



## Cognitive constraints on optimal foraging in frog-eating bats

Claire T. Hemingway<sup>a, b, \*</sup>, Michael J. Ryan<sup>a, b</sup>, Rachel A. Page<sup>b</sup>

<sup>a</sup> Department of Integrative Biology, University of Texas, Austin, TX, U.S.A.

<sup>b</sup> Smithsonian Tropical Research Institute, Balboa, Ancón, Panama

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Animals are expected to optimize energy intake when choosing between different foraging options. A common explanation for deviations from optimal economic decisions is that there is an imperfect relationship between physical reality and an animal's perceptual processes, which can constrain assessment of profitability. One such phenomenon that is apparently ubiquitous across taxa is proportional processing, where a perceived change in a stimulus is proportional to the change in stimulus magnitude. In this study, we investigated whether proportional processing explains how frog-eating bats, *Trachops cirrhosus*, discriminate between patches of frog choruses that vary in their number of calling frogs. To test this, we created artificial choruses consisting of one to six calling frogs. In the flight cage, we then tested the preference of bats ( $N = 17$ ) with every pairwise combination of chorus size. We found that while bats generally preferred larger choruses, preferences for larger choruses were better explained by the relative, not absolute, differences in chorus sizes. This indicates that *T. cirrhosus* is perceptually limited in its ability to discriminate between choruses of varying size as the choruses increase in size. Foragers are likely to be less choosy when choosing among larger patches.

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There has been considerable interest over the last five decades in understanding the decision rules that shape animal foraging behaviour (McFarland, 1977). Animals are expected to adhere to decision rules that maximize net energy intake when choosing between food sources that vary in quantity and quality (Charnov, 1976; Emlen, 1966; MacArthur & Pianka, 1966). While many studies of optimal foraging in animals have been focused on how decisions are made within patches, for many animals, prey items are not necessarily homogeneously distributed (Elton, 1949). For predators foraging on prey that can be found in discrete patches, decisions about which patches to feed in are likely under strong selection as predators may need to expend considerable energy travelling between patches (Charnov, 1976). Therefore, for animals foraging in patches, it is predicted that the optimal behaviour is to allocate as much available time as possible to patches with the greatest food abundance in order to maximize net energy intake (Pyke, Pulliam, & Charnov, 1977; Shettleworth, 2010).

Underlying the capacity to make foraging decisions that maximize fitness is the ability to evaluate patch quality by estimating resource density, variability or concentration (Cartar, 2004). Additionally, animals often need to explicitly compare two options to

one another to generate a more complex and comprehensive measure of magnitude (Jacob, Vallentin, & Nider, 2012). Several characteristics of perceptual and cognitive systems may place limits on the kinds of optimal choices that animals can make (Akre & Johnsen, 2014; Bateson & Healy, 2005). A common explanation for deviations from optimality is that the ability of sensory systems to detect differences in the physical values between different alternatives may be constrained by the perceptual processes that encode profitability (Livnat & Pippenger, 2008). One such perceptual limitation is 'proportional processing' (Akre & Johnsen, 2014). Proportional processing is ubiquitous across taxa and refers to the process in which the noticeable change in a stimulus is proportional to the actual stimulus value. This process is commonly known as Weber's law (Weber, 1978). Humans are among the many taxa that use proportional processing (Akre & Johnsen, 2014). For example, a person holding an item that weighs 100 g might not notice if 5 g are added, but if they were holding a 10 g item and 5 g were added, they would likely notice the difference. In this example, the absolute difference is identical, but the relative difference is not.

Proportional processing has the potential to create predictable deviations in behaviour that could be viewed as suboptimal in certain conditions (Nachev & Winter, 2012). Although substantial effort has been devoted to understanding how animals make decisions about foraging patches, tests of perceptual limitations in

\* Correspondence: C.T. Hemingway, Department of Integrative Biology, University of Texas, Austin, TX 78712, U.S.A..

E-mail address: [cheming@utexas.edu](mailto:cheming@utexas.edu) (C. T. Hemingway).

foraging decisions have so far been largely limited to decisions about food items within a patch or with a uniform distribution (e.g. Akre, Farris, Lea, Page, & Ryan, 2011; Nachev, Stich, & Winter, 2013; Toelch & Winter, 2007). For animals that forage on prey that are not homogeneously distributed, the fitness consequences of proportional processing when foraging within patches and between patches could be very different. Although the use of proportional processing has been broadly documented in foraging and mate choice decisions (Akre & Johnsen, 2014), perceptual limitations on patch choice decisions have not been widely explored (but see Abrahams, 1986; Kacelnik & Todd, 1992).

The frog-eating bat, *Trachops cirrhosus*, provides an interesting system for testing questions related to perceptual mechanisms involved in patch choice decisions. The túngara frog, *Physalaemus pustulosus*, is a preferred prey species eaten by *T. cirrhosus*. These small, Neotropical frogs call in leks, and frog-eating bats hunt túngara frogs by eavesdropping on their mating calls (Tuttle & Ryan, 1981). Much of the work done in this system has been focused on how *T. cirrhosus* makes decisions within patches; specifically, how these bats choose between calls of the same species varying along several call parameters (Akre et al., 2011; Page & Ryan, 2008; Tuttle & Ryan, 1981).

