

Rationality in decision-making in the fringe-lipped bat, *Trachops cirrhosus*

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Abstract

Most models of animal behavior assume rationality in animal's decisions, with animals maintaining strict preferences for different options (e.g., optimal foraging theory). In the wild, however, animals often choose among several options simultaneously, and their evaluation of each prey type may depend on the perceived relative values of other choices. Fringe-lipped bats (*Trachops cirrhosus*) are promising subjects for studying how animals make decisions. When given a choice between the calls of two species of frogs, *T. cirrhosus* will choose the more salient call that is associated with the higher capture rate. Although in the wild *T. cirrhosus* often choose among multiple call options, most tests of prey preferences in this system include only two options. In this experiment, we tested whether *T. cirrhosus* alters relative preference for two call types that differ along two acoustic dimensions (amplitude and complexity) when presented with a third, “decoy” option, inferior to the two original options along either one or both dimensions. Results from this study demonstrate that under these circumstances, *T. cirrhosus* evaluates all three options independently of one another, and thus, preferences remain consistent and rational in both the presence and

absence of a decoy. These results counter many other experiments suggesting irrationality in animal decision-making.

Significance statement

A fundamental assumption of animal behavior is that animals make rational decisions. However, most animals are tested in ways that rely on simple binary choice experiments. Because animals are often faced with multiple options simultaneously in the wild, these tests may often fail to capture the complexity necessary to understand cognitive limitations that naturally influence animal decisions. In certain cases, complex decisions can result in irrational behavior that is inconsistent with what is found in binary choice studies. Here, we conducted a test with fringe-lipped bats to determine whether their choices for specific frog calls were influenced by the number of options in a choice set. We found that, unlike many other animals, the fringe-lipped bats appear to make consistent decisions, even with more complex choice sets. Our results indicate that there are likely to be strong selective pressures on rational decision-making in this species, perhaps shaped by high metabolic requirements.

Keywords Bats · Túngara frogs · Rationality · Regularity · Decoy effect · Decision-making

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Introduction

There are striking similarities between economics and biology in the way that the two fields model decision-making behavior. Just as economic theory predicts that humans will act in ways that maximize financial gain, natural selection is expected to favor decision-making that maximizes fitness. In models of animal choice, animals are expected to evaluate options in absolute terms and assign some intrinsic, fitness-related utility value to

different options (Shafir 1994; Orr 2007). This utility can be associated with food acquisition or access to mates, shelters, or other resources. Models of behavior that assume utility maximization, such as optimal foraging theory, have been widely successful at predicting different aspects of animal behavior (e.g., MacArthur and Pianka 1966; Stephens and Krebs 1986).

A major consequence of assuming animals behave in ways that optimize this fitness-related utility is encompassed by the economic concept of rationality (Kacelnik 2006). In an economic sense, rationality refers to behaviors that result in maximized utilities. There are two main principles of rationality: *transitivity* and *independence from irrelevant alternatives* (McCleery 1978). Transitivity refers to a noncircularity in decision-making: if A is preferred to B and B is preferred to C, then A should be preferred to C (Navarick and Fantino 1972). The constant ratio rule, which is a probabilistic form of independence from irrelevant alternatives, states that the introduction of an irrelevant or inferior alternative into a choice set should not alter relative preferences between existing options (Luce 1959; Huber et al. 1982). In other words, if A is preferred to B, then this relationship should not change in the presence of C. Failure to adhere to these two axioms is referred to as “irrational” decision-making.

One apparent violation of rationality that has been empirically demonstrated in humans, and more recently in animals, is called the asymmetric dominance effect or “decoy effect” (Huber et al. 1982). In the decoy effect, two options are present that differ along two dimensions. When a third option, the “decoy”, is presented, which is inferior along both dimensions by one option (target) but only one dimension by the other (competitor), there can be a noticeable shift in preference between the first two options towards the target option (Huber et al. 1982). For example, if consumers are choosing between two cans of vegetables, one that is more expensive but organic (target) and another that is cheaper but not organic (competitor), there may be a 50/50 preference between the two. However, if a third can is introduced that is expensive and is not organic (decoy), consumers might exhibit a subtle shift in preference towards the first, expensive, and organic option (target). This is because the decoy is inferior on two dimensions by the target and only one by the competitor.

This effect has more recently been explored in foraging, mating, and habitat choices in animals. Attempts to investigate rationality in wild animals have mostly shown evidence for irrationality. For example, Bateson et al. (2002) have demonstrated that wild rufous hummingbirds, *Selasphorus rufus*, show violations of rationality in response to the addition of an asymmetrically dominated decoy. Similarly, Shafir et al. (2002) have demonstrated that foraging choices of gray jays, *Perisoreus canadensis*, and honeybees, *Apis mellifera*, are influenced by the addition of a third option to a choice set. Although we have substantial evidence for both irrational and rational behavior among diverse taxa (see Table 1), we have a fragmented

understanding of the ecological contexts in which comparative evaluation plays a role in decision-making across taxa.

