Transitive foraging behaviour in frog-eating bats

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Most models of animal foraging assume that individuals make decisions rationally. One expectation of rationality theory is that preferences should be hierarchical or transitive. For many animals, including humans, making decisions about what to eat can become difficult when various parameters of choices are not positively related to one another and no single option may be considered the best. These complex decisions can result in irrational behaviour, suggesting that the value of any particular option may vary depending on the other available options. Here, we tested whether frog-eating bats, *Trachops cirrhosus*, are transitive in their preferences for frog calls. These bats attend to several attributes of the calls, such as call amplitude and complexity, when choosing a frog to target in their attack. While acoustic preferences are largely understood in isolation, we have a limited understanding of how bats choose between calls that vary along several important acoustic dimensions. Here, we conducted a series of binary choice experiments manipulating amplitude and complexity both separately and together to evaluate whether these bats make transitive foraging decisions. We found that bats are transitive in their rankings of calls based on these acoustic dimensions, with preferences reflecting a trade-off between both amplitude and complexity. Overall, our results add support to the notion that bats' preferences obey the general principles of rational behaviour and support the use of optimality approaches to the study of animal behaviour and decision making.

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There is a compelling parallel between optimal foraging theory and economic theory in terms of how decision making is modelled. Foraging theorists depict animals as maximizing fitness (Parker & Maynard Smith, 1990; Stephen & Krebs, 1986), while economists depict individuals as maximizing some monetary utility value (Huber, Payne, & Puto, 1982). Because evolutionary fitness is often difficult to measure directly, choice models usually deal in the more easily measured currency of 'utility', which is assumed to contribute to fitness. This parallel suggests that examining animal behaviour from an economic perspective should produce comparable outcomes and perhaps new insights into the evolution and mechanisms of decision making in nonhuman animals (Shettleworth, 2010).

A key assumption in economics is that people maximize utility in consistent ways across time and contexts and thus behave 'rationally' (Kacelnik, 2006). Among other things, this means that choices should be transitive or noncircular. If option A is preferred to B and B is preferred to C, then A should also be preferred to C

(Navarick & Fantino, 1972). If individuals evaluate options independently of one another, all options should be given preference scores, and these preference scores should be ranked in transitive or hierarchical ways (Houston, McNamara, & Steer, 2007). In such cases, the value placed on different options should reflect an intrinsic property of each option and should not change in the presence of competing alternative options. Although normative models in economics and animal behaviour assume that individuals make decisions in consistent ways, these models do not always accurately predict choice behaviour of humans or other animals. A major challenge in understanding and predicting choice behaviour in humans and other animals is determining how individuals evaluate alternatives that differ along multiple dimensions.

Decisions become particularly complex in situations where several attributes of choices are inversely related to one another, with no single option always considered the best (Bateson & Healy, 2005; Gabel & Hennig, 2016). In nature, foraging animals often choose among several options simultaneously that may differ in several important attributes. A common example of this occurs with nectivorous species, which must attend to both the volume and the concentration of nectar solutions among other aspects of

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floral quality. Studies investigating rationality in nectarivores, such as honeybees (Shafir, 1994; Shafir, Waite, & Smith, 2002) and hummingbirds (Bateson, Healy, & Hurly, 2002, 2003; Hurly & Oseen, 1999), have found both irregular and intransitive preferences when these, and other, dimensions of floral choices are varied. Importantly, these seemingly irrational choices may also emerge from nonlinearities in the combination of dimensions into a single utility metric (Shafir, 1994). These violations in rationality are incompatible with expectations of economic and behaviour models of decision making, which assume that animals assign absolute utilities to different options (Shafir, 1994). Instead, they suggest that, in some cases, animals compare available options along their shared dimensions, and that the relative value of an option depends on the option with which it is compared (Bateson & Healy, 2005).

The use of comparative evaluation has now been demonstrated widely across contexts such as mate choice (e. g. Lea & Ryan, 2015), foraging (Shafir et al., 2002) and habitat choice (e.g. Sasaki & Pratt, 2011) and across a broad range of taxonomic groups, from slime moulds to humans (reviewed in Hemingway, Ryan, & Page, 2017). Comparative evaluation has likely evolved in these cases as a cognitive short cut that facilitates decision making, especially as the number of shared dimensions of a set of choices increases (Bateson & Healy, 2005). Even though comparative evaluation can sometimes result in irrational behaviour, with currency not always being optimized with every choice, it is assumed that the fitness consequences resulting from choosing suboptimal options are offset by either the time or the neural processing expenditures saved by these decision-making short cuts (Bateson, 2004; Bateson & Healy, 2005; Gigerenzer, 1997). While violations of rationality appear to be quite common and may reflect an intrinsic property of biological decision making, there are also examples of animals that adhere to rationality principles when tested in similar ways (e.g. Monteiro, Vasconcelos, & Kacelnik, 2013; Schuck-Paim, Pompilio, & Kacelnik, 2004). As a result, we have a limited understanding of how the ecological strategy, evolutionary history and context of decision making (foraging, mate choice, etc.) drive the evolution of comparative evaluation.

