ ) (see Appendix Figure 4). In addition birds did not significantly differ in the number of bouts which they took to complete the choice sets ( $F(2,8) = 3.173$ ,  $p = 0.0967$ ). There was no difference in the numbers of grams of sugar birds consumed per minute in the different choice sets ( $F(2,8) = 2.082$ ,  $p = 0.187$ . Figure 5, Appendix). In the Volume Treatment, I can be confident that birds experienced the differences in Volume as birds consumed an average 94.7% of the sucrose provided in each well that they visited (Figure 6, Appendix) and birds took different volumes of sucrose in each of the choice sets (Figure 7, Appendix). The amount of sugar which birds consumed per minute was altered by the addition of inferior options. Birds in the 5 $\mu$ l choice set consumed more sugar per minute than they did in the binary choice sets ( $F(2,8) = 7.761$ ,  $p = 0.032$ . Figure 8, Appendix). The amount of sugar that birds consumed per minute was not significantly different in binary and 15 $\mu$ l conditions ( $F(2,8) = 7.761$ ,  $p = 0.120$ ).

## Discussion

In both the Volume and the Concentration Treatments, the addition of a very poor option (5 $\mu$ l or %) to a choice set of options with values of 20 and 30 (%) or  $\mu$ l led to all of the birds reducing their preference for their favoured option. The addition of a slightly poorer option (15 $\mu$ l or %) did not, however, affect the birds' choices. In the

Volume Treatment 4 of the 5 birds preferred the smaller 20 $\mu$ l option. In the presence of the 5 $\mu$ l option birds decreased the proportion of choices made to this option, choosing the 30 $\mu$ l option more frequently. Birds took in more sugar per minute in the 5 $\mu$ l choice set than they did in the Binary choice. The presence of the 15 $\mu$ l option did not change the proportion of choices which birds made to the options. In the Concentration Treatment all birds chose the 30% option most frequently in the binary choice. When the 5% option was added to the choice birds decreased the proportion of choices which they made to the 30% option. Birds did not change the proportion of choices they made to the options when the 15% option was added to the options. The addition of the poorer decoy options did not change the amount of energy per minute that the birds consumed in the Concentration Treatment. These data firstly support our prediction that birds' preference for two favourable options would be affected by the addition of a poor option. Secondly, these data support our prediction that the change in response as a result of the addition of an inferior option would depend on the value of that inferior option. These data provide two key additions to attempts to understand whether or not animals make economically rational decisions: (1) the birds all made the same kind of (irrational) response to the addition of a poor decoy option to a choice set; (2) economically irrational choices were biologically rational as they were not necessarily poorer than the behaviour we would have expected if the birds had been economically rational.

Experiments which have found economically irrational decisions have often not found consistent changes in preference across individuals (Bateson et al., 2002, Shafir, 1994). If animals are economically rational then we would expect that the animals would not change their preference in the presence of a poor value option.

Whereas, if animals are using a common decision rule which is suitable for their environment we would expect that changes in preference would be consistent across individuals. Without predictable responses, it is difficult to determine whether the changes in preference could be a mistake on the part of individuals or if there is a decision making mechanism that is underpinning the changes in preference. It appears from our data that presenting options that vary in one dimension only may provide a powerful tool for addressing the rationality of decision making in animals. Not only did the birds make consistent choices in response to the poor decoy within a dimension (i.e. either sucrose concentration or sucrose volume), they all made the same kind of response across those dimensions. As all birds changed their preference in the same way it seems likely that there is a common process underlying these changes in preference.

The addition of a poor quality decoy to a choice set requires the animal to assess that option by drinking it and unless the animal takes the decoy in addition to the other options it would normally choose, that animal would reduce its energy intake by drinking the poorer option. It has been argued that changes in energy state could be responsible for some of the apparently irrational decision making we see in animals (Schuck-Paim et al., 2004). The birds did have to sample the poor decoys to learn about them. However, once the birds had learned the value of the 5 option, which they did within a handful of visits, the birds rarely chose this option again although the effect of the presence of that option was both immediate and relatively long-lasting (to our limit of 100 well visits, which took about a day), well beyond any immediate energetic deficit that would have been imposed by the intake of the 5 option. Furthermore, the effect was that the birds reduced their intake of their preferred option.

This effect is most clearly seen and interpreted in the Concentration Treatment, whereby the birds preferred 30% over 20% in the binary condition but reduced that preference for 30% in the presence of 5%.

In the Volume Treatment four of the five birds preferred the 20 $\mu$ l option over the 30 $\mu$ l option in the binary choice set. In addition, they did not appear to consider the 15 $\mu$ l option to be a poor decoy option either as when 15 $\mu$ l was presented alongside the 20 $\mu$ l and the 30 $\mu$ l options, they preferred 15 $\mu$ l as much as they did 20 $\mu$ l, and chose 30 $\mu$ l option least (Figure 2, Appendix). Birds left very little (less than 5%) in each well so it is clear that they must have experienced the different volumes of sucrose. It is not clear why in the binary choices birds would prefer the 20 $\mu$ l option as this provides a lower volume of sucrose than the 30 $\mu$ l option. Therefore if birds were trying to acquire a certain volume of sucrose or a particular amount of energy per bout birds would have to visit more wells to achieve this. Although the inclusion of the 15 option did not increase the preference for the 30 option (as would be expected by an energetic explanation), if the birds used a relative assessment of the options, the inclusion of a 15 option would be expected to cause the 30 option to seem less like the 20 option and this does seem to have been the outcome: in both dimensions, the birds differentiated very little between the 15 and 20 options. This is surprising, given both the energetic difference between the two and that these birds can readily distinguish the difference between 15 and 20 value options (Blem et al., 2000, Morgan et al., 2012, Tamm and Gass, 1986). All in all, it seems very unlikely that the changes in preference are caused by changes to the nutritional state of animals caused by sampling the ‘poor’ options.

Not only do our data show, for the first time, firstly, consistent responses to the addition to choice sets of poorer decoy options across birds and, secondly, that changes in energetic state do not account for those changes, we can also begin to distinguish amongst possible alternative mechanistic explanations for the birds' choices. There are, broadly, two classes of mechanism, one in which the birds can determine exactly the value of each option and choose accordingly (which could include ignoring that difference) and the other where the birds use a relative assessment of the options (e.g. one is sweeter/better than the other without an assessment of the actual value of the option). As hummingbirds can distinguish between the concentrations we used in this experiment, it could be that the hummingbirds do know the exact value of each of the options but choose not to act on this information. However, taken as a whole our data would seem to support the latter possibility more strongly, i.e. that, instead of making an assessment of the absolute value of the options, hummingbirds are instead making choices based on a relative assessment of the options available. So, as a very poor option is added to the choice set, the difference between the two good options seems less than it was when the poor option was not present. Mechanistically a relative assessment could be made in at least two ways, either at a perceptual level or at a later stage in information processing (Louie and Glimcher, 2012). Which (if not both) of these two processes is responsible for the changes in preference will be difficult to discriminate.

Whether or not we will eventually be able to determine whether irrational decisions are based on perceptual or cognitive mechanisms, we suggest that the single dimension paradigm we describe here is likely to be a productive step forward in the determination of the mechanisms of choice by animals.

## **Chapter 4: Context-dependent decision making in a single dimension: prior experience does not change preferences**

### **Introduction**

It is clear that the decision-making context can change the choices that animals make contrary to the predictions of rational choice theory. In Chapters 2 and 3 the local context (the options available at the time of the choice) changed the decisions made by hummingbirds. In Chapter 2 this was individual hummingbirds changing their preferences but those changes were not consistent over individuals, whereas in Chapter 3 the changes in preference were consistent across individuals. Previous experiments have also demonstrated that the local context can change the choices made by animals. For example, when inferior options are added to choice sets, animals will change their preferences for the favourable options (Bateson et al., 2002, Bateson et al., 2003, Hurly and Oseen, 1999, Latty and Beekman, 2011, Morgan et al., 2012, Shafir et al., 2002). In experiments where cats are presented with food choices, the presence of option that they can smell but not eat changes their feeding preferences (Scarpi, 2011). Previous experience, or the background context, can also influence the choices that animals make. For example, in starlings the energy state that the animal experienced when learning about an option can change the preference an animal has for that option in future choices: options that were experienced by starlings in poor condition were considered more favourably than would be expected from their energetic value when the starlings re-encountered them (Marsh et al., 2004, Pompilio et al., 2006). Background context also affected the choices made by jays, where the cost (in this case, the theoretical predation risk) required to obtain an item in previous choices

influenced the cost they were willing to pay to acquire that option in subsequent trials (Waite, 2001a).

In humans (who also make irrational choices) there have been various explanations suggested to explain violations of rationality. These include constraints on the decision maker in time, on their cognitive capacity, or on their perceptual systems as well as the use of decision-making strategies such as rules of thumb (Gigerenzer et al., 1999, Scheibehenne et al., 2007, Simon, 1997, Tversky and Kahneman, 1974). To understand why violations of rationality in animals may occur, we need first to determine the contexts in which they occur.

Here we aimed to examine the effect of local (options available at the time of the choice) and previous context on the decisions of foraging hummingbirds. Although hummingbirds make choices that are changed by the local context, changes that depend on the options present at the time of the choice, irrespective of whether the options vary in two dimensions (concentration and volume: (Bateson et al., 2002, Bateson et al., 2003), in a single dimension (concentration or volume: (Morgan et al., 2012) or differ in their variability (Hurly and Oseen, 1999), it is not clear whether background context (previous experience) has similar effects. Certainly the previous energetic intake of hummingbirds changes the degree to which the birds are risk averse: hummingbirds that experienced favourable background contexts were more risk averse than were birds that experienced a less favourable background context (Bacon et al., 2010). However, as in that experiment energetic state was explicitly manipulated, those data do not demonstrate that background context leads to irrational decision-making.

Aside from changes brought about by energy intake we know little about the way in which the experience of options in previous contexts may affect the future foraging preferences of hummingbirds. This is because in previous experiments in which the design is such that the birds are presented with a binary choice set and a trinary choice set in which the order of presentation is counterbalanced and the options for both choice sets are represented by different colours (even though the two options in the binary choice set occur in the trinary choice set), birds had to relearn all of the colour associations for each new choice set (Bateson et al., 2002, Bateson et al., 2003, Hurly and Oseen, 1999, Morgan et al., 2012). A consequence of this methodology is that it is not clear whether the choices the hummingbirds make are affected by knowledge of those options acquired in previous contexts.

To examine whether background context can change preferences, we attempted to manipulate the birds' knowledge of options without changing their energetic state. In order to do this, birds were split into two treatment groups and presented with three choice sets, consisting of the same options occurring in the same order (binary followed by trinary followed by binary). For each choice set, the options were identified by a colour. The difference between the treatments was that in one, the colours of the options in the first binary choice set matched those of the same options in the trinary choice set (Trinary Matched; Figure 1) and in the other, the colours of the options in the first binary choice set did not match those of the same options in the trinary choice set (Binary Matched). Both sets of birds, then, faced a trinary choice set having experienced the same favourable options (20% and 30% sucrose solution) alongside a new, much poorer option (5% sucrose solution).

I predict that birds will use prior information to inform their decisions and as such birds which have experienced options previously (as the colours are matched) will make different choices to birds without the experience of the options. If birds use prior information to inform their decisions in future contexts I would expect that when the colours of the options are matched birds would use the information that they had already learned and so make more choices to the 30% option than when the colours are unmatched. I would also predict that if birds change their preference in the trinary choice as a result of the addition of the poor 5% option (as they did in Chapter 3) that this change in preference would be greater when the colours are unmatched as these birds must relearn all of the colour associations and so may attend to local context more than birds with prior information.

## Methods

### *Subjects and study site*

The subjects were 12 wild male rufous hummingbirds defending feeding territories in a valley in the Eastern Range of the Rocky Mountains ( $49^{\circ} 35'N$ ,  $114^{\circ} 41'W$ , elevation 1400m), Alberta, Canada. The data were collected between May-July 2011. 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 marked by applying a small amount of waterproof, non-toxic ink to their breasts. The marks had faded by the time by the birds migrated in mid-July.

*Experimental procedure**Training*

The subjects were initially trained to feed from a small Plexiglas board containing three wells (10 mm deep, 3.5 mm in diameter) in a triangular formation set on a stake 80cm tall. The edge of each well was marked with a yellow paper reinforcement ring. The wells were filled with 25% sucrose, a concentration that was not used again in this experiment. Once the bird had fed from any of the wells in the board the feeder was removed. After each visit made by the bird to the board, the board was rotated 90° and the volume of sucrose in each well was lowered until the wells all contained 50 $\mu$ l. Once the bird had fed from each of the wells, this stage of the training was complete.

The small Plexiglas was then replaced with a larger Plexiglas board (28 cm x 21.5 cm x 1.2 cm) containing 18 wells (10 mm deep, 3.5 mm in diameter) that could hold a maximum of 120 $\mu$ l. These wells were arranged in an offset pattern with each well 5.2cm from each of its nearest neighbours. All of the wells were marked with yellow reinforcements and all contained 50 $\mu$ l of 25% sucrose solution. The board was initially parallel to the ground but each time the bird fed from the board the angle of the board was tilted by approximately 10° until it reached an angle of 45°. After each visit the board was rotated through 90°. Rotating the board changes the spatial arrangement of the wells, which means that birds can only learn the contents of the wells by the colour of the ring rather than the spatial location of the wells. Once the board had been rotated four times training was considered complete and the experiment proper began. Training took approximately two hours.

### *Experimental manipulation*

For the experiment, we used the larger Plexiglas boards described above. The wells were marked with coloured reinforcement rings to indicate the contents of the well. The board was mounted on a stake *ca.* 80 cm high at a 45° angle.

There were two experimental treatments with each choice set consisting of three choice sets, a binary choice set (30 $\mu$ l of 20% or 30% sucrose solution) followed by a trinary choice set (30 $\mu$ ml of 5%, 20% or 30% sucrose) followed by a second binary choice set (30 $\mu$ l of 20% or 30% sucrose; Figure 1). In the binary choice sets nine of the 18 wells were randomly assigned to contain one option and the other nine contained the second option. In the trinary choice sets a third (six) of the wells were randomly assigned to contain each option.

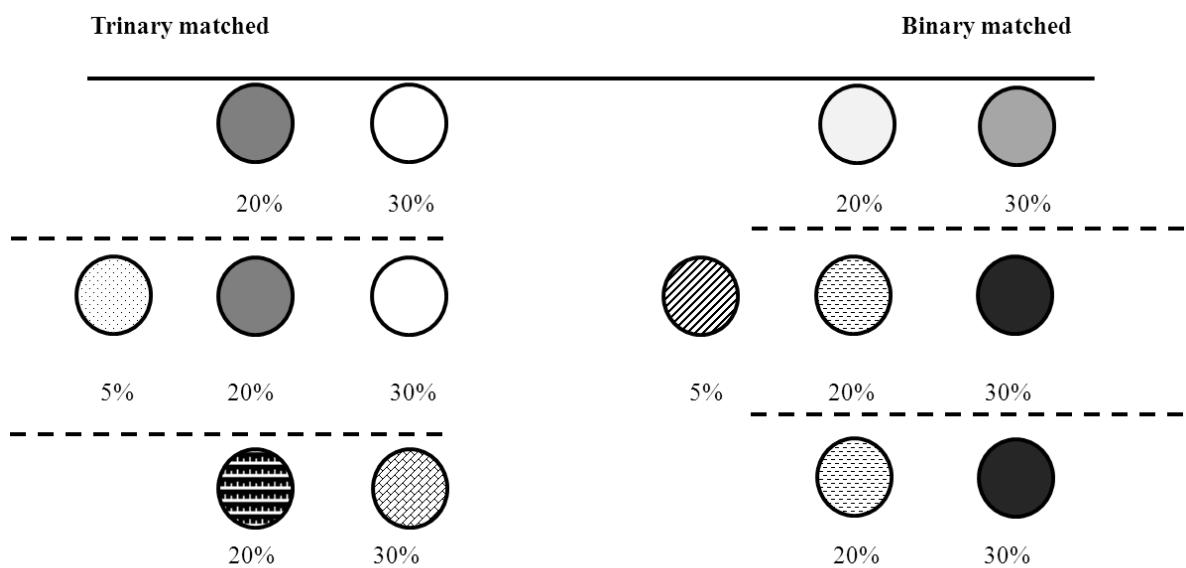


Figure 1. Schematic for Trinary Matched and Binary Matched treatments. Differently patterned circles represent different colours of the reinforcement surrounding each well type. In the Trinary Matched treatment the colours of the first binary choice and the trinary choice are matched but in the second binary the wells are

marked with a new set of colours. In the Binary Matched treatment the colours of the trinary are not the same as the preceding binary. In the final binary choice the colours are the same as the trinary choice which preceded it.

The treatments differed in the way that the colour which identified the contents of each well was assigned. In one treatment (Trinary Matched), the colours indicating the 20% and 30% options in the trinary condition matched those of the preceding binary condition (Figure 1). The colours changed for the second binary condition. The 5% option was a novel colour as this option was not present in the binary choice set. In the other treatment (Binary Matched), the colours indicating the 20% and 30% options in the trinary condition differed to those of the preceding binary condition but remained the same for the second binary condition.

The birds were presented with each choice set until they had visited 80 wells. During each visit to the board (a bout) the bird was allowed to visit as many wells as he wished and we recorded the colours of the wells that the bird fed from. Once the bird left the board, the remaining sucrose in the wells was removed and the volume of sucrose remaining was measured using a 20 $\mu$ l capillary tube. The well was then refilled with the concentration appropriate for the colour of that well. After each visit the board was rotated 90° and after the 4<sup>th</sup> visit to the board the board was replaced with another board with a new pattern of randomly assigned wells. If a bird failed to sample one well type after having visited the board four times then the bird received a board that contained only that well type. After he had visited the wells on this board he was presented with the board containing all the options and the count to a total of 80 well visits began from zero.

### *Statistics*

In both treatments we compared the proportion of choices to the 30% option in each of the different choice conditions using a repeated measures ANOVA with Bonferroni corrections. In the analyses we looked at the proportion of choices to the 30% option from the total choices made to the 20% and 30% options in each choice set. To allow time for learning about the options available, instead of looking at all the choices we looked at the last 20 well visits made. The last 20 visits were used so that I could examine the choices which birds had made after experience with options to the choices made in the first 20 well visits when birds were still learning about the options. I also tested the preferences of males around the time when options were added or taken away from choice sets. Paired samples T tests were used to test for these changes in preference using the last 20 well visits before the addition or removal of an option in addition to the first 20 well visits of the new choice set; I only did this when colours were matched in the choice sets being compared. An independent samples T test was used to look at the difference in choices birds made in the first 20 well visits of the trinary choice sets in both treatments. All of the data were analysed with IBM SPSS version 19.

## **Results**

In the Trinary Matched Treatment birds did not make different choices in the matched trinary than they did in the preceding binary ( $F(1, 5) = 0.178, p > 0.999$ ). In addition, birds chose the 30% option the same amount in the final binary that they had in the trinary choice ( $F(1, 5) = 0.178, p > 0.999$ ; Figure 2). Birds made fewer choices to the 30% option in the first 20 choices of the trinary choice set than they did in the last 20

well visits of the first binary ( $t(5) = 3.221$ ,  $p = 0.023$ ; Figure 3). For cumulative choices to each option in the trinary matched treatment see appendix figure 1.