In the wild, animals often choose among several options simultaneously that differ in more than one attribute. In situations in which acquiring and integrating information is time-consuming (Dukas 1999), and costly in terms of predation pressure (Dukas and Kamil 2000) and missed opportunities (Johnson et al. 2013), comparative mechanisms of decision-making can serve as economic “rules-of-thumb” (Bateson and Healy 2005). Comparative evaluations may lead to decisions that are irrational, in that they may not maximize any given utility. However, if they still outweigh the costs of absolute evaluations, they may still maximize *Darwinian fitness*, representing an adaptive decision-making strategy in some contexts (Gigerenzer and Goldenstein 1996; Bateson and Healy 2005; Johnson et al. 2013). Deviations in rationality have the potential to bias mate choice and foraging behaviors in predictable ways that have received little consideration (Bateson and Healy 2005; Ryan et al. 2009). Switches from absolute to comparative evaluation can be found in the human economic literature in which people tend to behave rationally when presented with few options, but fail to behave rationally in more complex, or contrived, scenarios reflecting underlying cognitive limitations (Heath and Chatterjee 1995; Gigerenzer and Goldstein 1996; Edwards and Pratt 2009). Advertisers have created very clever ways of exploiting human irrationality by manipulating the contexts in which options are presented in order to sway consumer decisions (e.g., Ariely 2010).

There has also been a more recent general interest in the cognitive mechanisms and ecological pressures involved in decision-making in bats (e.g., Simmons et al. 1990; Page and Ryan 2005; Winter and Stich 2005; Ghose and Moss 2006). Historically, most studies of cognition in mammals have been biased towards primates and rodent species (Shettleworth 2010), and bats are phylogenetically quite distant from both groups. Whether most bat species conform to predictions of rationality during foraging has not been investigated.

In this study, we tested for the effects of an asymmetrically dominated decoy option on foraging decisions in wild, fringe-lipped bats (*Trachops cirrhosus*). To test this, we evaluated the absolute and relative preference for two frog calls in the presence and absence of an asymmetrically dominated “decoy” call, using a series of choice experiments manipulating the relative amplitude and complexity of these calls. These two dimensions naturally vary for male calls in the wild and contribute to localization and preference (Tuttle and Ryan 1981; Page and Ryan 2008). If *T. cirrhosus* relies on comparative evaluation, then the addition of an alternative to a choice set should influence the relative preference of preexisting options (e.g., Shafir 1994; Bateson et al. 2002). Alternatively, if *T. cirrhosus* does not rely on comparative evaluation, we should not detect irrational behavior upon the addition of a decoy.

Table 1 Known studies testing for context-dependent violations of independence of irrelevant alternatives using the decoy effect in nonhuman animals

Taxa		Behavior	Study
Arthropods	Honey bees (<i>Apis mellifera</i>)	Irrational	Shafir et al. 2002
	Temnothorax ants (<i>Temnothorax curripinosus</i>)	Rational	Edwards and Pratt 2009
		Irrational (individual); rational (group)	Sasaki and Pratt 2011
	Fiddler crabs (<i>Uca mjoebergi</i>)	Irrational	Reany 2009
Birds	Gray jays (<i>Perisoreus canadensis</i>)	Irrational	Shafir et al. 2002
	Rufus hummingbirds (<i>Selasphorus rufus</i>)	Irrational	Hurly and Oseen 1999; Bateson et al. 2002, 2003; Morgan et al. 2012, 2014
	Starlings (<i>Sturnus vulgaris</i>)	Irrational	Bateson 2002
Rational		Schuck-Paim and Kacelnik 2004; Monteiro et al. 2013	
Amphibians	Túngara frogs (<i>Physallemus pustulosus</i>)	Irrational	Lea and Ryan 2015
Fish	Green swordtails (<i>Xiphophorus helleri</i>)	Irrational	Royle et al. 2008
	Peacock blenny (<i>Salaria pavo</i>)	Irrational	Locatello et al. 2015
Mammals	Cats (<i>Felis catus</i>)	Irrational	Scarpi 2011
	Rhesus macaques (<i>Macaca mulatta</i>)	Irrational	Parrish et al. 2015
Other	Slime mold (<i>Physarum polycephalum</i>)	Irrational	Latty and Beekman 2011