Frog-eating bats, *Trachops cirrhosus*, provide an interesting system for investigating mechanisms involved in decision making. These bats hunt frogs and insects by eavesdropping on their mating calls (Tuttle & Ryan, 1981). The túngara frog, *Physalaemus pustulosus,* is a lekking frog species that is a preferred prey 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 & Ryan, 1981; Ryan,

Tuttle, & Rand, 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 short broadband suffixes called chucks (see Fig. 1; Ryan, 1985).

Complex calls are longer, contain more total energy and have a larger range of frequencies than simple calls (Ryan et al., 1982). Ryan et al. (1982) found that adding chucks to a simple call makes the call significantly more attractive to frog-eating bats when tested in the field or in flight cages. There is no known relationship between a male's mass, length or body condition and the number of chucks with which he adorns his calls. Instead, the proportion of complex calls is better explained by a male's proximity to other males (Bernal, Rand, & Ryan, 2007). Male túngara frogs calling alone tend to produce just the whine, but when calling together they produce complex calls (Ryan et al., 1982). As a result, call complexity might indicate the density of individuals within a specific patch (Bernal et al., 2007). Additionally, complexity has been shown to aid bats in localizing a calling frog in a cluttered and noisy environment, which is consistent with the typical foraging environment of these bats (Page & Ryan, 2008).

Along with a greater preference for complex calls, *T. cirrhosus* has been shown to prefer higher-amplitude calls (Tuttle & Ryan, 1981). Higher-amplitude calls are likely preferred by bats for several reasons. First, amplitude likely reveals distance, with louder calls indicating closer calling frogs (Bernal, Page, Ryan, Argo, & Wilson, 2009; Ryan, 1986). Second, while localization performance has only been tested with call complexity, both complexity and amplitude are likely necessary in facilitating localization performance and increasing detectability, and likely both play an important role in the bats' foraging performance. Importantly, these two aspects of frog calls are not always positively correlated with one another.

Here, we conducted a series of experiments to test for transitivity in foraging behaviour of frog-eating bats by manipulating the amplitude and complexity of frog calls. Bats were given a series of binary choices between calls that varied in complexity (Fig. 1a) and amplitude (Fig. 1b) to test for transitivity independently along each dimension. For these two experiments we used three calls (low, medium and high). We also gave bats choices where amplitude and complexity were covaried inversely to one another. To do this we created three calls that varied in both amplitude and complexity (Fig. 1c): (A) high complexity, low amplitude; (B) medium complexity, medium amplitude; (C) low complexity, high amplitude. Thus, intransitive preferences could occur because these options all differed along two dimensions that are weighted
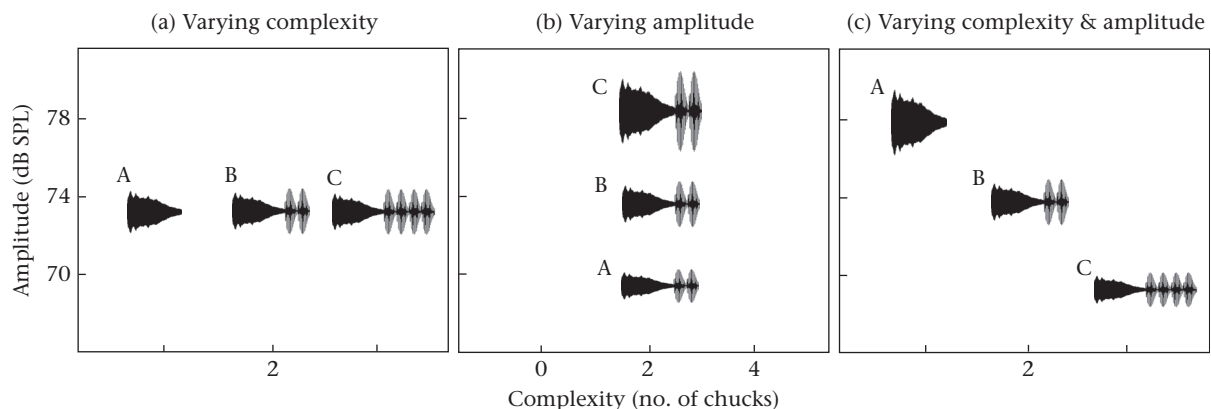
Figure 1. Experimental design. In every experiment, each animal was given every pairwise combination a total of 10 times each, resulting in 30 choices per experiment and 90 choices in total per bat. Oscillograms depict túngara frog mating calls, with size representing changes in amplitude and suffixes indicating chuck number.

differently by the bats. If frog-eating bats rely on absolute evaluation, preferences should be independent of the context in which the calls are presented, and thus ranked in a transitive order. Conversely, if the bats rely on comparative evaluation, preferences for calls might vary depending on the calls to which they are being compared.

METHODS

Subjects and Study Site

We caught wild, frog-eating bats ($N=14$ adults) using mist nets set along streams and rivers in Soberanía National Park, Panama. Bats were caught and tested between May and August of 2017. Upon capture, bats were maintained in a small mesh tent for 24 h and hand-fed bait fish. Following this acclimation period, bats were released and tested individually in large outdoor flight cages (5 × 5 × 2.5 m) under ambient temperature and humidity in Gamboa, Panama. Following the experiments, we released all bats at their initial capture location. For long-term identification and to avoid multiple testing of the same individual, each bat was injected subcutaneously on the back with a passive integrated transponder tag (PIT tag, 12 mm, ~0.1 g and ~0.3% of body mass; Biomark, Boise, ID, U.S.A.) prior to release. All experiments were licensed and approved by the Smithsonian Tropical Research Institute Institutional Animal Care and Use Committee (STRI IACUC protocol 2017-0102-2020-A8), the University of Texas at Austin (AUP-2015-00048) and the Government of Panama (Ministerio de Ambiente permit SE/A 69-15 and SE/AH-2-6).

