

Context-dependent preferences in wild fruit bats

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In models of choice, animals are expected to evaluate options in absolute terms and assign some fitness-related value to different options. These expectations are similar to those of economic rationality, and both predict consistent decisions across variable contexts. Evidence from humans and other animals suggests that decision-making mechanisms can lead to context-dependent choices, which are considered economically irrational. While there is widespread evidence that these mechanisms may influence animal decision making, we can now explore how the presence and degree of these biases may arise in different animals based on their taxonomy and ecology. Here, we investigated context-dependent decisions in wild Jamaican fruit bats, *Artibeus jamaicensis*. We found that bats were sensitive to the context of the choice, showing shifts in preference upon the addition of an irrelevant decoy option. These results contrast previous findings in a close relative, the frog-eating bat, *Trachops cirrhosus*, indicating that diet may play a critical role in these behaviours. We argue that comparative studies exploring the role of diet on these decision-making biases are critical for understanding how animals make foraging decisions in the wild.

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Whether choosing a mate or a meal, animals are constantly faced with a variety of choices. Models of decision making often assume that animals combine several attributes (e.g. energetic payoff, time investment, predation risk) of each option into a single measure of value related to fitness (Stephens & Krebs, 1986). Rational choice behaviour in economics similarly predicts that humans make decisions between options in ways that maximize some aspect of monetary or emotional value. According to economic theory, if these values are based on the intrinsic properties of the options, and individuals evaluate each option in absolute terms, then preferences based on these values should be transitive and independent of irrelevant alternatives (Luce, 1959; Tversky, 1969). Surprisingly often, people violate these principles of rationality (Todd & Gigerenzer, 2007), and more recent work flowing from this similarity between animal foraging and human consumer choice indicates that decision rules used by animals can produce decisions not always considered 'rational' according to most models of choice. Instead, the context of the choice can have important consequences for how decisions are made (Tversky & Kahneman, 1986; Tversky & Simonson, 1993).

One context that can lead to economically irrational behaviour is where the introduction of an irrelevant option, or decoy, can affect relative preferences between pre-existing options (Huber & Puto, 1983). For instance, if given a choice between two equally desirable options: a trip to Paris or to Rome both with free breakfast included, people may not show a strong preference between the two. If a decoy option is added, a trip to Rome without free breakfast, Rome with free breakfast quickly becomes the preferred option (Ariely, 2010). This decoy is irrelevant because it has less value than that of the other two and should not affect the preference, or perceived value, between the first two if options are evaluated independently of one another. There is growing evidence that introducing irrelevant decoy options into a set of options can create context-dependent decisions that violate principles of economic rationality in both humans and other animals (Ariely, 2010; Hemingway, Ryan, & Page, 2017). By adding the decoy, a direct comparison can be made between both trips to Rome, making Rome with breakfast seem like the best option available of the three (Ariely, 2010).

Most studies of economic rationality in animals come from species similar in their foraging behaviour, such as hummingbirds and bees (Bateson, Healy, & Hurly, 2002; Shafir, Waite, & Smith, 2002), and species commonly used in studies of cognition such as mice (Rivalan, Winter, & Nachev, 2017), jays (Shafir et al., 2002; Waite, 2001b) and starlings (Bateson, 2002). More recently, studies

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spanning a broader range of species such as slime moulds (Latty & Beekman, 2011), frogs (Lea & Ryan, 2015) and fish (Reding & Cummings, 2017), have all found evidence for economically irrational behaviour upon the addition of a decoy option to a choice set. While there appears to be widespread evidence for economically irrational behaviour across both humans and animals, the conditions that produce such violations are still poorly understood. Because the magnitude and rank order of preferences can vary in context-dependent ways (Bateson & Healy, 2005), the role of taxonomy and ecology in influencing such decision-making mechanisms deserves further inspection.

Here we investigated whether wild bats make rational decisions as we varied the context of their choice. We explore this question in a frugivorous species, the Jamaican fruit bat, *Aribeus jamaicensis*. We asked whether bats exhibit shifts in preferences between two preferred options, ripe banana and papaya, depending on the presence of a decoy option, unripe banana. If these bats make context-dependent decisions, the presence of a decoy might create noticeable shifts in preferences between the two preferred options, such that bats increase their preference for ripe banana in the presence of unripe banana. Alternatively, if bats evaluate the options in absolute terms, preferences should be stable regardless of whether the decoy is present or absent.

