



State-dependent learning influences foraging behaviour in an acoustic predator

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Humans and other animals have been shown to exhibit preferences for options previously associated with greater past need. Such studies indicate that animals are sensitive to both the physical properties of choices and their own state-dependent gains at the time of learning. Because this behaviour appears to occur across divergent taxonomic groups, it most likely reflects a common way that animals learn about food. Here we study this phenomenon in the frog-eating bat, *Trachops cirrhosus*. This carnivorous bat hunts by eavesdropping on frog and insect mating calls and its diet is both broad and seasonally variable. As a result, these bats must learn about new sources of food and possibly the state-dependent gains associated with those sources. In this experiment we trained bats to associate two different acoustic cues (ringtones) to two identical food rewards. Each ringtone was encountered in one of two nutritional states: hungry or pre-fed. We then tested preferences between these cues under both nutritional states. We found that bats overwhelmingly preferred the ringtone associated with previous greater deprivation regardless of their condition during testing. We argue that it is most likely adaptive for frog-eating bats to place a higher value on food rewards that are obtained when internal reserves are low.

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A fundamental assumption in models of decision making is that decisions are made in ways that maximize some aspect of an individual's fitness. Because evolutionary fitness is often difficult to measure directly, choice models usually deal in more easily measured currency, or 'utility' that is assumed to contribute in some way to fitness. Maximizing currency forms the basis of many optimal foraging models, including the standard models of prey choice and patch use (MacArthur & Pianka, 1966). In the context of an animal's foraging decisions, the net rate of energetic gain is an obvious currency to use as a proxy of fitness (Stephen & Krebs, 1986). All else being equal, animals are expected to choose options that offer a higher energetic gain and to be indifferent between options that offer the same quantity and quality of food. Both humans and animals, however, do not always reliably choose options that are considered optimal based on the physical properties of the choices, and one reason for such deviations is that an individual's internal state, or energy reserves, can influence how choices are made between alternatives (Houston, 1997).

Decisions influenced by an individual's internal state are considered rational in economics, psychology and behavioural ecology, and considering a decision maker's state has been informative in predicting behavioural outcomes (McNamara, Trimmer, & Houston, 2012). Bernoulli (1954) is credited with being one of the first to recognize that a gain of one thousand ducats is more valuable to a pauper than to a rich man even though both men gain the same amount. This difference in value between rich and poor can be explained in terms of their current state of need because the benefits that each person receives are drastically different. In nonhuman animals, we also see similar decision rules that take into account an individual's energetic states. For example, animals tend to partake in riskier strategies when their current energy reserves are lower and avoid risk when energy reserves are sufficiently high (Caraco, 1981; McNamara & Houston, 1992).

Most models of state-dependent foraging only consider an animal's current energetic state at the time that foraging decisions are made. Recent work has gone a step further by addressing how foraging decisions may also depend on the individual's state of need during prior experiences with alternatives. For example, starlings have been shown to prefer a reward that was previously encountered during higher need over one that was encountered during low need, even though both rewards were identical in their

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payoff. These preferences were robust when birds were tested at both high and low deprivation states (Marsh & Kacelnik, 2004). Pompilio and Kacelnik (2005) took this a step further to show that starlings still prefer a stimulus encountered in a hungry state over a stimulus encountered in a satiated state, even when the objective payoffs were higher in the pre-fed state. This behaviour has been termed state-dependent valuation or learning (Pompilio, Kacelnik, & Behmer, 2006) and it contradicts most normative models of decision making in behavioural ecology and economics that only consider the intrinsic properties of a choice and an individual's current state at the time of decision making.

