Context-dependent foraging decisions in rufous hummingbirds

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A core assumption implicit in economic models of animal choice is that subjects assign absolute utilities to options that are independent of the type and number of alternatives available. Humans sometimes appear to violate this assumption and employ relative, as opposed to absolute, currencies when making choices. Recent evidence suggests that animals too might sometimes employ relative choice mechanisms. We tested this idea by measuring the foraging preferences of rufous hummingbirds (*Selasphorus rufus*) faced with choices analogous to those in which human use of relative currencies is evident. The birds experienced three treatments: a binary choice between two artificial flower types designated concentration (20 μl, 40% sucrose solution) and volume (40 μl, 20%), and two trinary treatments in which a third decoy option (either concentration decoy: 10 μl, 30% or volume decoy: 30 μl, 10%) was added to the set. The birds' preferences differed significantly across the three treatments. In the trinary treatments, the effect of the decoy options was to increase the preference for the option that dominated the decoy. These results are similar to those reported in the human choice literature, and are compatible with the hummingbirds using a relative evaluation mechanism in decision making.

Keywords: asymmetrically dominated decoy; context-dependent choice; rationality; foraging; currency; decision making

1. INTRODUCTION

It is an implicit assumption in most models of animal choice that animals evaluate alternative options using absolute currencies, meaning that a fixed value, independent of the number and type of other options available, is assigned to each option (e.g. classical optimal foraging theory; Stephens & Krebs 1986). This focus on absolute currencies arises from the premise in behavioural ecology that the fitness consequences of choosing a particular option are absolute, and therefore that the short-term currencies used as surrogates for fitness in decision making should also be absolute (but see Houston 1997).

An important consequence of assuming that animals assign fixed values to options is that the preference for one option over another should not be affected by the presence of other options. For example, in the scenario represented in figure 1 the relative preference for the target option (T) over the competitor option (C) should not be affected by the presence of the decoy option (D). Thus, if option D is added to the binary choice of T and C then it should take choices from T and C in proportion to their original shares, maintaining the ratio of their preferences at a constant value (the constant-ratio rule; Luce 1959). A strong prediction that arises from assuming that animals assign fixed values to options is that it should never be possible for the absolute preference for an option to be *increased* by the addition of one or more options to the choice set. This is known as the principle of regularity, and is regarded as a hallmark of rational decision making (Luce 1977; Tversky & Simonson 1993).

Several studies have tested these predictions in humans, by examining the consequences of adding a third option to a binary choice. The results obtained show that when the options vary in two dimensions, violations of regularity can occur, specifically when the third option is an asymmetrically dominated decoy (Huber *et al.* 1982; Wedell 1991; Doyle *et al.* 1999; Sedikides *et al.* 1999). Option D in figure 1 is defined as an asymmetrically dominated decoy (Huber *et al.* 1982) because it is dominated by both T and C on dimension 2, but it is dominated only by T on dimension 1. One option is defined as dominating another if two conditions are met: first, in all dimensions the dominating option must be greater than or equal to the dominated options; and, second, in at least one dimension, the value for the dominating option must be greater than the value for the dominated option (Wedell 1991). The effect of adding an asymmetrically dominated decoy is to increase the preference for the dominant option. Thus, in the choice between T and C, D acts to increase preference for T.

The asymmetrically dominated decoy effect described above is not compatible with assuming that humans assign fixed values to options. Instead, it has been proposed that humans may assign value using a comparative mechanism, whereby the value of an option is computed relative to the other options currently available. A number of different psychological mechanisms have been suggested as explanations for the asymmetrically dominated decoy effect (Huber *et al.* 1982; Wedell 1991). However, empirical evidence favours the view that the decoys may influence evaluations by altering the dominance relationships between the options (Wedell 1991). By ranking between the target and the competitor in the dimension on which