METHODS

Subjects

Experiments were conducted in Gamboa, Panama, from May to July 2019 at the Smithsonian Tropical Research Institute. We captured 36 adult Jamaican fruit bats using mist nets in Soberanía National Park, Panama. Upon capture, bats were housed together in a small cage (L × W × H: 1 × 1 × 2.5 m) for one night and fed a mixture of banana and papaya. Following one night of acclimation, bats were released together into a larger outdoor flight cage (L × W × H: 5 × 5 × 2.5 m) that served as a home cage and experimental chamber. During training and testing, bat flights were recorded with three infrared security cameras (Amcrest, <https://amcrest.com/>) positioned on each of the feeding platforms. Individuals were identified by a combination of sex and a small haircut made on either the posterior or anterior part of the back fur. Following testing, bats were released at their initial capture location.

Ethical Note

For this study, mist nets were set up in close proximity (several hundred metres) to one another and checked every 10 min to ensure that bats were quickly removed upon capture. Bats that appeared distressed or anxious were immediately released upon capture. Following capture, bats were quickly (~15–30 min) transported in cloth bat bags directly to the flight cage, where they were released into cages with other individuals. We took every precaution to ensure that we reduced any activity such as quick movements or loud noises that would contribute to any unnecessary stress during the capture and transportation process. We did not observe any bats displaying distress upon release into the flight cage or across subsequent nights in captivity.

For short-term identification and to avoid multiple testing of the same individual, bats of the same sex were given a unique haircut (0.5 × 0.5 cm) on the anterior or posterior end of the dorsal side. Haircuts were given on the second night as bats were moved from the small holding cage into their larger training and testing cage. They were done quickly in the hand while bats rested atop a cloth bat bag (~15 s). Only 2 mm of hair was cut in order to reveal the

lighter hair underneath and to avoid close contact with the skin of the animal. No animals appeared distressed or sustained any injury during this process. We know from personal observation and recapture data that fur grows back within approximately 2 weeks.

Experiments were approved by the IACUC of University of Texas at Austin (AUP-2017-00292) and the Smithsonian Tropical Research Institute (2017-0102-2020), and by Panama's Ministry of the Environment, MiAmbiente (SE/AH-2-17).

Ripeness Measures

Bananas were measured according to a seven-stage colour scale (see Appendix, Fig. A3). Unripe bananas were selected by choosing bananas that fell between stages 1 and 2 based on colour and texture. These stages are categorized by a green peel with a trace of yellow. Structurally, the bananas are quite strong (60–70 N) during these early stages and require more energy to penetrate (30–37 J/mm). Ripe bananas were those that fell between stages 6 and 7. By stage 7, bananas are categorized by a yellow peel with brown speckles. Bananas at these stages are structurally quite weak (27 N) and require much less energy to penetrate (13.3 J/mm) (Soltani, Alimardani, & Omid, 2010).

Papaya ripening is characterized by a transition from green to yellow skin on the outside of the fruit. During this stage, the flesh with the fruit begins to darken and becomes more tender as the available sugar content increases. Lastly, the seeds turn from brown to black upon ripening (Zhou & Paull, 2001). Fruit used in this study met these requirements of yellow skin, tender/darker flesh and black seeds (Appendix, Fig. A4).

Pre-exposure Phase

All bats were trained in groups of three to four individuals, as these bats have been shown to respond poorly to being housed in isolation (Ratcliffe, Fenton, & Galef, 2003). Bats in each cohort were all caught on the same night and started the training together. We trained bats to retrieve food rewards from three feeding platforms. Three food rewards were used in this study: two preferred options (A: banana, B: papaya) and the decoy option (C: unripe banana). Ripeness was assessed by age, colour and texture according to Gomez, Lajolo, and Cordenunsi (2002) and Soltani et al. (2010). Feeding platforms were arranged in a triangle in the centre of the flight cage. Platforms were 1.5 m tall and were placed 2 m from one another. Fruit was presented on top of the feeding platform in 2 g pieces on a plastic tray. Trays were consistently used for one fruit type throughout the training of each cohort and each tray was thoroughly cleaned immediately after feedings.

The pre-exposure phase occurred over two nights with each reward type presented alone for 2 h at one of the feeding platforms. Each reward type was kept at a constant location during training and testing. At the beginning of each training block, 30 pieces (60 g total) of one of the fruit types was presented on a plastic tray placed on one of the three feeding platforms. During several training blocks, the tray was depleted during the 2 h period, at which point an additional 30 pieces were added to the tray. The order of presentation during training was randomized but counterbalanced across cohorts, meaning that if bats started with ripe banana on the first night of training, they would receive papaya first on the consecutive night. There were no criteria that bats were expected to meet in order to proceed to testing. This training period served mainly as a pre-exposure stage to ensure that bats learned to retrieve food rewards from the different feeding platforms. Because we were trying to control for the amount of exposure that each cohort had with each type of food reward, we kept the exposure time and the location of each food reward constant during the

training period. While training was to ensure that bats knew to visit each platform to obtain food rewards, we consider it likely that bats also learned to associate each platform with specific reward types. Previous studies in closely related frugivorous and nectivorous bats have shown that spatial locations are the most salient cues when learning about food rewards (Carter, Ratcliffe, & Galef, 2010; Thiele & Winter, 2005; Winter & Stich, 2005).