In the wild, however, *T. cirrhosus* is not just choosing between several frogs calling simultaneously but must also decide which group of calling frogs to approach. Túngara frogs often call from small, ephemeral ponds typically consisting of one to five calling males, although these numbers can vary substantially (Ryan, 1985). These ponds are often several metres or farther apart. *Trachops cirrhosus* hunts by flying over choruses of calling frogs and gleaning prey items off substrates (Jones, Hämsch, Page, Kalko, & O'Mara, 2017; Kalko, Friemel, Handley, & Schnitzler, 1999). Radiotracking data shows that *T. cirrhosus* leaves its day roost in the early evening for its foraging grounds, where it typically adopts a 'hang-and-wait' foraging strategy around a selected chorus of frogs (Jones et al., 2017; Kalko et al., 1999). Foraging from a perch has also been demonstrated in the flight cage for *T. cirrhosus* (e.g. Page & Ryan, 2008). How *T. cirrhosus* distinguishes the difference in the total number of frogs calling and uses this acoustic information to choose among choruses of frogs has not yet been explored.

In this study, we investigated the ability of *T. cirrhosus* to discriminate between patches that varied in their number of calling frogs. We created artificial choruses consisting of one to six calling frogs, which captures much of the typical range of one to five calling males in the wild (Ryan, 1985). In the flight cage, we then tested individual bat preferences for different chorus sizes with every combination of choruses in binary comparisons. Here, we propose three hypotheses about the mechanism by which *T. cirrhosus* discriminates between patches that vary in the number of calling frogs. Hypothesis 1 predicts that for patches ranging within these naturalistic parameters, *T. cirrhosus* can discriminate and choose the larger patch in absolute terms and thus, potentially maximize caloric intake. Hypothesis 2 predicts that if *T. cirrhosus* is limited in its ability to detect differences in the number of calling frogs as patches increase in size, preferences for larger patches may be predicted by proportional differences of patch sizes, and thus may not always optimize caloric intake. A recent study demonstrated that, when deciding which individual frog to approach within a prey patch, *T. cirrhosus* attends to proportional differences in the number of chucks with which male túngara frogs use to adorn their calls (Akre et al., 2011). Lastly, hypothesis 3 predicts that *T. cirrhosus* may not always prefer larger patches. Studies in túngara frogs have demonstrated higher vigilance in larger choruses (Ryan, Tuttle, & Taft, 1981). Additionally, many predators have more difficulty capturing prey when confronting a large group of prey, such as a swarm or school, than when confronting a smaller group of

individuals (Krakauer, 1995). If there is an optimal patch size necessary for *T. cirrhosus* to maximize both caloric intake as well as capture success, we might expect to see preference converge around an optimal number of calling frogs.

## METHODS

### Subject and Study Site

We captured 17 adult *T. cirrhosus* (10 males, 7 females) using mist nets set along streams and near small ponds in Soberanía National Park, Panama, from May to August 2016. All captured bats were held and tested in outdoor flight cages (5 × 5 × 2.5 m) in Gamboa, Panama. 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 Jones, Ryan, & Page, 2014; Page & Ryan, 2005). Each bat was then tested alone.

### Ethical Note

Following testing, bats were released at initial capture locations. For long-term identification and to avoid multiple testing of the same individual, each bat was injected with a subcutaneous passive integrated transponder (PIT) tag in the back (t-Tag100, Trovan Ltd, [www.trovan.com](http://www.trovan.com)). The PIT tags measured 2 × 12 mm and weighed close to 1 g, representing <3% of an individual's body weight. All procedures adhered to the ASAB/ABS guidelines for treatment of animals in behavioural research. Additionally, we regularly recapture bats previously tested in experiments (~60% of the bats in this study), which suggests that experimental procedures and pit tagging have minimal impact on their survivorship. All experiments were licensed and approved by the Smithsonian Tropical Research Institute (STRI IACUC protocol 2014-0101-2017), the University of Texas at Austin (AUP-2015-00048) and by the Government of Panama (Ministerio de Ambiente permit SE/A 69-15 and SE/AH-2-6).

### Experimental Stimuli

The experimental stimuli were modified using Adobe Audition 3. Stimuli were made from a modal túngara frog call (Ryan & Rand, 2003). Six choruses were synthetically constructed from the same model male frog call (whine + one chuck) and made to consist of one to six calling frogs, as males typically call in small ponds consisting of one to five individuals calling simultaneously (Ryan, 1985). Because chorusing males call about every 2 s and calls typically last around 333 ms (Ibáñez, Rand, Ryan, & Jaramillo, 1999), this was also the maximum number of calls that could be combined to produce nonoverlapping choruses that would not vary from one another in amplitude. While call rate is likely one attribute of calls to which bats attend, we consider it unlikely that choruses here may have been perceived by bats as single males that varied in their call rates. Túngara frogs are a common prey species of this bat and, in the wild, túngara frogs cannot call much faster than once every 2 s (Ryan, 1985), so our chorus with six calls would be extremely far outside of the natural range.

Each simulated chorus (1–6 frogs) was broadcast from a single speaker. In nature, these frogs call within centimetres of one another and the bat is often hearing these calls from metres away. Because the speakers were 15 × 15 cm, a single speaker was roughly the size of a chorus of males in the wild and adding more speakers would alter the spatial scale outside of a natural range. We also wanted to control for any visual and echo-acoustic cues that

bats could attend to by altering the number of speakers used for different chorus sizes.