Study system

The fringe-lipped bat, *Trachops cirrhosus*, is a Neotropical bat that hunts frogs and insects by eavesdropping on their mating calls (Tuttle and Ryan 1981). The túngara frog, *Physalaemus pustulosus*, is a preferred prey species of this bat. It produces two types of sexual advertisement calls, simple and complex, and both female frogs and predatory bats are attracted to simple calls but prefer complex calls (Rand and Ryan 1981; Ryan et al. 1982). Both simple and complex calls start with a whine, which is a frequency-modulated sweep. Complex calls differ from simple ones in that the whine is followed by one to seven chucks: short broadband suffixes (Ryan 1985, see Fig. 1a). Túngara frog males calling alone tend to produce just the whine, but when calling together, they produce complex calls (Ryan et al. 1982). There is no known relationship between the size of a male and numbers of chucks or the proportion of calls with which he adorns them (Bernal et al. 2007). Along with a greater preference for complex calls, *T. cirrhosus* has been shown to prefer higher amplitude calls (Tuttle and Ryan 1981). While, to date, the localization performance of *T. cirrhosus* has only been tested with call complexity, both complexity and amplitude are likely to play a role in localization success. Increased localizability likely serves as part of the basis for the bats' preferences both for increased complexity and increased amplitude.

Túngara frogs mainly call from small, ephemeral ponds typically consisting of around one-to-five individuals calling simultaneously (Ryan 1985). *Trachops cirrhosus* hunts by flying over patches of calling frogs and gleaning prey items off substrates (Kalko et al. 1999). Frogs have been shown to

sometimes detect an approaching bat after which they execute a series of evasive behaviors (Tuttle et al. 1982). Thus, the context of decision-making presented in this study is ecologically relevant as *T. cirrhosus* has a short period to detect and choose between multiple calling prey items.

Methods

Subject and study site

We captured 11 adult *T. cirrhosus* using mist nets set along streams and near small ponds in Soberanía National Park, Panama, from May to August 2015. All captured bats were held and tested in outdoor flight cages (5 × 5 × 2.5 m) in Gamboa, Panama. Each bat was tested alone. Following testing, each bat was released at its initial capture location. For long-term identification and to avoid multiple testing of the same individual, each bat was injected with a subcutaneous passive integrated transponder tag (PIT tags, Trovan, Ltd.). This technique has proven effective for long-term identification in *T. cirrhosus* and even smaller sized bats (Page person. comm.). All experiments were licensed and approved by the Smithsonian Tropical Research Institute (STRI IACUC protocol 2014-0101-2017) and the University of Texas, Austin (AUP-2015-00048) and by the Government of Panama (Ministerio de Ambiente permit SE/A 69-15). Following capture, bats were maintained in a small (142 × 127 × 203 cm) mesh tent for 24 h, where they were hand fed bait fish and then released into the flight cage (following Page and Ryan 2005; Jones et al. 2014).

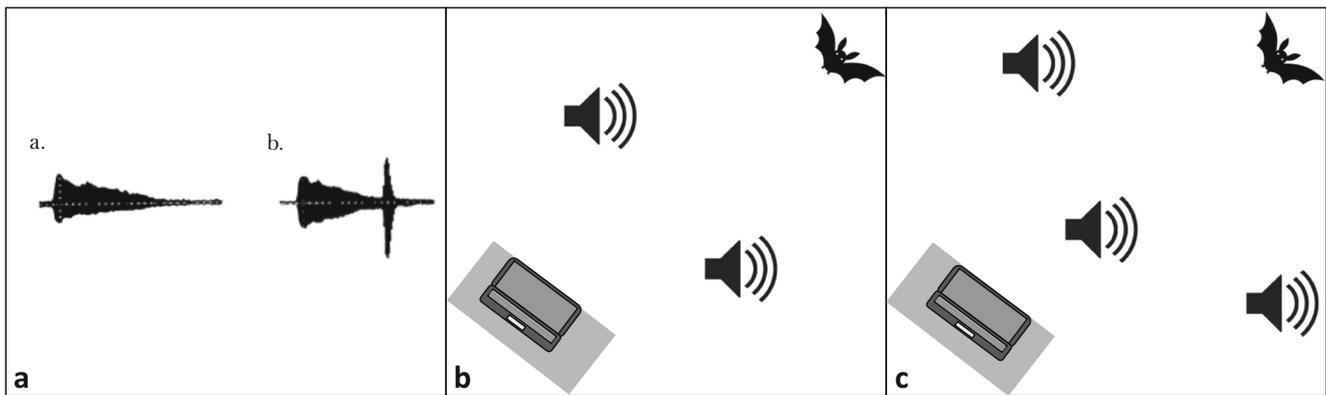


Fig. 1 **a** Call structure of a male túngara frog, *Physalaemus pustulosus*. Oscillogram of a whine (*a*; simple) and a whine paired with one chuck (*b*; complex) taken with permission from Ryan and Rand (1990). **b**

Experimental flight cage setup for binary choice test. **c** Experimental flight cage set up for trinary choice test. Experimenter station is in bottom left corner across from the bat roost

Experimental arena

In the flight cage, bats were positioned in a shelter with a perch to which they were trained to return between stimulus presentations. The flight cage was illuminated with a 25-W red light invisible to the bats. In the center of the flight cage, we placed Fostex FE103En speakers 1.5 m apart, each 2 m from the roost. The experimenters sat in the corner opposite the bat, with the video and playback equipment (see Page and Ryan 2005).