Food Rewards

Following release into the flight cage, bats were allowed one night to forage for food rewards (bait fish) in response to frog calls broadcast from a speaker under a screen placed randomly throughout the flight cage. During this period, we broadcast calls of other palatable frog species consumed by this bat in the wild (*Smilisca sila* and *Dendropsophus ebraccatus*) that were not the species later used in the experiment (*P. pustulosus*). Once bats successfully retrieved 10 fish rewards in response to frog calls in captivity, we began experimental trials.

Experiments were conducted between 1900 and 0200 hours each night for three consecutive nights. Because bats only respond to frog calls when hungry, trials were reinforced 50% of the time in a randomized order. Previous experiments have demonstrated that bats approach unrewarded speakers broadcasting frog calls and that they are attracted to the location of the frog call and not the food reward per se (Page & Ryan, 2008). Additionally, previous studies in this system using the same schedule of reinforcement detected no differences in preference based on the history of reward associated with different calls (Hemingway, Ryan, & Page, 2018; C. T. Hemingway, personal observation). Trials were partitioned into three separate feedings (1900, 2200, 0100 hours) each night. Feedings ended when bats were no longer motivated to feed. Bats typically ate around 4–6 g per feeding, consuming approximately 15 g per night.

Experimental Arena

Bats started all trials from a perch positioned in one corner of the flight cage. Stimuli were presented from Fostex FE103En speakers underneath 1 × 1 m screens positioned 2.5 m from each other and 2.5 m from the perch. The experimenter sat in the corner opposite the perch. The experimental stimuli were modified using Adobe Audition 3. All stimuli were constructed from the same modal túngara frog call (Ryan & Rand, 2003). Sound playbacks were broadcast from a Lenovo Thinkpad laptop through a Pyle Pro PTA2 amplifier to the speakers. We used two Sony Handycam DCR-SR45 cameras to record trials. One camera was positioned on the perch and recorded the bat's behaviour upon the onset of the stimuli. The second camera was positioned on the speakers to record the flight of the bat during trials. The flight cage was illuminated during experiments with two, high-powered LED IR lights (IR Yeshzhuanjia, model 80 AIR) for enhanced video recordings.

Phonotaxis Experiments

This study consisted of three experiments: (1) varying only call complexity (Fig. 1a); (2) varying only amplitude (Fig. 1b); (3) varying both complexity and amplitude simultaneously (Fig. 1c). For experiment 1, three calls, A (whine + 0 chucks), B (whine + 2 chucks) and C (whine + 4 chucks), were broadcast at the same amplitude (74 dB SPL, re. 20 μPa) at 1 m from the speaker. Bats were given three stimulus combinations (A versus B, A versus C, B versus C). Each bat was tested with each stimulus pair a total of 10 times in this experiment, for a total of 30 choices per animal. We manipulated stimuli based on amplitude in the same way. Three calls, A (70 dB SPL), B (74 dB SPL) and C (78 dB SPL), were broadcast at the same level of complexity (whine + 2 chucks). Each bat was tested with a random presentation of each stimulus pair a total of 10 times in this experiment, for a total of 30 choices per animal. Lastly, we varied the two call attributes simultaneously. Here we presented three calls that varied inversely along each dimension. Call A was low in complexity and high in amplitude (whine + 0 chuck; 78 dB SPL), call B was intermediate along both dimensions (whine + 2 chucks; 74 dB SPL) and call C was high in complexity and low in amplitude (whine + 4 chucks; 70 dB SPL). Again, each bat was given each pair 10 times totalling 30 choices per animal for this experiment.

Each bat was tested across each experiment in a repeated measures design. All stimuli were randomized by order, within and across experiments. Because each experiment consisted of 30 trials, each bat received a total of 90 trials, which typically spanned a period of 2–3 nights. Stimuli were also randomized between the left and right speaker, although we made sure each pairwise comparison was equally represented on both sides. Phonotaxis was defined here as flight within 50 cm of a speaker. Phonotaxis choices were later validated by an observer scoring video recordings without knowledge of the auditory stimuli that the bats received. We measured bat foraging preference as the proportion of times a bat chose one choice over the other. When determining whether bats ordered the calls in a linear way, we used a ≥60% cutoff to determine the directionality of preference. While this captures both weak and strong preferences, we consider 60% a sufficient cutoff to use here for several reasons. In other studies testing for transitivity, a more liberal preference cutoff at ≥50% has been used (Appleby, 1983; Kirkpatrick, Rand, & Ryan, 2006). Secondly, we used the data only to determine the directionality of preference and not the strength of preference.

Statistical Analysis

All statistics were carried out in R version 3.5.0 (R Development Core Team, 2018). We first determined whether bats generally prefer either of the two calls for every pairwise combination across the three experiments. To do this, we calculated the proportion of choices by each subject to one of the dyad options (Fig. A1) and used a two-tailed, one-sample t test for every pairwise comparison in each experiment to determine whether the proportion differed from our null expectation (0.5). We also calculated the mean

proportion across all bats as well as the 95% bootstrapped confidence intervals.