Stimuli were broadcast at 75 dB SPL (re. 20  $\mu$ Pa) at 1 m, which is consistent with call amplitude of these frogs in the wild (Rand & Ryan, 1981). Sound pressure level was measured using a handheld meter (Galaxy Audio CM160). Stimuli were broadcast from a Lenovo T500 Thinkpad laptop through a Pyle Pro PTA2 amplifier. The bat's flight from the speaker was videorecorded with two infrared cameras (Sony DCR-TRV340). The first camera was focused on the perch to capture latency to fly following the onset of the stimuli presentation; the second was focused on the speakers to record the bat's approach and stimulus choice. The flight cage was illuminated with two, high-power LED IR lights (IR Yeshzhuanjia, model 80AIR) and a 25 W red light.

#### Acclimation to Captivity

In the flight cage, bats were positioned in a shelter with a perch to which they were trained to return between stimulus presentations. In the centre of the flight cage we placed two Fostex FE103En speakers 1.5 m apart and both 2 m from the roost. The experimenter sat in the corner opposite the bat, with the video and playback equipment (see Page & Ryan, 2005; Fig. 1).

Following release into the flight cage, bats were allowed 1–2 nights to forage for food rewards (fish) in response to frog call stimuli broadcast from speakers. During this acclimation period, we broadcast the calls of different palatable nocturnal frog species (*Smilisca sila* and *Dendropsophus ebraccatus*) rather than the one later used in experiment (*P. pustulosus*). When the captive bats were accustomed to finding a food reward at the location of the frog call playback, we began the experimental trials.

#### Experimental Procedure

Bats were tested between 1900 and 0300 hours each night over an average of 2 consecutive nights. Experiments simultaneously served as feedings, where each bat typically ate approximately 3–4 g of fish in three separate feeding bouts (1900, 2200 and 0100 hours). We offered the bats every combination of six chorus types of one to six calls, for a total of 15 combinations of chorus sizes (see Fig. 1a). Each bat was tested with a random order of each pairwise comparison twice, resulting in 30 choices per bat.

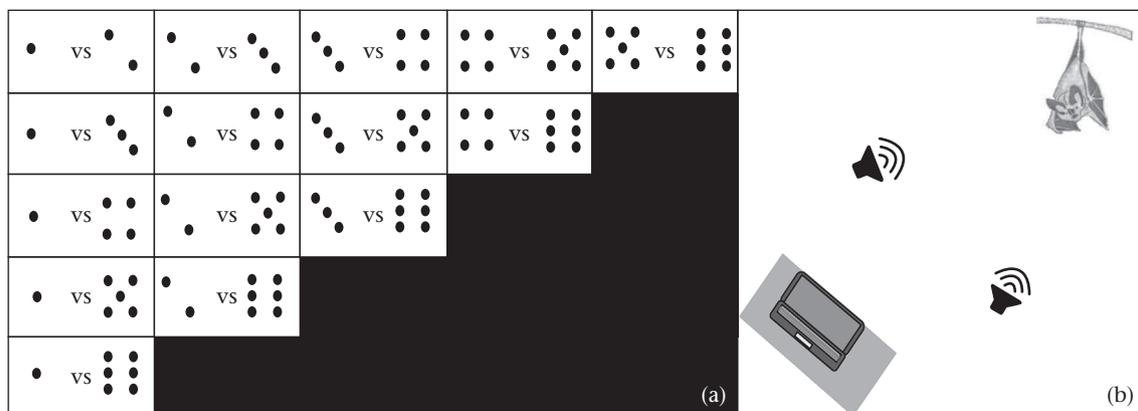
For every chorus combination, each chorus was broadcast from a single speaker in a binary choice test (see Fig. 1b). A distance of 1.5 m between the speakers allowed for clear discrimination between the two stimuli. Stimuli were broadcast simultaneously

until the bat flew, or until 60 s had passed, whichever came first (Fugère, O'Mara, & Page, 2015). If bats did not fly within 60 s, we allowed 60 s to pass before broadcasting the stimuli again. Choices were defined by flight within 50 cm of a speaker. To maintain high levels of motivation, we offered small food rewards on both speakers at a 50% variable ratio schedule of reinforcement. Intermittent, rather than constant, rewards also helped 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 choices (Page & Ryan, 2005). To prevent spatial associations with rewards, playbacks were randomized with constraints between the two speakers on each side of the flight cage, so the larger chorus was not presented more than three times in a row on the same side. To prevent side biases, if bats flew to the same side four times in a row, the experiment was paused, and the bat was rewarded on the other side of the flight cage, using one of the frog calls from the acclimation period. We also switched speakers nightly between the two speaker locations to prevent any biases based on a specific speaker. To minimize observer bias, one observer would present the auditory cue to the bat and the other would record which speaker the bat flew to. All trials were videorecorded. Choices were later validated by observers scoring choices without knowledge of the auditory stimuli that the bats were being presented.

#### Statistical Analyses

To test for an overall preference for larger chorus size, we used an exact binomial test to compare the proportion of larger chorus choices to chance expectations. We repeated this test within each treatment combination.