The experimental stimuli were modified using Adobe Audition 3 from a modal túngara frog call drawn from a sample of 300 male calls from 50 males (Ryan and Rand 2003). Stimulus period was 2 s and stimuli were broadcast between 71 and 77 dB sound pressure level (re. 20 μ Pa) at a distance of 1 m from the speaker, which is consistent with natural call rate and amplitude in the wild (Ryan and Rand 1981). Stimuli were broadcast from a Lenovo T500 Thinkpad laptop into an Edirol UA700 USB recording interface, which connected to speakers through a Pyle Pro PTA2 amplifier. The bat's flight from the speaker was videotaped with two cameras. The first video camera (Sony DCR-TRV340) was positioned on the perch to capture latency to fly following the onset of the stimuli presentation; the second was focused on the speakers to record bat approach and stimulus choice. Finally, the flight cage was additionally illuminated with two, high-power LED IR lights (IR Yeshzhuanjia, model 80AIR) for enhanced video recording in the dark flight cage.

Initial training

Following release into the flight cage, bats were allowed one to two nights to forage for prey rewards in response to frog call stimuli broadcast from a speaker placed in random positions within the flight cage. During this acclimation period, we broadcast the calls of different nocturnal frog species (*Smilisca sila* and *Dendropsophus ebraccatus*) than the one

later used in experiment (*Physalaemus pustulosus*). When bats were accustomed to finding a fish reward in response to a frog call in captivity, we began the experimental trials (Page and Ryan 2005).

Experimental procedure

We conducted experiments between 1900 to 0300 h each night over an average of four consecutive nights. Because experiments simultaneously served as feedings, bats were typically fed around 4 g of fish per feeding in three separate feedings each night (1900, 2200, and 0100 h). By conducting the trials and the associated feedings in multiple bouts in this way, we attempted to minimize fluctuations in hunger and satiation throughout the night. This likely helped to alleviate artifacts of state-dependence on potential violations of rationality that have been previously reported (Schuck-Paim et al. 2004; Waite et al. 2007; Monteiro et al. 2013).

In each treatment, the speakers were placed 1.5 m apart to allow for clear discrimination between stimuli (see Fig. 1); previous studies with this species have shown discrimination at around half of this distance (0.8 m) (Gomes et al. 2016). Stimuli were broadcast simultaneously until the bat flew. If the bat did not fly after 60 s, the playback was stopped for 120 s before it was played again (Fugère et al. 2015). If a bat did not fly after three sequential presentations, a feeding was stopped. Phonotaxis was defined by flight within 10 cm of a speaker. Food rewards (bait fish) were placed on all speakers to ensure that bats not only maintained motivation to fly towards playbacks but also to ensure that bat approaches were in response to acoustic stimuli and not to olfactory, echolocation, or visual cues that could potentially differ between the stimuli (Page and Ryan 2005; Gomes et al. 2016). Studies have also shown that bats do not approach baited speakers in the absence of acoustic stimuli emanating from the speakers and do not attend to other sensory stimuli associated with the food reward

(Page and Ryan 2008; Jones et al. 2014). To minimize spatial associations with rewards, playback location was randomized between speakers.

In the binary choice treatment, bats were given a choice between a normal amplitude whine +3 chucks broadcast at an amplitude of 74 dB SPL (option A) and a higher amplitude whine with no chucks broadcast at 77 dB SPL (option B) (Fig. 1b). These two options were selected in order to elicit an approximately 50/50 preference both within and between individuals, as both options dominate each other on respective axes (complexity or amplitude; see Fig. 2). We selected these stimuli following results of Ryan et al. (1982) which showed that a 4-dB difference between a whine and whine +1 chuck was sufficient to elicit a reversal of preference.

In the trinary treatment, a third speaker was added. Here, all three speakers were again spaced 1.5 m apart and 2 m from the roost. The additional speaker broadcasted a lower amplitude whine with no chucks, at 71 dB SPL (option C) (Fig. 1c). This call was inferior to A on both dimensions (complexity and amplitude) but to call B on only one dimension (amplitude). In this treatment, all three stimuli were presented simultaneously in a three speaker phonotaxis choice test. If bats behave irrationally in this context, the expectation is that preference for call A will increase in this treatment group. If bats maintain their original preference, the prediction is that response to A and to B should remain roughly 50–50.

Each bat was tested in each design. All bats were given roughly 60 choices in total (~30 in each treatment). Six of the 11 bats were tested first in the binary and then the trinary (30 + 30) choice experiments. The remaining five bats were tested in binary, trinary, binary, and trinary experiments (15 + 15 + 15 + 15) to account for order effects. Each bat spent between 3 and 5 days in the flight cage for experiments. To minimize observer bias, one observer would present the auditory cue to the bat and the other would blindly record which speaker to which the bat flew. All trials were also video recorded. In cases in which it was not immediately clear from observation, trials were scored from the recorded video by a naïve observer.