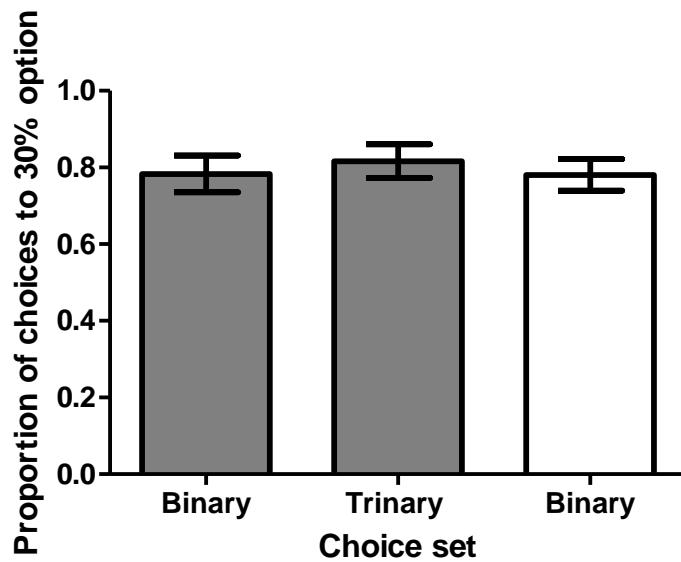


Figure 2. The proportion of choices that birds made to the 30% option in the Trinary Matched Treatment. Where the bars are grey, the colours used to mark each well are the same. In this treatment the colours of the 20% and 30% options in the trinary were matched to those of the preceding binary choice, the 5% options was a novel colour as it was not in the binary choice. The data are means  $\pm$  1 s.e. (N=6).

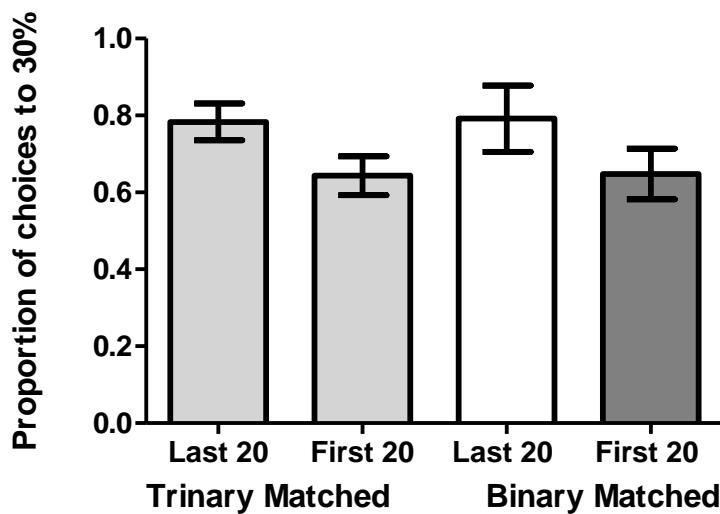


Figure 3. The proportion of choices birds made to the 30% option in the final 20 well visits of the first binary choice sets and the first 20 well visits of the trinary choice. In the choice sets where the bars are the same shade, the colours used to mark each well in the experiments are the same, so in this Trinary Matched treatment the colours of the 20% and 30% options in trinary were matched to those of the preceding binary. The data are means  $\pm$  1 s.e. (N=12).

In the Binary Matched Treatment birds chose the 30% option the same amount in the first binary and the trinary choice set ( $F(1, 5) = 0.020, p > 0.999$ ). Birds also did not make different choices in the trinary choice set than they did in the final binary matched choice set ( $F(1, 5) = 0.020, p > 0.999$ ). There was also no difference in the proportion of choices that birds made to the 30% option in the binary choice set compared to the binary matched choice set ( $F(1, 5) = 0.020, p > 0.999$ ; Figure 4). The removal of the 5% option in the second binary choice did not change the choices birds made to the 30% option ( $t(5) = 0.601, p = 0.574$ ). Birds did not make different choices to the 30% option in the first 20 choices of the trinary choice set than they did in the last 20 well visits of the first binary ( $t(5) = 1.899, p = 0.116$ ; Figure 5). For cumulative choices to each option in the binary matched treatment see appendix figure 2.

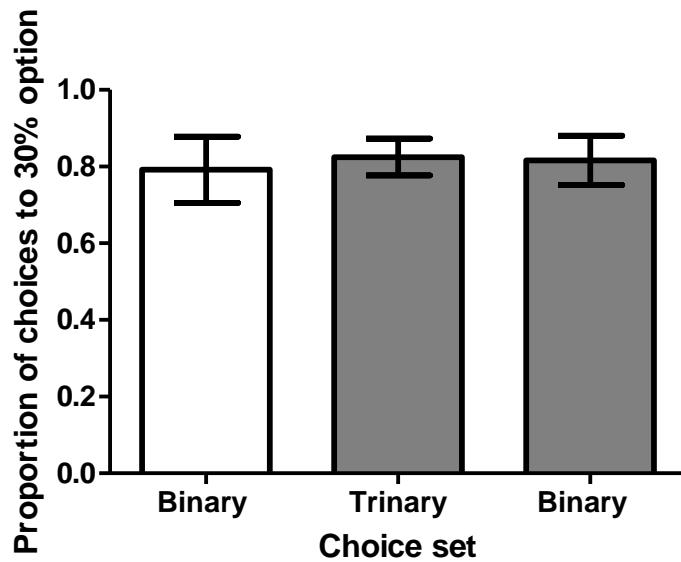


Figure 4. The proportion of choices that birds made to the 30% option in the Binary Matched Treatment. Where the bars are grey, the colours used to mark each well are the same. In this treatment the colours of the 20% and 30% options in the binary were matched to those of the preceding trinary choice. The data are means  $\pm$  1 s.e. (N=6).

The proportion of choices that birds made to the 30% option in the first 20 choices of the trinary treatment were not different in the Binary Matched and Trinary Matched Treatment ( $t(10) = 0.089$ ,  $p = 0.931$ ; Figure 4). Birds in the Trinary Matched Treatment made fewer choices to the 30% option in the first 20 choices of the second binary choice set than birds in the Binary Matched Treatment ( $t(10) = -3.616$ ,  $p = 0.005$ ; figure 5).

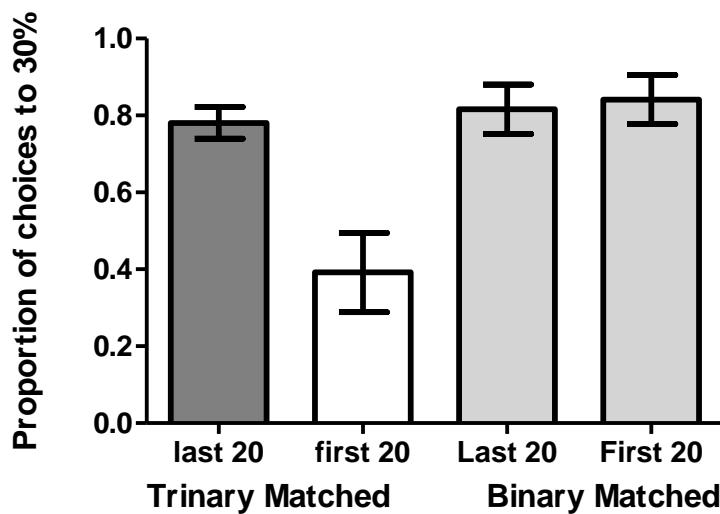


Figure 5. The proportion of choices birds made to the 30% option in the final 20 well visits of the trinary choice set and the first 20 well visits of the final binary choice set. Where the bars are the same shade, the colours used to mark each well in the experiments are the same, so in this Binary Matched treatment the colours of the 20% and 30% options in binary were matched to those of the preceding trinary. The data are means  $\pm$  1 s.e. (N=12).

## Discussion

In this experiment the choices birds made in the last 20 well visits in both of the binary and the trinary choice sets were not different in the two treatments. In addition within a treatment birds did not make different choices to the options in the last 20 well visits of any of the choice sets. In both treatments birds did not make different choices in binary and trinary choice sets. I also compared the first 20 choices made in a choice set to the final choices of the choice set which preceded it. In both treatments birds made fewer choices to the 30% option in the first 20 wells visits of the trinary than they did in the final 20 well visits of the binary choice, whether the colours of the 20% and 30% options in the trinary choice matched the binary made no difference to the preference

(Figure 3). However, the choices in the first 20 well visits of the final binary were affected by whether the colours matched the preceding trinary. When the colours were unmatched birds made fewer choices to the 30% option in the first 20 well visits of the binary than they did in the final 20 well visits of the trinary. But when the colours indicating the 20% and 30% options were the same in the trinary and binary choice sets birds made the same number of choices in the first 20 well visits of the binary than they did in the final 20 well visits of the trinary.

When I looked at the choices the birds made in the last 20 well visits for each context, we could find no evidence for an effect of prior experience on their decisions. In addition, when the 5% option was added in the trinary choice set there was no difference in the choices made to the 30% option between birds that had experienced the 20% and 30% options in the same colours and birds that had not experienced the same colours. In the final binary choice, however, experience of the options did appear to change the choices made by birds in the first 20 well visits. In the first 20 well visits of the final binary choice birds that experienced options with their colours matched to the previous trinary making made more choices to the 30% option than birds which had to relearn the colours (Figure 5).

There are several possible explanations for the lack of evidence for experience having an impact on the choices made by birds by the end of each context. Firstly, hummingbirds could update their information about the options available throughout the experiment so that by the end of each set of 80 choices, prior experience is no longer affecting their choices. Alternatively, hummingbirds might not use prior experience at all when making choices about those same options. However, this second possibility seems unlikely as, in this experiment the choice of the 30% option in the

final binary context was altered by prior experience: birds with experience chose the 30% option more than did birds without this experience. This suggests that prior experience is having some effect as the birds with prior experience of an option in a trinary choice are using that information at the start of the following binary choice. However, birds only use prior information when options are removed from choice sets, not when the number of options is increased. It is possible that when a new item is added to the choice set the birds noticed that the range of options available for them to choose from had changed and as a result the birds responded to this by sampling all of the options again to update their knowledge of the options. When an option is removed, however, they need not update their knowledge in the same way, especially if the option removed is poorer than those that remain.

In this experiment we only looked at one kind of prior experience, which was the knowledge the birds had of the experimental options and their colour associations. In addition to experience of options and their colour associations, there other types of prior experience that might change the choices made by hummingbirds. For example, animals that experienced a good option prior to a choice set of two reasonably good options might make different choices than individuals which experienced a poor option prior to the choice. Ants (*Temnothorax curvispinosus*) have different preferences due to prior experience of good or poor options, those experienced a poor nest before a choice of a new nest move to their new nest slower than ants that had experienced a good nest prior to the choice (Healey and Pratt, 2008). Another type of prior experience which can change the decisions made by animals is the effort previously required to acquire a particular option. For example, Gray jays (*Perisoreus Canadensis*) were presented with a task in which they could obtain a reward (raisins)

for different costs (walking different lengths down a tube); these jays made different choices depending on their prior experience. Jays that had previously experienced a highly rewarded option (in this case three raisins) with little cost (a short way into the tube) were less likely to choose this same option when the cost of obtaining these three raisons was larger than birds with no experience of the option at little cost (Waite, 2001b). Waite (2001a) suggested that experience of the option at the reduced cost had devalued the option, so birds with experience of the option at a lower cost than selected this option less frequently than birds with no experience. Previous experiments with hummingbirds looking at prior experience have found that they are more risk prone when they had foraged on high concentrations of sucrose than when they had experienced low concentrations of sucrose (Bacon et al., 2010). As differences in the energetic state of hummingbirds changes their future foraging choices (Bacon et al., 2010) in this experiment we kept the energetic state the same in the two treatment groups. Prior experience did not have a lasting impact on the choices made by the birds. To determine the full role of prior experience in the choice of hummingbirds further experiments would need to be conducted that changed prior experience in other ways, such as altering the cost of acquiring an option. However, these experiments would need to control the energy state of the animals as we know that changes in energy state can change the preferences of the birds.

In this experiment learning the association between an option and its colour in a previous context did not have a lasting impact on the choices birds made to that option in subsequent choice sets. Although the choices made by hummingbirds in this experiment were not changed by knowledge of previous options their choices might be changed by other types of prior experience. We suggest that future work with

hummingbirds might be best focused on looking at other types of previous experience in hummingbirds. This will enable examination of whether hummingbirds use any prior experience (beyond their energy status) to guide their future foraging choices or if the choices of hummingbirds are influenced by local context only.

## **Chapter 5: Simultaneous or sequential presentation changes the choices made by hummingbirds**

### **Introduction**

In order to maximise their fitness animals are predicted to evaluate the fitness benefit of the options in decisions and choose the option with the greatest fitness benefit (Charnov, 1976, Pyke et al., 1977). However, there is accumulating evidence that animals, like humans, are making relative decisions (Bateson, 2002, Bateson et al., 2003, Hurly and Oseen, 1999, Latty and Beekman, 2011, Morgan et al., 2012, Sasaki and Pratt, 2011, Scarpi, 2011, Waite, 2001a). The discovery that humans make relative decisions led to the formulations of new theories of decision making and the mechanisms that might underpin those decisions. Before we can do this for animal decision-making we need first to characterise the circumstances in which animals make relative decisions. One plausible way to do this is to use the human data as a model to make predictions regarding those circumstances.

It is clear from the human literature that a key component of relative decision making is the manner in which the options are presented. Options that are presented sequentially are judged to be more similar than options that are presented simultaneously (Dato-on and Dahlstrom, 2003, Geiselman et al., 1984, Jordan and Uhlarik, 1985): for the reverse result see Wedell et al., 1987). This might also be true for animals, as both in experimental situations and in the real world animals encounter both simultaneous and sequential choices. For example, grouse females will encounter a number of males effectively simultaneously (Gibson, 1996) whereas bowerbird females visit the bowers of several males before choosing (Borgia, 1995).

In this experiment then, we examined what effect presenting options sequentially or simultaneously caused on the choices made by foraging hummingbirds. In foraging hummingbirds relative decision-making is demonstrable by comparing the choices birds make between two favourable options with the choices birds make among those same options with an inferior option added to the choice set. To examine the effect of manner of presentation on decision making, then, I presented birds with one of two treatments. In one treatment birds were presented with three options (30 $\mu$ l of 5%, 20% and 30% sucrose solution) simultaneously. In the other treatment birds were presented with each of these options sequentially. Although we expect a difference between the treatments, it is not clear from the human literature the direction in which the manner of presentation should affect the hummingbirds' choices.

## Materials and Methods

### *Subjects and study site*

The subjects were 14 wild male rufous hummingbirds defending territories in the Westcastle Valley in the eastern range of the Rocky Mountains (49° 21'N, 114° 25'W), Alberta, Canada. In mid-May commercial hummingbird feeders containing 14% sucrose were placed in potential territories and by late May most of the feeders were defended by males. Territorial males were caught using a drop-door trap surrounding the feeder and individually marked by a small application of non-toxic, waterproof ink to the breast feathers enabling birds to be identified without recapture.

The data were collected from 7:00 to 20:00 hours Mountain Standard Time during May-July, 2011. All work was approved by the University of St Andrews Ethical Committee, conducted according to the requirements of the Canadian Council on Animal Care and was carried out under permits from Environment Canada and the Alberta Sustainable Resource Development Fish and Wildlife division.

### *Training*

The subjects were trained initially to feed from a Plexiglas board (28 cm x 21.5 cm x 1.2 cm) containing 18 wells (10 mm deep, 3.5 mm in diameter) that could hold a maximum of 120 $\mu$ l and set on a stake 80cm tall. These wells were arranged in an offset pattern with each well 5.2cm from each of its nearest neighbours. All of the wells were marked with yellow paper reinforcements and all contained 50 $\mu$ l of 25% sucrose solution. The board was at an angle of 45° and after each visit it was rotated a quarter turn clockwise and the stake and board moved a short distance (10-20cm). This was to ensure that the birds did not learn the spatial location of the well contents. Once the board had been rotated four times training was considered complete and the experiment proper began. This training phase typically took approximately two hours.

### *Experimental procedure*

Each bird experienced one of two experimental treatments: a Simultaneous Treatment ( $n = 7$ ) or a Sequential Treatment ( $n = 7$ ).

*Simultaneous Treatment*

In the Simultaneous Treatment, we presented each bird with a board with the 18 wells divided into three types: six wells contained 30 $\mu$ l of 5%, six wells contained 30 $\mu$ l of 20% and the remaining six wells contained 30 $\mu$ l of 30% sucrose solution. The wells were marked with coloured reinforcement rings to indicate the contents of the well to the bird. A bird was allowed to visit the board and feed from the wells to a total of 80 well visits. If there was any sucrose remaining in the wells after a visit to the board then the remaining sucrose was removed and the empty wells were refilled. After each visit the bird made to the board, the board was rotated through 90°. After four visits the board was replaced with another board with a different set of randomly assigned wells. If a bird failed to sample every option within the first 10 visits to the board we forced him to sample the avoided option by presenting him with a board containing only the unsampled option.

*Sequential Treatment*

In the Sequential Treatment birds were presented with a series of boards such that he experienced each of the three options on a board alone. Each bird was presented with an 18-well board with wells containing 30 $\mu$ l of only one of the three options (5%, 20% and 30%). Each option was presented until the bird had visited 20 wells. He was then presented with a board with only one of the other options for 20 visits, followed by a board of the third option for a further 20 visits. The wells were marked with coloured reinforcement rings to indicate the contents of the well to the bird. The order

of the presentation was pseudo randomised across birds. Following the presentations of boards containing single options only, the birds were presented with a board with all three options available to choose among (six wells of each; Figure 1). The birds were allowed 20 visits to this mixed board. When all of the options were simultaneously available, a third of the wells were randomly assigned to contain each option.

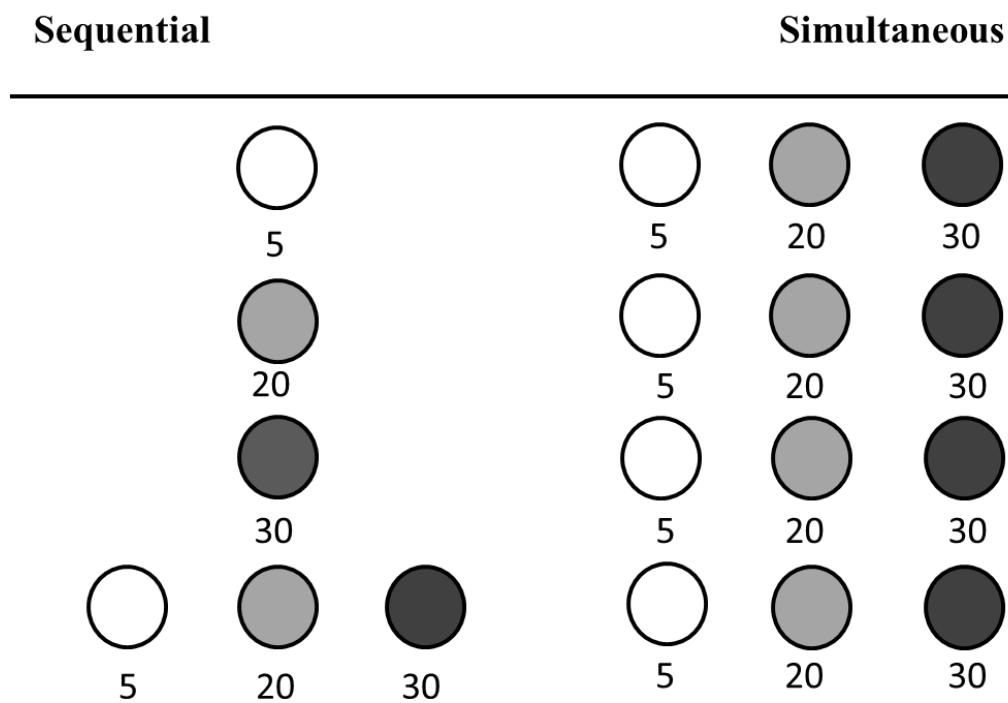


Figure 1.

