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ORIGINAL ARTICLE

Effects of information load on response times in frogs and bats: mate choice vs. prey choice

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Abstract

Decisions tend to become more challenging as the number of available options increases and choice sets become more complex. Choosing between multiple options may require additional information processing time and effort. Here, we asked if response time increases with stimulus number and attractiveness by female frogs (*Physalaemus pustulosus*) and their predators, frog-eating bats (*Trachops cirrhosus*), when comparing the mating calls of male túngara frogs. We found that frogs' response time is significantly longer when presented with two calls, compared with one. Bats also take longer to respond when presented with two calls but only when they were complex calls. Although the frogs and bats behave somewhat similarly in this experiment, the decisions that these animals are making are occurring in different domains (mating vs. foraging) and have different fitness consequences. Given these differences, we find it especially interesting that for both frogs and bats, we see similar temporal patterns in response times as a function of information load.

Significance statement

Animals are often faced with several options simultaneously. One cost of decision-making is the time involved in choosing the best option within a choice set. Here, we asked whether female frogs and frog-eating bats take longer to respond when presented multiple frog mating calls simultaneously. We also asked whether the attractiveness of those frog calls influences the time it takes frogs and bats to respond to them. We found that the time to respond was influenced by both the number and attractiveness of frog calls for both bats and frogs; however, frog response time seemed to be more greatly influenced by the number of frog calls, while bat response time seemed to be more influenced by the attractiveness of frog calls. In general, our results suggest that there may be similar mechanisms involved in decision-making for both animals.

Keywords Decision-making · Response time · Mate choice · Foraging · Túngara frogs · Frog-eating bats

Introduction

When presented with a mating or feeding opportunity, animals must often decide not just whether to pursue a presented opportunity or not but also which of multiple alternatives to pursue (Vasconcelos et al. 2013). While larger choice sets allow decision-makers to learn more about the range of available options (Hadar and Sood 2014), choosing from larger, more complex choice sets has its own suite of negative consequences. In general, decisions tend to become more challenging as the number of available options increases and as choices vary in their attractiveness (Iyengar and Lepper 2000; Chernev and Hamilton 2009). The negative effects of more choices on the decision-maker have been termed "choice overload" and occur when the complexity of the choice exceeds the cognitive resources of the individual making the decision (Chernev et al. 2015; Sasaki et al. 2018).

A variety of factors are likely to influence choice overload—including, but not limited to, the number of options available, option attractiveness, and experience with available options (Chernev et al. 2015). We often observe cases in which animals, including humans, simplify their decision-making processes by relying on simple heuristics

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(Gigerenzer 1997; Gigerenzer and Gaissmaier 2011), which may lead to suboptimal choices or irrational decisions such as "decoy effects" (e.g. Bateson et al. 2002) or intransitive preferences (e.g. Shafir 1994). Similarly, animals can be susceptible to the worsening of decision quality with increasing numbers of options due to the increasing potential for negative outcomes and risks that may result from making the wrong choice (Iyengar and Lepper 2000; Scheibehenne et al. 2010; Chernev et al. 2015).

While most studies of decision-making in animals focus on a subject's ability to choose the best option, they often overlook how much time it takes an animal to actually make a decision (Chittka et al. 2003). Because obtaining high-quality information often increases sampling time, especially under noisy conditions (Dukas 1999), speed of decision-making can be an important measure of performance. When evaluating multiple options, animals must sample alternatives for some time until a decision is reached and acted upon (Chittka et al. 2009; Kacelnik et al. 2011). Computational models of decision-making, such as drift diffusion models, suggest that evidence favoring each alternative is integrated over time and a decision is made when there is sufficient evidence favoring one alternative (Ratcliff and McKoon 2008). This process has been compared with a jury deliberating and weighing the evidence before reaching a final verdict (Gold and Shadlen 2007).

Several psychophysical laws have been used to describe changes in response times as choice sets increase in size (Hick 1952; Hyman 1953) and as options vary in stimulus magnitude (Piéron 1913). Hick-Hyman's law states that the time for a decision-maker to respond increases linearly with the amount of information that needs to be processed. Piéron's law states that response times decrease according to stimulus magnitude. Both have been powerful at predicting response times in non-human animals (e.g. Shimp et al. 2007; Reina et al. 2018).