Because bats were trained in groups, there was no way to differentiate between individuals during the two training nights using the video recordings. To ensure that all bats had experience with the food rewards and were eating during the 6 h training block, all bats were caught and checked quickly for visible and palpable signs of a full stomach. On average, training cohorts ate 54 pieces of ripe banana, 90 pieces of ripe papaya and 38 pieces of unripe banana across the two nights of training.

Testing

We determined whether bats shift their preference between ripe banana and papaya in the presence of a decoy option (unripe banana). Following two nights of training, two of the bats from each cohort were randomly selected for testing. A total of 18 bats were tested in this experiment (9 males, 9 females). Each bat was tested in both a two-choice test (A and B) and a three-choice test (A, B and C). Both the two-choice and three-choice tests lasted for 1.5 h each (3 h in total per bat). Each bat was tested individually. While one bat was being tested, the other would be housed in a holding cage without food. Between choice tests, bats were swapped, and the tested bat would be placed in the holding cage while the other bat was being tested. This allowed the bats to regain hunger between choice tests. In total, testing took 6 h per night. The order of testing was kept consistent within cohorts but randomized across cohorts (Appendix, Table A1).

During both choice tests, 30 pieces of fruit (2 g each) were presented on each feeding platform. Foraging preferences were recorded as the number of fruit pieces taken from each platform during the testing period. Although the unripe banana was not expected to be preferred, video recordings during testing show that bats visited the decoy platform during the testing period, indicating they were aware of that option (see Supplementary material, Video S1). Similar to the training protocol, fruit trays were kept consistent for the different fruit types during the testing period. All trays were washed and dried thoroughly between each bat and each choice test.

Analyses

The constant-ratio rule is a probabilistic form of rationality and states that the relative preference between two options (A and B) should not change in the presence of a third option (C) (Luce, 1959). Relative preferences were calculated for bats in both the two-choice and three-choice tests by dividing the number of choices for banana by the number of choices for both banana and papaya ($A/(A + B)$). We did not include choice for the decoy as a measure of preference in the trinary test as we were mainly interested in whether the presence of the decoy option would influence the relative preference between the two pre-existing options.

To test for decoy effects, we analysed whether the relative preference for ripe banana differed between the two test conditions (two and three choices) using a permutation test. We first calculated the mean change in preference for ripe banana by subtracting the mean preference during the two-choice test from the mean preference during the three-choice test. To test whether this difference was greater than expected by chance, we compared this observed mean difference to those from 5000 null data sets where

we permuted the choice label (three and two choices) within the same bat to control for repeated measures. We also calculated a 95% confidence interval around the mean within-bat change in preference using nonparametric bootstrapping (Bca method; Puth, Neuhäuser, & Ruxton, 2015). Using this method, we also compared the mean change in preference for both bats that started with the two-choice test and bats that started with the three-choice test to evaluate the data for potential order effects.

Additionally, for each individual, we ran chi-square tests to detect preference shifts. Two bats from the B cohort (Beatrice and Barnaby) were not included in the analysis as we were unable to access the fruit market on the day of testing for these individuals, and therefore did not have unripe banana that fit the requirements for testing. All analyses were done using R v.3.5.3 (R Core Development Team, Vienna, Austria). Data and R script are available on Figshare.

RESULTS

Figure 1 shows the changes in relative preference for ripe banana across all individuals from the two-choice to three-choice test. Bats did not have an overall initial preference for banana over papaya in the two-choice test (Fig. 1). We found a 20% higher preference for ripe banana in the three-choice test relative to the two-choice test (mean change = 0.2, 95% CI: 0.08–0.35, $N = 18$, permutation $P < 0.005$; Fig. 2a). Distribution of null expected effects from data permutations are shown in the Appendix (Fig. A1). The mean change did not depend on whether the bat was first tested in a two-choice or three-choice condition (mean change_{two-choice}: 0.09; 95% CI: 0.02–0.18, $N = 8$; mean change_{three-choice}: 0.28; 95% CI: 0.08–0.53, $N = 10$; Appendix, Fig. A2). Additionally, although the unripe banana was sampled, it did not appear to be a preferred food type in this experiment. It is common in experiments with decoys for individuals to sample the decoy options, while showing stronger preferences for the initial two options (e.g. Bateson, Healy, & Hurly, 2003; Edwards & Pratt, 2009). Overall, we recorded a total of 15 choices for the decoy compared to 69 choices