Schematic for Sequential and Simultaneous Treatments. Differently patterned circles represent different colours surrounding each well type. In the Sequential Treatment options were learned one at a time before being presented together at the end. In the Simultaneous treatment all options were present at the same time.

On a visit to a board, the bird could feed from as many wells as he wished. If there was any sucrose remaining in the wells then the volume of sucrose that was

remaining was removed and the empty wells were refilled. When there was only one option presented, the board was rotated through 90° after each visit to bird made to the board. When all three options were presented together on the board, the board was rotated through 90° after each visit and after the bird made four visits to the board it was replaced with another board with a different set of randomly assigned wells. The stake with board was moved after each 4<sup>th</sup> visit. If a bird did not sample one of the options when all three were present, he was not forced to try the avoided option.

### *Statistical Analysis*

All of the data were analysed using IBM SPSS version 19. Independent samples Mann-Whitney U-tests were used to compare the choices made by birds to each of the options across the two treatments.

## **Results**

There was a trend for birds to choose the 30% option more often in the last 20 well visits of the Simultaneous Treatment than they did in the Sequential Treatment ( $U = 39.00$ ,  $z = 1.886$ ,  $p = 0.059$ ; Figure 2) but they chose the 5% and the 20% options equally often in the two treatments (5% :  $U = 17.50$ ,  $z = -1.468$ ,  $p = 0.142$ ; 20% :  $U = 11.00$ ,  $z = -1.748$ ,  $p = 0.080$ ; Figure 2). Although there are insufficient data for analysis, in the sequential treatment order of presentation of the 5% or 30% options does not seem to change the number of choices made to those options (see appendix Figures 1 and 2).

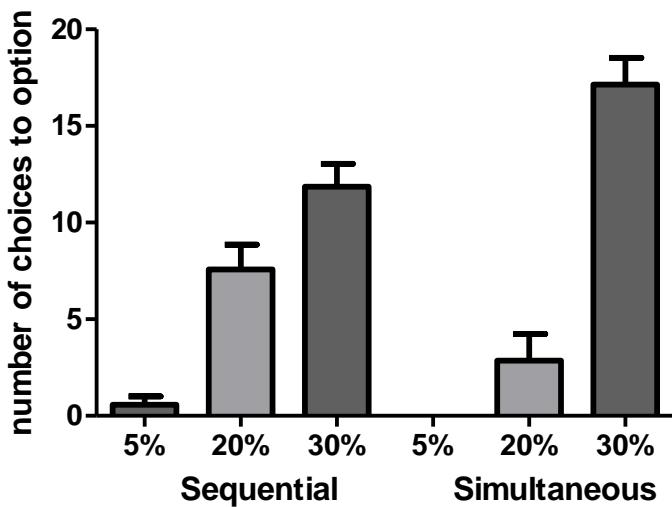


Figure 2.

Number of choices which birds made to the 5%, 20% and 30% options in the last 20 well visits made in the Simultaneous and Sequential Treatments. The data are means  $\pm$  s.e. ( $N = 14$ ).

However, birds in the Simultaneous Treatment have had more experience of the 30% option than had the birds in the Sequential Treatment. To examine whether experience might have caused the birds in the simultaneous treatment to choose the 30% option more often we compared the preference for 30% after birds from both groups had experienced that option 20 times. Birds in the Simultaneous Treatment chose the 30% option after having 20 experiences more frequently than did birds in the Sequential Treatment having experienced the 30% option 20 times ( $U = 40.00$ ,  $z = 2.009$ ,  $p = 0.044$ ). The first 20 visits to the 30 option by birds in the Simultaneous Treatment were interspersed with visits to the 5% and 20% options. Birds chose the 5% option equally often in the Simultaneous Treatment after having twenty

experiences of the 30% option as birds in the final 20 well visits of the Sequential Treatment (5% :  $U = 17.50$ ,  $z = -1.468$ ,  $p = 0.142$ ). The 20% option was also chosen the same amount after 20 wells visits to the 30% options in the Simultaneous Treatment as for birds in the Sequential Treatment (20% :  $U = 12.50$ ,  $z = -1.556$ ,  $p = 0.128$ ; Figure 3).

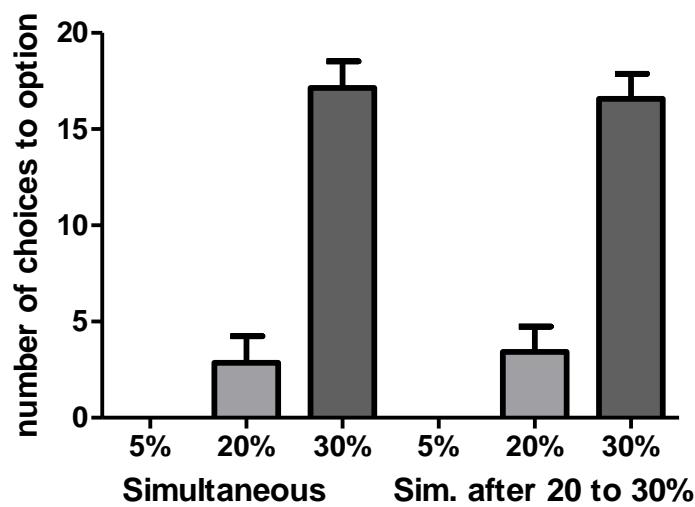


Figure 3. Number of choices which birds made to the 5%, 20% and 30% options in the last 20 well visits of the Sequential Treatments and the choices birds made to these options in the 20 choices after birds had experienced the 30% option 20 times. The data are means  $\pm$  s.e. ( $N = 14$ ).

We then wanted to ask whether the birds in the Sequential Treatment had learned anything about the options from the preceding experience of the options presented alone. Birds chose the 30% option as often in the first 20 well visits of the Simultaneous Treatment as they did in the last 20 well visits of the Sequential Treatment (30%:  $U = 25.00$ ,  $z = 0.065$ ,  $p = 0.948$ ). They also chose the 20% options

equally often (20%:  $U = 16.00$ ,  $z = -1.111$ ,  $p = 0.276$ ). Birds chose the 5% option more often in the first 20 well visits of the Simultaneous Treatment than they did in the last 20 well visits of the Sequential Treatment ( $U = 45.00$ ,  $z = 2.763$ ,  $p = 0.006$ ).

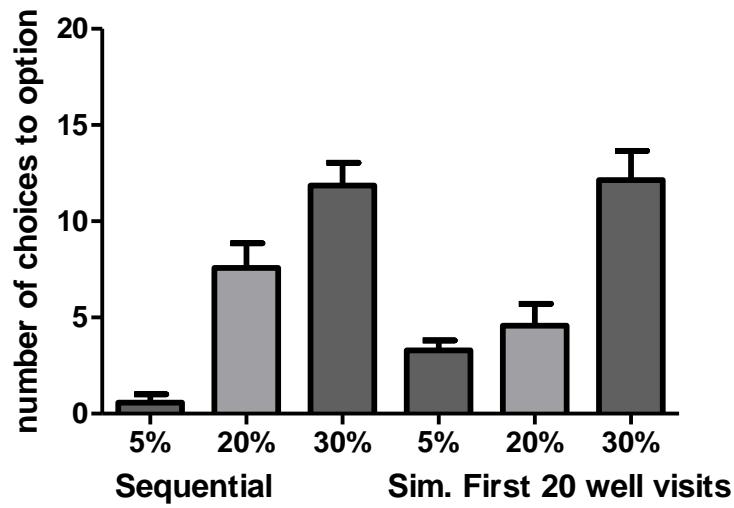


Figure 4. Number of choices which birds made to the 5%, 20% and 30% options. In the Simultaneous Treatment these were the first 29 choices and in the Sequential Treatment this was the final 20 well visits. The data are means  $\pm$  s.e. ( $N = 14$ ).

## Discussion

Manner of presentation appears to have changed the preferences of hummingbirds for the most favourable option; birds preferred 30% option more when options had been presented simultaneously than when they were presented sequentially. A larger preference for the 30% option in the Simultaneous Treatment could be due to a difference in the ability of the birds to compare the options available. Comparing the

options with one another is likely to be easier for birds in the Simultaneous Treatment than for birds in the Sequential Treatment as the options are experienced alongside one another and therefore may explain the larger preference for the 30% option. However, the results are also consistent with prior experience having no discernible impact on the choices of the sequential birds. This could be because either they did not remember the options when presented alone or alternatively they did not use that information when confronted with the options presented simultaneously. To determine whether either of these possibilities could explain the result from Experiment 1 we carried out Experiment 2.

## **Experiment 2**

To determine whether the experience of an option presented alone prior to the presentation of a trinary choice set makes a significant contribution to the changes in preference seen between binary and trinary contexts I conducted Experiment 2. Ie presented birds with one of two treatments consisting of two choice sets each, birds completed both choice sets. In one treatment (No Experience Treatment) birds were presented with two options (either 30 $\mu$ l of 20% and 30% sucrose solution or 30 $\mu$ l of 5% and 20% sucrose solution) followed by a choice of three options (30 $\mu$ l of 5%, 20% and 30% sucrose solution). In the other treatment (Experience Treatment) birds were also presented with a choice of the same two options as in the previous treatment (30 $\mu$ l of 20% and 30% or 5% and 20% sucrose solution) only in this treatment birds experienced the new option (either 30  $\mu$ l of 5% or 30%) prior to the choice of three options.

If birds use prior information about options that are experienced alone to guide their choices when those options are presented together I would expect that birds with prior experience of options would make more choices to preferred options and fewer choices to non-preferred options than birds with no experience. Therefore I expect that if birds use information learned when options are presented alone birds in the Experience Treatment will make more choices to the 30% option when it has been presented alone prior to the trinary choice set than birds in the No Experience Treatment that have not experienced the 30% option alone. I also predict that birds in the Experience Treatment that experience the 5% option prior to the trinary choice set will make fewer choices of this option than birds in the No Experience option that do not have prior experience of the 5% option.

## Materials and Methods

### *Subjects and study site*

The subjects were 11 wild male rufous hummingbirds defending territories in the Westcastle Valley. Eight birds had participated in Experiment 1 and received no further training. The three birds that had not taken part in Experiment 1 were trained in the manner described in Experiment 1. The data were collected from 7:00 to 20:00 hours Mountain Standard Time in June- July in 2011. All work was approved by the University of St Andrews Ethical Committee, conducted according to the requirements of the Canadian Council on Animal Care and was carried out under permits from

Environment Canada and the Alberta Sustainable Resource Development Fish and Wildlife division.

### *Experimental procedure*

The experimental apparatus was as described for Experiment 1. Each bird experienced one of two experimental treatments: the Experience Treatment ( $n = 5$ ) and the No-Experience Treatment ( $n = 6$ ).

### *Experience treatment*

In the Experience Treatment there were two components and birds completed both. In the 5% component birds were presented with a binary choice of 30 $\mu$ l of either 20% or 30% sucrose solution. Birds then had an experience of the 5% option where they had a board containing only the 5% option which they visited for one bout. After the experience of the 5% option birds were presented with a trinary choice of 30 $\mu$ l of 5%, 20% and 30% sucrose solution. In the 30% component birds were presented with a binary choice of 30 $\mu$ l 5% and 20%. Birds then experienced the 30% option alone for one bout before completing a trinary choice of 30 $\mu$ l of 5%, 20% and 30% sucrose solution (Figure 5).

### *No Experience treatment*

In the No Experience Treatment there were also two components and birds completed both. In the No Experience treatment birds also had a binary and a trinary choice set but birds did not experience the new option alone before the trinary choice. In the 5% component birds were presented with a binary choice of 30 $\mu$ l of either 20% or 30% sucrose solution. After this binary choice birds were presented with a trinary choice of 30 $\mu$ l of 5%, 20% and 30% sucrose solution. In the 30% component birds were presented with a binary choice of 30 $\mu$ l of 5% and 20%, followed by a trinary choice of 30 $\mu$ l of 5%, 20% and 30% sucrose solution (Figure 5).

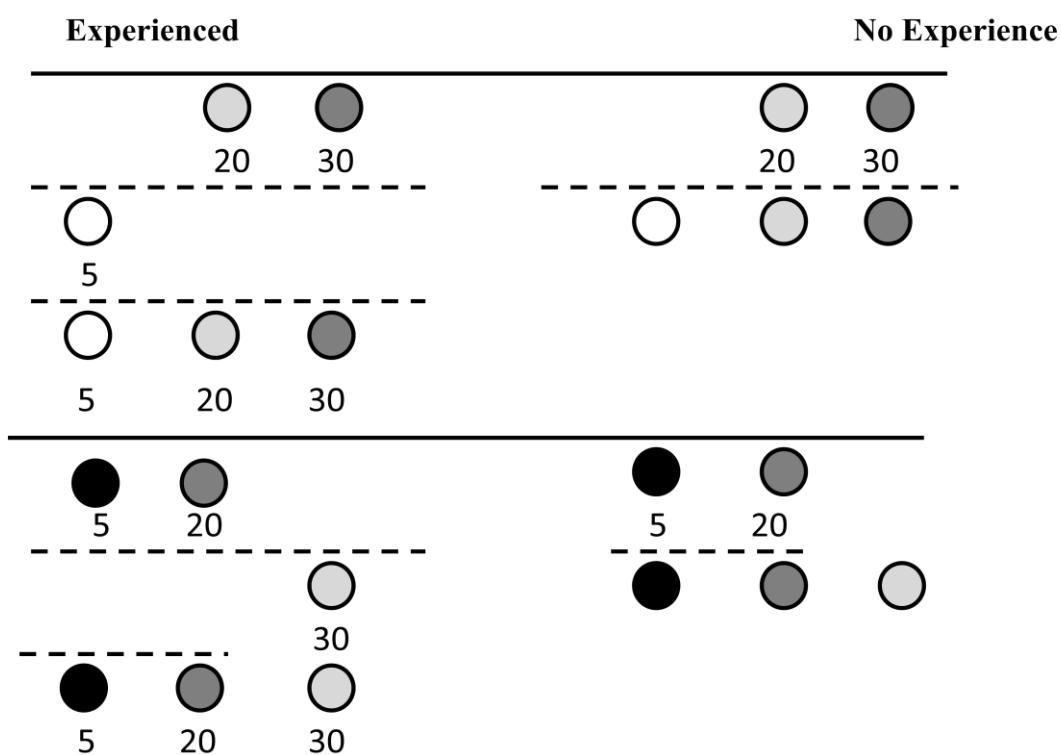


Figure 5. Schematic for Experience and No Experience Treatments. Differently patterned circles represent the different colours surrounding each well type. In both the

Experience and the No Experience Treatments birds had a binary choice followed by a trinary choice. However, birds in the Experience Treatment experienced the new option alone before the trinary choice and birds in the No Experience Treatment did not experience the new option prior to the trinary choice. In both treatments birds experienced both a binary choice of 20% and 30% followed by a trinary of all three options as well as a binary choice of 5% and 20% followed by another trinary choice set.

In both treatments for the binary and trinary choice sets birds made in a total of 20 well visits to the options they wished. The order of presentation of the 5% and 30% components were counter-balanced across birds with birds completing both 5% and 30% components. In binary choice sets half of the wells were randomly assigned to contain each option and in trinary choice sets a third of wells were assigned to contain each of the options. When birds in the Experienced Treatment had an experience of either the 5% or the 30% option all wells were filled with the option. Each option was indicated to the birds by a colour reinforcement placed around the well. After each visit to the board the remaining sucrose was removed, the wells refilled and the board was rotated. The contents of each well were indicated to the bird by a coloured paper reinforcement placed around the well.

### *Statistical Analyses*

All of the data were analysed using IBM SPSS version 19. I looked at the difference in the number of choices birds made to the 30% option in the 30% component between the Experience treatment (where birds had experienced the 30% option alone) and the

No Experience treatment (birds had no experience of the 30% option). I also looked at the number of choices made to the 5% option in the 5% component of the Experienced and No Experience Treatment. The differences in the number of choices birds made to the 5% and 30% options were calculated using an Independent Samples Mann Whitney U test.

## Results

In the 5% component there was no difference in the number of choices birds made to the 5% option in the trinary choice set by birds in the Experienced Treatment (where birds had experience of the 30% option prior to the trinary choice) and No Experience Treatment (where birds had no experience of the 30% option) ( $U = 21.50$ ,  $z = 1.212$ ,  $p = 0.226$ ; Figure 6a).

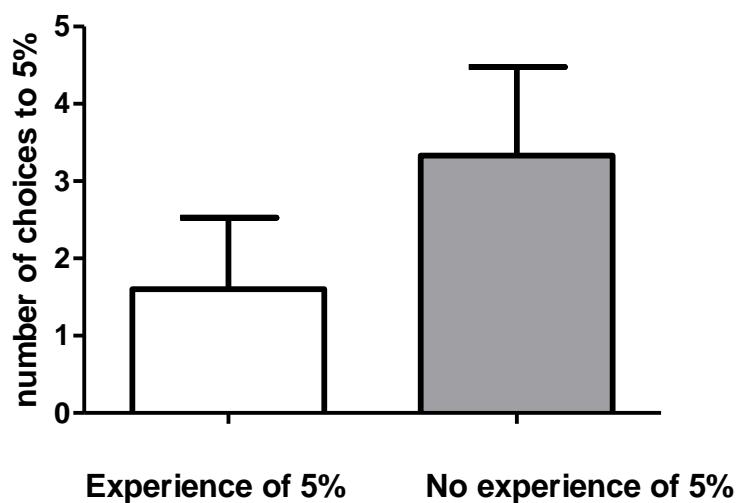


Figure 6(a). Number of choices made by birds to 5%, 20% and 30% options when birds either had prior experience of the 5% option (Experience) or no experience with

the 5% option (No Experience). The data are mean number of choices to each option  $\pm$  s.e. (N=11).

In the trinary choice set of the 30% component, birds in the Experience Treatment did not choose the 30% option differently than birds in the No Experience Treatment ( $U = 6.50$ ,  $z = -1.555$ ,  $p = 0.120$ ; 6b).

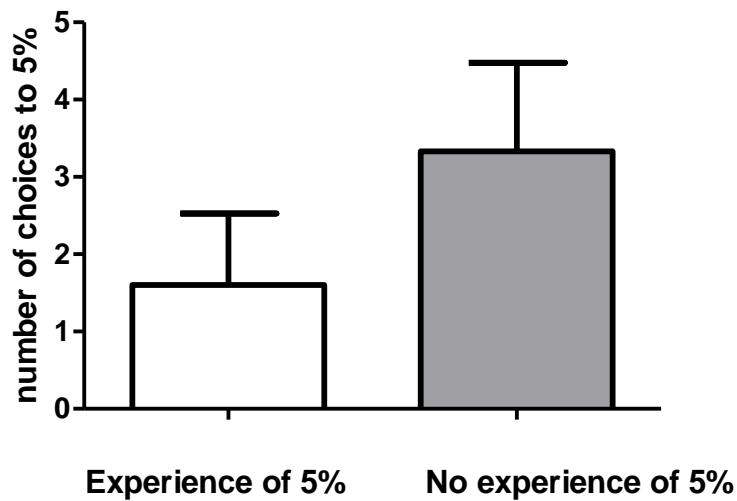


Figure 6(b). Number of choices made by birds to 5%, 20% and 30% options when birds either had prior experience of the 30% option (Experienced) or no experience with the 30% option (No Experience). The data are mean number of choices to each option  $\pm$  s.e. (N=11).