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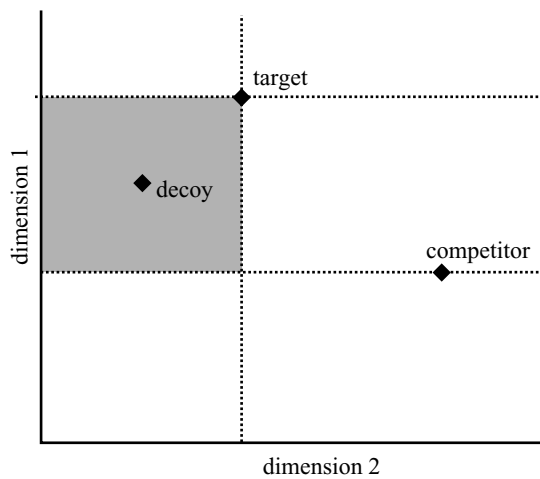DOI 10.1098/rspb.2003.2365

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Figure 1. Three options, a target (T), a competitor (C) and a decoy (D), that differ along two independent dimensions. The shaded area indicates the range of positions in which D is an asymmetrically dominated decoy for T.

the target is superior to the competitor, an asymmetrically dominated decoy decreases the ranking of the competitor relative to the target. This constitutes a comparative evaluation mechanism because rank can be defined only relative to the other options present. It is important to note that such a mechanism can operate only in cases where a subject has to take into account more than one dimension when making a decision.

Animals frequently have to make choices between two or more options that differ along two or more dimensions; therefore, the above findings in humans have raised the question of whether animals might also use comparative evaluation mechanisms in decision making (Shafir 1994; Real 1996). Table 1 summarizes the three recent studies that have investigated the effects of asymmetrically dominated decoys in foraging animals (Bateson *et al.* 2002; Shafir *et al.* 2002). Two studies have examined the effects of a single asymmetrically dominated decoy on the preference between a target and a competitor option (hummingbirds; Bateson *et al.* 2002; grey jays; Shafir *et al.* 2002). Both of these studies found that the addition of the decoy option affected preference. However, in the hummingbird study, the effects were in the opposite direction to those predicted, with the decoy option increasing the relative preference for the competitor option. Although we interpreted this finding as evidence for a comparative evaluation mechanism, it is also possible that it could have occurred as a result of the decoy option merely amplifying a pre-existing preference by diluting the effects of random responses ('random dilution effect'; Bateson (2002) and below). This latter possibility raises the question of whether the context effects observed in animals are occurring via the same mechanism as those reported in humans. A stronger test of the asymmetrically dominated decoy effect involves the comparison of the effects of two decoys, each of which acts as an asymmetrically dominated decoy for one of the two options compared in a binary choice. The asymmetrically dominated decoy effect predicts that such decoys should have opposite effects on the preference between the target and

competitor options, whereas the random dilution effect predicts that both decoys should have the same effect of increasing any preference present in the binary choice. Only one animal study on foraging bees has so far compared the effects of more than one decoy option in a single design (the bee experiment; Shafir *et al.* 2002). Although the data do not support the random dilution effect, only one of the decoys worked as predicted by the asymmetrically dominated decoy effect, and the experimental design did not counterbalance the order of treatment presentation because all trinary tests were preceded by binary tests. This latter point is potentially important since previous experience (background context) has been shown to affect preference (Waite 2001a).

The current experiment is designed to test the effect of asymmetrically dominated decoys on the foraging decisions of rufous hummingbirds using a design that brings together in a single experiment the merits of exploring the effects of more than one decoy option and a balanced order of testing in the binary and trinary contexts. As in Bateson *et al.* (2002) we investigated choice between flowers differing in the dimensions of nectar volume and nectar concentration, because both of these attributes have independently been shown to be important in explaining hummingbird flower preferences, with birds preferring higher volumes (Gass & Sutherland 1985) and higher concentrations (Roberts 1996) within a given range. We designed four artificial flower types corresponding to a concentration option (C, so called because it had the highest nectar concentration), a volume option (V, so called because it had the highest nectar volume), a concentration decoy (D^C) and a volume decoy (D^V). The actual nectar volumes and concentrations used are given in figure 2. In contrast to Bateson *et al.* (2002), the values of nectar volume and concentration for each flower type were chosen such that the variance in each dimension between flower types was equal. The two decoy options were both asymmetrically dominated, such that D^C was dominated by C but not by V and D^V was dominated by V but not by C (see figure 2). We tested the birds' preferences between the flowers in three treatments:

(i) binary: C versus V;
(ii) trinary with D^V (trinary D^V): C versus V versus D^V; and
(iii) trinary with D^C (trinary D^C): C versus V versus D^C.