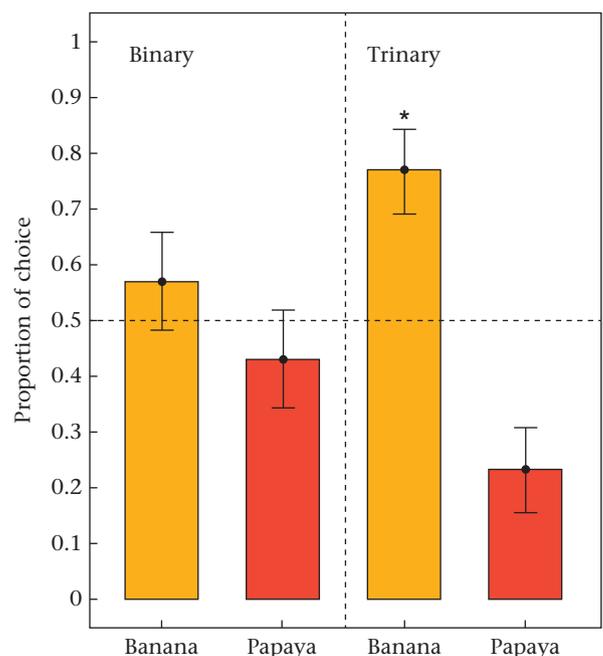


Figure 1. Relative preferences (mean ± SE) across all bats for ripe banana and papaya in both the two-choice test and the three-choice test. $N = 18$ for each test. * $P < 0.01$ (Wilcoxon signed-rank test).

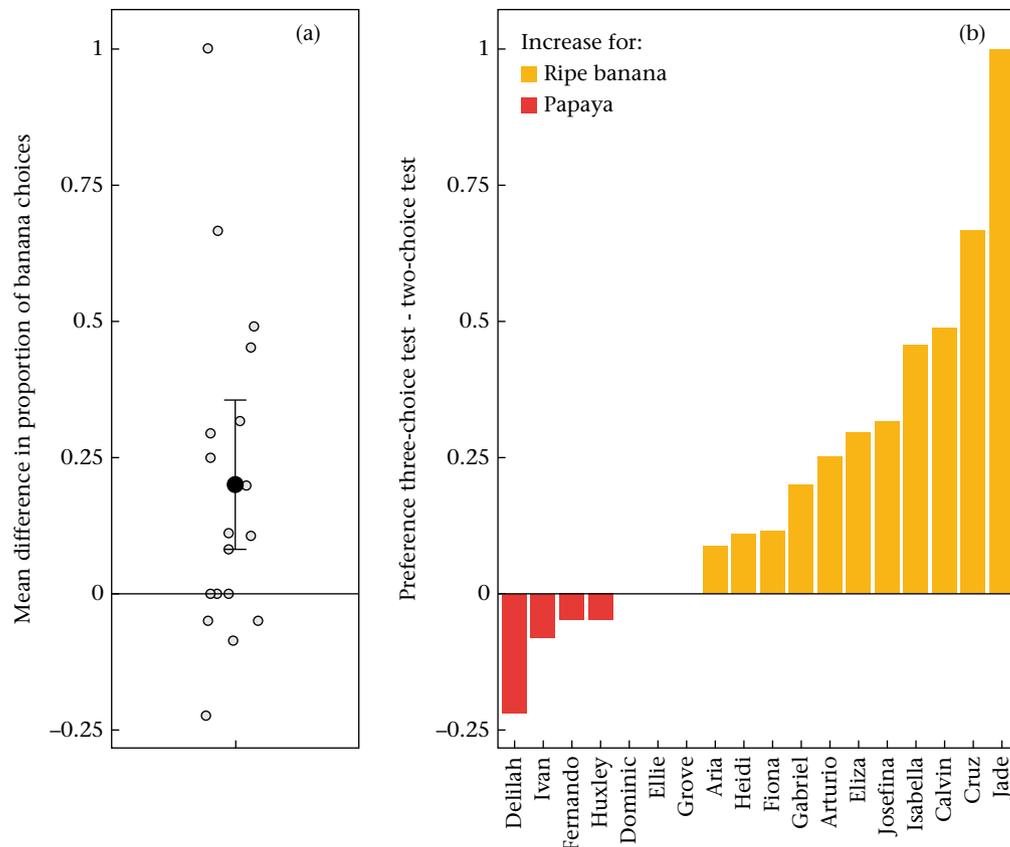


Figure 2. (a) Difference in preference for banana (preference in three-choice – preference in two-choice). Each point represents a single bat. (b) Differences in preference for banana in the two treatments across all individuals.