## Discussion

It appears that prior experience of an option presented alone had no major effect on the decisions made by hummingbirds. Birds with experience of the non-preferred 5% option did not make fewer choices to this option than birds in the No Experience

Treatment. Similarly, birds in the Experience Treatment did not make more choices to the preferred 30% option after they had experienced this option alone than birds in the No Experience Treatment that had not had experience of this option alone.

It seems that when an option is presented alone birds do not remember or use this information to inform their future choices when the options are later presented simultaneously. However, although not significant, when birds had experience of the options they made fewer choices to the 5% option and more choices to the 30% option than birds in the No Experience Treatment. It could be that there is an effect but we did not see it for one of three reasons: (1) the sample size was too small; (2) prior experimental experience for many of the birds tested in Experiment 2 increased the variation in response; (3) the effect with regard to 5% is difficult to show because the birds learn this option very quickly.

## General Discussion

In Experiment 1 hummingbirds made more choices to the sweeter option (30% sucrose) when the options were presented simultaneously than when birds experienced options sequentially. In the Sequential Treatment the order in which the boards of single options only were presented did not affect the choices made to the 30% option in the trinary choice. Birds that had learned about options sequentially made fewer choices to the poor 5% option than naïve birds. However, there was no difference in the choices made to the 30% option by naïve birds and the choices made by birds that had experienced the options sequentially. In Experiment 2, hummingbirds with

experience of either a poor option or a preferred option presented alone prior to a choice set did not make different choices than birds with no experience.

Presenting the three options together as in the Simultaneous Treatments appears to have led to an exacerbated preference for 30% and an enhanced avoidance of 5%. This effect can already be seen by the first 20 experiences of the 30% option in the Simultaneous Treatment. In effect these birds have learned very rapidly which options are best and which are poorest. For the simultaneous birds in spite of having experienced the best and the poorest options it appears that this does not aid them in determining which is the best option when all three are presented together although it might aid them in avoiding the poorest option.

The avoidance of 5% in the trinary of the sequential treatment suggests that birds have not forgotten about the options, which they learned alone. The data from Experiment 2 however suggest that it is not easy to demonstrate that animals have not forgotten information learned previously. There is a methodological corollary to this point in that in the past birds that did not visit one of the options early in the experiment were forced to experience the option presented alone. As it is now not clear what impact this would have on the birds' future choices perhaps this practice should be discontinued. Those birds that do not visit the choice presented early in the experiment should be excluded from the experiment.

As with human experiments the mode of presentation makes a difference. However, there is no clear pattern in the human data to the way in which mode of presentation impacts on context dependent choice. Our data would suggest that experiments in which options are presented simultaneously may be more likely to

result in more striking differences in the preferences for the available options. This could mean for example that peahens experiencing multiple males simultaneously have stronger preferences for some males than do bower bird females experiencing males sequentially. Alternatively this could mean that testing mate preferences should be done using the mode of presenting mate options that is consistent with the mode in which those animals experience those options in the wild. Given that most non-lekking species will encounter possible mates sequentially, examining mate preferences in those species in the lab simultaneously might lead to exaggerated preferences. The data presented here might suggest that experiments which present options simultaneously may over emphasise the value of one trait over another. This possibility requires experimental testing. It seems unlikely that this would best be done with peahens or bowers birds.

**Chapter 6: Context effects the assessment of health in human faces****Introduction**

When making decisions, we expect that individuals should consistently choose options that confer the largest benefit (Edwards, 1961, Simon, 1959, Schoemaker, 1982, Rieskamp et al., 2006). Since the benefits conveyed to the individual when choosing a particular option are independent of the benefits of choosing an alternative option, an individual's selection of that option should also be independent of the presence of inferior options ((Rieskamp et al., 2006). However, contrary to this prediction the choices made by both humans and animals do appear to be influenced by the presence of inferior options (Bateson, 2002, Bateson et al., 2003b, Edwards and Pratt, 2009, Hurly and Oseen, 1999, Shafir et al., 2002, Tversky and Simonson, 1993, Wedell, 1991, Huber et al., 1982). In humans, when inferior options are added to choice sets containing options that vary in multiple attributes, people increase the proportion of choices they make for the option that is similar to the inferior option but better than it in at least one dimension (Doyle et al., 1999, Bateman et al., 2008). Even when the options vary only in a single dimension the choices made by both humans and animals can be changed by the addition of poorer options (Hurly and Oseen, 1999, Morgan et al., 2012, Wedell et al., 1987).

In humans, there is a considerable literature on the facial features used to choose among possible partners, or at least, that are considered most attractive. How attractive possible partners are can also be changed by the context in which those options occur. For example, after seeing an attractive female, males are more likely to rate subsequent average females as less attractive (Kenrick and Gutierres, 1980).

However, it is not clear what decision-making mechanisms underpin the evaluation of the faces as the focus is usually on which of the facial features are used (Geiselman et al., 1984, Kenrick and Gutierres, 1980, Melamed and Moss, 1975, Wanke et al., 2001).

Here we set out to test one suggested mechanism for the context-dependent effects, which is the compromise effect. The compromise effect is an increase in preference for an option that lies between two extreme options, which has been widely reported when consumers choose among products (Dhar et al., 2000, Simonson, 1989, Simonson and Tversky, 1992). To determine whether the addition of a poor option to a choice set of two options can cause changes in the preferred choice via the compromise effect, we exploited the finding that the degree of yellow in the skin influences how healthy and attractive the face appears: a moderate increase in the yellowness of faces is seen as more attractive than are either very yellow faces or faces with much less yellow (Stephen et al., 2011, Stephen et al., 2009, Whitehead et al., 2012). Participants were presented with pairs or trios of faces that varied in the degree of yellow in the faces. The pairs of faces both had relatively healthy levels of facial yellow but the trios consisted of two relatively healthy faces accompanied by a third face that was coloured yellow to a degree considered much less healthy (Stephen et al., 2009). If participants' perception of a face's health is context dependent, the addition of either of the inferior options (Yellow 2- or Yellow 2+) should alter the perceived health of the moderately yellow faces (Yellow – and Yellow +). If the compromise effect underpins this alteration in preference, participants should prefer the option that is the intermediate of the three options. This would mean that the addition of a very yellow option (Yellow 2+) should increase participants' preference for the slightly

more yellow faces (Yellow +) while the inclusion of the much less yellow option (Yellow 2-) should increase the preference for the slightly less yellow option (Yellow-).

## Methods

### *Participants*

31 undergraduate students at the University of St Andrews volunteered to take part in an experiment investigating the effect of skin-colour changes on the perception of health. 24 of the participants identified themselves as Caucasian and 7 did not give their ethnicity. 17 participants identified themselves as male, 12 identified as female and 2 participants did not give their gender. The experiment took place in a small white room containing only a computer between 9am-5pm. Participants were alone when they completed the experiment, which took roughly an hour. Participants were made aware that they could withdraw from the experiment at any time without explanation. Ethical approval was obtained from the University of St Andrews Teaching and Research Ethics Committee, and prior to the experiment we obtained informed written consent from all participants. Participants first completed a questionnaire identifying their sex, country of residence, ethnic origin and sexual preference (for questionnaire see appendix).

### *Image creation*

The faces we used in the experiment were of 29 Caucasian females without makeup and with neutral expressions. The photographs were taken using a Fujifilm FinePix S5Pro digital SLR camera (60mm fixed length lens) in a booth painted with

achromatic matt grey paint. For these images illumination was from three 6504K bulbs (VeriVide, Ltd). The camera was white-balanced according to a GrectagMacbeth white balance card in these lighting conditions. Participants held a grey painted board over their shoulders to prevent reflections from clothing. A GrectagMacbeth Mini ColorChecker was included in each image to color-calibrate images. Images were color-corrected by transforming observed values of each of the 24 color-checker patches towards known values of these same patches using a least-squares transform from an 11-expression polynomial expansion (Stephen et al., 2009, Stephen et al., 2011, Whitehead et al., 2012). Matlab was used to calculate mean colour values across skin pixels for each face image and these colour values defined the starting colour for each face. The colour of the faces was then adjusted by using Matlab to produce masks of colour, these masks were used to increase or decrease the yellowness of the faces. The masks applied were Gaussian blurred at the edges of the face ( $SD \pm 3$  pixels), to prevent final images having an obvious color border. The mask changed the colour of the face including lips and ears but the eyes, hair and background were unchanged. Four versions of each face were created which varied in the Yellowness only. The least yellow shade was the Yellow2- shade; and the yellowness of this shade was reduced by 2.666 units. The Yellow- shade had the yellowness increased by 2.666 and in the Yellow+ shade the yellowness was increased by 7.999 units of yellowness. For Shade Yellow2- the yellowness of each face was increased by 13.333 units (Figure 1). Images were presented to the participants on a 19 inch Iiyama Vision Master 1451 monitor. Each image was 6cm by 8cm and presented on a black background. The images were numbered from left to right so that participants could identify each image. The positions of the images on the screen were randomized.

Figure 1.



Figure 1. An example face set showing one face in all of the four shades of yellow: Yellow2-, Yellow-, Yellow+, Yellow2+.

#### *Experimental Procedure*

The experiment was conducted in a windowless testing room ( $\approx 2\text{m} \times 3\text{m}$ ) with an office desk, a chair and the computer used to run the experiment. Participants were tested singly. On arrival each participant completed a consent form and the experimental procedure was described to them. Once a participant had agreed that they understood the procedure the experimenter left the room. The computer screen showed the questionnaire concerning the participant's details. Once the participant had completed the on screen questionnaire, the following screen informed them which of two treatments was about to follow (Sequential or Simultaneous). The participants were presented with pairs or trios of faces and asked to choose the face they considered to be healthiest from each set. In each pair (binary) or trio (trinary set) the images were of the same face, each differing only in the yellowness of the face. Binary choice sets consisted of a choice between the faces that were Yellow - and Yellow +, both of which are considered to be relatively healthy. Trinary choice sets

consisted of a Yellow – face, a Yellow + face and either a Yellow 2+ face or a Yellow 2- face. After each choice set participants were asked to identify the healthiest face and its relative health on a ten-point scale ranging from very healthy to very unhealthy. The ten point scale was presented as a horizontal line with unnumbered checks across the middle of the screen. The left hand end of the line was labeled “very unhealthy” and the right hand end was labeled “very healthy”. Using the mouse the participants clicked at the point along the line they considered to represent the “health” of the healthiest face. Then they confirmed the end of the trial by clicking ok and the next set of faces was presented.

As the order of presentation can influence choices, for half of the trials the faces were presented simultaneously, and in half the trials, the faces were presented sequentially (Damisch et al., 2006, Dato-on and Dahlstrom, 2003, Geiselman et al., 1984, Jordan and Uhlarik, 1985, Wanke et al., 2001, Wedell et al., 1987). In the Sequential Condition the faces were presented one after another before participants were asked to choose a face whereas in the Simultaneous Condition all of the faces were presented on the screen at the same time. For both the Simultaneous and Sequential Conditions there were three choice sets for each face (one binary and two trinary, comprising of all of the four versions of the face). The order of the choice sets was pseudo-randomized so that choice sets using the same face did not occur adjacent to one another.

In both the Sequential and the Simultaneous Conditions the images were presented for a total of five seconds of exposure per image. This meant that in the binary choice set in the Simultaneous condition the two images were presented simultaneously for ten seconds and in trinary choice condition the three images were

presented simultaneously for fifteen seconds. In the Sequential Condition, the first image was presented for five seconds, followed by blank screen for two seconds before the presentation of the second image (followed by a further two seconds of blank screen and then the third image for the trinary condition). In the Sequential Condition the images were presented on the same position on screen as they were presented in the Simultaneous Condition and the faces were numbered left to right to allow participants to identify the face which looked healthiest.

Each participant completed 90 trials in each of the Sequential and the Simultaneous Conditions and the order of conditions was pseudo randomized across the participants. After 180 trials, which took 50-60 minutes, the screen instructed the participants to inform the experimenter that they had finished the experiment.

### *Analysis*

I analysed participants' decisions about the face they thought looked the healthiest by examining the choices to Yellow+ faces divided by the sum of choices to Yellow+ and Yellow-. As the proportional data were not normally distributed, they were transformed prior to analysis using an arcsine square root transformation. I compared preference across the conditions using repeated-measures ANOVAs and if the data violated the assumption of sphericity then they were corrected using a Greenhouse-Geisser correction.

## Results

In the binary choice when options were presented simultaneously participants preferred the Yellow + option ( $t(30) = 2.035, p = 0.051$ ). When faces of Yellow + and Yellow – were presented simultaneously with faces of Yellow 2+, participants chose the Yellow + as the healthiest face more frequently than when Yellow + faces were presented only with Yellow – faces set ( $F(1.451, 43.535) = 49.343, p < 0.001$ ; Figure 2a). When faces of Yellow + and Yellow – were presented simultaneously with faces of Yellow 2-, however, participants chose the Yellow - as the healthiest more frequently than when Yellow + faces were presented only with Yellow – faces ( $F(1.451, 43.535) = 49.343, p < 0.001$ ). For changes in preference shown by individual participants when options were presented simultaneously see Appendix Table 1.

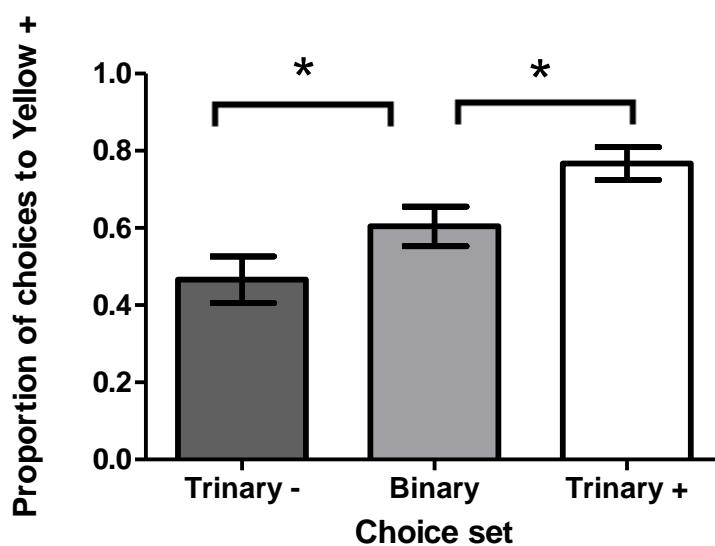


Figure 2a. The proportion of choices participants made in the Simultaneous Condition to the Yellow Plus shade when options were presented simultaneously in binary and trinary choice sets. Binary indicates participants had a choice between Yellow and Yellow plus shades. The Trinary Minus choice was between shade Yellow Minus,

Yellow and Yellow Plus. The Trinary Plus comprised a choice between Yellow, Yellow Plus and Yellow Two Plus. The asterisk indicates significance at  $p \leq 0.05$ . The data are means  $\pm$  s.e. ( $N = 31$ ).

When images were presented sequentially, in the binary choice participants also preferred the Yellow + face ( $t(30) = 4.336, p < 0.001$ ). We saw the same pattern of results in the Sequential Treatment: the addition of Yellow 2+ to the choice set of Yellow – and Yellow + led to an increased choice of Yellow + faces as the healthiest while the addition of Yellow 2- led to an increased choice of Yellow – faces as the healthiest (addition of Yellow 2+:  $F(1.539, 46.181) = 44.054, p < 0.001$ ); addition of Yellow 2-:  $F(1.539, 46.181) = 44.054, p < 0.001$ ; Figure 2b). For changes in preference shown by individual participants when options were presented sequentially see Appendix Table 2.

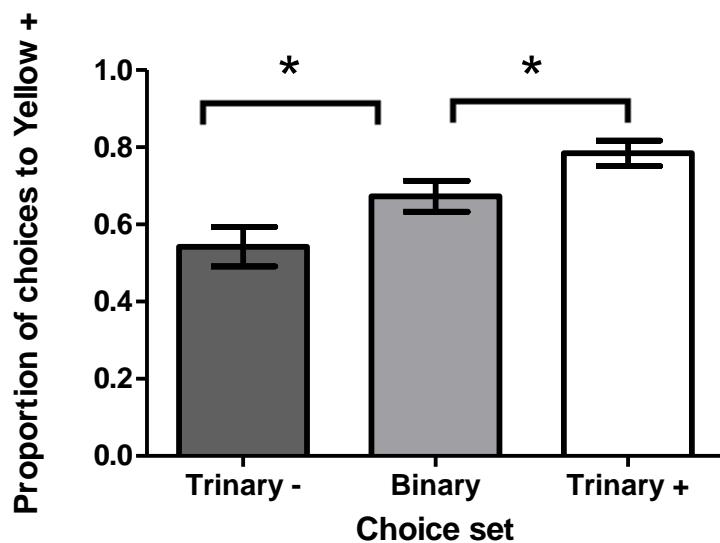


Figure 2b. The proportion of choices participants made in the Sequential Condition to the Yellow Plus shade when options were presented simultaneously in binary and trinary choice sets. Binary indicates participants had a choice between Yellow and Yellow plus shades. The Trinary Minus choice was between shade Yellow Minus, Yellow and Yellow Plus. The Trinary Plus comprised a choice between Yellow, Yellow Plus and Yellow Two Plus. The asterisk indicates significance at  $p \leq 0.05$ . The data are means  $\pm$  s.e. ( $N = 31$ ).

When the images were presented sequentially, participants choose the Yellow+ faces as the healthiest more frequently than they did when the options were presented simultaneously ( $t(30) -2.035$ ,  $p = 0.051$ ). There was a similar effect when Yellow 2- was added to the choice set of Yellow + and Yellow – conditions: participants in the Sequential Treatment decided that the Yellow - faces were more healthy than when images were presented simultaneously ( $t(30) -2.269$ ,  $p = 0.031$ ). However, the addition of Yellow 2+ to the choice set of Yellow + and Yellow – in the Sequential Condition did not differ from its impact in the Simultaneous Condition ( $t(30) = -0.352$ ,  $p = 0.727$ ).

The gender of the participants did not affect the proportion of choices made to the Yellow+ in any of the contexts ( $F(1, 27) = 0.005, p = 0.946$ ). See Appendix for choices made by individuals in each choice set.

## Discussion

When participants were asked to rate health among trios of faces that varied in their yellowness, they tended to choose the face with the intermediate degree of yellow. The addition of a much yellower face to a choice set of two relatively healthy faces increased the choice of the yellower of the two healthy faces while the addition of a much less yellow face decreased the choice of the yellower of the two healthy faces. When faces were presented sequentially participants chose the Yellow + faces as the healthiest more frequently than did participants when presented with faces simultaneously. However, the pattern of changes in preference upon the addition of the decoys did not differ depending on the mode of presentation.