On the assumption that hummingbirds respond in a similar way to humans to asymmetrically dominated decoys, it is predicted that D^C should act to *increase* the relative preference for C over V, and that D^V should act to *decrease* the relative preference for C over V. Relative preference for C over V should therefore be highest in trinary D^C, intermediate in binary and lowest in trinary D^V. If violations of regularity are observed, it is predicted that absolute preference for C should be higher in trinary D^C than in binary, and absolute preference for V should be higher in trinary D^V than in binary. Conversely, the random dilution effect predicts that any preference seen in the binary treatment should *increase* in both trinary treatments irrespective of the nature of the decoy.

Table 1. *Summary of studies that have tested the effects of asymmetrically dominated decoys on foraging decisions in animals.*
(Treatments: binary, T versus C; trinary, T versus C versus D.)

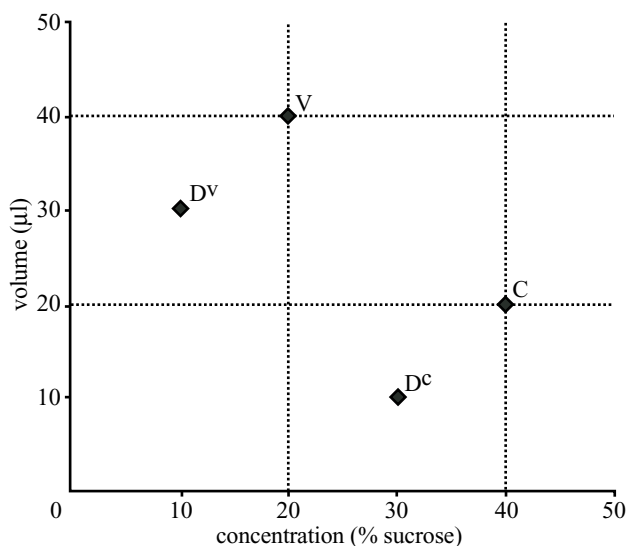| subject	dimensions	target (T)	competitor (C)	decoy (D)	treatments	effect of decoy	reference
honeybees (*Apis mellifera*)	length of flower (mm)/ volume of nectar (μl)	40/2	50/3	40/1	binary → trinary → binary	no effect	Shafir *et al.* (2002)
		50/3	40/2	100/3	binary → trinary → binary	increased relative preference for T	
grey jays (*Perisoreus canadensis*)	distance into tube (cm)/ number of raisins	56/2	28/1	84/2	binary → trinary → binary	increased absolute preference for T	Shafir *et al.* (2002)
		56/2	28/1	84/2	trinary → binary → trinary	increased absolute preference for T	
rufous hummingbirds (*Selasphorus rufus*)	volume of nectar (μl)/ concentration of nectar (% sucrose)	15/40	45/30	10/35	binary → trinary	decreased relative preference for T	Bateson *et al.* (2002)
		15/40	45/30		trinary → binary	decreased relative preference for T	

Figure 2. Relative positions on the concentration and volume dimensions of the four flower types used in the current experiment. The volume flower (V) contains 40 μl of 20% sucrose, the concentration flower (C) 20 μl of 40%, the volume decoy flower (D^V) 30 μl of 10% and the concentration decoy flower (D^C) 10 μl of 30%. In the trinary D^V treatment, V is the target, C the competitor and D^V the asymmetrically dominated decoy, whereas in the trinary D^C treatment, C is the target, V the competitor and D^C the asymmetrically dominated decoy.