for papaya and 155 for ripe banana across all bats in the three-choice test (Appendix, Table A2). Removing bats that sampled the decoy from the analysis did not change our results (mean change = 0.26, 95% CI: 0.12–0.48, $N = 12$, permutation $P = 0.003$; Appendix, Fig. A5).

Although individual preferences were highly variable across bats in both the two-choice and three-choice tests, we observed a general trend of an increase in preference for ripe banana in the three-choice test. Out of 18 bats, 11 showed an increase in preference for the ripe banana in the three-choice test, three showed the same preference across both choice tests and the remaining four showed a decrease in their preference (Fig. 2b). Only two bats exhibited significant shifts in preference following multiple test corrections (Appendix, Table A2), but both bats increased their preference for the ripe banana in the three-choice test. This is likely due, in part, to a lack of power as most bats made fewer than 20 choices in each treatment.

DISCUSSION

Decoy effects can serve as an indication of the decision rules that guide behaviour. Economically irrational decisions may arise when items in a choice set are not evaluated in absolute terms, but are instead compared to other items available, often along shared attributes (Tversky & Simonson, 1993). In this study, when we altered the context of the choice that bats were making, we found that bats increased their relative preference for ripe banana over papaya in the presence of unripe banana, suggesting that fruit bats make decisions that are influenced by the context of the choice. This is considered a violation of the constant-ratio rule, which states that the addition of an irrelevant option (i.e. one lower in value) to a

choice set should not alter the relative preference between the original two options (Luce, 1959).

One proposed explanation for violations to the constant-ratio rule is the ‘random-dilution effect’, which states that individuals allocate some fixed proportion of responses to a preferred option and choose randomly between other available options (Bateson, Healy, & Hurly, 2002; Luce, 1959). This explanation seems unlikely to explain our results for several reasons. First, the preference for ripe banana increased in the three-choice test, which is inconsistent if animals allocate fixed responses to ripe banana. Second, while we observed some choices for the decoy option in the three-choice test, unripe banana was selected far less than papaya. Instead, our results appear consistent with the explanation that options are evaluated relative to other options available, leading to context-dependent preferences.

Most studies testing for decoy effects are set up so decoys are asymmetrically dominated by two options, such that one option beats the decoy on two dimensions and the other only on one (Huber, Payne, & Puto, 1982). Studies in humans have shown that decoy effects can also occur when a decoy is relatively inferior to one option, representing a compromise (Herne, 1999; Pettibone & Wedell, 2000). Although the unripe banana in this experiment was not asymmetrically dominated by the ripe banana, it may have still altered the perceived relationship between the two preferred options. As a result, the bats may have considered the ripe banana as a compromise when presented with all three options. While our aim was to select two options that were equally preferred, bats did appear to have a slight preference for banana over papaya in the two-choice test. There were also several cases in the three-choice test where the unripe banana was eaten more frequently than the papaya, indicating that at least some bats may have preferred

any banana over papaya. Experiments using unripe papaya as a decoy could shed light on how our patterns were influenced by the specific food type as well as the context of the choice.

Jamaican fruit bats are considered fruit generalists and fig specialists, with figs comprising a large component of the diet. In addition to figs, these bats also eat the fruit, flowers, pollen and nectar of over 100 other tropical species (Gardner, 1977), including banana and papaya, both of which can be found at the study site. Because our experiments were conducted with wild animals, it is possible that bats used in this study had previous experience with banana or papaya in the wild, which could have potentially guided preferences between different fruit options. If bats had previous experience with one or more food type, this could have altered the perceived utility or value of these options in ways not predicted solely by the physical properties of the options (Pompilio & Kacelnik, 2010; Waite, 2001a). In the present study, we did not observe dramatic changes in preferences over time or significant differences in preferences between bats based on treatment order. We did, however, see that the three individuals who showed the greatest change in preference all received the three-choice test with the decoy first. In a study testing for decoy effects in honey bees, *Apis mellifera*, and grey jays, *Perisoreus canadensis*, Shafir et al. (2002) similarly found that previous experience with a decoy did not appear to influence later choices. Studies exploring how the type and duration of prior experience with available options might influence context-dependent decisions would be an interesting avenue for future research.