The change in participants' choice of healthy faces is the outcome that would be expected from the compromise effect. When three options are available the choice is expected to be directed to the middle option. To determine whether the "middle" is the average or any option between the two extremes requires testing with multiple intermediate options. However, tests using multiple intermediate options are not straight forward because there is debate as to whether the discriminability of options might change based on the position or density of the options added (Krumhansl, 1978, Parducci, 1965). An alternative explanation for the results is that exposure to faces biases the perception of novel faces. Faces similar to the faces previously presented are viewed as more typical than they would otherwise be rated (Little et al., 2011).

However, experiments which show adaptation to extreme facial features frequently only present in the extreme faces prior to the choice (Leopold et al., 2001, Leopold et al., 2005, Rhodes et al., 2001, Webster et al., 2004, Webster and MacLin, 1999) rather than at the time as is the case with this experiment. Therefore it seems unlikely that this would explain the results. It is also plausible that participants were not assessing the health of the faces, but would have chosen the middle option even if we had asked another question. There would be two ways to exclude this possibility, either participants could be given the same set of faces and asked to rate some other feature unrelated to health or participants could be presented with faces which are much less yellow and so seen as unhealthy. In these cases we would expect that participants would all choose the yellowest faces every time which would demonstrate that participants were assessing the health of the faces rather than simply choosing the intermediate option.

Although the compromise effect is commonly seen in consumer research (Dhar et al., 2000, Simonson, 1989, Simonson and Tversky, 1992), this is, to my knowledge the first demonstration that the compromise effect may also impact on decisions regarding perception of human health. The data show that the face that is considered the healthiest depends on the range of faces presented: extending the range of options towards more yellow in the face led to participants choosing the slightly more yellow face as the healthiest. However, those same participants deemed the slightly less yellow face to be the healthiest when the range of faces to choose among was extended to include much less yellow faces. Participants were not then able to decide which the healthiest face was. This may mean that the quest for determining the healthiest or most attractive face is unlikely to lead to a single value.

It seems plausible that other context dependent effects might impact on decisions as to which is the healthiest or most attractive option. For example in this experiment presenting faces sequentially rather than simultaneously apparently led to more participants considering the slightly yellower face to be healthier than the slightly less yellow face. Although this might suggest that prior experience might play some role in decision making the time scale over which that experience might have an impact is not clear.

More generally these data suggest that the interpretation of data from experiments in which animals are required to choose between two options only may also not represent absolute preferences.

## **Chapter 7: Context does not change the assessment of health in human faces**

### **Introduction**

The judgements that people make about the health and attractiveness of others are not independent of the context in which the options are placed. Rather, those judgements (often based on images of faces) are influenced by the presence of other options, including inferior options (Kenrick and Gutierres, 1980, Kenrick et al., 1989, Melamed and Moss, 1975). The most frequent of these effects is that faces or bodies of average attractiveness are judged as more attractive when presented alongside images of less attractive people and are judged as less attractive when presented together with images of very attractive people (Kenrick and Gutierres, 1980, Kenrick et al., 1989, Melamed and Moss, 1975). The effect of context on attractiveness assessments can even be demonstrated when the figures or faces are represented schematically e.g. as line drawings (Wedell and Pettibone, 1999, Wedell et al., 2005).

Determining the mechanism(s) that underpins these context effects is somewhat difficult as to date, the range of faces from which choice sets are drawn are usually sets of manipulated faces, in which only one feature of interest is manipulated. However, when most attributes of a face are manipulated, that manipulation usually impacts on the assessment of other features. For example, changing the distance separating the eyes will lead to changes in the relative distance of the eyes to all other points on the face (Wedell and Pettibone 1999). In this experiment, therefore, we attempted to examine whether context-dependent effects occur in assessments of health when only a single feature is manipulated, by using faces in which variation occurred only in the colour of the face. We manipulated the degree of yellow in the

faces because even a moderate increase in yellowness increases the perceived health of a face (Stephen et al., 2011, Stephen et al., 2009, Whitehead et al., 2012). This may be because yellowness of the skin increases with dietary consumption of carotenoids (Whitehead et al., 2012), which are antioxidants that may offer protection from free radicals (Alaluf et al., 2002, Sies, 1997). Facial yellowness also decreases with at least some illnesses (Darvin et al., 2008).

In Chapter 3, hummingbirds' choices of two favourable options were differently affected by two poorer options: the inclusion of the better of the poor options did not change the choices made by birds while the inclusion of the poorest option led to a decreased proportion of choices for the best option. In this experiment, the aim was to determine whether a similar effect could be demonstrated when human participants were assessing the health of faces. Participants were presented with choice sets of either two or three faces (variations of the same face), which varied only in their yellowness and asked to judge which face looked the healthiest. As in Chapter 3 with hummingbirds, in binary choice sets participants were presented with two faces that were both moderately yellow, but one a little more yellow (Yellow +) and one a little less yellow (Yellow -). In this experiment, however, one trinary choice set consisted of a Yellow + face, a Yellow - face, and a face that was a little less Yellow (Yellow 2-) while in the other trinary, the choice was among Yellow + face, a Yellow - face, and a face that was even less Yellow (Yellow 3-).

If humans respond to the presence of the poor options in a choice set in the way that the hummingbirds did, we expected the addition of the slightly less healthy option (option Yellow 2-) to slightly increase the choice of Yellow + as being the healthiest

face while we expected the addition of the much less healthy option would increase the perceived health of the Yellow - option.

## Methods

### Participants

19 students at the University of St Andrews volunteered to take part in an experiment investigating the effect of skin-colour changes on the perception of health. 11 of the participants identified themselves as Caucasian, two identified as Latin American and six did not give their ethnicity. Six participants identified themselves as male, twelve identified as female and one participant did not give their gender. The experiment took place between 9am-5pm in a small testing room with plain white walls containing a desk, chair and a computer. Once the experimenter had explained what the participants were required to do, the experiment left the room for the participants to complete the experiment, which took roughly an hour to complete.

I obtained ethical approval from the University of St Andrews Teaching and Research Ethics Committee, and prior to the experiment we obtained informed written consent from all participants. Participants were made aware that they could withdraw from the experiment at any time without explanation. Before they began the experiment, they completed a questionnaire identifying their sex, country of residence, ethnic origin and sexual preference (for questionnaire see appendix). Although preference for yellowness has been shown cross culturally, a preference for yellower faces is stronger in same ethnicity faces (Stephen et al., 2012), I asked participants to identify their ethnicity so that we could assess whether this played any role in the participants' preferences.

### *Image creation*

The faces we used in the experiment were of 29 Caucasian females without makeup and with neutral expressions. The photographs were taken using a Fujifilm FinePix S5Pro digital SLR camera (60mm fixed length lens) in a booth painted with achromatic matt grey paint. For these images illumination was from three 6504K bulbs (VeriVide, Ltd). The camera was white-balanced according to a GrettagMacbeth white balance card in these lighting conditions. Participants held a grey painted board over their shoulders to prevent reflections from clothing. A GrettagMacbeth Mini ColorChecker was included in each image to color-calibrate images. Images were color-corrected by transforming observed values of each of the 24 color-checker patches towards known values of these same patches using a least-squares transform from an 11-expression polynomial expansion (Stephen et al., 2009, Stephen et al., 2011, Whitehead et al., 2012). Matlab was used to calculate mean colour values across skin pixels for each face image and these colour values defined the starting colour for each face. The colour of each of the faces was adjusted by applying a mask of colour over the face which either increased or decreased the yellowness of the faces. The masks applied were Gaussian blurred at the edges of the face ( $SD \pm 3$  pixels), to prevent final images having an obvious color border. The mask changed the colour of the face including lips and ears but the eyes, hair and background were unchanged. Four versions of each face were created which varied in the Yellowness only. The least yellow shade was the Yellow 3- shade the yellowness of this shade was reduced by 10.666 units. The Yellow 2- shade had the yellowness decreased by 5.333 units and in the Yellow - shade the yellowness was decreased by 2.666 units of yellowness. For Shade Yellow + the yellowness of each face was increased by 2.666 units (Figure 1)

this shade appeared in the experiment in Chapter 6 and was the Yellow Minus shade in that experiment. Images were presented to the participants on a 19 inch Iiyama Vision Master 1451 monitor. Each image was 6cm by 8cm and presented on a black background. The images were numbered from left to right so that participants could identify each image. The positions of the images on the screen were randomized.



Figure 1. An example face set showing one face in all of the four shades of yellow: Yellow 3-, Yellow 2-, Yellow -, Yellow +.

### *Experimental Procedure*

The participants were presented with pairs or trios of faces and were asked to choose the face they considered to be healthiest. There were either two or three faces in each set and all of the options were presented on the screen at the same time. In each binary or trinary set the images were of the same face, each differing only in the yellowness of the face. Binary choice sets consisted of a choice between the faces that were Yellow - and Yellow +. Trinary choice sets consisted of a Yellow – face, a Yellow + face and either a Yellow 2- face or a Yellow 3- face. After each choice set participants were asked to identify which face they thought looked the healthiest and to rate that health on a 10-point scale, ranging from very healthy to very unhealthy.

Each participant made health assessments of faces in the three contexts: one binary and two trinary, comprising all of the four versions of the face. In binary choices the images were on the screen for ten seconds and in trinary choices the images were on the screen for 15 seconds. The images were numbered left to right to allow participants to identify the face which looked healthiest. Each participant completed 90 trials.

### *Analysis*

To assess the effects of context, we looked at the choices made to the two options that were present in every choice set (Yellow- and Yellow+).

As the data were not normally distributed, they were transformed prior to analysis using an arcsine square root transformation. Differences in the proportion of choices made to the Yellow + option in the different choice sets and different in the rating of the options was calculated using repeated measures ANOVAs. All results were Bonferroni corrected.

### **Results**

Participants did not change their health assessment of the Yellow + face as a result of the addition of either the Yellow 2- option ( $F(2, 18) = 3.052, p = 0.107$ ) or the Yellow 3- option ( $F(2, 18) = 3.052, p > 0.999$ ). The proportion of choices to the Yellow + faces as the healthiest was not different between the two trinary conditions ( $F(2, 18) = 3.052, p = 0.243$ ; Fig 2).

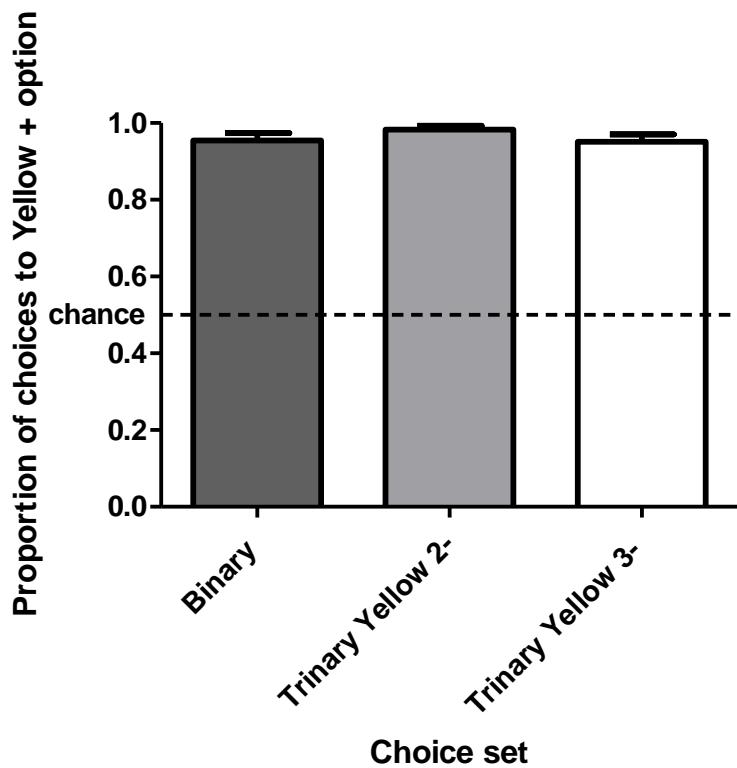


Figure 2. The proportion of choices participants made to the Yellow+ shade when options were presented in binary and trinary choice sets. Binary choice sets contained Yellow+ and Yellow- faces, one trinary set contained Yellow+, Yellow- and Yellow2- and the other trinary set contained Yellow+, Yellow- and Yellow 3-. The dotted line represents no difference in preference between Yellow+ and Yellow-. The data are means  $\pm$  s.e. ( $N = 19$ ).

Participants also rated how healthy they thought the face that they had chosen looked on a scale of 1-10. Participants' rating of the Yellow + option did not change as a result of the inclusion of the Yellow 2- option ( $F(2, 18) = 1.616, p = 0.347$ ) or of the Yellow 3- to the choice sets ( $F(2, 18) = 1.616, p = 0.648$ ). The rating of the Yellow + option was also not different between the two trinary choice sets ( $F(2, 18) = 1.616, p > .999$ ; Figure 3).

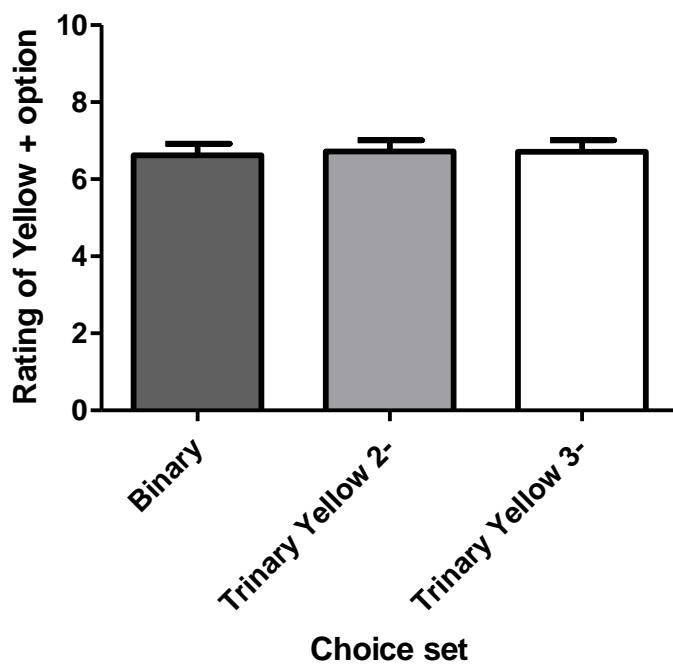


Figure 3. The average rating of the Yellow+ faces when options were presented in binary and trinary choice sets. Binary choice sets contained Yellow+ and Yellow- faces, one trinary set contained Yellow+, Yellow- and Yellow2- and the other trinary set contained Yellow+, Yellow- and Yellow 3-. The data are means  $\pm$  s.e. ( $N = 19$ ).

Participants chose the Yellow + option as the healthiest more often than they chose the Yellow - option in all of the choice sets (binary: ( $M = 0.95$ ,  $SE = 0.019$ )  $T (18) = 23.669$ ,  $p < 0.001$ , Trinary Yellow 2-: ( $M = 0.98$ ,  $SE = 0.019$ )  $T (18) = 48.895$ ,  $p < 0.001$ , Trinary Yellow 3-: ( $M = 0.95$ ,  $SE = 0.019$ )  $T (18) = 23.423$ ,  $p < 0.001$ ).

## Discussion

The addition of less healthy faces to choice sets of two moderately healthy faces did not change the assessments of health for those healthy faces. In all of the contexts, participants overwhelmingly assessed the Yellow + faces as being healthier

than the Yellow – faces.

It would appear that humans do not necessarily respond to the presence of poorer options in choice sets in the way that hummingbirds do. It is possible that the rating of the health of faces, or using the degree of yellow in that face to do so, is not context dependent. However, the data from the experiment in Chapter 6, as well as from experiments on other aspects of attractiveness, demonstrate that the preference for particular faces and bodies is, usually, influenced by the presence of other options (Wedell et al., 1987, Wedell and Pettibone, 1999, Wedell et al., 2005).

Rather, it seems possible that the lack of effect of the inclusion of the less healthy faces was due to the rating by the participants of the healthy faces. Unlike the participants in the earlier experiment where the options were much yellower, here the participants almost exclusively chose the Yellow + face as the most healthy. Much of the theory underpinning context-dependence is based on the assumption that effects will only be seen when preferences are incomplete i.e. when one option is not obviously better and strongly preferred over all others (Gerasímou, 2010) (Bateman et al., 2008, Colman et al., 2007, Dato-on and Dahlstrom, 2003, De Martino et al., 2006, Doyle et al., 1999, Huber et al., 1982), it is perhaps not surprising that the inclusion of the less healthy faces did not cause participants to change their assessments. However, the almost exclusive selection of the yellowest face as the healthiest face does confirm that in Chapter 6 participants were assessing the health of the faces available rather than simply choosing the intermediate option. If participants were just choosing the intermediate option for reasons other than the assessment of health then participants would have also chosen the intermediate face in this experiment. As they did not and instead overwhelmingly chose the yellowest shades we can be confident that

participants in Chapter 6 were assessing the health of the faces.

At this point, then, it is difficult, to assess whether the variation in the decoy options would exert a similar effect on health assessments as seen in the hummingbirds experiment (Chapter 3). This needs to be examined in an experiment where participants rate the two options in the binary context more similarly.

## Chapter 8: General discussion

In this thesis, I set out to determine whether context affects the choices that hummingbirds make when foraging. In addition, as human experiments are often used to make predictions about how context might change the choices made by animals, I wanted to determine how similar the effects of context on hummingbird decision making are to the effects of context on decision making by humans.

Initially I varied the options provided to hummingbirds in two dimensions, volume and concentration of sucrose solution. As is consistent with previous work on hummingbirds (Bateson et al., 2002, Bateson et al., 2003), in Chapter 2 hummingbirds changed their preferences when inferior options were added to choices sets. The explanations I predicted prior to the experiment were that birds could change their choices due to changes in energy state (Schuck-Paim et al., 2004) or that birds may show the decoy effect (Bateson et al., 2002, Bateson et al., 2003, Doyle et al., 1999). However, the choices made by birds were inconsistent with one another and were not consistent with either of these hypotheses. There are several possible explanations for these inconsistent preferences. The first is that the changes which birds showed were mistakes rather than departures from economic rationality. The second is that birds may have been attending to different cues, therefore when inferior options were added some birds changed their preference in one direction and other individuals showed a different change in preference. If this were the case I would expect that birds would show consistent context-dependent preferences when options varied in a single dimension as birds could only attend to a single cue. To test this I conducted the experiment in Chapter 3, where I looked at the effect of the addition of

inferior options to a choice sets when options were varied in a single dimension. The addition of much poorer options to choices sets changed birds' preferences with all birds reducing their preference for their preferred option. As the manipulation of options which varied in a single dimension produced preference changes where all birds were consistent with one another, in subsequent experiments I continued to use options which varied in a single dimension only.

In human decision-making presentation context makes a difference to the choices which people make, so to see if presentation also changes the decisions animals make in Chapter 4 I presented hummingbirds with options either simultaneously or sequentially. When options were presented simultaneously birds chose preferred options more frequently and made fewer choices to non-preferred options than when the options were presented sequentially. In both human and animal decision making prior experience of options can change the choices made to those options in future choices (Simonson and Tversky, 1992, Waite, 2001b), in Chapter 5 I manipulated the amount of prior experience a hummingbird had of the options by either matching the colours of options to those already learned or not matching the colours. The choices made by hummingbirds were only temporarily altered by the prior experience of the options, which suggests that having prior experience of options does not have a lasting impact on the decisions made by hummingbirds. As the rufous hummingbird migrates long distances and the availability and species of flower varies considerably over the breeding season, it is perhaps not surprising that the birds are not influenced by options they have previously experienced. As they live in seasonal environments so the options experienced in the recent past may not be a good indicator of future foraging options.