Our main statistical question was whether the number of bats that ordered their preferences in transitive ways differed from a null expectation based on possible ranking combinations. Based on an individual's preferences between pairwise choices in every experiment, individuals were categorized as either transitive or intransitive depending on whether their preferences were ordered in circular or linear ways. With three stimuli, there are six possible transitive ways to rank the stimuli and two possible intransitive rank orders (see Fig. A1; Shizuka & McDonald, 2012). As a result, individuals exhibiting random preferences would lead to 75% of individuals making decisions that appear transitive and 25% of individuals making decisions that appear intransitive. We used binomial tests to determine whether the number of bats ranking the calls in transitive orders differed from our null expectation (75%

transitive = 6/8 transitive combinations). All binomial tests were two tailed. Because each bat was tested with every pairwise combination 10 times, it was possible for bats to show no preference (5–5). Across all three experiments, there were six instances where individuals exhibited no preference between the two options within an experiment. In cases where this occurred, bats were not included for that experiment as preferences did not follow any of the eight possible outcomes and individuals could not be classified as either transitive or intransitive. Data from these bats were only used when measuring population-level preferences.

RESULTS

In experiment 1, when complexity was varied alone, we found a significant preference for call B (74 dB, 2 chucks) over call A (74 dB, 0 chucks) (0.864 ± 0.058; $t_{13} = -11.21$, $P < 0.001$; Fig. 2a). We did not
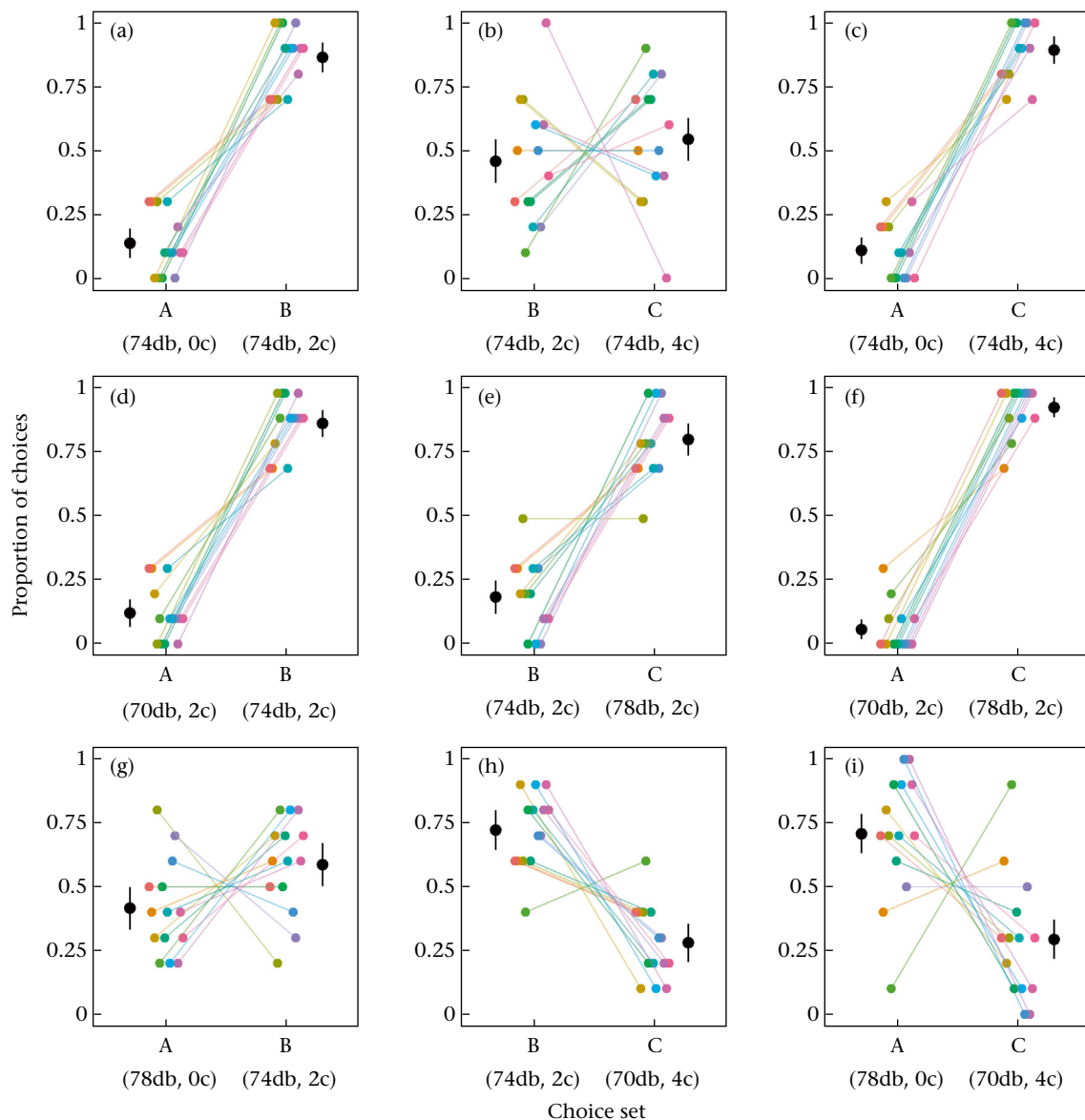
Figure 2. Individual responses in choice experiments in which three options (A, B, C) were tested against each other in binary choice tests. Error bars represent bootstrapped 95% confidence intervals for mean proportions. (a–c) Results from experiment 1, where only complexity was manipulated. (d–f) Results from experiment 2, where only amplitude was manipulated. (g–i) Results from experiment 3, where both complexity and amplitude were manipulated inversely to one another. The *X* axis represents the binary choice presented to the bats. The *Y* axis represents the proportion of times that each bat made a choice.