The fact that most bats in this experiment sampled the decoy call at least once suggests that the bats are able to hear the decoy call in both the binary and trinary treatments. Alternatively, if the bats could not hear the decoy call, it is possible that bats were flying to decoy speakers due to learned spatial association of a previous reward. To discriminate between these possibilities, we conducted a series of binary choice tests in a separate experiment, in which bats were given a choice between a speaker broadcasting either a whine or a whine + chuck at 75 dB and another speaker that was baited but silent. A series of 55 trials were conducted using a separate group of 17 bats from Soberanía National Park, Panama. All bats tested in this experiment had been trained in similar ways and had received a minimum of 30 unrelated trials prior to

testing. Therefore, all bats had been rewarded on both speakers in the exact same location.

Statistical analyses

For each bat, we computed the proportion of choices made for options A and B in both the binary and trinary choice tests. Relative preferences were computed as $P(A)/(P(A) + P(B))$. Although trinary choice tests consisted of three options, for this study, we were only interested in the relative preferences between options A and B. Therefore, we did not include flights to option C in the analysis, and the remaining proportion reflects flights to A or B. To be sure that option C was not a preferred option, we performed a chi-square test to determine if the flights to call C were significantly different than one third of all trials.

A two-tailed binomial test was conducted to test for overall preference for either option A or B for all bats in both the binary and trinary treatment groups. This was done to determine whether one call type was preferred over the other, regardless of treatment group. We then performed two-tailed Fisher's exact test to test for a difference in proportion of flight to A and B in the presence and absence of the third call type, C, at a group level.

For each individual bat, we also conducted a two-tailed binomial test on preference for A or B in both treatments. Fisher's exact test was then run on each individual's preference in both treatments to test for a difference in proportion of flights to A in the binary and trinary conditions. This was done to determine whether there is individual variation in rational behavior within a population.

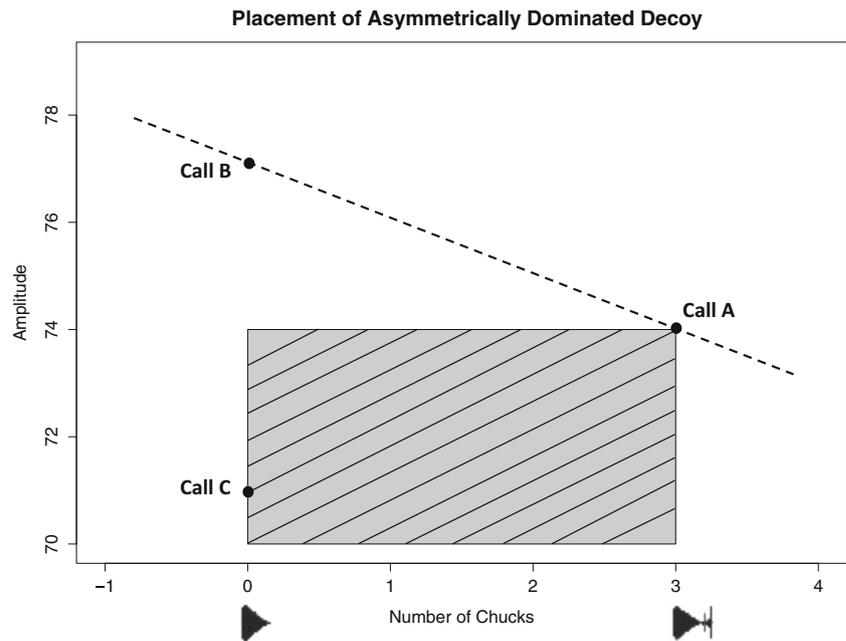
A mixed-effects linear model was run in R 3.0.2 (R Developmental Core Team 2015) using the lme4 package to test for the effect of treatment on the proportion of choices for the target and competitor calls. This model also allowed us to test for other potential covariates on the proportion of flights to either call. Covariates included night, feeding, side, and order. Bat individual was included as a random intercept.

Lastly, for the separate binary choices between a broadcasting and silent speaker that were both baited, we ran two-tailed binomial test preferences between the two speakers. This was done to control for any learned associations between the location of the speaker and a food reward. All data are available in the supplementary material.

Data availability statement

All data generated or analyzed during this study are included in this published article and its supplementary information files.