In addition to experiments with hummingbirds I also tried to create analogous experiments with humans to compare the choices made by humans and hummingbirds. In Chapter 6 I offered participants choices of faces which varied in their yellowness. I found that the perception of health in faces could be altered by the addition of non-preferred options to the choice, as is the case in animals. As the preference for the yellowness of faces was context dependent, in Chapter 7 I designed an experiment with humans using the yellowness of faces which replicated the hummingbird experiment in Chapter 3. In Chapter 7 participants had an overwhelming preference for one of the options. They did not change their preference for this option when non preferred options were added to the choice sets. As a result of the overwhelming preference of the participants for the yellowest face I was not able to compare the results of this experiment with those of Chapter 3.

One of the aims of this thesis was to determine how similar the effects of context are on the choices made by animals and humans. The reason I wanted to look at this is that many of the experiments looking at context-dependent choice are inspired by behavioural economics experiments, for example, many experiments with animals create asymmetrically dominating decoys and make the prediction that when a decoy is added animals (like humans) will increase their preference for the option that is most similar to the decoy (Bateson et al., 2002, Bateson et al., 2003, Latty and Beekman, 2011, Royle et al., 2008, Shafir et al., 2002). The changes in preference that occur in these experiments are not always in the predicted direction which suggests that there may be a different process underlying the changes in preference in humans and animals (Bateson et al., 2002, Royle et al., 2008). If the process underlying the changes in preference in human and animal decision-making is very different then

continued experiments which use the same paradigms as those in the human literature might not be the best course of study and instead we should build new theories focusing only on animal data.

One of the reasons why it is not clear whether the processes underlying the choices made by humans and animals are similar is that the experiments with humans are difficult to replicate with animals. Human participants are typically told about the options whereas animals have to assess the options themselves. In order to design comparable experiments in humans and animals I designed experiments with humans which replicated some of the main features of experiments with animals. In chapter 6 I confirmed that humans made context dependent decisions when the options varied only in the yellowness of the faces available to choose from. Chapter 7 was a replication of the hummingbird experiment in Chapter 3. In this experiment human participants were given choices between faces which varied in the yellowness only. In Chapter 3 the options which hummingbirds choose between vary in concentration with the most concentrated option (30% sucrose solution) having a concentration higher than many hummingbird flowers (Stiles, 1976, Baker, 1975) but less concentrated than the concentrations of sucrose hummingbirds prefer in experiments (Blem et al., 2000), (Stiles, 1976, Morgan et al., 2012, Blem et al., 1997, Stromberg and Johnsen, 1990). Therefore, in order to make the experiments as comparable as possible the options available for humans to choose between were also less yellow than the option they have the greatest preference for. However, this resulted in participants just choosing the yellowest option in each choice set; as a result I was not able to determine if the changes in preference between human and animal decisions are the same. Given that the hummingbirds had a split preference for the 20% and 30% sucrose solutions, it is

possible that the preference curve for the hummingbirds is not centred around as high a concentration as 50%. In addition the preference curve for the choice of yellowness in humans is a bell-shaped curve whereas in hummingbirds it is more flattened. Therefore only experiments in the lower concentrations and lower end of the yellowness scale of faces will have the same shape of preference curve. In order to use this experiment to answer questions about the similarity of human and animal decision-making, options would need to be chosen where participants did not have an overwhelming preference for one of the options, perhaps using the two faces from the binary choice in Chapter 6 where preference was not absolute.

Although I was not able to directly compare the choices made by humans and hummingbirds there are at least some differences in the choices made by hummingbirds and humans as the predictions made about the changes in preference that might be seen in Chapter 2 were based on the well-studied concept of asymmetrically dominating decoys. In humans the changes in preference are well documented and predictable. However, in the experiment in Chapter 2 the inconsistent changes in preference caused by the addition of decoys are not consistent with the data from humans which suggests that the mechanisms which may underpin economically irrational choice in humans and hummingbirds are likely to not be the same. Until experiments are conducted which provide both humans and animals with complimentary choices in order to help to establish whether or not economically irrational choice in humans and animals share any features, it seems doubtful that explaining animal decision-making using patterns of behaviour seen in humans will lead to new understanding.

In this thesis I found that context can affect the decisions made by hummingbirds in a number of different ways; Chapters 2 and 3 shed light on how context can affect the choices made by hummingbirds as the addition of inferior options in both single dimensional and multidimensional choice changes the preferences birds show between options. These changes in preference are not consistent with animals making economically rational choices and are not able to be easily explained by changes in energetic state of the animals during the experiments. In Chapter 2 birds changed their preference in response to the addition of poorer decoy options but the changes in preference observed were not consistent across birds. This is a difficult result to explain as you might expect that if there was a decision making mechanism which caused birds to make economically irrational choices, it would change choices in the same way for each bird. Therefore, it is possible that these changes in preference were mistakes on the part of the birds and so do not represent a significant departure from economic rationality. Alternatively, each bird may be attending to a different cue, either volume or concentration. Birds might attend to different cues due differences in their prior experiences. However, even if the birds were each using either volume or concentration of the options to guide their decisions it is unexpected that the different cues would both change the birds' preference in the same way.

In order to investigate whether the hummingbirds made consistent choices when there was only one cue I conducted the experiment in Chapter 3 where the options varied on only volume or concentration. When options varied in concentration only all birds reduced the proportion of choices they made to the most concentrated option. Whereas when options varied in volume only all birds decreased the proportion

of choices they made to their favoured option. However, for only one of the five birds was this the option with the highest volume, as unexpectedly four out of five birds did not prefer the option with the largest volume. There is no clear explanation for birds not choosing the option with the largest volume, as birds consumed almost all of the sucrose contained in the wells so obviously experienced the manipulation. They would be predicted to distinguish between options of different volumes as this would allow birds to visit the fewer wells to obtain a particular volume of sucrose. In the Concentration Treatment birds made economically irrational choices because they changed their preference upon the addition of a much poorer option (5%) to the choice. Although this was economically irrational it wasn't necessarily biologically irrational as birds consumed the same amount of energy per minute in the binary choice as they did when the 5% option was added to the choice. In the Volume Treatment birds also made economically irrational choices as they changed their preferences when the 5 $\mu$ l option was added to a choice of 20 $\mu$ l and 30 $\mu$ l. In the Volume Treatment birds consumed more energy per minute in the presence of the poorer option than they did in the binary choice. So although birds made economically irrational choices there was a biological advantage to doing so as they had a higher energy intake. This could be interpreted as either birds making better choices (by favouring the option with the larger volume) as a result of an adaptive decision making mechanism or alternatively that judging decisions by looking at economically irrational choices is not appropriate as that decision-making should not be expected to be consistent across contexts. I think that looking at economically irrational choices in animals may help us to examine decision-making mechanisms but that choices should not be judged as poor if they are economically irrational.

In this thesis hummingbirds changed their preferences when non-preferred options were added to choice sets. It has been suggested that one explanation for changes in preference in foraging experiments as a result of non-preferred options being added to the choice sets might be changes in energy state (Schuck-Paim et al., 2004). In previous experiments the addition of non-preferred options which have lower energy contents caused an increase in preference for the option with the greatest energy content (Bateson et al., 2002), which could be explained by changes in energy state as the birds would be consuming more of the best option to compensate for sampling the poor non-preferred option. In Chapters 2 and 3, the addition of a poorer option actually decreased the preference for the option which had the highest energy, which shows that not all context-dependent changes in preference in foraging animals can be explained by changes in energy state. However, despite changes in energy state not explaining all of the context-dependent foraging choices made by animals, it may still play an important role in the choices made and therefore should be controlled for. In foraging experiments energy is very difficult to exclude but energy state could be controlled by either presenting options that contain the same amount of energy, or by controlling the energy state of animals through supplementary feeding and the monitoring of their weight. If these alternatives are not possible then experiments into the decision-making mechanisms of animals might be best investigated in a non-foraging context, for example, mate choice.

In this thesis the majority of the experiments conducted with hummingbirds and all of the experiments with humans looked at choice amongst options which varied in a single dimension, which for the hummingbirds was either concentration or volume of sucrose solution and for human participants was the yellowness of faces. The

advantages of using options which vary in only a single dimension are a greater level of control. When options vary in more than one dimension (as in Chapter 2) it is not clear whether all of the animals are paying attention to the same cue. Therefore, when all birds did not make the same decisions it is not clear why. When options vary in more than one dimension individuals could pay attention to different cues, assess the cues different and weight the cues differently than other individuals. But when options are manipulated in only one dimension, as there is only one thing changing we can be confident that birds are either indifferent to the manipulation or they are paying attention to the only cue which is altered. However, there are some disadvantages of manipulating options in only a single dimension, for many animals (although not all) foraging on options which vary in only a single dimension might be somewhat artificial. Although it is worth noting that there will be other animals (particularly specialists with little variation in their diets) for whom options varying only in a single dimension would be more realistic than options which varied in multiple dimensions. In addition, many of the experiments carried out in both humans and animals occur when the items vary in more than one dimension, therefore, it is more challenging to make predictions about the effects we might expect when options only vary in a single dimension as there is a smaller volume of experimental evidence and theoretic ideas.

In this thesis hummingbirds did change their decisions in response to changes in context but these changes did not always occur and are not always consistent across individuals. As such it is difficult to assess the possible mechanisms which may or may not underpin these choices and it is not clear how important irrational decisions might be in an individual's lifetime. If animals were systematically economically irrational it would not necessarily mean that they made poor choices, as was the case in

Chapter 3; economically irrational choices might be better than economically rational choices. There are two possible explanations for economically irrational choices; the first is that these choices might be sufficiently rare as to make little difference to the life of the animal, perhaps occurring in experiments but rarely in the animal's natural decision making environment. Alternatively if animals were systematically economically irrational this might suggest that economically irrational choices are adaptive. Economically irrational choices could be adaptive if there were a cost to rational decision making that could be reduced by making an irrational choice. If the benefits of making an irrational choice outweighed the cost then irrational decision making could be selected for. An example of this might be a time cost associated with economically rational decision making. If the animal could use a heuristic which would allow the animal to make a good but not necessarily economically rational choice more quickly, then this would be selected for if the benefit of the shorter decision time outweighed the cost of occasionally not making the correct choice. Here choices would be economically irrational but biologically rational as over the course of the animal's lifetime these choices would be expected to maximise its fitness. Finding economically irrational choices does not necessarily imply that animals are not foraging optimally for their environment; instead it could suggest an adaptive mechanism enabling the animal to reduce the cost of decision making.

Using wild free living rufous hummingbirds in decision making experiments has advantages and disadvantages. One of the advantages of using free living hummingbirds is the choices the birds make are not consequence free; as the birds feed almost exclusively from the options available in the experiments they are highly motivated to make good choices. In addition, the birds are also defending their

territories and mating whilst the experiment is in progress, as a result birds making choices under the normal levels of time pressure which they would if they were foraging from flowers. Therefore, the choice the hummingbirds make are likely to be ecologically relevant so we can be confident that the context-dependent effect we observe is not due to a lack of motivation or a unnatural level of time pressure and therefore is not likely to impact on the birds choices in natural situations. There are also some drawbacks to using wild hummingbirds for decision making experiments as there is a reduced level of control. For example, in Chapter 5 I manipulated the prior experience of the birds in the experiment, however, I could only look at the prior experienced received in the experiment, experience prior to the experiment could not be controlled. As not all birds were marked at the same point in the season and there was variation between the capture of birds to mark and their entry into the experiment it seems unlikely that body mass would provide a useful measure of prior experience.

The use of the yellowness of faces also has advantages and disadvantages. Faces could be a good way of looking at context-dependent choice in humans as there are several aspects of faces, such as yellowness, which are able to be manipulated independently. In addition humans, like animals, need to assess the faces rather than be told about the values of each of the options. Also importantly, the preference for these faces is context-dependent and in a single dimension options could be created which did not take all of the choices. However, the use of faces also has challenges as people can have very strong preferences and the situation is somewhat artificial with people rating different versions of the same face.

### Future directions

Looking at the natural history of context-dependent decision making might help us to understand the reasons why we might not expect animals to be economically rational. If for example we only saw context-dependant choices when the consequences of making a poor choice were low and decisions needed to be made quickly we might conclude that context-dependent decision making might not be a mistake but instead could be caused by an adaptive process to enable animals to make decent, but not perfect, quick choices. In addition to a range of animals, the natural history of context-dependent choice would also look at the range of decision making contexts which are affected by context (mate choice, foraging etc.). Although looking at the natural history of the trait might not be able give a definitive answer to why context dependent choices are made, it could help to find areas which warrant further investigation.

In addition to the natural history, understanding what the brain is doing in decision-making may well prove crucial for the understanding of context. For example, there is some evidence that the coding of value is not absolute and instead is changed by the presence of other options (Kable and Glimcher, 2007, Louie and Glimcher, 2012). It has been argued that the systems for coding value are structurally similar to those which send perceptual information. Perceptual information is influenced by context and these effects are thought to be at least in part due to the coding structure of perceptual systems, if the decision making system is structurally similar we might also expect it to be influenced by context (Louie and Glimcher, 2012).

A third method for the further investigation of context-dependent decision-making is mapping the decision space. For example in two dimensions, like volume and concentration of sucrose, what impact does a decoy have when placed in a variety of possible positions relative to the main options? Also what impact does adding more than three options have on the choices made? Answering these questions would help us to understand what information is used and what information is ignored when making choices. In addition if humans choice was also investigated in this way using comparable decision-making experiments it would allow a good understanding of how human and animal decision-making is linked and if it is appropriate to continue to use human decision making experiments to inspire experiments with animals. Specifically leading on from the experiments presented in this thesis the next step would be to continue to look at the similarities or differences between human and animal decision-making. The two experiments that would be the next steps would be to replicate the human experiment in Chapter 6 with hummingbirds, where birds were given options of intermediate concentration of sucrose in addition to one option which is much more concentrated and one option which is much less concentrated. The other experiment would be to redo the experiment from Chapter 7 but to use the options present from the binary choices in Chapter 6, this would mean that participants did not overwhelmingly choose one of the options.

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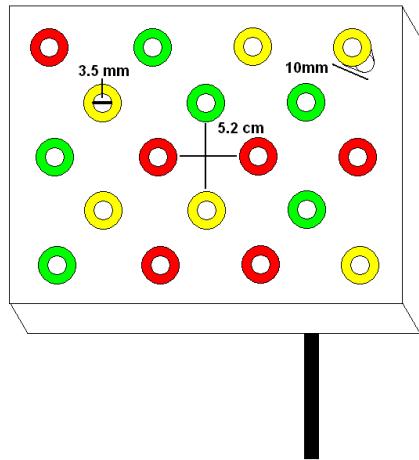
**Chapter 2. Context-dependent decision making in hummingbirds: the role of decoys****and energetic state on preference**

Figure 1. Layout of the Plexiglas board displaying a trinary choice. The space between each of the wells as well as the depth and diameter of the wells are displayed.

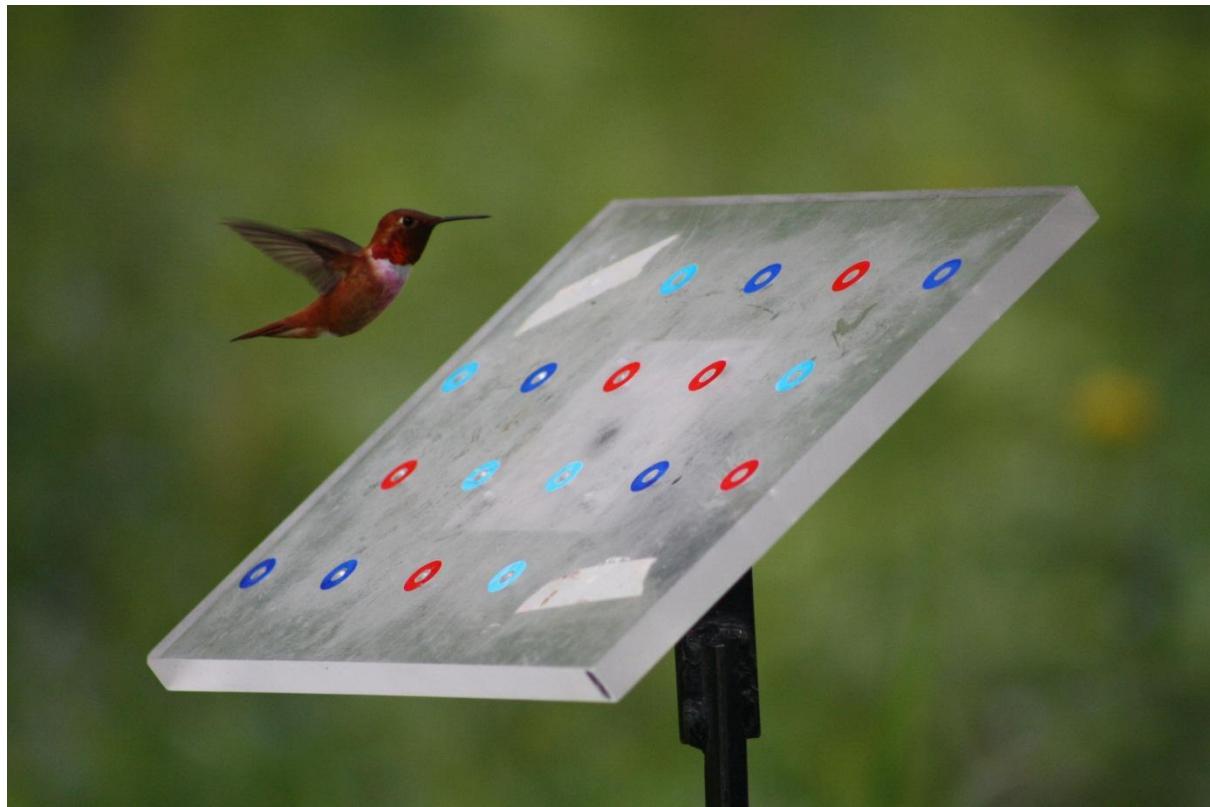


Figure 2. An image showing a hummingbird approaching the Plexiglas board to make a choice to one of three possible options, these options are indicated to the bird by the colour of the paper reinforcement around each well. This bird's identifying mark is a pink line of ink and can be seen on the white feathers of the breast.

Equation 1.

*Proportion of choices to Concentration option*

$$= \frac{\text{Choices to Concentration option}}{\text{Choices to Concentration option} + \text{Choices to Volume option}}$$

Equation 2.

*Proportion of Choices to Volume option*

$$= \frac{\text{Choices to Volume option}}{\text{Choices to Volume option} + \text{Choices to Alternative Concentration option}}$$

Equation 3.

*Proportion of choices to the most rewarding option*

$$= \frac{\text{Choices to most rewarding option}}{\text{Choices to most rewarding option} + \text{Choices to other option}}$$

**Chapter 3: Context-dependent decision making in a single dimension: inferior options make a difference**

Figure 1.