2. MATERIAL AND METHODS

(a) *Subjects and study site*

The subjects were 11 wild male rufous hummingbirds observed in the Westcastle Valley in southwestern Alberta, Canada, in the eastern range of the Rocky Mountains (49°29′ N; 114°25′ W, elevation of 1400 m). During mid-May, commercial hummingbird feeders containing 14% sucrose solution were placed in potential territories, and by late May most feeders were successfully defended by males. Males defending feeders were individually marked by spraying their breasts with a small amount of waterproof non-toxic ink. All birds had previous experience of different choice experiments, and were already trained to feed from artificial flowers of the type used in this experiment. Data were collected between 0800 and 1930 Mountain Standard Time in June–July 2001.

(b) *Experimental procedure*

The experimental apparatus consisted of a Plexiglas plate (28 cm × 21.5 cm × 1.2 cm) drilled with 18 wells (10 mm deep × 3.5 mm in diameter) arranged in a hexagonal pattern such that nearest-neighbour distances were 5.2 cm. The wells (flowers) could hold a maximum of 120 μl of sucrose solution (nectar) and were marked with coloured reinforcement rings that were used to indicate the contents of the flower. The flowers were presented to the birds by mounting the plate at a 45° angle on a stake *ca.* 80 cm high.

Each bird was tested in all three treatments, with the order of presentation balanced across birds. In each treatment, the different flower types were indicated to the bird by the colour of the reinforcement ring surrounding the well of nectar. We used eight colours (blue, green, lilac, orange, pink, red, white and yellow) for each bird, such that each flower type in each treatment was indicated by a different colour, in order that the birds had to re-learn all the colour associations in each of the treatments they received. Colours were assigned to flower types such that the pairs and trio of colours used in each treatment was unique for each bird.

In the binary treatments, nine out of the 18 wells on the plate were randomly chosen as volume flowers and the remaining nine as concentration flowers, whereas in the trinary treatments six of the wells were randomly chosen as volume flowers, six as concentration flowers and six as decoy flowers (either D^{V}s or D^{C}s depending on the treatment).

Birds visited the plates of flowers approximately every 15 min throughout the day. On a visit, a bird was allowed to feed from as many wells as he wished, and the colours of the wells from which he fed were recorded. Once a feeding bout had finished and the bird had flown away, the wells from which he had fed were cleaned and refilled with the appropriate volume and concentration of nectar. The plate was rotated through 90° between visits. Every four visits a new board was used with a different random pattern of flowers, and the plate was moved *ca.* 1 m to encourage the bird to learn the association between the colour

of a flower and its contents, as opposed to learning the spatial locations of preferred flower types.

In the event that a bird failed to sample all the available flower types in the course of its first 10 flower visits in the binary treatment or the first 15 visits in the trinary treatments, the bird was forced to visit the same number of flowers of the non-chosen colour, or colours, by presenting it with plates consisting of flowers of only the non-chosen type or types. Following this correction procedure, the choice experiment was restarted. Flower visits made before and in the course of the correction procedure were not included in the dataset.

Each treatment was continued until a bird had made at least 150 choices of volume and concentration flowers. A single treatment typically took between 1 and 3 days to complete, with trinary treatments taking longer than binary treatments because the birds allocated some of their choices to the decoy flowers. Breaks taken by observers for the night, lunch or rain were ignored since they did not seem to have any effect on the subsequent choices made by the birds.

(c) *Analysis*

Given that there were only six flowers of each type in the trinary treatments, the preferences of a bird could span the complete range of preference from 0 to 100% for a given flower type only if he visited six flowers or fewer per bout. For this reason, we analysed only the first flower visited in each bout.

We computed both absolute and relative measures of preference. The absolute proportion of choice for an option is equal to the number of times that option was chosen divided by the total number of choices. We compared absolute preferences in the binary and trinary treatments to test for violations of regularity. The relative proportion of choices for option C over option V is defined as the total number of choices of C divided by the total number of choices of either C or V. If the values assigned to options are fixed, then relative preference should not be affected by the presence of a decoy option, thus relative preference was used to test the constant-ratio rule.