Fig. 2 Placement of the asymmetrically dominated decoy. Call A dominates call C on both axes (complexity and amplitude), whereas call B only dominates call C on one axis (amplitude). Shaded area represents all potential placements of the decoy to be asymmetrically dominated by call A and call B. Figure modified from Huber et al. 1982 (created in R Studio and modified in Inkscape)



Results

Figure 3 shows the proportion of choices to options A and B in both the binary and trinary choice tests. Mean preference for option A in the binary choice test was 0.52 ± 0.091 (mean \pm SE, $n = 11$), which was not significantly different from preference for B ($p = 0.48$). This roughly 50–50 preference for A vs. B in the binary test was as predicted by the researchers' choice of approximately matching stimuli. We found that nine of the 11 bats flew to the decoy call at least one time with an average of 2.9 choices for the decoy call across all bats. As seen in Fig. 3, choices for the decoy call made up about 9% of all choices in the trinary choice test. Additionally, the decoy call was chosen across all three speakers for the two flight cages used for experiments, indicating that while the decoy was less preferred than the other calls, they were in fact detectable ($\chi^2 = 88.92$, $df = 2$, $p < 0.0001$).

Preference for option A in the trinary choice test was 0.51 ± 0.087 (mean \pm SE, $n = 11$), which was also not significantly different from preference for option B ($p = 0.65$). Overall, there was not a significant shift in preference for either option A or B between the binary and trinary choice tests ($p = 0.94$) demonstrating regularity in the bats' decisions on a group level.

Table 2 shows the proportions of choices to each of the options in the binary and trinary treatments. Within the binary condition, two of the 11 bats tested flew to A significantly more than to B (bat F: $p = 0.002$; bat H: $p = 0.018$). Also, within the binary test, one individual flew to B more than A (bat J: $p = 0.0001$). The binary choices of the remaining eight bats were not significantly different from chance ($p > 0.05$,

Table 2). These data indicate that not all bats had an initial preference for either option A or B in the binary treatment, and there was high variability in preference across bats in the binary treatment. Within the trinary treatment, three bats showed a significant preference for call A (bat A: $p = 0.013$, bat F: $p = 0.014$, and bat H: $p = 0.011$), and one bat had a significant preference for call B (bat E: $p = 0.04$). Only one bat (bat A)

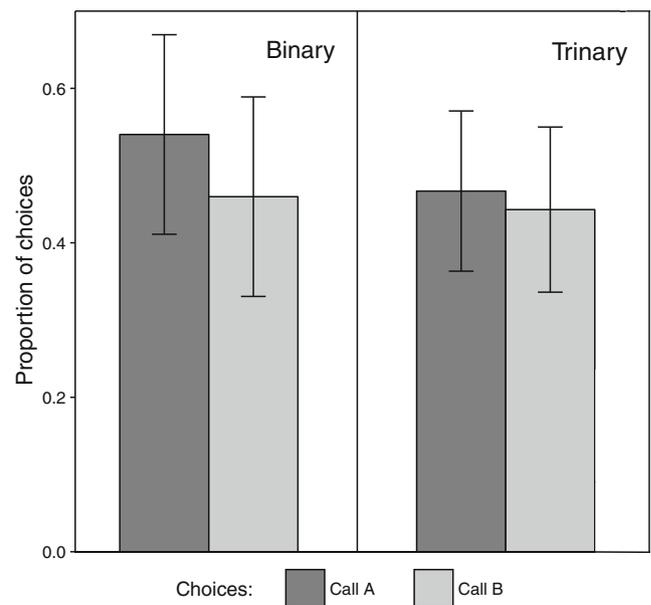


Fig. 3 Introduction of a decoy does not change the relative proportions of choices for call A vs. call B. Proportions represent the mean number of proportions across all individuals for calls A and B in the binary choice tests and calls A, B, and C in the trinary choice tests with 95% confidence intervals. We found no significant difference between preferences for the target or competitor calls in the binary vs. trinary treatments. Figure 3 created in R Studio and modified in Inkscape

Table 2 Proportion of choices for Call A over Call B in both binary and trinary choice test across individuals

Animal	Binary		Trinary		Fisher's exact
	p (A, B)	P	p (A, B)	P	
A	0.45	0.719	0.75	0.014*	0.033*
B	0.70	0.444	0.47	0.857	0.115
C	0.58	0.472	0.46	0.849	0.439
D	0.34	0.111	0.43	0.582	0.603
E	0.40	0.363	0.30	0.044*	0.589
F	0.80	0.002**	0.75	0.014*	0.757
G	0.63	0.201	0.64	0.186	1.000
H	0.73	0.018*	0.77	0.011*	1.000
I	0.50	1.0	0.46	0.841	0.791
J	0.13	0.0001***	0.32	0.110	0.114
K	0.50	1.0	0.30	0.055	0.177

Fisher's exact test displays two-tailed difference between these two preference scores in each treatment (* = $p < 0.05$, ** = $p < 0.005$, *** = $p < 0.0005$)

showed a significant shift towards option A between the two treatment groups ($p = 0.03$). The remaining 10 bats did not exhibit a significant shift ($p > 0.05$). These results demonstrate that only one of 11 bats exhibited irrationality across the two treatment groups.