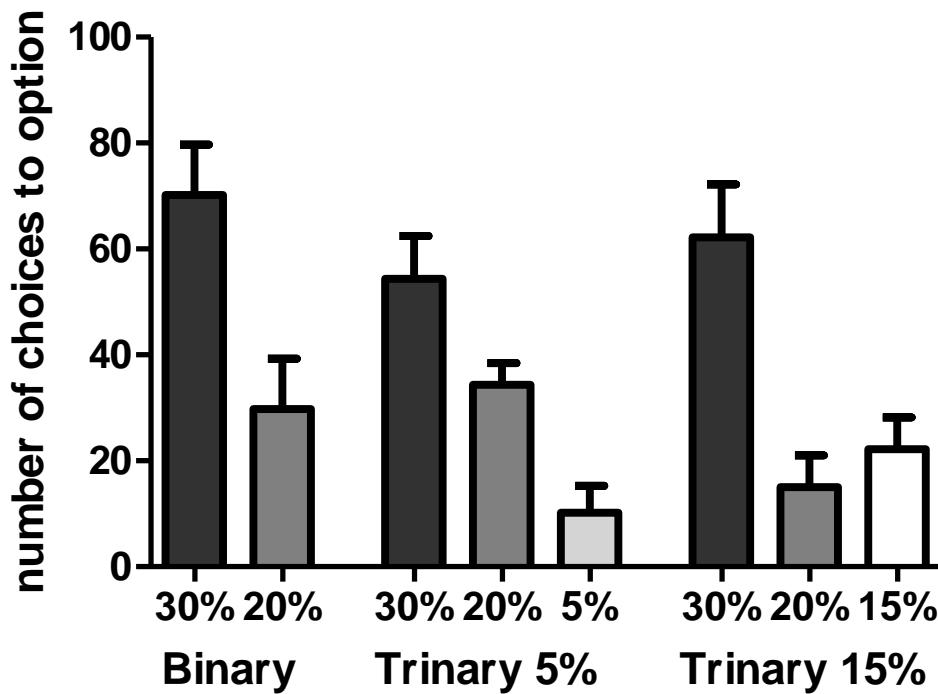


Figure 1.

The total number of choices made by the birds to each of the options in the binary and trinary choice sets of the Concentration treatment. For all conditions the data are means  $\pm$  s.e. ( $N = 5$ ).

Figure 2.

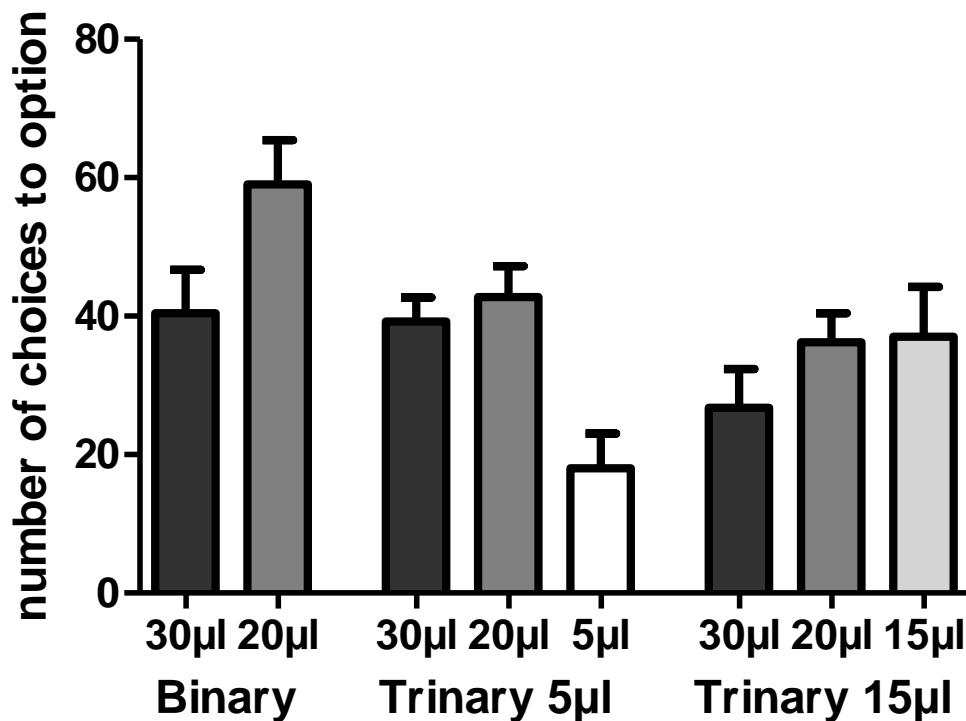


Figure 2.

The cumulative number of choices made by the birds to each of the options in the binary and trinary choice sets of the Volume treatment. For all conditions the data are means  $\pm$  s.e. ( $N = 5$ ).

Figure 3.

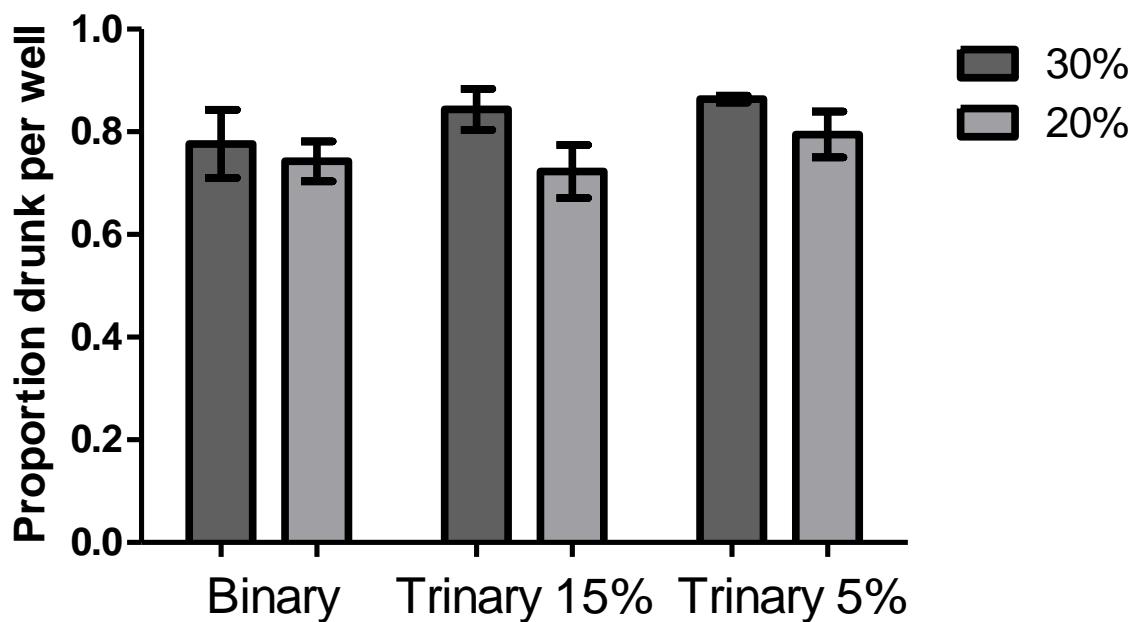


Figure 3.

The mean proportion of sucrose which birds consumed from the 20% and 30% options in the binary and trinary choice sets of the Concentration treatment. The data are means  $\pm$  s.e. ( $N = 5$ ).

Figure 4.

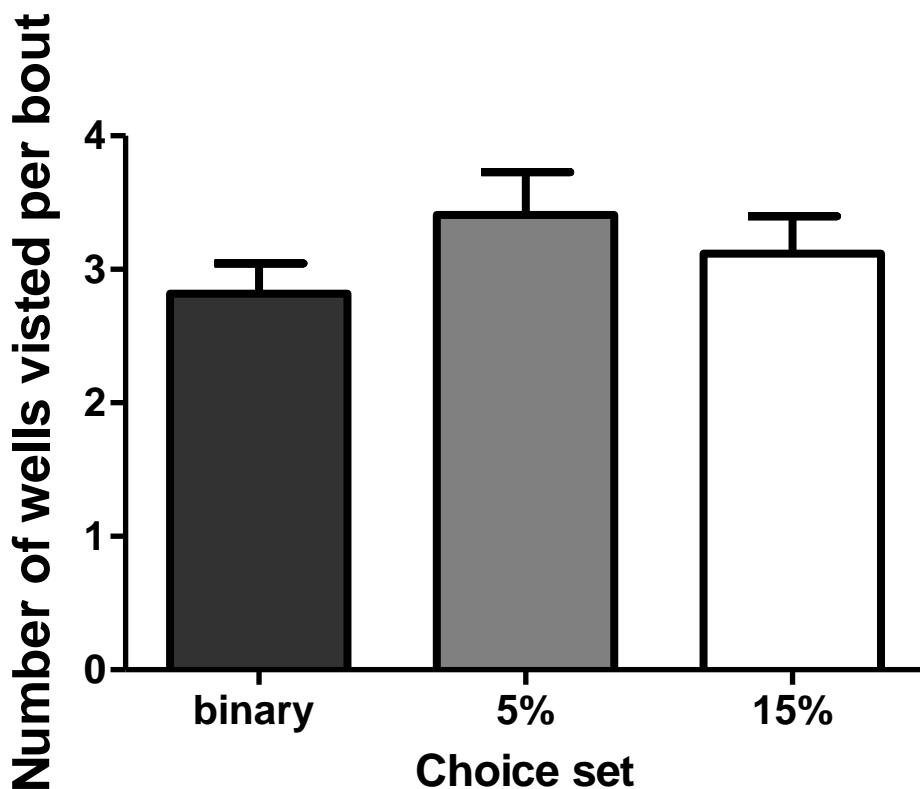


Figure 4.

The number of wells birds visited per bout in the binary and trinary choice sets of the Concentration treatment. The data are means  $\pm$  s.e. ( $N = 5$ ).

Figure 5.

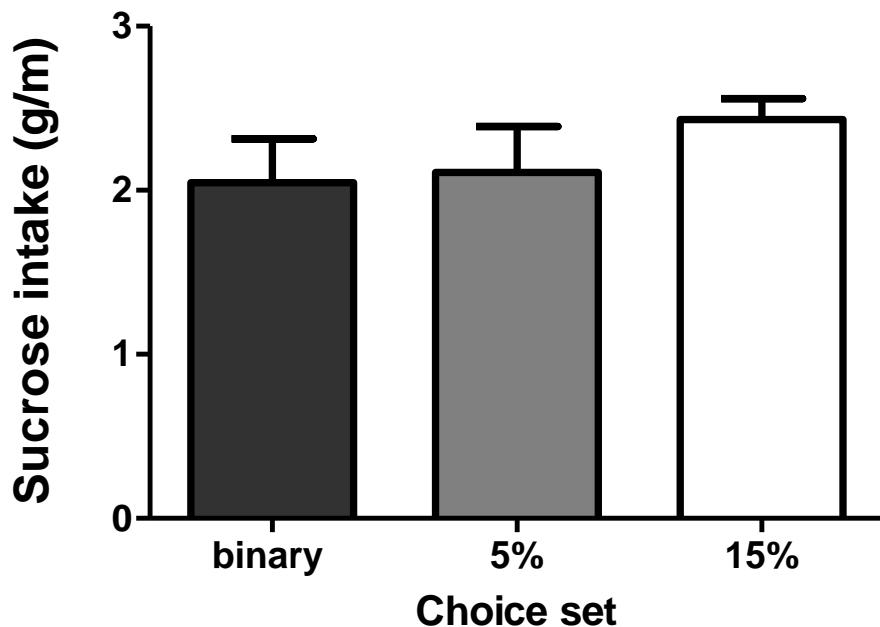


Figure 5.

The number of grams of sucrose per minute birds consumed in each of the choice sets of the Concentration treatment. The data are means  $\pm$  s.e. ( $N = 5$ ).

Figure 6.

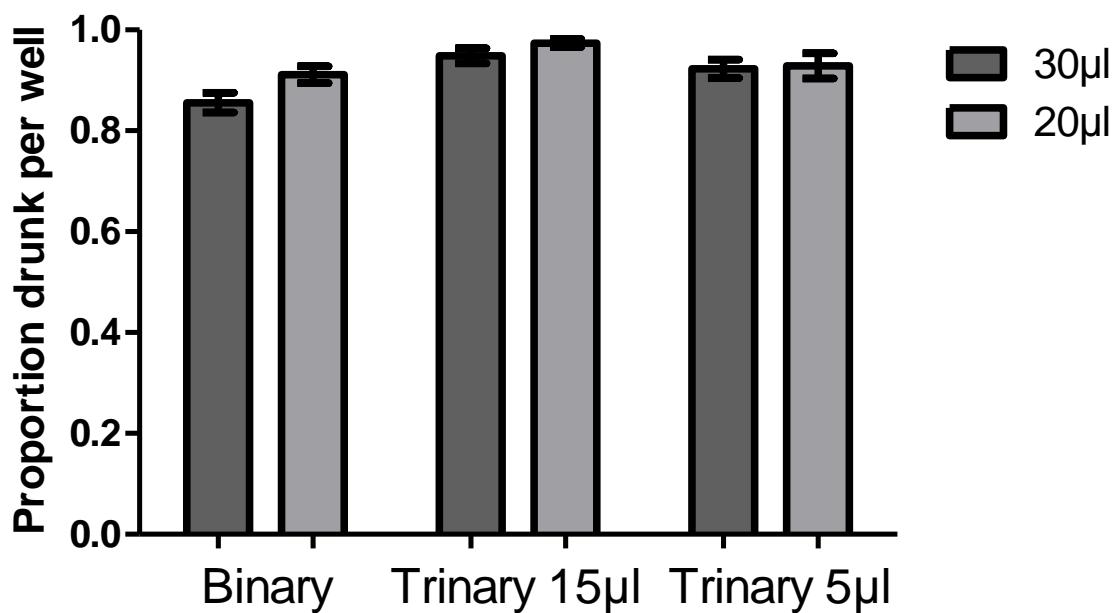


Figure 6.

The mean proportion of the sucrose available in each well which birds consumed from the 20µl and 30µl well types in the binary and trinary choice sets of the Volume Treatment. The data are means ± s.e. (N = 5).

Figure 7.

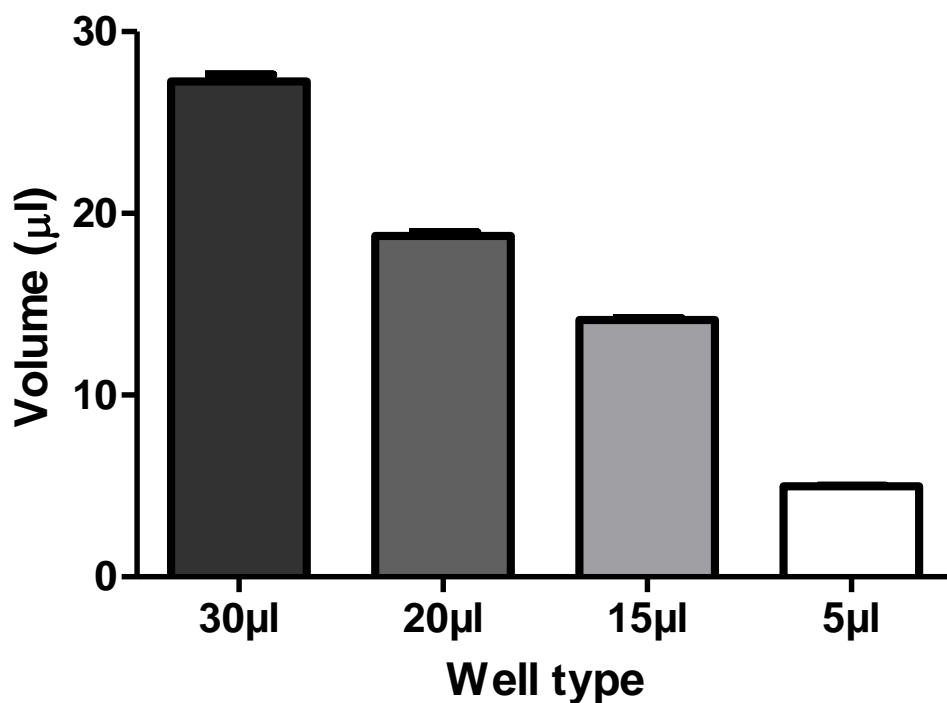


Figure 7.

The volume of sucrose birds drank from each well type in the Volume Treatment. The data are means  $\pm$  s.e. (N = 5).

Figure 8.

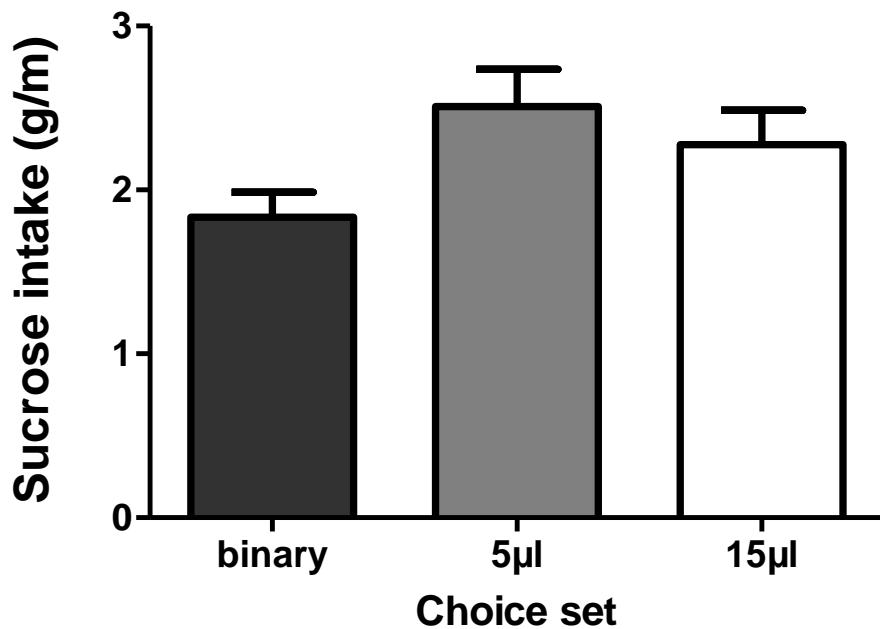


Figure 8.

The number of grams of sucrose birds consumed per minute in each of the choice sets of the Volume treatment. The data are means  $\pm$  s.e. (N = 5).