find a significant preference between call B (74 dB, 2 chucks) and call C (74 dB, 4 chucks) (0.543 ± 0.084; t_{13}=-0.65, P=0.53; Fig. 2b). Lastly, when given a choice between call A (74 dB, 0 chucks) and call C (74 dB, 4 chucks), we did find a significant preference for call C (0.893 ± 0.051; t_{13}=-12.88, P<0.001; Fig. 2c).

In experiment 2, where we varied amplitude alone, bats showed a significant preference for the louder call in every pairwise combination. When given a choice between call A (70 dB, 2 chucks) and call B (74 dB, 2 chucks), bats significantly preferred call B (0.879 ± 0.056; t_{13}=-12.63, P<0.001; Fig. 2d). When given a choice between call B (74 dB, 2 chucks) and call C (78 dB, 2 chucks), bats preferred call C (0.814 ± 0.067; t_{13}=-8.05, P<0.001; Fig. 2e). Lastly, when given a choice between call A (70 dB, 2 chucks) and call C (78 dB, 2 chucks), we found that bats significantly preferred the higher-amplitude call (0.943 ± 0.040; t_{13}= -17.67, P<0.001; Fig. 2f).

In experiment 3, when we varied amplitude and complexity at the same time, we found that bat preferences generally reflected a trade-off between these two dimensions. When given a choice between call A (78 dB, 0 chucks) and call B (74 dB, 2 chucks), call B appeared to be more preferred, although this preference was not significant (0.586 ± 0.08; t_{13}=-1.71, P=0.11; Fig. 2g). When given a choice between call B (74 dB, 2 chucks) and call C (70 dB, 4 chucks), bats preferred call B (0.721 ± 0.076; t_{13}=5.61, P<0.001; Fig. 2h). Lastly, when choosing between call A (78 dB, 0 chucks) and call C (70 dB, 4 chucks), bats preferred call A (0.707 ± 0.078; t_{13}=3.11, P=0.008; Fig. 2h).

When testing for transitivity, we first varied complexity alone in experiment 1 and found that individuals that were transitive in their preferences for calls with varying chuck numbers did not differ from the number of individuals expected by chance (12 transitive, 0 intransitive; binomial: P=0.06). Seven bats that ranked the calls in a transitive way showed consistent preference for more chucks (C>B>A; Fig. 2a–c). The other five bats were also found to be transitive but showed a different preference ranking of the calls (B>C>A; Fig. 2a–c). When amplitude was varied alone in experiment 2, we found that all individuals exhibiting preferences were transitive in those preferences (13 transitive, 0 intransitive; binomial: P=0.042), indicating that the number of bats showing transitive preferences exceeded that expected by chance. These preferences were also consistent across all individuals, with bats always preferring the higher amplitude calls (C>B>A; Fig. 2d–f). Lastly, when we varied both amplitude and complexity at the same time in experiment 3, we found that all bats showing preferences were transitive in those preferences (11 transitive, 0 intransitive; binomial: P=0.084). Although this result was not significantly different from our null expectation, we consider this strong evidence for transitive decision making along these two dimensions. Interestingly, although all bats in this experiment were transitive in their preferences, not all bats were consistent in their rank order for these three calls (Fig. 2g–i). Individual preferences for all experiments are shown in Table A1.

DISCUSSION

In this study, we manipulated call amplitude and call complexity of prey, both separately and together, in a series of binary choice tests to evaluate whether frog-eating bats attend to these call attributes of their prey when making complex foraging decisions, specifically testing whether bats rank calls transitively along multiple dimensions. We found that frog-eating bats generally preferred calls of higher complexity and higher amplitude when dimensions were manipulated separately. When making decisions about both dimensions simultaneously, bats appeared to have transitive preferences for túngara frog calls, with preferences reflecting a trade-off between each acoustic dimension.

When manipulating complexity alone, we found no evidence that bats preferred more complex calls over less complex calls, as there was no statistical preference between call B and C on a population level. We also found no evidence for intransitive preferences. We did find, however, that individuals did not rank the three calls in the same way. Seven of the 12 bats that showed preferences between all three calls preferred call C to both B and A, and call B to call A (C>B>A). The remaining five bats preferred call B to both call A and call C, and call B to call A (B>C>A). While the preferences of these latter five bats did not follow the expectation that bats prefer more complex calls, their preferences were also transitive and adhered to expectations of economic rationality.