For each stimulus combination, we calculated the absolute difference in call number between the two choruses and the relative difference (i.e. the absolute difference between the two stimuli, divided by the mean number of calls of the two stimuli; Toelch & Winter, 2007). Additionally, we calculated the ratio between the two choruses, which is mathematically related to the relative difference (see Table 1). To determine whether relative or absolute differences in chorus sizes better explain preferences for larger choruses, we fitted two generalized linear mixed models (binomial family) with absolute difference and relative difference as predictor variables in R (v.3.0.2, package 'lme4', R Developmental Core Team, 2015). Individual bat was included as a random factor to account for our repeated measures design. We then compared these two models, as well as a null model that just included bat as a random effect, based on their  $\Delta$ AIC values (Burnham & Anderson, 2004).



**Figure 1.** Experimental stimuli and arena. (a) Every pairwise presentation that bats were offered. (b) Experimental testing arena. The experimenter sat in the corner opposite the bat perch and presented each set of stimuli from two speakers.

**Table 1**  
Discrimination performance for different chorus size combinations in *T. cirrhosus* foraging decisions

Stimuli	Average <sup>a</sup>	Abs. diff. <sup>b</sup>	Ratio <sup>c</sup>	Rel. diff. <sup>d</sup>	N visits <sup>e</sup>	Prop. <sup>f</sup>
1 vs 2	1.5	1	0.5	0.67	30	0.8824
1 vs 3	2	2	0.33	1	31	0.9118
1 vs 4	2.5	3	0.25	1.20	28	0.8235
1 vs 5	3	4	0.2	1.33	28	0.8235
1 vs 6	3.5	5	0.167	1.43	27	0.7941
2 vs 3	2.5	1	0.67	0.4	28	0.8235
2 vs 4	3	2	0.5	0.67	21	0.6176
2 vs 5	2.5	3	0.4	0.857	22	0.6471
2 vs 6	4	4	0.33	1	25	0.7353
3 vs 4	3.5	1	0.75	0.286	16	0.4706
3 vs 5	4	2	0.6	0.5	24	0.7059
3 vs 6	4.5	3	0.5	0.667	23	0.6765
4 vs 5	4.5	1	0.8	0.22	22	0.6471
4 vs 6	5	2	0.67	0.4	25	0.7353
5 vs 6	5.5	1	0.83	0.182	17	0.5000

Bats ( $N=17$ ) were presented with each chorus combination a total of two times (34 total choices).

<sup>a</sup> Average difference between the number of frogs in two choruses.

<sup>b</sup> Absolute difference is calculated as the number of frogs in the larger chorus minus the number in the smaller chorus.

<sup>c</sup> Ratio is calculated as the difference between the smaller and larger chorus.

<sup>d</sup> Relative difference is calculated as the difference between the two choruses divided by the average of the concentrations.

<sup>e</sup> N visits represents the total number of times (out of 34 possible) that bats visited the larger chorus.

<sup>f</sup> Proportion of choices for the larger chorus.

Additionally, we tested other potential covariates that may have contributed to variation in preferences. These included the side of the flight cage and order of presentation. We tested all factors using a forward model selection method starting with the model above that had the lowest AIC. For these nested models, in addition to AIC, model fits were compared using maximum likelihood chi-square tests. If a factor did not significantly improve the fit of the model, we removed it.

Lastly, we wanted to investigate whether there was some optimal chorus size that the bats preferentially targeted. One way for checking for nonlinearity in data is to fit a polynomial model and determine whether the polynomial model fits the data better than the linear model. We used this approach to compare the fit of a linear model for the proportion of choices for each chorus size to a

polynomial model with a quadratic fitted to this proportion based on chorus size. We compared the fit of both models using an  $F$  test.

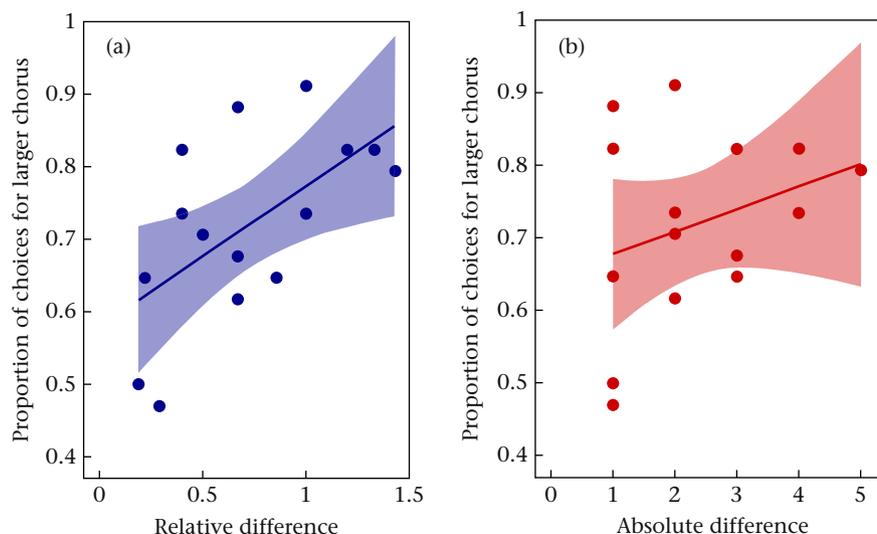
## RESULTS

Overall, bats chose the larger of the two choruses significantly more often than they chose the smaller (368 times out of 511 total responses; binomial test:  $P < 0.001$ ). Within each combination, we found significant preferences for the larger chorus in 10 of the 15 chorus size combinations across all bats (see Appendix, Table A1).