For analysis of variance (ANOVA), proportions and relative proportions were arcsine square-root transformed to correct the distribution of residuals. All *t*-tests are two-tailed, and an alpha level of 0.05 is assumed throughout.

3. RESULTS

(a) *Regularity*

Figure 3 shows the absolute proportion of choices for each option in each of the three treatments. Overall, the birds preferred C to V (binary treatment, one-sample *t*-test against a test mean of 0.5: $t = 2.283$, $n = 11$, $p = 0.0181$).

The mean absolute proportion of choices of V is not significantly different in the trinary D^V and binary treatments (paired *t*-test: $t = 0.114$, $n = 11$, $p = 0.9112$). The mean absolute proportion of choices of C is also not significantly different in the trinary D^C and binary treatments (paired *t*-test: $t = 0.110$, $n = 11$, $p = 0.9150$). Thus, overall there are no significant violations of regularity, because in neither trinary treatment is the absolute proportion of choices of the target option significantly increased by the presence of an asymmetrically dominated decoy.

Whereas the overall data show no violation of regularity, such violations are evident for some individual subjects. To test whether these violations of regularity in individual
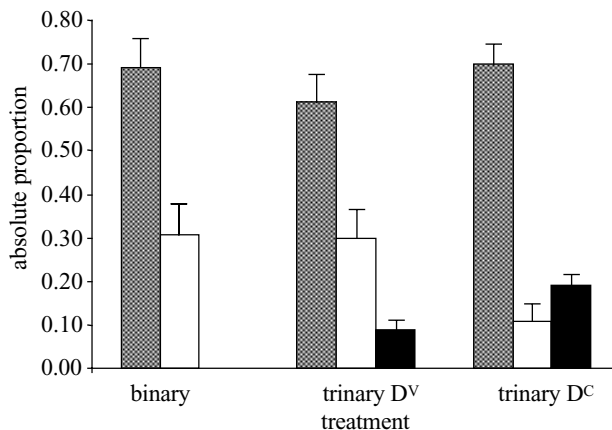

Figure 3. Absolute proportions of first flowers visited in each treatment. The bars show the means + 1 s.e. ($n = 11$). Grey bars, concentration; open bars, volume; black bars, decoy.

birds are significant, we conducted a contingency-table analysis of the number of choices made of C and V in the binary and trinary D^V treatments. Five birds' preferences differed significantly between treatments: three birds increased their preference for V (χ^2-tests, PK3: $\chi^2 = 10.42$, d.f. = 1, $p = 0.0012$; PK12: $\chi^2 = 24.18$, d.f. = 1, $p < 0.0001$; RD18: $\chi^2 = 10.38$, d.f. = 1, $p = 0.0013$), whereas two birds increased their preference for C (χ^2 tests, BK45: $\chi^2 = 4.03$, d.f. = 1, $p = 0.0447$; GN8: $\chi^2 = 5.45$, d.f. = 1, $p = 0.0196$). In the comparison between the binary and trinary D^C treatments four birds' preferences differed significantly between treatments: two birds increased their preference for C (χ^2-tests, BL165: $\chi^2 = 19.12$, d.f. = 1, $p < 0.0001$; RD10: $\chi^2 = 24.16$, d.f. = 1, $p < 0.0001$) and two birds increased their preference for V (χ^2-tests, PK12: $\chi^2 = 4.21$, d.f. = 1, $p = 0.0402$; RD18: $\chi^2 = 4.72$, d.f. = 1, $p = 0.0298$). Thus, in summary, five out of 11 birds showed significant violations of regularity in the direction predicted by the asymmetrically dominated decoy effect in one of their two treatments (PK3, PK12, RD18, BL165 and RD10); however, no individual bird showed the predicted effect in both treatments. Four birds showed significant violations of regularity in the opposite direction from that predicted in one of their two treatments (GN8, BK45, PK12 and RD18). Using Fisher's technique (Sokal & Rohlf 1995) to combine the *p* values from the five birds that had violations of regularity in the predicted direction and the *p* values from the four birds that had violations of regularity in the non-predicted direction, we see that the effect is much stronger in the former group ($\chi^2 = 105.08$, d.f. = 10, $p \ll 0.0001$ for the predicted-direction group versus $\chi^2 = 27.53$, d.f. = 8, $p = 0.0005$ for the non-predicted-direction group).