As predicted by the Hick-Hyman law, decision-makers also typically face a very clear tradeoff between speed and accuracy, such that faster responses can be produced at the expense of accuracy (Seow 2005). Conversely, individuals can improve accuracy by spending more time gathering information (Trimmer et al. 2008; Chittka et al. 2009). Rapid decisions might lead to decreased accuracy and are more likely when it takes a long time to solve a difficult task and the potential costs of errors may be low (Chittka et al. 2009). When accuracy is of prime importance, additional time might be needed to ensure costs are not incurred for poor decisions (Ings and Chittka 2008). Depending on the species and the potential consequences of a particular choice, selective emphasis might be placed on either speed or accuracy (Chittka et al. 2009). Empirical evidence supports the notion that these tradeoffs exist between decision speed and accuracy in many foraging behaviors, such as predators choosing prey and pollinators choosing flowers (Chittka et al. 2003, 2009).

Here, we investigate the temporal aspect of decision-making using two vertebrates that differ greatly in their information processing systems but make decisions in the wild based on the same set of stimuli. Our two test subjects are the túngara frog, *Physalaemus pustulosus*, and the bat that eats it, the frog-eating bat, *Trachops cirrhosus*. Although they are very different animals, their natural histories are intricately intertwined. Male túngara frogs vocally advertise for females from small, ephemeral ponds typically consisting of one to five calling males, although these numbers can vary substantially (Ryan 1985). Frog-eating bats hunt túngara frogs by eavesdropping on their mating calls (Tuttle and Ryan 1981). These mating calls are initiated by a whine and can be followed by 0 to 7 chucks (Ryan 1985). Both female frogs and frog-eating bats are preferentially attracted to calls with chucks (Akre et al. 2011). As a result, both bats and frogs are often choosing between several calling males simultaneously.

In the present study, we are not concerned with whether animals are choosing optimally or what "optimal" means for a frog or a bat in a given context. Rather we are interested in how the context of a decision influences the time it takes to make a choice. We use response time or the time from the onset of the stimulus until a choice is made as a proxy for decision-making time in both frogs and bats. In this study, we ask (1) whether response time differs between a more attractive and less attractive option in a one-speaker test, (2) whether response times differ when choosing between one and two identical options in a two-speaker test, and (3) whether response times differ between two-speaker tests that differ in their attractiveness.

Methods

Frogs

Frog phonotaxis experiments were conducted at the Smithsonian Tropical Research Institute in Gamboa, Panama (9° 07.0 N, 79° 41.9 W) in July 2009. Females were collected in amplexus with males from the field and tested between 1930 and 0430 h that night/morning. All applicable international, national, and/or institutional guidelines for capture and testing of frogs were followed.

We conducted phonotaxis trials in an Acoustic Systems (ETS-Lindgren, Austin, TX, USA) sound attenuation chamber (2.7 × 1.8 m × 2 m high). We broadcast calls at 82-dB SPL (re. 20 μPa) at the release point of the female, 110 cm from the speaker(s), and at the natural túngara call rate of one call every 2 s (Ryan 1985). We used synthetic calls that are as effective in eliciting female phonotaxis as natural calls (Rand et al. 1992).

Frogs were presented with one-speaker tests (whine alone, whine-chuck alone) and two-speaker tests (whine vs. whine, whine-chuck vs. whine-chuck, broadcast antiphonally). Each of 20 females completed all four tests in randomized order for a total of 4 presentations per female. Trials lasted a maximum of 10 min; we scored a choice if the subject approached within 10 cm of the speaker. Latency to choose was measured from the moment a release funnel was raised to the moment the frog made a choice. After testing, frogs were released at their original site of capture. Additional details on the phonotaxis procedure can be found in (Rand et al. 1992).

Bats

Bat phonotaxis experiments were conducted at the Smithsonian Tropical Research Institute in Gamboa from May to August 2016. We captured 17 adult *T. cirrhosus* using mist nets in Soberanía National Park. Bats were released into a large, outdoor flight cage (5 × 5 × 2.5 m) and allowed to forage for prey rewards. Once bats fed readily in captivity, we commenced behavioral trials. Bats were tested individually between 1800 and 0200 h. All applicable international, national, and/or institutional guidelines for capture and testing of bats were followed.