We have two nonmutually exclusive explanations for this result. A previous study found that bats preferred calls with more chucks, but as more chucks were added to both calls and, thus, the relative difference in chuck number between the two calls decreased, this preference was no longer detectable (Akre, Farris, Lea, Page, & Ryan, 2011). In our study, it is possible that bats were attending to relative, not absolute, differences in chuck number, but in Akre et al. (2011), bats still showed ~70% preference for calls with four chucks when they were given a choice between calls that had two and four chucks added to the whine. There is also substantial evidence that the value of zero is treated numerically different from other values (Shampanier, Mazar, & Ariely, 2007). Choices between calls that do and do not have chucks are likely different to the bats than choices between calls that differ in chuck number. This may explain why we found stronger preferences when choices were made between calls with and without chucks (zero versus two chucks, zero versus four chucks), but not when bats were choosing between calls with two versus four chucks. This would indicate that bats attend more readily to the presence or absence of chucks, rather than to the number of chucks.

In the second experiment our results also support and extend upon earlier findings, in which bats significantly preferred higher-amplitude calls when given a choice between two calls broadcast at 74 and 78 dB SPL (Tuttle & Ryan, 1981). In our study, we found that bats significantly preferred the higher-amplitude calls for every binary combination when amplitude was manipulated on its own in experiment 2. We also found that 13 of the 14 bats showed preferences for every pairwise combination of calls that varied in amplitude, and that all 13 of these bats exhibited transitive and consistent rankings of preferences. Taken together, these results suggest that amplitude may be an important aspect of frog calls that bats attend to in the wild. Additionally, our results provide further support that bats are capable of discriminating between calls that differ by 4 dB.

When both dimensions, amplitude and complexity, were manipulated simultaneously in experiment 3, we found that bats were transitive in their preferences. We generally found that bats ranked all three calls in a linear way (B>A>C), although there was a lot of variation in preference among individuals. Importantly, even though individuals varied in their preferences, we found that all individuals were transitive in the ways that they ranked these three calls (Fig. 2). These data suggest that when both properties of calls are varied, bats include both attributes in an assignment of a utility value that is then ranked to produce consistent, transitive decisions. This adherence to transitivity is compatible with models of animal behaviour and suggests that these bats are likely using absolute evaluation when choosing between two frog calls that vary in these attributes.

At a population level, the ranking of frog calls demonstrates that the more preferred call falls in the middle of these two dimensions (medium complexity, medium amplitude), suggesting that bats make trade-offs between amplitude and complexity of frog calls, where poor values along one dimension can be compensated for by

high values in another. This makes biological sense as we know that bats attend to both dimensions based on previous research (Hemingway et al., 2017; Tuttle & Ryan, 1981). Interestingly, this trend occurred along both dimensions. We found strong preferences for higher-amplitude calls across every pairwise presentation. Conversely, preferences for more complex calls seemed to drop off and did not follow the same linear trend. Importantly, the preference for calls of medium amplitude and medium complexity over calls of high amplitude and low complexity was not significant, although it approached significance, and this may reflect some nonlinear preference across this dimension. Indeed, several individuals preferred the higher-amplitude call regardless of complexity even as both dimensions were covaried, indicating that amplitude may be a more salient aspect of frog calls that bats attend to.

Although call complexity is important for localization success (Page & Ryan, 2008), amplitude may also either serve to help with localization, or be used by bats as a measure of distance. In a study of acoustic radiation patterns of male túngara calls, the vertical active space of calls was much greater than the horizontal active space (Bernal et al., 2009). As a result, any increase in amplitude could asymmetrically increase the frog's conspicuousness to eavesdropping bats (Bernal et al., 2009). Whether or not both aspects of the call contribute to localization, or whether amplitude is used by the bats to estimate distance requires further investigation.

Irrationalities caused by comparative evaluation are more likely in cases with two or more dimensions and as stimuli encompass a wider range of parameter space (Bateson & Healy, 2005; Tversky, 1969). In this study we wanted to know whether bats are transitive when deciding between calls in the wild. Although there are other dimensions that bats likely attend to, such as frequency modulation and call duration (Fugère, Teague O'Mara, & Page, 2015), amplitude and complexity are likely the two most salient aspects of calls for foraging bats. It also seems likely that using a wider set of parameter values (i.e. higher amplitudes, more chucks) may make comparisons of frog calls more difficult, so we chose parameter values that best matched those in which foraging bats would encounter in the wild. Túngara frogs can produce up to seven chucks (Ryan, 1985), but they only add chucks to their calls in the presence of male competitors. As a result, males often produce just a whine, but they tend to produce about two to four chucks per call, on average (Bernal et al., 2007). The amplitude ranges chosen for this study also matched those found in the wild (Ryan, 1985).

Our results are also consistent with a previous study of foraging preferences of frog-eating bats that investigated another aspect of economical rational behaviour — independence from irrelevant alternatives, which requires that the introduction of a new option to a choice set should not change the relative preferences between pre-existing options (Luce, 1959). In this earlier study, we tested whether bats changed their relative preferences between two calls upon the addition of a decoy that was inferior to one call in both amplitude and complexity and inferior to the other call just by amplitude, and we found that bats maintained strict preferences even in the presence of the decoy call (Hemingway et al., 2017). Taken together, these studies provide strong support for the notion that bats' preferences obey general principles of rational behaviour.