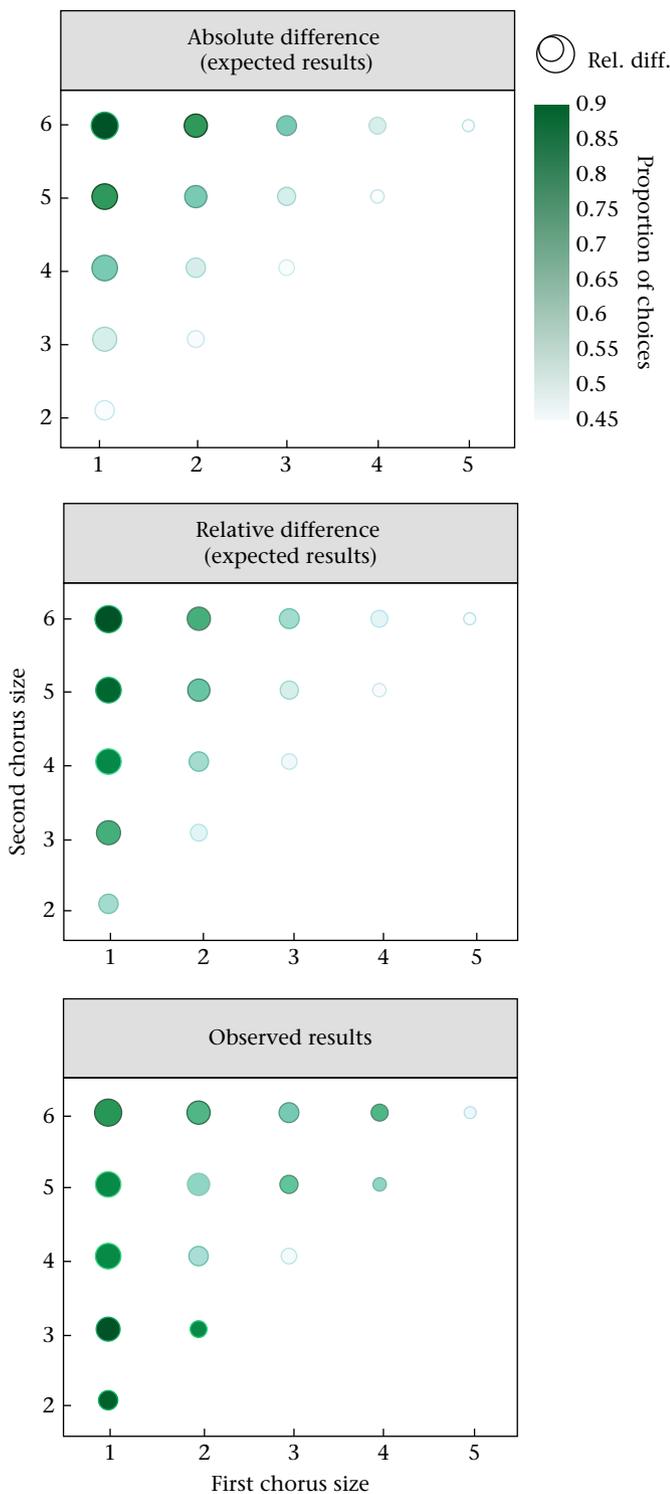
The most probable model based on  $\Delta$ AIC comparison included relative difference as a predictor variable (AIC = 598.15,  $Z = 3.56$ ,  $P < 0.001$ ). The model that included absolute difference had a higher AIC (AIC = 608.44,  $Z = 1.75$ ,  $P = 0.08$ ) than the model with relative difference as did the null model (AIC = 609.57,  $Z = 8.73$ ,  $P < 0.001$ ). A  $\Delta$ AIC of  $>10$  is considered sufficient evidence of better model fit (Burnham & Anderson, 2004). Thus, preferences for larger choruses appear to be better explained by relative, rather than absolute, differences. This is highlighted in Fig. 2, which shows how relative differences in chorus size better explain preferences for larger choruses than absolute differences across all bats.

Adding relative difference significantly improved the fit of the model when compared to the null model (AIC = 598.15,  $\chi^2_1 = 13.419$ ,  $P < 0.005$ ). Additionally, including both absolute and relative difference significantly improved the fit of the model when compared to the model that just included relative difference (AIC = 591.9,  $\chi^2_1 = 8.2833$ ,  $P = 0.004$ ). This makes sense given the design of the study. There are multiple cases where the two stimuli have a relative difference of 0.5 but vary in their absolute difference (1 versus 2, 2 versus 4, and 3 versus 6). In such cases, absolute difference would also be necessary to explain preferences for larger choruses. Our best-fitting model, however, included relative difference, absolute difference and side of presentation as fixed effects when compared to the null model (AIC = 584.7,  $\chi^2_1 = 9.1838$ ,  $P = 0.002$ ; Appendix, Table A2, Fig. A1).

Many of the similar choice tests that have been done in this system have resulted in some subtle side bias towards either the right or the left side of the cage. Importantly, we made sure that the acoustic stimuli of the larger chorus were presented on each side with equal probability. We also traded the speakers each night between the two speaker locations in the flight cage to control for



**Figure 2.** Total proportion of choices for larger choruses across all bats as explained by (a) relative differences between chorus sizes and (b) absolute differences between chorus sizes.