We broadcast natural calls, using a modal túngara frog call drawn from a large sample of natural túngara frog calls (Ryan and Rand 2003). Unlike with the female frogs (Rand et al. 1992), we have not determined if synthetic and natural calls elicit the same responses in the frog-eating bat. Stimulus pairs were presented simultaneously because the bats show a strong tendency to respond to the first call they hear. Calls were broadcast every 2 s at 69-dB SPL at the bat's perch. We placed speakers 1.5 m apart, each 2 m from the roost. We quantified latency to choose as the time from the onset of stimuli presentation to the bat's flight from the roost. Bats were presented with the same four combinations of stimuli used for the female frogs: two one-speaker tests (whine alone, whine-chuck alone) and two two-speaker tests (whine vs. whine, whine-chuck vs. whine-chuck). Each bat was presented with these stimuli three times (12 total presentations per bat); presentation order was randomized. Additional details of the bat phonotaxis experiments can be found in Page and Ryan (2005).

Measuring response times in frogs and bats

For frogs, choices were considered made when individuals arrived within 10 cm of a speaker. Response times were measured from the moment the release funnel was raised until the moment the frog made a clear choice. We were conservative in this choice metric. We recognize that this conservative approach may confound other aspects of choice such as motivation and locomotion. The alternative would have been to measure the latency from time the frogs first moved from the arena's center rather than from the moment the release funnel was raised, but we know that initial direction does not always coincide with the final choice that they make. Thus, we cannot assume that the frog's final decision, or any decision, has been made when the frog first moves. Conversely, in the bats, we quantified response time as the time from the onset of stimuli presentation to the bat's flight from the roost. Unlike frogs, bats typically flew straight from the perch directly to a speaker. Thus, latency to leave the perch is likely quite similar to, and highly correlated with, the time it takes them to arrive at the speaker. For both frogs and bats, latency times were measured by an observer who was blind to the experimental stimuli.

Importantly, we do not compare the actual latency times between species but rather only within species. Between species, we compare more general patterns that occur according to stimulus number and attractiveness. For both bats and frogs, we are also comparing their responses to the same stimuli they would encounter in nature, providing us with a rare opportunity to understand processes that take place in the wild in two very different species making different decisions, choosing a meal or a mate, based on identical stimuli. Although we cannot assume that we are perfectly capturing the time during which a decision must have taken place, we are certainly bracketing the behavioral criteria that we are using as proxies for decisions. Such challenges highlight the difficulty in studying decision-making in mate choice and foraging choice behaviors, especially in a comparative framework.

Statistics

We used linear mixed models (LMM) with restricted maximum likelihood (REML) to analyze the influences of speaker number and signal complexity (whine only vs. whine-chuck) and their interaction (speaker number * signal complexity) on response time. In both bats and frogs, latency distributions were left-skewed. We used a natural-log transformation prior to using the linear modeling procedure and back-transformed the estimated marginal means (EMMs) for ease of interpretation. Subjects were treated as random intercepts. For frogs, trial order contributed significantly to the variance and therefore also included as a random effect; similarly, feeding contributed significantly to variance among bat latencies and thus included as a random effect. Degrees of freedom for EMMs were calculated using the Kenward-Roger method, and p values in post hoc pairwise tests were adjusted for 6 test combinations using the Holm method (Holm 1979). Statistical analyses were conducted in R v3.5 utilizing the following packages: *lmer*, linear mixed model fit (Bates et al. 2015); *car*, Anova type II p value calculation; *emmeans*, post hoc pairwise contrasts (Fox and Weisberg 2011).

Results

Frogs

There was a significant effect of speaker number, one vs. two ($X^2 = 18.94$, df = 1, $p < 0.001$), and stimulus, whine only vs. whine-chuck ($X^2 = 7.76$, df = 1, $p = 0.005$); but there was no interaction between speaker number and stimulus ($X^2 = 3.01$, df = 1, $p = 0.082$).

