Cognitive constraints on optimal foraging in frog-eating bats

Claire T. Hemingway [a, b, *], Michael J. Ryan [a, b], Rachel A. Page [b]

[a] Department of Integrative Biology, University of Texas, Austin, TX, U.S.A.
[b] Smithsonian Tropical Research Institute, Balboa, Ancón, Panama

ARTICLE INFO

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.
© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

There has been considerable interest over the last five decades in understanding the decisions 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 (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). 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