The frequency and importance of such paradoxes in natural settings are not known, although there appears to be widespread taxonomic evidence in humans and other animals that preferences more closely reflect the subject's state at the time of learning than at the time of choice (McNamara et al., 2012). While the adaptive advantages of such mechanisms may not be obvious, theoretical work has proposed that state-dependent valuation can be favoured by natural selection in changing and uncertain environments (McNamara et al., 2012). Individuals who allow hunger to affect learning for future decisions may enjoy longer-term fitness benefits (Kacelnik & Marsh, 2002). It has therefore been proposed that irrational behaviour can arise because of state-dependent mechanisms of evaluation that have evolved to be advantageous in a broader context (Houston, 1997; Houston, McNamara, & Steer, 2007).

Here we tested whether frog-eating bats, *Trachops cirrhosus*, exhibit state-dependent valuation when learning about novel food items. Frog-eating bats are generalist predators that forage on frogs and other small vertebrates as well as many insect species (Giannini & Kalko, 2005). They passively eavesdrop on mating calls of prey and have been shown to associate several aspects of prey quality, such as prey size and palatability, with the calls of their prey species (Tuttle & Ryan, 1981). These bats also have a seasonally variable diet that differs in prey availability between the Neotropical wet and dry seasons (Jones, Ryan, & Page, 2014). As a result, these animals must constantly update their internal knowledge about what is available, when, and at what payoff.

In this study, we manipulated the hunger state of the bats in a flight cage while they were trained to associate novel sounds with identical food rewards. Each bat encountered two identical rewards each paired with its own unique ringtone. Each ringtone was encountered in one of two nutritional states: hungry or pre-fed. We then gave bats a series of choices between the two ringtones when the bats were both in hungry and satiated states. We predicted four possibilities for how bats could value each reward. If bats just learn about the physical properties of each reward without incorporating knowledge of their internal state during learning, we expected there to be no preference between the two options (magnitude priority). If, however, bats differentially value each option based on past gains, they may prefer either the option experienced when they were in a low nutritional state (value priority) or the option associated with a high nutritional state (state priority) regardless of their state at the time of testing. Lastly, bats may favour the options that they learn about only when they are in the same state in which they learned about them (state-option association) (Marsh & Kacelnik, 2004; Pompilio et al., 2006).

METHODS

Animal Capture and Care

Experiments were conducted in Gamboa, Panama, from May to September 2018 at the Smithsonian Tropical Research Institute. We captured bats ($N = 12$) using mist nets set over streams and across

flyways in Soberanía National Park, Panama. Upon capture, bats were held in a small mesh tent for 24 h and hand-fed bait fish. Following one night of acclimation, bats were released into a larger outdoor flight cage ($5 \times 5 \times 2.5$ m) that served as both a home cage and an experimental chamber. During the experiment, bats were positioned in a shelter with a perch to which they were trained to return between stimulus presentations. The experimenter sat in the corner opposite the bat, with video and playback equipment. Stimuli were broadcast through a Lenovo Thinkpad laptop and a Pyle Pro PTA2 amplifier. Fostex FE103En speakers were placed under 1×1 m screens on the floor of the flight cage. The flight cage was illuminated with two infrared lights (IR Yeshzhuanhua model 80AIR) and a 25 W red light. For both training and testing trials, bat flights were recorded with two infrared cameras (Sony DCR-TRV340). One camera was focused on the ground facing the speaker and the other was focused on the bat in the perch.

Experimental Overview

The experiment consisted of three components: pretraining, training (40 trials) and testing (20 trials). Fig. 1 provides a flowchart of the experimental design. Methods for each component are outlined in more detail below. The experiment lasted for 4 days per bat and all bats were trained and tested individually. Tested bats were individually marked with PIT tags (Biomark Ltd, Boise, ID, U.S.A.) for long-term identification and to avoid multiple testing of the same individual. Following testing, bats were released at their initial capture location.