It is also worthwhile to consider how the feeding ecology of fruit bats and the chemical ecology of fruit defences may have several important consequences on decision making in this context. Unripe fruit pulp can harbour higher levels of defensive fruit secondary compounds than ripe fruit pulp (Maynard et al., 2020). It also leads to altered gut retention time (Baldwin & Whitehead, 2015), meaning consumed unripe fruit pulp might simply not remain in the intestinal tract of fruit bats long enough to yield sustainable caloric benefits. If bats in our study started with a slight preference for ripe banana and then increased their preference for ripe banana when faced with three choices, this could be a consequence of having ingested numerous pieces of unripe banana (with potentially low caloric yields) early in the night and having to deal with the ensuing relative caloric deficit. In such cases, changes in internal state could potentially lead to apparent violations of rationality (Schuck-Paim, Pompilio, & Kacelnik, 2004). Our results indicate, however, that four of the six bats that sampled the decoy option (Ellie, Elize, Fernando and Huxley) received the two-choice test first (see Appendix, Table A1), meaning they did not have access to the unripe banana until later in the night. Additionally, when we removed from the analysis the six bats that sampled the decoy, we still observed a significant shift in preference between both choice tests. Taken together, we argue that shifts in preference observed here are more likely explained by comparative evaluation mechanisms leading to differences in perceived quality, rather than changes in internal state during the course of testing.

Although comparative evaluation has the potential to produce economically irrational behaviours, these decision mechanisms may still be favoured by natural selection. Trade-offs between the efficiency of decision making and the accuracy of resulting choices have been argued to select for decision-making shortcuts that might produce economically irrational behaviours in some situations, but that are considered rational in a broader, ecological context (Bateson & Healy, 2005; Gigerenzer, 1997; Houston, McNamara, & Steer, 2007). Evidence for decoy effects has been found broadly across many taxonomic groups such as insects, amphibians, fish, birds and mammals (reviewed in Hemingway et al., 2017), suggesting that comparative evaluation is quite

common. A handful of studies have also shown that several species seem immune to decoy effects (e.g. Edwards & Pratt, 2009; Hemingway et al., 2017), suggesting that comparative evaluation may not be a general property of decision making in all animals, but instead, an adaptive solution to ecological pressures surrounding decisions in the wild. This has important consequences for our understanding of how selection operates on both animal decision making but also the targets of those decisions such as mating displays (Bateson & Healy, 2005; Lea & Ryan, 2015) or floral characteristics (Bateson et al., 2002; Shafir et al., 2002).

Our findings raise interesting questions about when and where these decision mechanisms might evolve. Because economically irrational behaviour occurs across such a wide taxonomic breadth, other factors, such as diet, might be an important selective force in producing such behaviours. For instance, hummingbirds (Bateson et al., 2002), honey bees (Shafir et al., 2002), and now fruit bats have been shown to exhibit decoy effects, all of which fly, consume sugar-rich food and interact with plants in a mutualistic manner. These three groups, however, differ considerably in their neural architecture. Additionally, while hummingbirds and bees forage during the day using primarily visual stimuli, fruit bats are nocturnal and rely heavily on echo-acoustic and olfactory cues to find food. In previous work, we have shown that frog-eating bats, *Trachops cirrhosus*, are not susceptible to decoy effects when choosing among frog calls (Hemingway et al., 2017). Frog-eating bats also appear to make transitive decisions (Hemingway, Ryan, & Page, 2019), upholding the other main assumption of rational choice theory. Not only are both bat species in the same family (Phyllostomidae), but they can often be found in the same forested habitats. Taken together, these results suggest that diet may play a critical role in the evolution of these decision-making strategies.

Whether this difference between these closely related species is caused, at least in part, by diet is only one possibility. For both fruit bats and frog-eating bats, differences in rational behaviours could be explained by how these bats forage, rather than what they are eating. Predators feeding on mobile, evasive prey may have evolved different decision-making strategies than animals foraging on mutualistic prey such as pollinators or frugivores. More generally, there may be a difference between ephemeral prey and more stable food sources that could alter the information that the individual gets from a decoy option. For fruit bats, it is possible that the presence of unripe bananas in natural environments may provide information on future availability of this food type. In the present study, rather than comparing unripe and ripe bananas directly, bats may have been assessing the current abundance of banana relative to papaya. Different foraging strategies may then select for differences in decision-making mechanisms. Comparative studies carefully controlling for phylogeny would be beneficial in understanding how taxonomy and ecology might jointly influence the presence and magnitude of these biases in decision-making behaviours of different animals.