(b) *Constant-ratio rule*

The relative preference for C over V shows the pattern predicted by the asymmetrically dominated decoy effect, decreasing relative to the binary treatment in trinary D^V and increasing in trinary D^C (figure 4). Repeated measures ANOVA shows a significant main effect of treatment on relative preference ($F_{2,20} = 3.937$, $p = 0.0362$). *Post hoc* Tukey tests show that all three pairwise comparisons are significant ($Q = 2.5299$, $p < 0.05$), thus confirming the
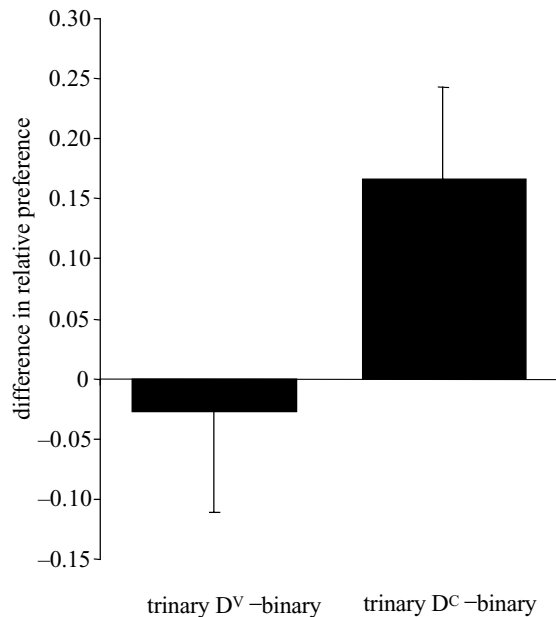
Figure 4. Relative preferences for the concentration flower (C) over the volume flower (V) was calculated as the number of choices of C divided by the sum of the numbers of choices of C and V. This figure illustrates the difference in this relative measure between each of the trinary treatments and the binary treatment. The bars show the means + 1 s.e. ($n = 11$).

predicted rank-order of relative preference in the three treatments.

4. DISCUSSION

We tested the preferences of wild rufous hummingbirds choosing between artificial flowers in both binary and trinary choice contexts. Specifically, we investigated the effects on preference of adding a third option, defined as an asymmetrically dominated decoy, to a binary choice between a target and a competitor. In both trinary treatments, the decoy option acted to increase the relative preference for the option that dominated it. Although the overall effects on relative preference were in violation of the constant-ratio rule, five individual birds also increased their absolute preference, thus also violating the principle of regularity. This is the first animal study to find significant effects of multiple decoys on preference as predicted by the asymmetrically dominated decoy effect (Huber *et al.* 1982).

The finding that asymmetrically dominated decoys affect choice is compatible with hummingbirds using comparative evaluation mechanisms to make foraging decisions. For example, the finding that asymmetrically dominated decoys act by increasing preference for the target option is compatible with hummingbirds evaluating the available flower types by comparing their relative ranks separately on each dimension (Huber *et al.* 1982; Wedell 1991). In the binary treatment the volume flower outranks the concentration flower on the volume dimension, but the concentration flower outranks the volume flower on the concentration dimension. However, when the D^V flower is added, the relative rankings of the volume and concentration flowers on the concentration dimension

remain unchanged, but their rankings on the volume dimension are altered such that the concentration option is now ranked third, below the D^V (see figure 2). Hence, the value of the volume flower increases relative to that of the concentration flower in the trinary D^V treatment when the relative ranks in both dimensions are taken into account. An equivalent but opposite argument can be made for the effect of the D^C. This mechanistic hypothesis needs to be tested further by exploring the effects of adding options in different locations in the two dimensional space defined by concentration and volume (e.g. Huber *et al.* 1982; Wedell 1991).