The fit of the null model, with only the random intercept, was not significantly improved by adding a main effect of treatment ($\chi^2 = 0.495$, $df = 4$, $p = 0.48$). Interestingly, there was a significant interaction between two of the covariates, night and flight cage used ($\chi^2 = 22.93$, $df = 8$, $p < 0.001$); however, we are unable to explain these findings as these flight cages are identical, located 6 m apart, and are likely subject to the same ambient sounds. Additionally, eight bats were tested in one flight cage, whereas three bats were tested in the other.

Of the 17 bats tested separately for the effects of the silent speaker, we found that out of 55 total binary trials that were baited, only one instance of a bat flying to the silent speaker over the broadcasting speaker was recorded ($p < 0.0001$). Therefore, these experimental results suggest that bats flying to the decoy speaker in this experiment were perceiving the decoy call.

Discussion

The influence of irrelevant alternatives on choice behaviors has recently become of great interest to behavioral ecologists in terms of predicting deviations in mating and foraging decisions (Bateson and Healy 2005). The majority of literature on decisions made in the presence of a decoy suggest that most animals behave irrationally (Table 1). These results seem to

span animals across taxa and decisions made in a variety of contexts (mate choice, foraging, habitat choice, etc.).

In a series of binary and trinary choice tests between túngara frog calls that differ in complexity and amplitude, we tested whether *T. cirrhosus* would be susceptible to the decoy effect. We have demonstrated that *T. cirrhosus* does fit the predictions of economic rationality principles, specifically adhering to the axiom of independence of irrelevant alternatives. Similar studies in other species have documented predictable, irrational, shifts in preference between choices when a third, decoy, option was added to a choice set (see Table 1). Given the economic principles described above, we would have expected that preferences in the trinary treatment would shift towards call A, since call A dominated call C in both complexity and amplitude, whereas call B only dominated call C in amplitude (see Fig. 2). These results indicate that within the context of this experiment, *T. cirrhosus* appears to rely on absolute evaluation when choosing between three multiply calling prey items.

A fundamental assumption in this experiment was that bats would be able to discriminate between all three calls presented simultaneously and make decisions based on the two dimensions manipulated in this study. This assumption was met in our experiment, and it was clear that bats could detect all three calls, as most bats sampled the decoy call at least once. We also have evidence that bats do not fly to silent speakers over broadcasting speakers based on learned associations with baited speakers. Therefore, we believe that these results reflect decision-making mechanisms of *T. cirrhosus* in the wild in similar contexts. Furthermore, the parameters used in this study match naturalistic conditions to the best of our knowledge. While choruses of calling males in the wild can be up to several hundred individuals (Ryan et al. 1981), it is much more common to find smaller patches consisting of one-to-five calling frogs in smaller, more ephemeral ponds (Ryan 1985). Given our results, we expect that in these scenarios, *T. cirrhosus* is largely making rational decisions in the wild when choosing among three or fewer frog calls. Whether these patterns hold when *T. cirrhosus* chooses between four or more frogs calling simultaneously is subject to further investigation.

On an individual level, 10 of the 11 tested bats adhered to the principle of regularity in this study. Because we did not account for multiple comparisons in the interpretations of our p values, it is possible that the one bat in which we detected a significant change could be attributed to random shifting. This, however, would not change the interpretation of our results. We also observed that there was high variability in preference for either call A or call B across individuals and treatments. This suggests that while there is high variability across bats in their preference for different call attributes, individual bats are highly consistent in their preferences. Our results correspond to those of Morgan et al. (2014), which showed that individual hummingbirds were consistent in their

preferences for sugar solutions that vary in both concentration and volume; however, variation in preference was not detectable at the group level in their study.

Bats provide a promising system for studying cognitive mechanisms involved in decision-making in mammals. They have the highest metabolisms among mammals (Shen et al. 2010) due to powered flight and have likely faced very strong selection pressures on different aspects of their cognition necessary to match energy requirements. It is possible that evolution has shaped aspects of bats' cognition in ways that prevent them from using comparative evaluation or rules-of-thumb, which would likely result in subtle decrements of energy over time. If the selection pressures operating on this aspect of decision-making indeed reflect the metabolic demands of bats, this may explain why these bats behave rationally even in contexts and situations in which other animals often fail to do so (see Table 1). Perhaps high metabolic rates coupled with their mobile, evasive preys have worked in concert to shape this aspect of cognition in *T. cirrhosus*. Although hummingbirds are highly constrained metabolically as well, fast decision-making might not be a selective requirement for these decisions due to stationary prey items. Further, other studies investigating different aspects of cognition have shown significant differences between hummingbirds and nectivorous bats that have likely been shaped by metabolic demands (e.g., Winter and Stich 2005).