Remarkably, studies across diverse taxa, from humans to slime moulds, have largely demonstrated evidence for comparative decision-making processes, suggesting that this form of evaluation may be an intrinsic feature of biological decision making (Latty & Beekman, 2011). In some cases, selection may favour more intensive absolute evaluation strategies in certain species or contexts (Latty & Beekman, 2011), although the underlying ecological and

phylogenetic drivers of these mechanisms remain unclear. Most studies investigating rationality have done so in a foraging context, with a few exceptions of studies investigating rationality in mate choice (Arbuthnott, Fedina, Pletcher, & Promislow, 2017; Dechaume-Moncharmont, Freychet, Motreuil, & Cézilly, 2013; Gabel & Hennig, 2016; Kirkpatrick et al., 2006; Lea & Ryan, 2015; Reding & Cummings, 2018) and habitat choice (Edwards & Pratt, 2009; Sasaki & Pratt, 2011). While these studies of rationality traverse a broad taxonomic range, including arthropods, birds, amphibians, fish, mammals, and even slime moulds (reviewed in Hemingway et al., 2017), there do not appear to be any clear patterns in the specific phylogenetic relationships or in the diets of animals that use comparative evaluation. Uncovering the specific ecological conditions and taxonomic groups of animals in which comparative mechanisms of evaluation are commonly used in decision-making processes is important for constructing models of the evolution of mate choice preferences, predator/prey interactions and signal evolution (Kirkpatrick et al., 2006; Ryan, Page, Hunter, & Taylor, 2019).

Rationality in animals has also been studied largely in visual and olfactory/gustatory modalities (e.g. Arbuthnott et al., 2017), with few studies investigating economic rationality in other sensory modalities. Receiving and processing acoustic information is inherently different from other modalities, and incorporating auditory information from multiple sources of sound may be a particularly difficult task for most vertebrates (Farris & Ryan, 2011; Farris & Taylor, 2016). Studies of rationality in acoustic preferences in both frogs and crickets have shown irrational preferences when making mate choice decisions along multiple, acoustic dimensions (Gabel & Hennig, 2016; Lea & Ryan, 2015). Whether irrational decisions represent conserved features of decision-making mechanisms or vary depending on the sensory modality involved in decision making largely remains unexplored.

The fitness consequences of comparative evaluations, as well as the selection pressures that they impose, are not as straightforward as absolute evaluation. As a result, the use of comparative evaluation in decision-making mechanisms has important implications for the way that we model choice behaviours. This may be important considering that most experiments are designed so that the animals do not encounter every pairwise combination of choices (Shafir, 1994). This may also mean that animals that do exhibit absolute evaluation do so because selection has operated on this aspect of decision making to optimize certain currencies. This may be particularly relevant to bat foraging behaviour due to bats' exceptionally high metabolisms (Shen et al., 2010). Bats in this study, for example, weighed around 35 g, on average, and consumed around 15 g of food per night, on average, which is close to half of their body weight. If frog-eating bats are under strong selection to optimize their foraging success, they likely must make decisions in ways that consistently lead to the highest possible payoffs. Hummingbirds also have very high metabolisms, and a variety of studies of hummingbird foraging behaviour have found evidence for irrational behaviour (e.g. Bateson et al., 2002). Comparative studies testing such questions in other closely related bat species that have different foraging strategies, perhaps those more similar to hummingbirds, or in distantly related bats with similar foraging behaviours could be done to help disentangle the role that phylogeny, diet and metabolism may play in shaping these behaviours.

Overall, our results provide further support for the notion that when choosing between calls that vary in amplitude and complexity, frog-eating bats adhere to expectations of decision-making models that predict that animals assign a single

preference score that is independent from other options present. This also suggests that the predatory selection that these bats impose on the calling behaviour of male frogs are not influenced by the background chorus in the same ways that they are influenced by female frogs (Lea & Ryan, 2015). These results also support the continued use of optimality approaches to modelling animal behaviour in certain contexts and species, although further work is necessary to fully understand whether we should consider rationality to be the rule or the exception.

Acknowledgments

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Appendix

Table A1
Preferences are shown for the second call in each test type across all three experiments