Pretraining

Bats were first trained to fly to a speaker broadcasting a frog call and retrieve a food reward (bait fish) placed on a screen positioned over the speaker. Once bats flew readily to frog calls, we trained bats to associate ringtones with a food reward, following Jones, Ryan, Flores, and Page (2013). To initially train bats to approach ringtones, we created stimuli in which we faded the preferred

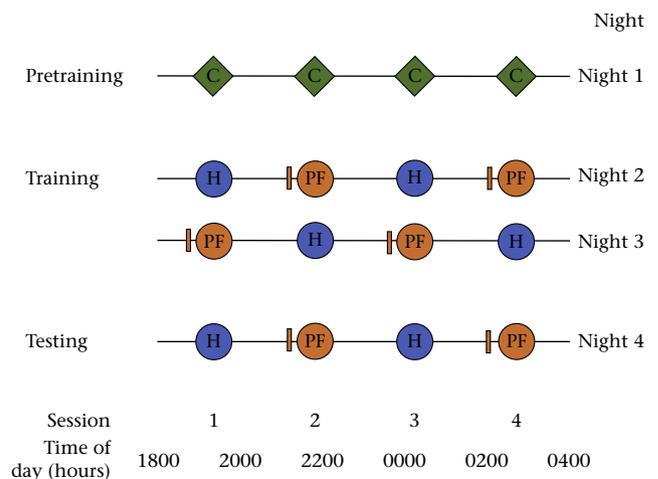


Figure 1. Schematic of experimental overview. Pretraining lasted for one night and consisted of four conditioning sessions (green diamonds marked 'C' for conditioning) in which bats learned to associate ringtones with a food reward. We then trained bats for two nights to associate one ringtone with a food reward only when in a hungry state (H) and another ringtone with an equal reward when in a pre-fed state (PF). During each training session, bats were given five presentations of the same ringtone paired with a food reward. In pre-fed training sessions, bats were fed 15 min prior to training, which is represented by the vertical bar. Following training, bats were given a series of two-choice tests between the two ringtones previously used in training and were also either pre-fed or hungry.

stimulus (call of a túngara frog, *Physalaemus pustulosus*) into the novel stimulus (ringtone) using Audacity v.2.2.2 (Audacity Team, 2018). In a series of training trials, we decreased the amplitude of the frog call and increased the amplitude of the ringtone (Page & Ryan, 2005). On average, it took about 10 of these merged playbacks for bats to fly to ringtones alone. All stimuli were broadcast through a single speaker that was positioned on the floor in the centre of the flight cage.

We made sure that bats were equally exposed to both ringtones (A and B) that we later used in this experiment by switching between the two during fading trials. To prevent generalization to all ringtones, we also intermittently played three other ringtones (C, D, E) that were not used in this experiment, and which were not rewarded. Bats quickly learned not to fly to them within two or three trials. Once bats flew three times consecutively to ringtones A and B and did not fly to any other ringtones, we began the training trials.

Training

Every subject learned to associate food rewards with two ringtones, A and B. Ringtones were selected as experimental cues for several reasons. First, ringtones were similar in duration (0.6 s) and frequency (750 Hz) to the mating call of túngara frogs, a preferred prey item of this bat (Ryan & Rand, 1990). Second, frog-eating bats have been shown to rapidly associate these specific ringtones with food rewards and do not show any initial bias or preference for either of the two ringtones (Jones et al., 2013). Lastly, the bats used in this experiment had no prior experience with any ringtones.

Each night, 20 training trials were partitioned into four training sessions. In each training session, bats experienced a single ringtone played five times and always paired with a food reward. Each bat was trained for two consecutive nights for a total of eight training sessions and 40 training trials (see Fig. 1). All individuals received an equal number of reinforcement trials with each ringtone over this 2-day training regime (20 trials per ringtone).

During each training session, subjects were either hungry (H) or pre-fed (PF). We always alternated between hungry and pre-fed sessions each night but randomized which session the bat encountered first each night. If a bat experienced a hungry training session first in night one of training, it would start with a pre-fed session on the following night. In pre-fed training sessions, bats were fed 1.5 g of bait fish from a speaker broadcasting a frog call 15 min prior to the training session. In hungry training sessions, bats did not receive any food prior to training. Training sessions started exactly 2 h following the completion of the last session. These bats typically eat about half of their body weight (~15 g of food) each night in captivity during an 8 h period (Hemingway, Ryan, & Page, 2018). In the wild, these bats also fly to a foraging area where they will remain for several hours (Kalko, Friemel, Handley, & Schnitzler, 1999). In between feeding bouts in the wild, bats most likely groom or rest until they get hungry again. Taken together, we believe that 2 h is a sufficient amount of time for bats to return to a state of hunger.