**Figure 3.** This plot shows all different patch size combinations. The darker the colour, the more often bats chose the correct, larger chorus (darker=better performance). The larger the circle, the greater the relative difference. As you go up the Y axis in each column, the absolute difference increases. If bats use only absolute difference between choruses when choosing the larger chorus, the proportion of choices should resemble the first panel. If the bats use only the relative difference when choosing the larger chorus, preferences should appear similar to the second panel. Our data are shown in the third panel. Our data better resemble the second model (relative differences) than the first model (absolute differences).

any potential biases created by a specific speaker. We randomized the location that was rewarded first in every trial. Lastly, we do not think that the environment within or around the flight cage influenced these biases, as biases were detected for both the left and right side of the flight cage across multiple experiments. For our data, although a side bias was present, it did not appear to swamp out the bat's preference for the larger chorus. Further experiments could be done to determine whether there is an inherent population-level bias in this species or whether biases may result from common behavioural patterns in the wild.

For tests of the optimal chorus size, we found that the fit of the linear and quadratic models was not significantly different (quadratic:  $R^2 = 0.89$ ,  $P = 0.033$ ; linear:  $R^2 = 0.81$ ,  $P = 0.015$ ; ANOVA:  $F_{4,3} = 2.54$ ,  $P = 0.21$ ). This indicates that, while there may be a preference for some intermediate chorus size, we did not have enough power in this study to detect it. Fig. 3 shows how, even though relative difference explained preferences better than absolute differences, the best performance of the bats of selecting the larger chorus was when given a choice between 1 versus 2 and 1 versus 3 rather than 1 versus 6 as predicted by either model, providing additional clues that point to an optimal chorus size.

## DISCUSSION

Consistent with models of optimal foraging, we found that bats in this study generally had a significant preference for large chorus sizes; however, *T. cirrhosus* discriminated between choruses depending on the relative, not absolute, difference in chorus size (Fig. 2). Within the range of tested chorus sizes, bats either visited the larger chorus significantly more, or showed no preference between the two. This supports our second hypothesis that bats attend to differences in the number of calling frogs as the relative difference between patches increases. Thus, *T. cirrhosus* appears to adhere to predictions of Weber's law, as seen in another study in this species (Akre et al., 2011).

*Trachops cirrhosus*, unlike many other predators, evaluates multiple patches from a distance (Pyke et al., 1977). Because these bats use passive localization to eavesdrop on prey-emitted cues (Tuttle & Ryan, 1981), they are potentially able to assess multiple patches simultaneously when making decisions about where to forage, depending on how the prey patches are distributed. Patches of túngara frogs can range from one to hundreds of calling frogs, but it is more common to find patches consisting of one to five frogs (Ryan, 1985). Because *T. cirrhosus* can eat up to 16 g each night (~10 túngara frogs), it seems reasonable to expect that selection has shaped their preferences towards larger patches. The discrimination capabilities detected in our study, however, may represent trade-offs between increased sensory processing and the resulting energy payoff. In situations where bats are making decisions about which patches to fly to when presented with several patches that all have more than six calling frogs, the fitness costs of choosing the smaller of two relatively larger patches may be marginal.

Studies of perceptual processing in both humans and animals focus on perceptual invariances in sensory phenomena that vary along a single continuum. Both our study and a study by Akre et al. (2011) investigated psychophysical limitations in acoustic modalities, however, the ways in which these acoustic stimuli are being categorically grouped may have different fitness consequences for *T. cirrhosus*. While Akre et al. focused on decisions about frogs within a single patch, our study focused on decisions about entire patches that bats chose to feed on. The fact that *T. cirrhosus* attends to proportional differences when choosing between calls that vary

in their number of chucks as well as when choosing between choruses that vary in their number of calling frogs, indicates that proportional processing is likely a conserved aspect of decision making in this bat. Akre et al. (2011) also found that bats and frogs attended to more chucks (at around 70%) when the chuck number ratio was around 0.4. In this study, we found that bats preferred larger patches around 70% of the time when this ratio was at 0.6. This difference could mean that *T. cirrhosus* is capable of discriminating differences between stimuli at larger magnitudes when choosing between the number of calling frogs than when choosing between calls that differ in their number of chucks. This seems likely, considering the energetic consequences between the two types of decisions being made.

Auditory proportional processing has also been described in other groups of animals, although in different contexts. For example, female lions, *Panthera leo*, can extract information about the size of a rival group from the number of roars and relate it to the number of their own group. Lions use this information to compute a ratio of their respective group sizes when deciding whether to attack the rival group (McComb, Packer, & Pusey, 1994). Similarly, chimpanzees, *Pan troglodytes*, use acoustic signals from rival groups when deciding whether to attack another troop, and only attack if the ratio of group sizes is 1.5 or higher (Wilson, Britton, & Franks, 2002).

Proportional processing in foraging behaviour has also been demonstrated in other Neotropical bats in the same family as *T. cirrhosus* (Phyllostomidae). Nachev and Winter (2012) found that the degree of diet specialization on sugar-rich flower nectar tends to negatively correlate with the psychometric discrimination threshold in nectarivorous phyllostomids. These trends could be driven by the costs associated with sensory processing. Comparative studies of gleaning phyllostomids could test whether and how stimulus discrimination differs between generalists like *T. cirrhosus*, which eats both insects and small vertebrates, and closely related gleaning bats, such as *Lophostoma silvicolum*, which specialize on katydid (Giannini & Kalko, 2005).