In one vs. two-speaker tests, latencies were significantly longer for whine only but not whine-chuck (EMM±SE, pairwise contrasts): whine only: one-speaker (56.8 ± 1.2 s) vs. two-speaker (96.5 ± 1.2 s) ($t = 3.98$, df = 48.0, $p = 0.001$); whine-chuck: one-speaker (51.4 ± 1.2 s) vs. two-speakers (64.5 ± 1.2 s) ($t = 1.76$, df = 56.6, $p = 0.25$) (Fig. 1a). Within speaker number, latencies in the two-speaker whine only test were significantly longer than those of the two-speaker whine-chuck test, but the stimulus effect was not significant in the one-speaker tests (two-speaker: whine only vs. whine-chuck ($t = 2.87$, df = 23.7, $p = 0.034$), one-speaker: whine only vs. whine-chuck ($t = 0.72$, df = 31.6, $p = 0.709$).

Bats

There was no significant effect of speaker number on latency to choose ($X^2 = 2.44$, df = 1, $p = 0.12$). There was, however, a significant effect of stimulus, whine vs. whine-chuck ($X^2 = 4.06$, df = 1, $p = 0.044$), and a significant interaction of speaker number and stimulus on latency to choose ($X^2 = 4.68$, df = 1, $p = 0.030$).

The effect of speaker number on latency depended on the stimulus (Fig. 1b). Latency was greater in the two-speaker test compared with the one-speaker test only when the stimulus was a whine-chuck, not when it was a whine (whine only: one-speaker (4.3 ± 1.2 s) vs. two-speaker (4.0 ± 1.2 s) ($t = 0.44$, df = 183.8, $p \sim 1$); whine-chuck: one-speaker (2.7 ± 1.2 s) vs. two-speaker (4.1 ± 1.2 s) ($t = 2.63$, df = 184, $p = 0.046$)). In the one-speaker tests, latencies were significantly shorter for whine-chuck tests than whine only ($t = 2.96$, df = 183.5, $p = 0.021$). There was no difference, however, between the latencies in the two-speaker whine and the two-speaker whine-chuck tests ($t = 0.087$, df = 183.97, $p \sim 1$).

Discussion

In economics, it is often assumed that money is the utility that humans strive to maximize. In animals, however, the utility being maximized is Darwinian fitness. There are costs and benefits to both slow and fast decision-making (for example, in humans see Kahneman (2011)). Slow decision-making might enhance accuracy but can also increase exposure to predators and parasites and lost opportunities. On the other hand, fast decision-making might be less accurate but more risky (Chittka et al. 2009). The expectation that complex decisions take time and that there is a tradeoff between speed of