Each ringtone was always associated with a specific state, hungry or pre-fed. We exposed six of the bats to ringtone A when hungry and ringtone B when pre-fed and the other six to the reverse. Food rewards were identical in size and energy content and bats in this experiment primarily received food during the experiment. During training, bats were rewarded with 0.5 g of bait fish for each trial (5 trials per session = 2.5 g). With four sessions (20 training trials) per night, each bat consumed 10 g of bait fish per night. Additionally, for the two pre-fed sessions each night, bats were fed 1.5 g of fish prior to training for an extra 3 g per night. In total, bats were fed 13 g per night during the experiment. To ensure

that bats were fully satiated, all animals were fed ad libitum at the end of the night, following the training or testing trials. Bats typically ate 1–2 g more food, if any, during this time.

Testing

Following two nights of training, bats experienced one night of two-choice tests. Similar to training, these trials were also partitioned into four sessions with five trials per session. The state of the bats at the time of testing was manipulated in the same way as the training period. Whether bats were tested first in a hungry or pre-fed state was randomized but counterbalanced across all bats. In choice trials, bats were presented with each ringtone played simultaneously from two different speakers concealed under separate screens and positioned 2 m from one another and from the roost. Ringtones were alternated between sides to control for potential side biases.

Choices were scored as flights within 10 cm of the speaker. There were several instances where bats approached a speaker in an attack flight but were unable to retrieve the food reward. Such flights were considered choices. Because testing sessions consisted of five rewarded trials to control for food intake, several bats made more than 20 choices during the testing phase of the experiment.

Ethical Note

Animal capture in Soberanía National Park, Panama was approved by the Panamanian authorities (Autoridad Nacional del Ambiente, ANAM permit number SE/AH-2-17). All experiments were conducted according to protocols approved by the Institute for Animal Care and Use Committee at the University of Texas (AUP-2017-00292) and the Smithsonian Tropical Research Institute (2017-0102-2020).

Data Analysis

If bats differentially value each option based on past gains, they may prefer either the option learned when in a low state or a high state, regardless of their state at the time of testing. Therefore, our first question was whether ringtone preferences could be predicted based on the state the bats were in when they learned about each ringtone. To test for this, we used a linear mixed effect model with arcsine square-root transformed proportions of choices for each ringtone as our response variable and tested for a fixed effect of ringtone identity (trained to when hungry versus trained to when pre-fed). Because of our repeated sampling design, we included bat identity as random effect.

Additionally, we wanted to know whether bats favour the options that they learn about only when they are tested in the same state during which the options were learned. To test for an effect of the testing session (tested when hungry versus tested when pre-fed), we tested for an interaction effect between training and test block on preferences. In addition to these models, we calculated the mean and bootstrapped 95% confidence intervals for each proportion (Puth, Neuhäuser, & Ruxton, 2015). All statistics were done using the 'lmer' and 'lmerTest' packages in R v.3.5.1 (R Core Team, 2018) and our data set and code are available on figshare (<https://figshare.com/account/home#/projects/56810>).