Bat	AB	BC	AC	Preference order	Violations
Experiment 1					
1	0.70	0.70	0.80	C>B>C (6)	
2	0.70	0.50	0.80	(not included)	
3	1.00	0.30	0.70	B>C>A (4)	
4	0.70	0.30	0.80	B>C>A (4)	Strong
5	1.00	0.90	1.00	C>B>A (6)	
6	1.00	0.70	1.00	C>B>A (6)	
7	0.90	0.70	1.00	C>B>A (6)	
8	0.70	0.80	0.90	C>B>A (6)	
9	0.90	0.40	0.90	B>C>A (4)	
10	0.90	0.50	1.00	(not included)	
11	1.00	0.80	1.00	C>B>A (6)	
12	0.80	0.40	0.90	B>C>A (4)	Strong
13	0.90	0.00	0.70	B>C>A (4)	Strong
14	0.90	0.60	1.00	C>B>A (6)	
Experiment 2					
1	0.70	0.70	1.00	C>B>A (6)	
2	0.70	0.70	0.70	C>B>A (6)	
3	0.80	0.80	1.00	C>B>A (6)	
4	1.00	0.50	0.90	(not included)	
5	0.90	0.80	0.80	C>B>A (6)	Strong
6	1.00	1.00	1.00	C>B>A (6)	
7	1.00	0.80	1.00	C>B>A (6)	
8	0.70	0.70	1.00	C>B>A (6)	
9	0.90	1.00	0.90	C>B>A (6)	Strong
10	0.90	0.70	1.00	C>B>A (6)	
11	0.90	1.00	1.00	C>B>A (6)	
12	1.00	0.90	1.00	C>B>A (6)	
13	0.90	0.90	1.00	C>B>A (6)	
14	0.90	0.90	0.90	C>B>A (6)	
Experiment 3					
1	0.50	0.40	0.30	(not included)	
2	0.60	0.40	0.60	B>C>A (4)	
3	0.70	0.10	0.20	B>A>C (3)	
4	0.20	0.40	0.30	A>B>C (1)	Strong
5	0.80	0.60	0.90	C>B>A (6)	
6	0.50	0.20	0.10	(not included)	
7	0.70	0.40	0.40	B>A>C (3)	Strong
8	0.60	0.20	0.30	B>A>C (3)	
9	0.80	0.10	0.10	B>A>C (3)	
10	0.40	0.30	0.00	A>B>C (1)	
11	0.30	0.30	0.50	(not included)	
12	0.80	0.20	0.00	B>A>C (3)	Strong
13	0.60	0.10	0.10	B>A>C (3)	
14	0.70	0.20	0.30	B>A>C (3)	

Bats are numbered in the order in which they were tested. Preference order is indicated for each individual. We also indicate which numbered example (1–6) this corresponds to in Fig. A1. Violations of weak stochastic transitivity occur when preferences cannot be ordered in a linear way (i.e. A<B<C). Violations of moderate stochastic transitivity occur when the preference between the weakest preferred option and greatest preferred options (i.e. A<C) is not as strong as the weakest pairwise relationships between the extremes (i.e. A<B and B<C). Violations of strong stochastic transitivity occur when the preference between the weakest preferred option and the greatest preferred option (i.e. A<C) is not as strong as the strongest pairwise relationships between the extremes (i.e. A<B and B<C).
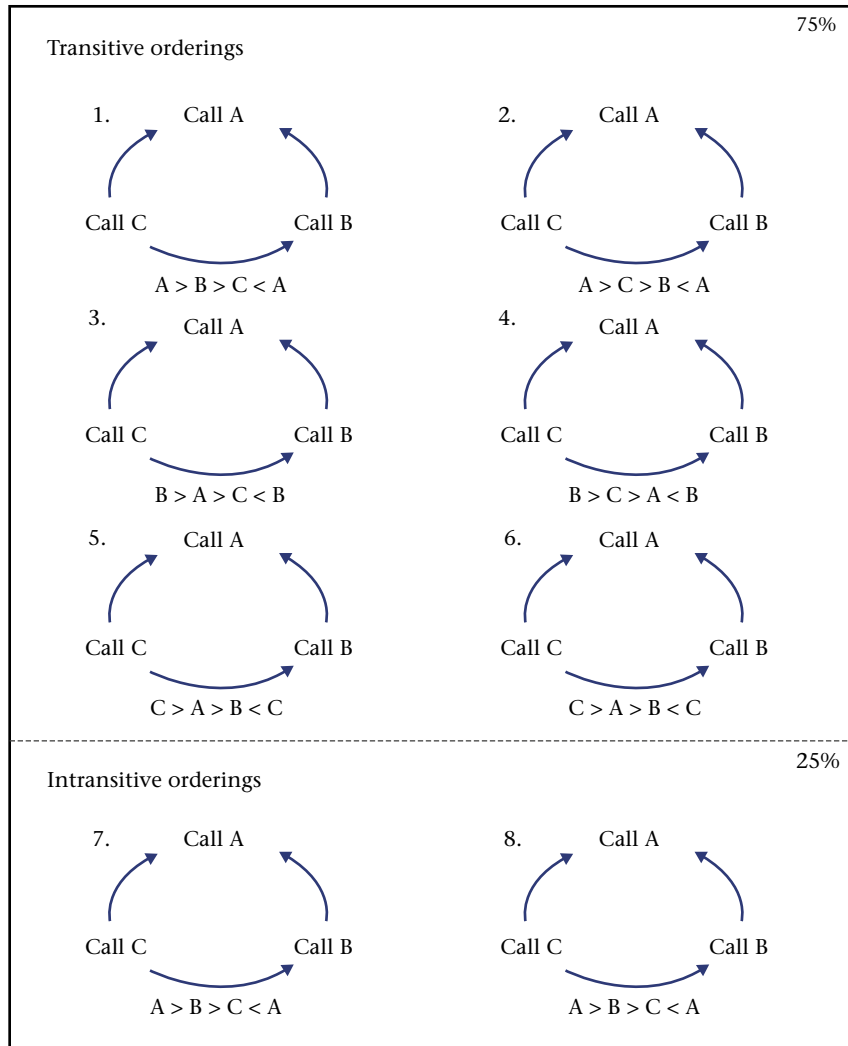
Fig. A1. Six possible transitive rank orders and two possible intransitive rank orders when ranking preferences for three options.