In a previous study that tested for the asymmetrically dominated decoy effect in rufous hummingbirds, the decoy had an effect on relative preference, but, contrary to predictions, it increased the preference for the high-volume competitor option as opposed to the target option (Bateson *et al.* 2002). However, a problem with that experiment was that the variation in volume between the options was much greater than the variation in concentration, potentially creating a situation in which the concentration dimension was completely overshadowed by the volume dimension. Based on this discrepancy between the two dimensions, we argued that it was possible that the birds perceived variation in only a single dimension (volume), and that this might explain why the asymmetrically dominated decoy effect (which requires options to vary in at least two dimensions) was not observed. This argument is supported by the results from the current experiment, because when the stimulus values for volume and concentration were chosen to give equal variance along the two dimensions, the asymmetrically dominated decoy effect was observed.

One aim of this study was to determine whether contextual effects on choice might be explained by the random dilution effect outlined in Bateson (2002). This mechanism is capable of producing increases in relative preference in response to increases in the size of the choice set, as reported previously in foraging hummingbirds and starlings (Bateson 2002; Bateson *et al.* 2002). The random dilution effect relies on animals assigning some proportion of their choices according to a fixed preference, while the remaining responses are allocated amongst the available options at random. As the number of options in the choice set is increased, the responses allocated at random are distributed among more options and thus dilute the actual preference less. Thus, unlike the comparative mechanism described above, the random dilution mechanism can produce changes in relative preference without the need to abandon the traditional assumption that animals assign absolute values to alternative options. It is important to note that the random dilution mechanism can only enhance existing preferences, and can only produce changes in relative preference; it cannot explain preference reversals or violations of regularity. Although this mechanism can explain the increase in relative preference seen for the concentration option in the trinary treatment with the D^C, it cannot explain either the increase in relative preference for the volume option seen in the trinary treatment with the D^V or the violations of regularity seen in some birds.

The current results add to a series of recent reports that provide data that suggest a role for comparative evaluation mechanisms in animal decision making (Shafir 1994;

Hurly & Oseen 1999; Waite 2001*a*;*b*; Bateson 2002; Bateson *et al.* 2002; Shafir *et al.* 2002). Since most of the existing theory on foraging behaviour is based on the assumption that animals evaluate alternative options using absolute currencies, such as long-term rate of energy intake, short-term rate of energy intake, efficiency or risk, the acknowledgement that animals may assign values to different foraging options using a comparative mechanism will provoke a rethinking of many optimal foraging models, and of the design of experiments to test these models. It seems surprising, given that Shafir (1994) first made this suggestion nearly a decade ago, that it has been largely ignored in the literature on animal decision making. Experimental tests of different choice currencies have previously focused on binary choice scenarios (e.g. Reboreda & Kacelnik 1991; Bateson & Kacelnik 1995, 1996; Brito-e-Abreu & Kacelnik 1999). However, the growing evidence for comparative choice mechanisms raises the uncomfortable prospect that many results obtained from such experiments may be limited in their generality (but see Schuck-Paim & Kacelnik 2002). It should however be stressed that evidence for comparative choice mechanisms does not constitute evidence that the foraging decisions of animals have not been shaped by natural selection. Although comparative evaluation mechanisms sometimes result in seemingly irrational and maladaptive behaviour, it is possible that such heuristics could be favoured by natural selection if they are computationally more efficient. Gigerenzer *et al.* (1999) has recently argued that often the most useful heuristics in decision making are those that are fast to compute and make use of only a limited range of information. Therefore, the heuristics used by foraging animals could result from an evolutionary trade-off between speed of computation and the quality of the decision reached. Further research is needed to establish the precise nature of the heuristics used by animals and the reasons that these decision-making rules have been favoured by natural selection.

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