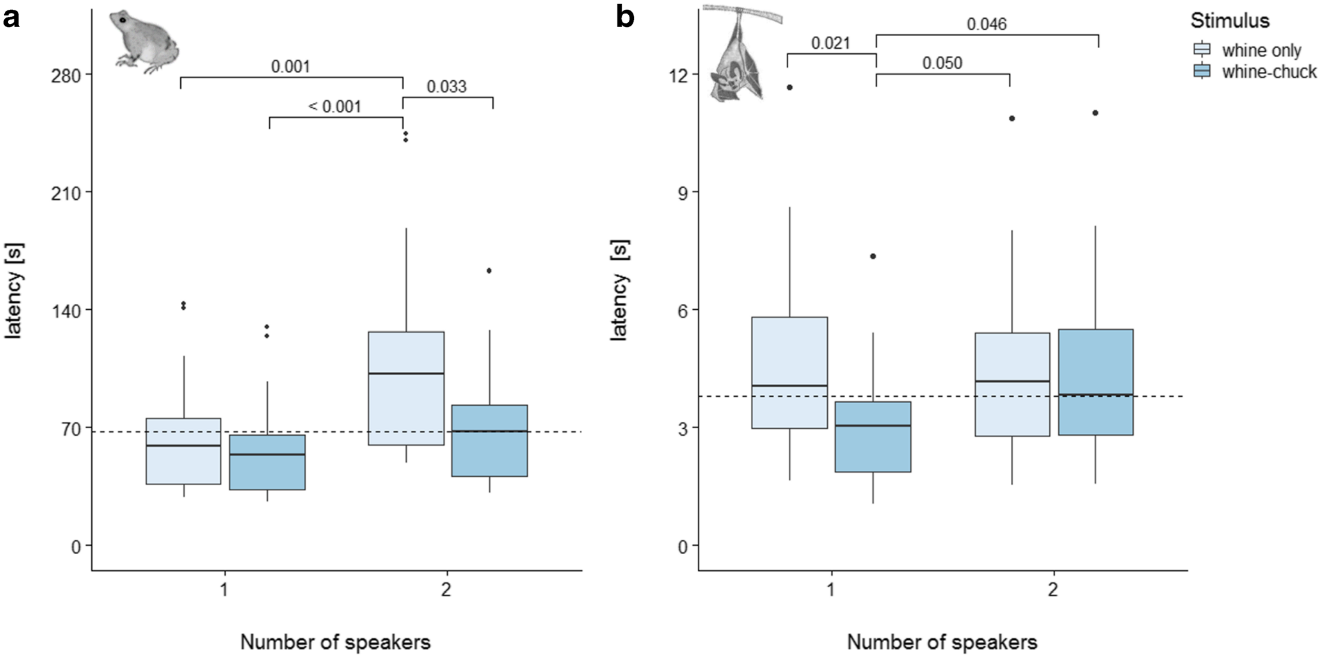

Fig. 1 Latency distributions for frogs (**a**) and bats (**b**) measured in response to a frog call stimulus broadcast from either one or two speakers. Boxplots represent medians and interquartile ranges (IQR) of the model-predicted values. Whiskers extend to the most extreme data points within ± 1.5 IQR. Dotted lines represent grand means (EMMs) for each species (frogs, bats). Only p values for significant pairwise contrasts ($p \leq 0.05$) are included in the figure

action and accuracy of decision is a logical expectation, but it is still subject to empirical research.

Here, we asked if decision-making time increases with the same number and attractiveness of frog calls being compared both by female frogs and their predators, frog-eating bats. Consistent with predictions of Hick-Hyman's law, we generally found that decisions took longer with more options although differences in response times based on speaker number alone were only significant for frogs. For both frogs and bats, and in accordance with Piéron's law, we found that latency to respond also differed according to the attractiveness of the stimuli. For female frogs, response time was significantly longer when presented with two vs. one exemplars of the whine and nearly so in response to the two vs. one exemplars of the whine-chuck. Bats also took longer to respond in the two-speaker test than in the one-speaker test for one of the two stimuli. Interestingly, the main effect in bats is seen with the whine-chuck while in the frogs the main effect is with the whine.

Previous túngara frog studies have shown that decision time between two stimuli varies with how different the stimuli are in dominant frequency and inter-call interval (Bosch et al. 2000). Phelps et al. (2006) assigned an "attractiveness" score to túngara frog calls based on females' choices in one-speaker tests; when these stimuli were then paired in two-speaker tests, latency to choose was predicted by the differences in these relative attractiveness scores, with females showing shorter latencies for more preferred calls. A similar relationship between latency and attractiveness has been shown in frog-eating bats, with bats flying more quickly to preferred calls (Fugère et al. 2015). Synthesizing these results with our current study strongly suggests that time devoted to responding to male frog calls in túngara frogs and frog-eating bats is influenced by the number of and relative differences between options, with more choices resulting in longer response times.

Apart from the differences in species-level patterns, we also found a substantial amount of individual variation in decision latencies within species. It has been proposed that there might be consistent between-subject differences when making decisions, such that some individuals consistently make "fast-and-sloppy" decisions, whereas others are slower and more accurate (Chittka et al. 2009). Chittka et al. (2003) found these differences in bumblebees when discriminating between different colored flowers. Burns and Rodd (2008) found similar individual variation in guppies when performing a spatial memory task.

Although stimulus number and attractiveness appear to influence response times in both bats and frogs, the decisions that these animals are making are actually quite different. First, they are operating in different domains: bats are looking for a meal and frogs are looking for a mate (Tuttle and Ryan 1981; Ryan et al. 1982). The cost of lost opportunities that can arise from longer decision times more likely influences the bats than the frogs: in the presence of bats, calling túngara frogs quickly stop calling to decrease their conspicuousness. In contrast, in the presence of females, calling frogs increase their conspicuousness (Akre and Ryan 2011). There is always a surfeit of males available as mates (Ryan 1985). Lost opportunities thus probably have a greater impact on the bats than the frogs. Experience with available options is another factor that can contribute to choice overload and ultimately lead to differences in time to respond to alternative options. There are clear, biological differences between both the frogs and the bats in terms of how experience may play a role in decision-making time. While frogs are innately predisposed to respond to conspecific calls (Dawson and Ryan 2012), bats likely first learn that calls of male túngara frogs indicate a palatable source of food. Differences in experience could account for some of the variation that we observe both between species and also within individual bats in this study.