Another question that remains to be answered is whether (ir) rational decision making is a domain-specific or domain-general process in different species. Although studies have explored rational decision making in different domains such as foraging, mating and habitat choice, to our knowledge, no studies have been conducted exploring rational decisions within a single species across multiple domains. Within a single domain there is evidence that the emergence of economic irrationalities can be task dependent in some animals. For example, starlings have been shown both to adhere to strict rationality in certain contexts (Monteiro, Vasconcelos, & Kacelnik, 2013) and to deviate from principles of rationality in different tasks (Pompilio & Kacelnik, 2010; Vasconcelos, Monteiro, & Kacelnik, 2013). Across domains, there is also evidence that other behaviours, such as social learning, appear to be domain general. For instance, in humans, women that exhibit

mate-choice copying are also more likely to use other forms of social information for decisions unrelated to mate choice (Street et al., 2018). While studies of domain specificity have not directly addressed economic rationality, such general outcomes suggest that some behaviours may be more general than previously thought. Whether or not rational choice in fruit bats, as well as other animals, is task dependent or domain dependent remains to be answered.

The integration of cognitive psychology with the study of behavioural ecology has led to an appreciation of the role of cognitive mechanisms in producing or failing to produce 'rational' decisions (Dukas, 1998). Because most studies of animal choice present only two options, while animals often choose among many, the generality of studies based on preferences between two options deserves further scrutiny. Comparative decision rules could also result in predictable, but largely unconsidered, deviations from choices considered optimal in models of behaviour (Bateson & Healy, 2005). Because most models assume absolute evaluation, the currencies we use to model animal decisions may fail to predict behaviour in more complex, naturalistic conditions (Bateson et al., 2002). More multifaceted models may be necessary to better capture how animals are making decisions in the wild.

Data Accessibility

Data, including the R codes, have been uploaded to figshare digital repository (<https://doi.org/10.6084/m9.figshare.12515474.v4>).

Author Contributions

C.T.H. and J.A. collected the data. C.T.H. carried out the analysis. All authors contributed to the writing and editing of the manuscript. All authors approve the final version of the manuscript and agree to be held accountable for the content therein.

Competing Interests

We declare no competing interests.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2021.06.016>.

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Appendix

Table A1

Treatment order of cohorts during testing

Cohort	1st	2nd
A	Two-choice	Three-choice
C	Three-choice	Two-choice
D	Three-choice	Two-choice
E	Two-choice	Three-choice
F	Two-choice	Three-choice
G	Three-choice	Two-choice
H	Two-choice	Three-choice
I	Three-choice	Two-choice
J	Three-choice	Two-choice

Table A2

Choices for banana and papaya in the two-choice and three-choice tests for individual bats

Bat	Two-choice			Three-choice				χ^2	P
	A	B	P (A)	A	B	C	P (A)		
Arturo	10	6	(0.625)	7	1	0	(0.875)	0.630	0.43
Aria	11	1	(0.917)	21	0	0	(1.00)	0.083	0.77
Calvin	1	7	(0.125)	8	5	0	(0.615)	3.067	0.08
Cruz	4	8	(0.333)	9	0	0	(1.00)	7.072	<0.01
Dominic	7	0	(1.00)	8	0	0	(1.00)	*	1.0
Delilah	7	0	(1.00)	7	2	3	(0.778)	0.327	0.57
Ellie	13	0	(1.00)	5	0	3	(1.00)	*	1.0
Eliza	12	5	(0.706)	7	0	3	(1.00)	1.123	0.29
Fiona	8	1	(0.889)	8	0	0	(1.00)	0.0	1.0
Fernando	1	19	(0.05)	0	16	1	(0.00)	0.0	1.0
Gabriel	8	2	(0.80)	13	0	0	(1.00)	0.89	0.35
Grove	8	1	(0.889)	8	1	0	(0.889)	0.0	1.0
Heidi	9	3	(0.75)	6	1	0	(0.857)	0.0	1.0
Huxley	1	19	(0.05)	0	5	3	(0.00)	0.0	1.0
Ivan	9	4	(0.692)	17	11	0	(0.607)	0.032	0.86
Isabella	3	11	(0.214)	8	4	2	(0.667)	3.723	0.05
Josefina	2	7	(0.222)	14	12	0	(0.538)	1.57	0.21
Jade	0	16	(0.00)	9	0	0	(1.00)	20.85	0.0

Choices for each option in the two-choice and three-choice tests. Relative preferences for banana (shown as P (A); calculated as: A/(A + B)) are shown for each choice test. P values reported are those before Bonferroni corrections. Individuals who showed a significant change in preference after multiple test corrections are shown in bold.