**Chapter 4: Context-dependent decision making in a single dimension: prior experience****does not change preferences**

Figure 1a

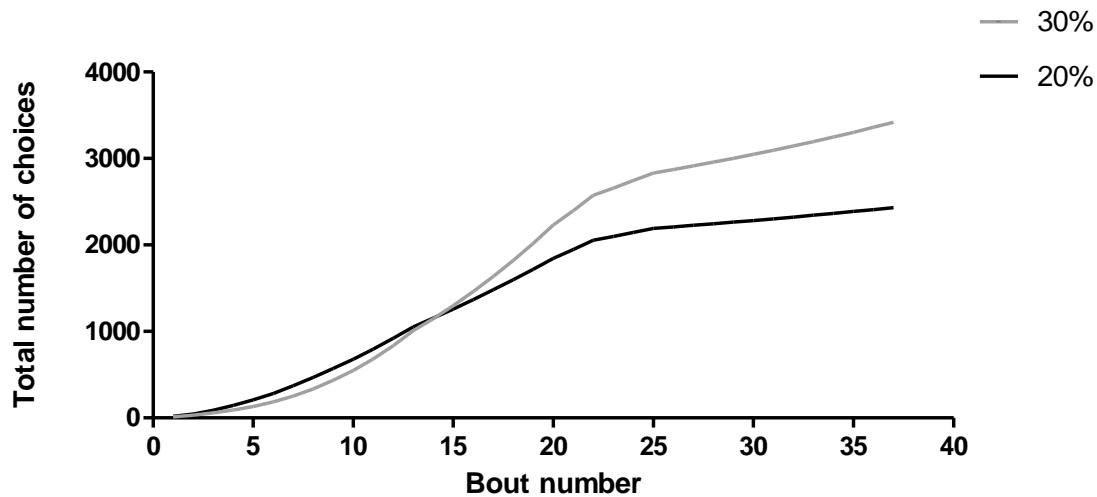


Figure 1b

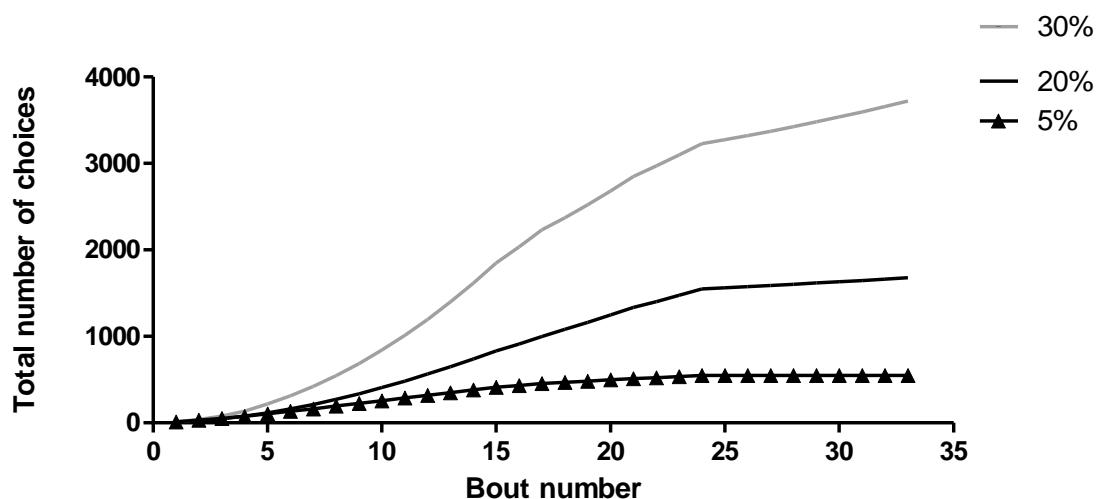


Figure 1c

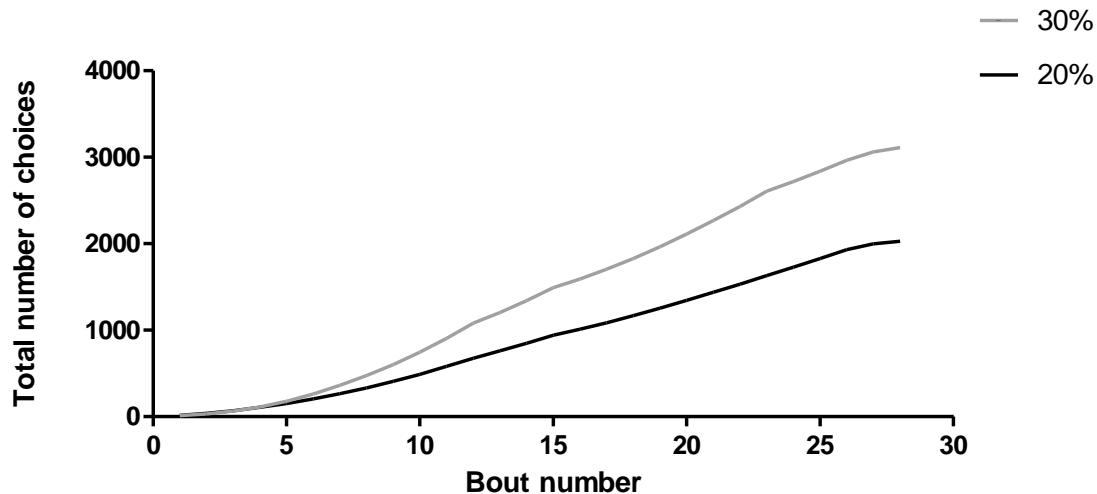


Figure 1.

The cumulative number of choices made by the birds to each of the options in the binary and trinary choice sets of the Trinary Matched treatment.

(A) Binary: cumulative choices to 20% and 30% options through the binary treatment.

(B) Trinary : cumulative choices to 20%, 30% and 5% options through the trinary

condition where the colours of those options are matched to the preceding Binary

(C) Binary Matched: cumulative choices to 20%, 30% options.

For all conditions the data are means ( $N = 5$ ). The dotted line indicates 50 well visits.

Figure 2a

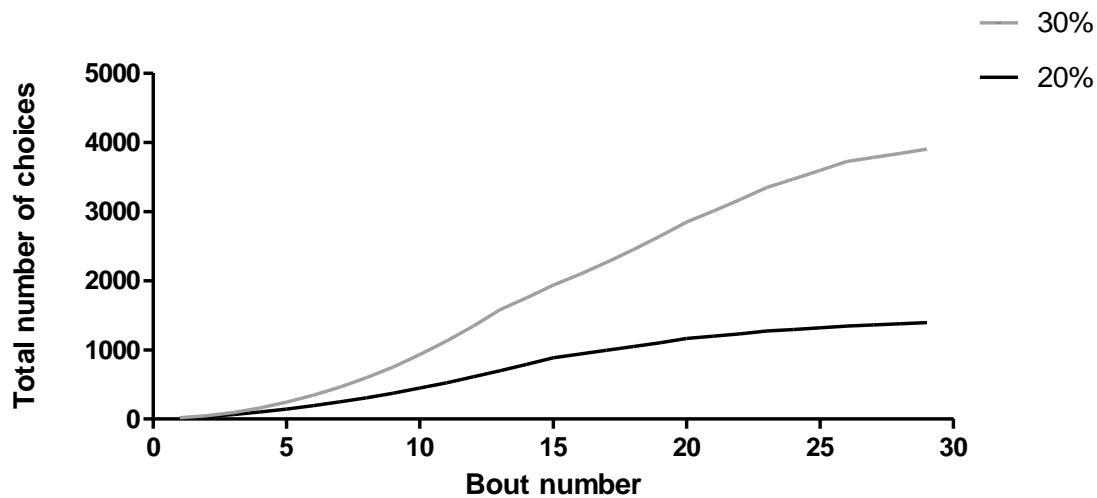


Figure 2b

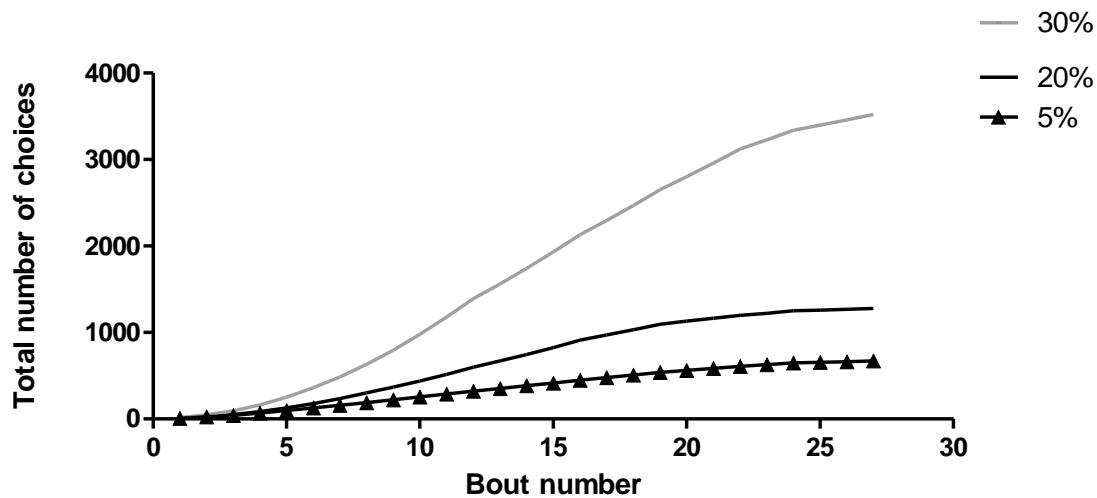


Figure 2c

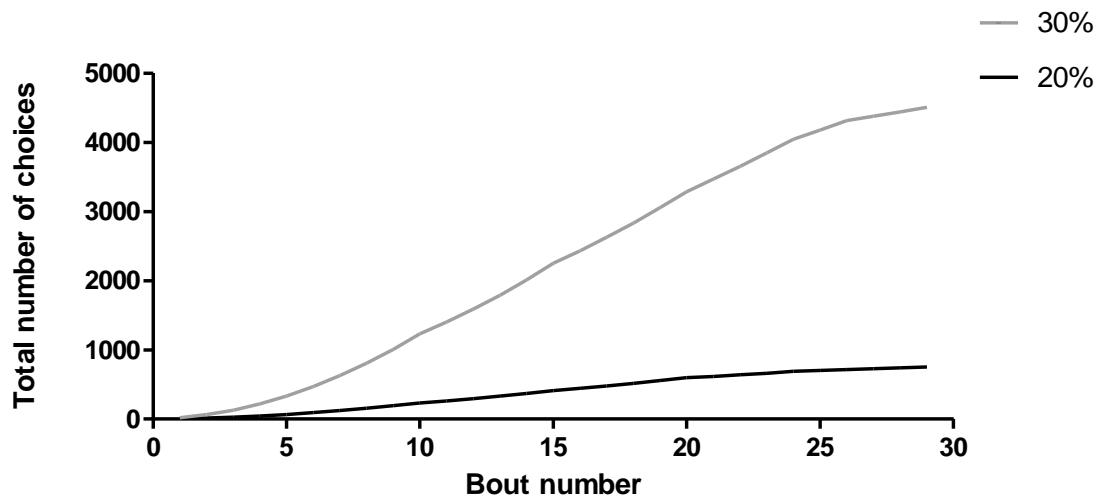


Figure 2.

The cumulative number of choices made by the birds to each of the options in the binary and trinary choice sets of the Binary Matched treatment.

(A) Binary: cumulative choices to 20% and 30% options through the binary treatment.

(B) Trinary: cumulative choices to 20%, 30% and 5% options through the trinary condition.

(C) Binary Matched: cumulative choices to 20%, 30% options where the colours of those options are matched to the preceding trinary

For all conditions the data are means ( $N = 5$ ). The dotted line indicates 50 well visits.

**Chapter 5: Simultaneous or sequential presentation changes the choices made by  
hummingbirds**

Figure 1.

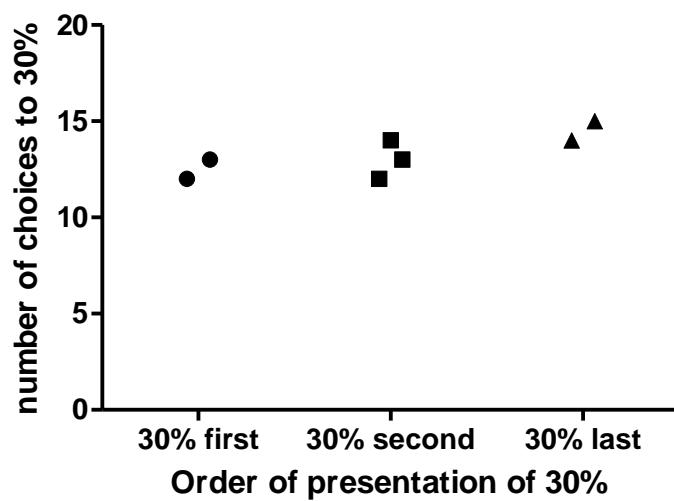


Figure 1.

*Separate Treatment.* (a) Number of choices birds made in the three-option choice set made to 30% option when the 30% option was experienced first, second and last (i.e. immediately before the three-option choice set). The data are from individual birds ( $n = 7$ ).

Figure 2

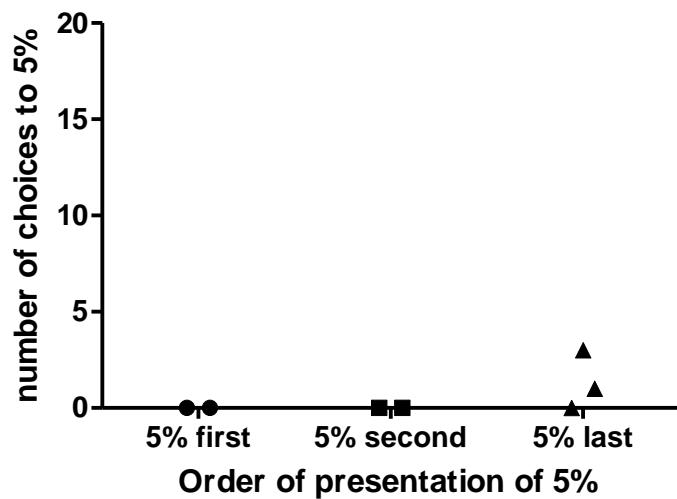


Figure 2.

*Separate Treatment.* (b) Number of choices which birds made in the three-option choices set made to the 5% option when the 5% option was presented first, second and last (i.e. immediately before the three-option choice set). Data are from individual birds ( $n = 7$ ).

## Chapter 6: Context affects the assessment of health in human faces

Participant number	Treatment	Proportion of choices to Yellow plus in the Trinary Minus choice	Proportion of choices to Yellow plus in the Binary choice	Proportion of choices to Yellow plus in the Trinary Plus choice	Trinary Minus different from Binary? (P value)	Trinary Plus different from Binary? (P value)	Follow the expected pattern?
1	Simultaneous	0.310345	0.466667	0.466667	0.288	1.000	Yes
2	Simultaneous	0.448276	0.766667	0.965517	0.017	0.052	Yes
3	Simultaneous	0.166667	0.533333	0.933333	0.006	0.001	Yes
4	Simultaneous	0.655172	0.833333	0.962963	0.143	0.197	Yes
5	Simultaneous	0.266667	0.5	0.733333	0.110	0.110	Yes
6	Simultaneous	1	0.966667	1			No
7	Simultaneous	0.793103	0.833333	0.809524	0.748	1.000	No
8	Simultaneous	0.083333	0.066667	0.517241	1.000	<.001	No
9	Simultaneous	0.62069	0.666667	0.758621	0.789	0.567	Yes
10	Simultaneous	0.966667	0.966667	0.9375	1.000	1.000	No
11	Simultaneous	0.111111	0.333333	0.333333	0.610	1.000	Yes
12	Simultaneous	0.083333	0.533333	0.758621	0.001	0.103	No
13	Simultaneous	0.7	0.833333	1	0.360		Yes
14	Simultaneous	0.423077	0.5	0.714286	0.601	0.114	Yes
15	Simultaneous	0.391304	0.5	0.827586	0.579	0.013	Yes
16	Simultaneous	0.862069	1	0.954545			No
17	Simultaneous	0.033333	0.333333	0.466667	0.006	0.430	Yes
18	Simultaneous	0.5	0.733333	0.966667	0.111	0.026	Yes
19	Simultaneous	0.321429	0.3	0.62069	1.000	0.019	No
20	Simultaneous	0.37037	0.666667	0.9	0.035	0.057	Yes
21	Simultaneous	0.896552	0.9	1	1.000		Yes
22	Simultaneous	0.6	0.7	0.727273	0.571	1.000	Yes
23	Simultaneous	0.3	0.533333	0.766667	0.115	0.103	Yes
24	Simultaneous	0.862069	0.9	0.954545	0.706	0.629	Yes
25	Simultaneous	0.9	0.9	0.923077	1.000	1.000	No
26	Simultaneous	0.173913	0.333333	0.766667	0.225	0.002	Yes
27	Simultaneous	0.344828	0.366667	0.642857	1.000	0.065	Yes
28	Simultaneous	0.733333	0.833333	0.892857	0.523	0.707	Yes
29	Simultaneous	0.214286	0.6	0.758621	0.004	0.267	Yes
30	Simultaneous	0.344828	0.533333	0.551724	0.192	1.000	Yes
31	Simultaneous	0.615385	0.633333	0.862069	1.000	0.072	Yes

Table 1. The proportion of choices made by participants in the Simultaneous Treatment to the

Yellow + option by individual participants in the Binary, Trinary Minus and Trinary Plus choice sets. In addition the table also shows the result of chi squared tests which compare the choices made by each participant in both Trinary Plus and Trinary Minus choice sets with the choices made by that participant in Binary choice sets.

Participant number	Treatment	Proportion of choices to Yellow plus in the Trinary Minus choice	Proportion of choices to Yellow plus in the Binary choice	Proportion of choices to Yellow plus in the Trinary Plus choice	Trinary Minus different from Binary? (P value)	Trinary Plus different from Binary? (P value)	Follow the expected pattern?
1	Sequential	0.15	0.37	0.60	0.129	0.120	Yes
2	Sequential	0.52	0.83	0.93	0.021	0.423	Yes
3	Sequential	0.56	0.77	0.79	0.103	1.000	Yes
4	Sequential	0.72	0.93	1.00	0.042		Yes
5	Sequential	0.86	0.83	0.89	1.000	0.709	No
6	Sequential	0.93	0.93	0.91	1.000	1.000	Yes
7	Sequential	0.92	0.83	0.82	0.431	1.000	No
8	Sequential	0.36	0.33	0.37	1.000	0.788	Yes
9	Sequential	0.59	0.73	0.87	0.279	0.333	No
10	Sequential	0.89	1.00	1.00			Yes
11	Sequential	0.00	0.03	0.07		1.000	Yes
12	Sequential	0.00	0.20	0.63		0.001	Yes
13	Sequential	0.76	0.83	0.91	0.532	0.685	Yes
14	Sequential	0.37	0.50	0.64	0.425	0.301	Yes
15	Sequential	0.50	0.67	0.81	0.286	0.365	Yes
16	Sequential	0.97	0.87	1.00	0.353		No
17	Sequential	0.23	0.33	0.53	0.554	0.192	Yes
18	Sequential	0.59	0.83	0.93	0.047	0.424	Yes
19	Sequential	0.03	0.13	0.28	0.353	0.209	Yes
20	Sequential	0.04	0.27	0.77	0.026	<0.001	Yes
21	Sequential	0.93	0.97	1.00	0.619		Yes
22	Sequential	0.64	0.60	0.80	0.788	0.216	Yes
23	Sequential	0.10	0.57	0.73	<.001	0.279	Yes
24	Sequential	1.00	1.00	1.00			Yes
25	Sequential	0.93	0.93	0.92	1.000	1.000	No
26	Sequential	0.32	0.47	0.69	0.407	0.115	Yes
27	Sequential	0.32	0.33	0.48	1.000	0.290	Yes
28	Sequential	0.83	0.87	0.96	0.731	0.367	Yes
29	Sequential	0.12	0.60	0.72	<.001	0.412	Yes
30	Sequential	0.25	0.63	0.54	0.007	0.595	No
31	Sequential	0.66	0.73	0.96	0.580	0.026	Yes

Table 2. The proportion of choices made by participants in the Sequential Treatment to the Yellow + option by individual participants in the Binary, Trinary Minus and Trinary Plus choice sets. In addition the table also shows the result of chi squared tests which compare the choices made by each participant in both Trinary Plus and Trinary Minus choice sets with the choices made by that participant in Binary choice sets.