The information gleaned from the calls might be another important difference between the frogs and bats. When deciding what to eat, there is a variety of circumstances in which favoring either speed or accuracy would be advantageous. For pollinating insects visiting different flowers, there is a low cost of visiting incorrect or less favorable flowers. Costs of errors are much greater for predators choosing between toxic and edible prey, where choice accuracy can have lethal consequences (Chittka et al. 2009). Túngara frog calls probably give the bats little information about their nutritional quality outside of the prey being edible (Bernal et al. 2007), but the calls do provide important information for localization (Page and Ryan 2008). The same mating calls indicate to the female túngara frogs if a male is a conspecific or heterospecific (Ryan 1985), large or small (Ryan 1985), and infected or not infected by the chytrid fungus (S. Rodríguez-Brenes and MJR, unpublished data). Suboptimal choices in any of these comparisons could negatively impact a female frog's fitness.

Another explanation for potential differences in patterns we observed in frogs and those that we observed in bats in this study might be, in part, attributed to the difference in how we measured latency to respond in the two different species. While for the bats, we are quite confident that what we were measuring was decision-making time, for the frogs, our metric includes decisions and potentially other behaviors. When presented with the stimuli, bats in this study flew quickly and directly towards the speaker. Conversely, frogs must have traveled at least 90 cm for a clear choice to be recorded and often did not do so in a direct path. While the response times that we measured for the frogs did include decision-making time, it is likely that the frogs were using some sort of Bayesian updating to inform their decision, and this likely contributed to increased latency times (Baugh and Ryan 2010). Due to the biological differences between animals and the way that we can measure preferences in the lab, this is one aspect of our study that demonstrates the challenges in conducting comparative studies of behavior.

Considering the temporal components of decision-making can also help elucidate which underlying cognitive mechanisms are at play. Two general decision-making models have been proposed which each predict differences in decision-making times (Kacelnik et al. 2011). The tug-of-war model states that multiple options are simultaneously "tugging" at the individual while the individual compares the options to one another. As a result, a decision-maker facing two or more alternatives takes more time to evaluate them and hence is slower to act than when each alternative is encountered on its own. In contrast, the sequential choice model assumes that options are evaluated successively, and latency to decide occurs once any single option reaches a decision criterion (Kacelnik et al. 2011). According to this model, adding options to the set should not increase decision time because the individual only needs to compare each option to a fixed threshold for acceptance, and both options either do or do not meet the threshold criteria.

Here, we asked if decision-making time increases with the number of calls being compared, allowing us to address some, but not all, of the predictions of these two models. Overall, our data lend some support for the tug-of-war model. Frogs had longer latencies with an increase in number and relative differences between options as predicted by this model. In bats, the effect of call number was dependent on the call type. The more attractive whine-chuck did in fact elicit a shorter latency when presented in isolation than when presented in the two-speaker test, also lending support to the tug-of-war model. Importantly, we did not see this same pattern in the bats when the single stimulus was a whine.

This study uses a largely unexplored case of two options being faced by the subject that are identical in every respect. The fact that the animals are asked to choose between identical stimuli makes this a case of Buridan's ass, in which a theoretical donkey dies of starvation when placed exactly equidistant between two equally attractive hay piles. As a result, there is no clear prediction: when facing two equally attractive targets, the animal can do anything without contradicting either model. The frogs in our study behave similarly to the hypothetical donkey, taking longer to decide between the two identical stimuli for both the whine and whine-chuck than they took when presented with either stimulus in isolation. The bats, on the other hand, only took longer when choosing between two whine-chucks vs. one whine-chuck but did not show any evidence for increased latency when presented with one or two whines.