Our data also appear tentatively consistent with our third hypothesis that there may be some optimal intermediate patch size for *T. cirrhosus*. There appears to be a peak in preferences across bats for choruses that consist of three calling frogs (Fig. 3), although we need more responses to test this. If there is an optimal chorus size that increases capture success for the bats, it may represent a trade-off between dealing with the vigilance levels of a small chorus of frogs and the challenges of localizing a single male in a large chorus of frogs. If a chorus is too small, frogs are hypervigilant and cease calling very quickly (Dapper, Baugh, & Ryan, 2011; Ryan et al., 1981). If a chorus is too large, then it may be difficult for the bats to localize a single auditory stream amidst the cacophony of a chorus (Jones, Farris, Ryan, & Page, 2013). In another bat species that eavesdrops on auditory signals in a lekking moth species, it was found that bats did not have a preference for the larger lek when given a choice of two aggregation sizes. Additionally, the per capita predation risk on a single moth decreased as lek size increased (Alem, Koselj, Siemers, & Greenfield, 2011). Experiments in frog-eating bats specifically investigating strike rate success with chorus sizes that vary in number of calling frogs could be done both in the flight cage and in the wild to measure capture success of different patch sizes.

Another possible explanation for apparent deviations from optimal foraging decisions is that decisions in the wild may be influenced by conspecific competitors. Ideal free distribution theory is often used to describe how animals make patch choice decisions and distribute themselves spatially when foraging with competitors (Fretwell & Lucas, 1969). In certain situations, foraging

animals may not always choose the larger patch if there are higher levels of perceived competition at more resource-dense patches. It is possible that perceived competition plays a role in patch choices by *T. cirrhosus*. Although *T. cirrhosus* roosts with conspecifics and have been caught together (Page & Ryan, 2005), most captures consist of a single individual at a given foraging location (C. T. Hemingway, personal observation). Therefore, we still have a very limited understanding of the ways in which patch choice decisions are influenced by conspecific behaviour, if at all. New technologies are allowing us to understand the foraging patterns of multiple individual *T. cirrhosus* at once. Such studies suggest that these bats do indeed forage in the same place at the same time (Ripperger et al., 2016). More study is needed to fill this critical gap in our knowledge.

Sampling multiple patches that vary in size may also allow *T. cirrhosus* to update information about its environment while foraging. Trial and error is necessary to collect information and can cause deviations from many optimality models that assume perfect information. In a study investigating optimal patch choice in titmice, Smith and Sweatman (1974) found that birds deviated slightly from optimality model predictions by allocating the greatest amount of time to the area with the highest food abundance, but still sampling areas with lower abundance. The authors argued that this behaviour may be adaptive in fluctuating environments (Smith & Sweatman, 1974). It is possible that *T. cirrhosus* may also make suboptimal choices to sample the options available. Patches of túngara frogs can be either stable or ephemeral depending on environmental conditions, such as rainfall, and vary seasonally.

Accounting for cognitive processing can lead to more realistic optimal foraging models. A consideration of cognitive mechanisms can refine existing theories and better explain many of the decision rules that animals appear to follow. This sentiment is supported by a model developed by Abrahams (1986), which examines how animals with limited abilities to perceive differences in patch quality affects an ideal free distribution by foragers. Results from this model indicate that perceptual constraints can produce a characteristic bias such that patches with a small proportion of resources are relatively overused and patches with larger proportions of resources are relatively underused. Similarly, Kacelnik and Brito e Abreu (1998) have demonstrated that accounting for perceptual or processing errors based on Weber's law provides a better approach for predicting partial preferences between two choices in both humans and nonhumans.

Psychophysical approaches to understanding behaviour can provide insight into underlying mechanisms involved in decision making. Although the use of proportional processing has been broadly documented in foraging and mate choice decisions (Akre & Johnsen, 2014), the use of proportional processing on patch choice decisions has not been widely explored. Additionally, Morse and Fritz (1982) argued that laboratory studies of optimal foraging could limit our understanding of these processes in the wild. Here, we demonstrate that wild frog-eating bats use proportional processing when making foraging decisions about patches of calling frogs.

### Conflicts of Interest

We declare no conflicts of interest.

### Data Availability

All data have been uploaded to Figshare (<https://doi.org/10.6084/m9.figshare.6794081>).