Further investigation in other species of bats could shed light on whether this aspect of cognition is an evolutionarily shared trait among closely related species or is unique to the ecology of this species. Within this family of bats (Phyllostomidae), there are frugivorous, nectivorous, insectivorous, sanguivorous, carnivorous, and omnivorous species, making it the most ecologically diverse family of bats (Fleming 1986). Within this family, comparative studies could be conducted to determine whether rationality is a shared ancestral trait or whether it is unique to the predatory foraging strategy of *T. cirrhosus*. Alternatively, *Cardioderma cor* is another carnivorous, gleaning bat found in the Old World that eavesdrops on prey-emitted sounds (Ryan and Tuttle 1987) but does not belong to the family Phyllostomidae. This provides a possible ecological comparison to determine whether there is convergent evolution of this cognitive trait in another species with both a high metabolism and a predatory foraging strategy. Whether rationality in *T. cirrhosus* is the result of some conserved cognitive property of bats within this family or whether it is unique to the ecology and life history of *T. cirrhosus* provides an avenue for further investigation.

For comparative evaluation to elicit a decoy effect, attributes must be compared along multiple dimensions (Huber et al. 1972). Therefore, another possible explanation for our results is that the two attributes we chose to vary are not in fact evaluated along separate dimensions. If complexity and amplitude are both necessary for increasing localization, then

both attributes may simultaneously contribute information to the bats necessary to optimize capture success. If two calls are equally localizable, they may be chosen at random and would not be subject to the decoy effect. This may be possible given the preference for the two calls across all individuals did not differ from random expectations; however, five bats showed a significant preference for either the target or competitor call in the binary and trinary choice tests.

One potential limitation in this study is that for both the decoy and competitor option, the value of each option on the complexity dimension was 0 chuck (whine only). Although the decoy used in this study fits within the parameters of where a decoy must fall between the target and competitor to create a predictable shift in preference, using zero for a dimension can lead to a different form of irrational behavior. There is substantial evidence in the human literature that zero is treated in a numerically distinct way from other numbers (Shampanier et al. 2007). For instance, the effect of zero vs. one is often treated differently than one vs. two or other quantity increments. This form of irrationality involves attentional switching away from the aspect that is absent in several of the options, in this case complexity. It is possible that this may have prevented noticeable shifts towards the decoy (call C), although this effect of zero has not been observed with *T. cirrhosus* when given a choice between whine + zero chucks vs. whine + one chuck and whine + one chuck vs. whine + two chucks (Akre et al. 2011). Furthermore, it is common for bats in the wild to choose between frogs calling with zero and one chuck.

Another commonly proposed explanation for why irrationalities occur in decision-making is that the individual's physiological or informational state varies across decisions, and thus, decisions are not consistently made in the same contexts (Pompilio and Kacelnik 2005; Pompilio et al. 2006; Waite et al. 2007). In this study, there was no apparent effect of feeding time on the proportion of choices made for call A or B in either the binary or trinary choice tests. Therefore, it is unlikely that the state or hunger levels of individuals played a strong role on the preferences of individuals in this study. It is possible that because all individuals in this study were fed to satiety each day of the experiment, that state plays a larger role in decision-making of *T. cirrhosus* in more naturalistic conditions. Follow-up studies specifically manipulating the condition and satiety levels of individuals would be necessary to fully understand the role that state plays on decision-making in this species.

Although the bats in this study adhered to strict preferences, the majority of published studies testing for decoy effects report deviations from rationality. In a simple search on Google Scholar and web of science, using the keywords "rationality," "decoy effect," and "regularity," we compiled a table of relevant studies in animals investigating economic principles of rationality, and specifically independence from

irrelevant alternatives, in decision-making. Of the 19 studies we reviewed, 15 (78%) report irrational behavior and only four (22%) report rational behavior. There are two possible explanations for reported irrationalities across many different species of both vertebrates and invertebrates. Either there is a publication bias towards studies that find irregularity in choice behavior (see Table 1), as rationality is the null expectation for most studies, and “negative” results are published less frequently (Duval and Tweedie 2000). Or comparative evaluation mechanisms are more common than previously thought. Further investigation is necessary to determine whether we should consider rationality as the exception rather than the rule and how it may or may not be adaptive in different ecological contexts. We encourage research to be published demonstrating both rationality and irrationality to better understand how selection operates on this component of cognition.

Irrationalities should not arise if animals are evaluating options independently of one another, as predicted by normative models of animal foraging behavior (e.g., optimal foraging theory, MacArthur and Pianka 1966; but see McNamara et al. 2014 for a counter argument). We argue that rationality principles should remain an integral part of these models. Furthermore, when rationality fails, it gives strong indication of the underlying mechanisms of decision-making (Sanfey et al. 2006). Because these rationality deviations appear to be such ubiquitous phenomena, they bear widespread implications for choice models of animal behavior. This effectively makes dichotomous choice tests, where animals are presented with only two options, representing two extremes, less effective at describing mating or foraging preferences in the wild.

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