It has been suggested that most animals encounter options in a sequential, not simultaneous, fashion (Vasconcelos et al. 2010). One notable exception is animals that aggregate in leks to attract females (Bradbury and Gibson 1983). In such cases, females approach aggregations of males and likely have some opportunity for simultaneous evaluation. Kacelnik et al. (2011) have argued that this is still likely a series of sequential encounters with females going from male to male. We argue that for both bats and frogs, there is at least some point where they are making a choice based on options that they are encountering simultaneously. This initial assessment is how they decide which frog to target in their approach. It is entirely likely, especially for the female túngara frogs, that as they approach, there may be more opportunity for sequential evaluation processes to occur as they sample multiple males. For bats eavesdropping on these leks, it does seem likely that there is much sequential assessment, especially when they are targeting these choruses in flight. Instead, bats likely target a single male in their attack and must reach this decision prior to attacking calling males.

Given the differences between frogs and bats in their cognitive complexity, the domains in which they are making decisions, and the different types of information they can glean from the frog's call, it is especially interesting that for both frogs and bats, we see similar temporal patterns in decision-making.

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Authors' contributions AML and CTH conducted the experiments with the frogs and bats, respectively, and analyzed the data. MJR conceived of the study, RAP and MJR supervised this study, and all authors contributed to writing the manuscript. All authors of this manuscript have read and agreed on the content.

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Data availability All data are deposited in figshare (frogs: https://doi.org/10.6084/m9.figshare.8476025.v1; bats: https://doi.org/10.6084/m9.figshare.8475533.v1).

Ethical approval All experiments were approved by the Smithsonian Tropical Research Institute (STRI IACUC, bats: 2014-0101-2017, frogs: STRI IACUC, 2009-0825-02), the University of Texas at Austin (bats: AUP-2015-00048, frogs: AUP-2011-00105), and the Government of Panama (Ministerio de Ambiente; bats: SE/A 69-15, frogs: SE/A-29-09).

Conflict of interest The authors declare that they have no conflict of interest.

References

Akre KL, Ryan MJ (2011) Female túngara frogs elicit more complex mating signals from males. Behav Ecol 22:846–853

Akre KL, Farris HE, Lea AM, Page RA, Ryan MJ (2011) Signal perception in frogs and bats and the evolution of mating signals. Science 333:751–752

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bateson M, Healy SD, Hurly TA (2002) Irrational choices in hummingbird foraging behaviour. Anim Behav 63:587–596

Baugh AT, Ryan MJ (2010) Ambient light alters temporal-updating behaviour during mate choice in a Neotropical frog. Can J Zool 88: 448–453

Bernal XE, Rand AS, Ryan MJ (2007) Sex differences in response to nonconspecific advertisement calls: receiver permissiveness in male and female túngara frogs. Anim Behav 73:955–964

Bosch J, Rand AS, Ryan MJ (2000) Signal variation and call preferences for whine frequency in the túngara frog, *Physalaemus pustulosus*. Behav Ecol Sociobiol 49:62–66

Bradbury JW, Gibson RM (1983) Leks and mate choice. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 109–138

Burns JG, Rodd FH (2008) Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. Anim Behav 76:911–922

Chernev A, Hamilton R (2009) Assortment size and option attractiveness in consumer choice among retailers. J Mark Res 46:410–420

Chernev A, Böckenholt U, Goodman J (2015) Choice overload: a conceptual review and meta-analysis. J Consum Psychol 25:333–358

Chittka L, Dyer AG, Bock F, Dornhaus A (2003) Bees trade off foraging speed for accuracy: psychophysics. Nature 424:388–388

Chittka L, Skorupski P, Raine NE (2009) Speed–accuracy tradeoffs in animal decision making. Trends Ecol Evol 24:400–407

Dawson B, Ryan MJ (2012) Female preferences are not altered by early acoustic experience in the Neotropical frog *Physalaemus pustulosus*. J Herpetol 46:535–538

Dukas R (1999) Costs of memory: ideas and predictions. J Theor Biol 197:41–50

Fox J, Weisberg S (2011) An R companion to applied regression. Sage Publishing, Newbury Park

Fugère V, O'Mara MT, Page RA (2015) Perceptual bias does not explain preference for prey call adornment in the frog-eating bat. Behav Ecol Sociobiol 69:1353–1364

Gigerenzer G (1997) Bounded rationality: models of fast and frugal inference. Swiss J Econ Stat 133:201–218