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## Appendix

**Table A1**  
Binomial tests for every chorus size combination

Stimuli	N choices small	N choices large	Prop. large	P
1 vs 2	4	30	0.8824	<0.001
1 vs 3	3	31	0.9118	<0.001
1 vs 4	6	28	0.8235	<0.001
1 vs 5	6	28	0.8235	<0.001
1 vs 6	7	27	0.7941	<0.001
2 vs 3	5	28	0.8235	<0.001
2 vs 4	11	21	0.6176	0.055
2 vs 5	12	22	0.6471	0.062
2 vs 6	9	25	0.7353	0.005
3 vs 4	18	16	0.4706	0.432
3 vs 5	10	24	0.7059	0.013
3 vs 6	11	23	0.6765	0.029
4 vs 5	12	22	0.6471	0.062
4 vs 6	9	25	0.7353	0.005
5 vs 6	17	17	0.555	0.567

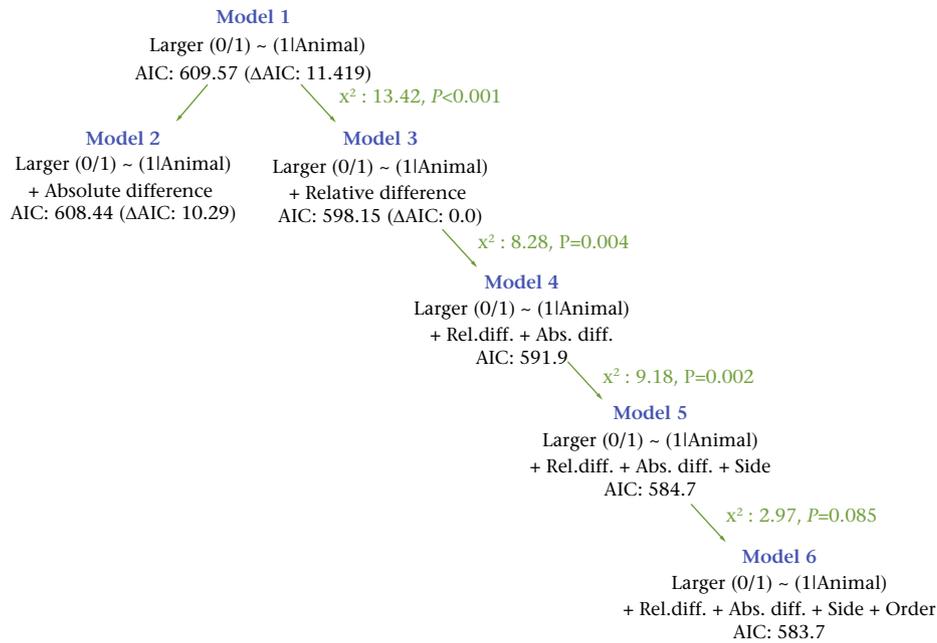
Significant P values are shown in bold (one-tailed binomial tests).

**Table A2**

Model results for binomial generalized linear mixed-effect models investigating the influence of main effects (relative difference, absolute difference, side and order) on preferences for larger chorus sizes by bats

Model	Estimate	SE	Z	P	Exp(b)	AIC	ΔAIC	Chi-square difference between models
<b>Model 1</b>								
Larger (0/1) ~ (1 Animal)								
Intercept	0.952	0.19	8.73	<0.001	2.59	609.57	11.419	
<b>Model 2</b>								
Larger (0/1) ~ (1 Animal) + Absolute difference								
Intercept	0.626	0.21	2.94	0.003	1.87			
Abs. diff.	0.143	0.08	1.75	0.081	1.15	608.44	10.29	
<b>Model 3</b>								
Larger (0/1) ~ (1 Animal) + Relative difference								<b>Model 1 vs Model 3</b> $\chi^2 = 13.42, P < 0.001$
Intercept	0.285	0.21	1.36	0.175	1.32			
Rel. diff.	0.968	0.27	3.56	<0.001	2.63	598.15	0.0	
<b>Model 4</b>								
Larger (0/1) ~ (1 Animal) + Rel. diff. + Abs. diff.								<b>Model 3 vs Model 4</b> $\chi^2 = 8.28, P = 0.004$
Intercept	0.459	0.22	2.10	0.037	1.58			
Rel. diff.	2.361	0.57	4.10	<0.001	10.60			
Abs. diff.	-0.495	0.18	-2.81	0.005	1.64	591.9		
<b>Model 5</b>								
Larger (0/1) ~ (1 Animal) + Rel. diff. + Abs. diff. + Side								<b>Model 4 vs Model 5</b> $\chi^2 = 9.18, P = 0.002$
Intercept	0.934	0.27	3.41	<0.001	2.53			
Rel. diff.	2.110	0.58	3.62	<0.001	8.25			
Abs. diff.	-0.437	0.18	-2.46	0.014	0.64			
Side	-0.667	0.22	-2.97	0.002	1.94	584.7		
<b>Model 6</b>								
Larger (0/1) ~ (1 Animal) + Rel. diff. + Abs. diff. + Side + Order								<b>Model 5 vs Model 6</b> $\chi^2 = 2.97, P = 0.085$
Intercept	1.469	0.42	3.52	<0.001	4.26			
Rel. diff.	2.127	0.58	3.64	<0.001	8.39			
Abs. diff.	-0.440	0.18	-2.47	0.013	1.55			
Side	-0.674	0.23	-2.99	0.002	1.96			
Order	-0.352	0.21	-1.72	0.085	1.42	583.7		

Variation in individual preference is accounted for by including bat as a random factor in the model. Model statistics and odds ratios are presented for all tested models. Models were compared using ΔAIC values to determine whether absolute or relative difference alone was better at predicting preferences for larger chorus size. For nested models, model fit was also compared using maximum likelihood chi-square tests in a forward stepwise selection process. Chi-square and P values are included to show the difference between models with added main effects. See flowchart for model selection in Fig. A1.



**Figure A1.** Flowchart for model selection and comparison. Model statistics and odds ratios are presented for all tested models in Table A2.