* Denotes chi-square comparison not possible with zero preference for papaya in both choice tests.

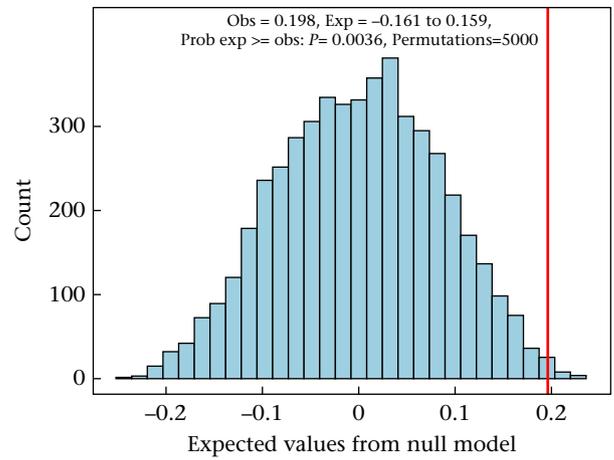


Figure A1. Permutation test results of the difference in preference between the two-choice and three-choice tests (mean change = 0.2, 95% CI: 0.08–0.35, N = 18, permutation P < 0.005). The vertical red line denotes the observed values.

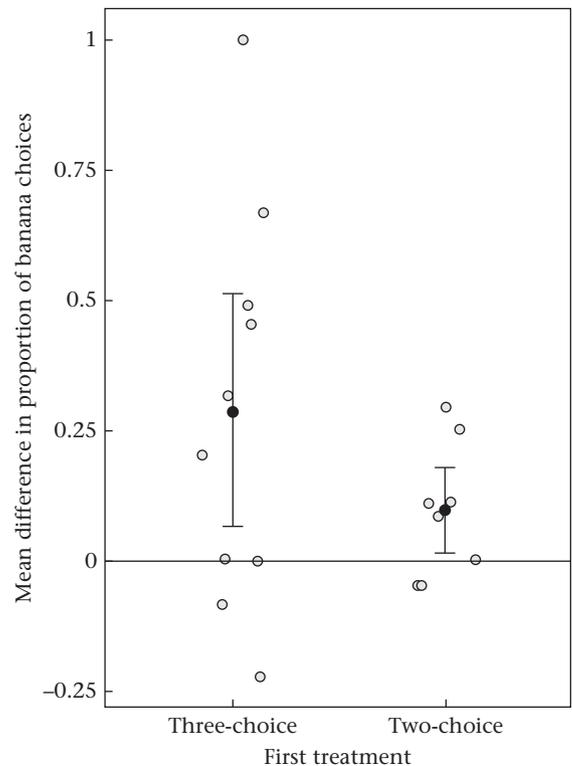


Figure A2. Mean difference in preference for banana in two- and three-choice tests by treatment order. Bats that received the three-choice test first are shown on the left and bats that received the two-choice test are shown on the right. Order of presentation for each cohort is given in the Appendix (Table A2).



Figure A3. Seven stages of banana ripeness. Unripe bananas were selected from stages 2–3 and ripe bananas were selected from stages 6–7.



Figure A4. Ripe papaya is characterized by yellow skin, darker flesh and black seeds.

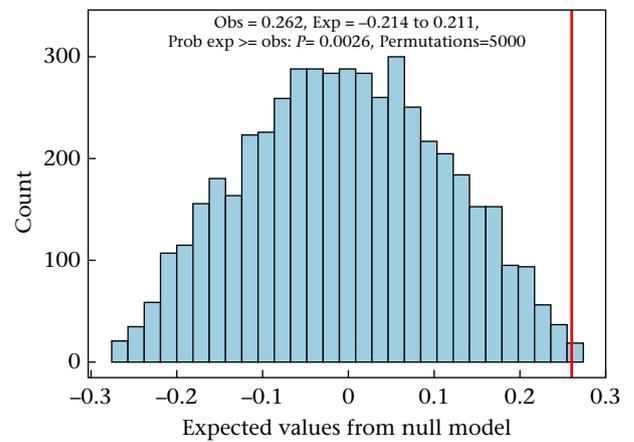


Figure A5. Results of the same permutation test outlined in Fig. A1 with the bats that sampled the decoy removed from the analysis. Shift in preference between the two-choice and the three-choice test (mean change = 0.26, 95% CI: 0.12–0.48, $N = 12$, permutation $P = 0.003$).