Gigerenzer G, Gaissmaier W (2011) Heuristic decision making. Annu Rev Psychol 62:451–482

Gold JI, Shadlen MN (2007) The neural basis of decision making. Annu Rev Neurosci 30:535–574

Hadar L, Sood S (2014) When knowledge is demotivating: subjective knowledge and choice overload. Psychol Sci 25:1739–1747

Hick WE (1952) On the rate of gain of information. Q J Exp Psychol 4: 11–26

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6:65–70

Hyman R (1953) Stimulus information as a determinant of reaction time. J Exp Psychol 45:188–196

Ings TC, Chittka L (2008) Speed-accuracy tradeoffs and false alarms in bee responses to cryptic predators. Curr Biol 18:1520–1524

Iyengar SS, Lepper MR (2000) When choice is demotivating: can one desire too much of a good thing? J Pers Soc Psychol 79:995–1006

Kacelnik A, Vasconcelos M, Monteiro T, Aw J (2011) Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice. Behav Ecol Sociobiol 65: 547–558

Kahneman D (2011) Thinking, fast and slow. Farrar, Straus and Giroux, New York

Page RA, Ryan MJ (2005) Flexibility in assessment of prey cues: frog-eating bats and frog calls. Proc R Soc Lond B 272:841–847

Page RA, Ryan MJ (2008) The effect of signal complexity on localization performance in bats that localize frog calls. Anim Behav 76:761–769

Phelps SM, Rand AS, Ryan MJ (2006) A cognitive framework for mate choice and species recognition. Am Nat 167:28–42

Piéron H (1913) Recherches sur les lois de variation des temps de latence sensorielle en fonction des intensités excitatrices. Ann Theor Psychol 20:17–96

Rand AS, Ryan MJ, Wilczynski W (1992) Signal redundancy and receiver permissiveness in acoustic mate recognition by the Túngara frog, *Physalaemus pustulosus*. Am Zool 32:81–90

Ratcliff R, McKoon G (2008) The diffusion decision model: theory and data for two-choice decision tasks. Neural Comput 20:873–922

Reina A, Bose T, Trianni V, Marshall JAR (2018) Psychophysical laws and the superorganism. Sci Rep 8:4387

Ryan MJ (1985) The Túngara frog, a study in sexual selection and communication. University of Chicago Press, Chicago

Ryan MJ, Rand AS (2003) Sexual selection in female perceptual space: how female túngara frogs perceive and respond to complex population variation in acoustic mating signals. Evolution 57:2608–2618

Ryan MJ, Tuttle MD, Rand AS (1982) Bat predation and sexual advertisement in a Neotropical anuran. Am Nat 119:136–139

Sasaki T, Pratt SC, Kacelnik A (2018) Parallel vs. comparative evaluation of alternative options by colonies and individuals of the ant *Temnothorax rugatulus*. Sci Rep 8:12730

Scheibehenne B, Greifeneder R, Todd PM (2010) Can there ever be too many options? A meta-analytic review of choice overload. J Consum Res 37:409–425

Seow S (2005) Information theoretic models of HCI: a comparison of the Hick-Hyman law and Fitts' law. Hum Comput Interact 20:315–352

Shafir S (1994) Intransitivity of preferences in honey bees: support for "comparative" evaluation of foraging options. Anim Behav 48:55–67

Shimp CP, Froehlich AL, Herbranson WT (2007) Information processing by pigeons (*Columba livia*): incentive as information. J Comp Psychol 121:73–81

Trimmer PC, Houston AI, Marshall JAR, Bogacz R, Paul ES, Mendl MT, McNamara JM (2008) Mammalian choices: combining fast-but-inaccurate and slow-but-accurate decision-making systems. Proc R Soc Lond B 275:2353–2361

Tuttle MD, Ryan MJ (1981) Bat predation and the evolution of frog vocalizations in the Neotropics. Science 214:677–678

Vasconcelos M, Monteiro T, Aw J, Kacelnik A (2010) Choice in multi-alternative environments: a trial-by-trial implementation of the sequential choice model. Behav Process 84:435–439

Vasconcelos M, Monteiro T, Kacelnik A (2013) Context-dependent preferences in starlings: linking ecology, foraging and choice. PLoS One 8:e64934