RESULTS

Overall, we found that bats preferred the ringtone to which they were trained in a hungry state (t test: $t_{46} = -12.72$, $P < 0.0001$; Fig. 2). This was true regardless of their state during testing (interaction: $t_{44} = -0.06$, $P = 0.96$). When tested in a hungry state,

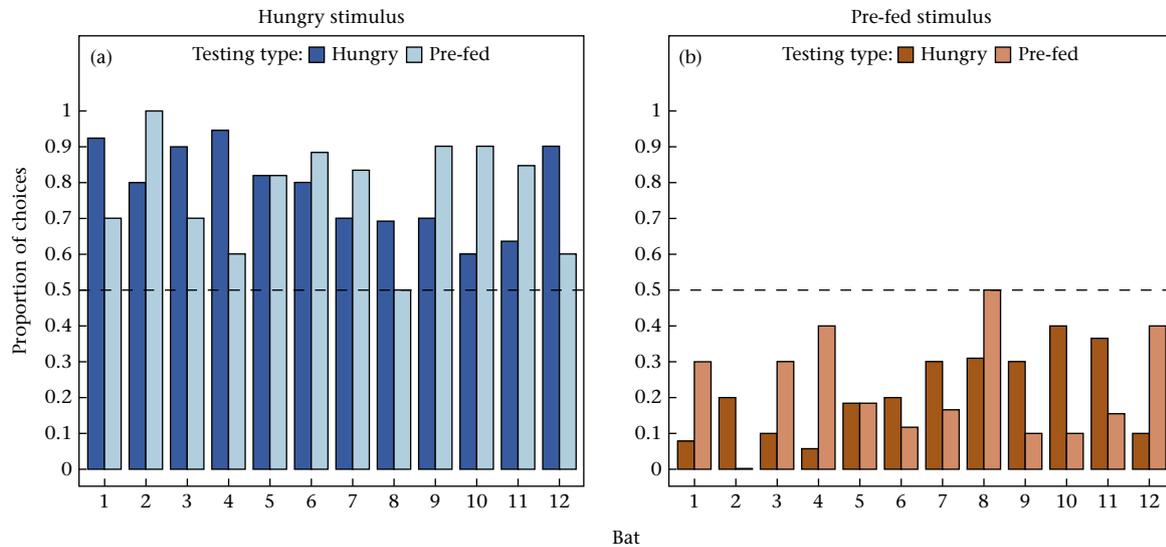


Figure 2. Preferences for hungry and pre-fed ringtone stimuli across all individuals (a) when the hungry stimulus was learned, then tested in a hungry and pre-fed state, and (b) when the pre-fed stimulus was learned, then tested in a hungry and pre-fed state.

bats preferred the hungry stimulus (mean = 0.79, 95% CI = 0.72 – 0.85) over the pre-fed stimulus (mean = 0.21, 95% CI = 0.15 – 0.28; Fig. 3a). When tested in a pre-fed state, bats still preferred the hungry stimulus (mean = 0.77, 95% CI = 0.69 – 0.85) over the pre-fed stimulus (mean = 0.23, 95% CI = 0.15 – 0.31; Fig. 3b).

DISCUSSION

Models of adaptive behaviour assume that, all else being equal, animals should choose options that confer higher rewards and behave indifferently to options that are equal in their payoff (Houston et al., 2007). We know, however, that the benefits of different choices may vary depending on the state of the individual (Schuck-Paim, Pompilio, & Kacelnik, 2004) and the remembered fitness benefits at the time of learning may influence future decisions (McNamara et al., 2012). Here, we were interested in whether frog-eating bats attend to internal cues when learning about novel food types. We presented bats with two identical food

rewards each paired with a unique ringtone. One ringtone was only encountered when individuals were hungry and the other when they were pre-fed. We then presented each bat with a choice between the two ringtones in both hungry and pre-fed states. We found that bats overwhelmingly preferred the ringtones for the food items that they learned about when hungry regardless of their state when later tested.

The type of learning that we observe in this study is not purely controlled by an individual's current state and the physical properties of the reward, but also past associated energetic gains, supporting the predictions of the value priority hypothesis in which animals place higher value on options that they initially encounter in a state of low reserves. Similar results have been found in other animals, in which individuals are sensitive to both the quality of the reward as well as their own internal state and integrate both sources of information during learning. Additionally, these findings appear to be taxonomically widespread, with evidence for state-dependent valuation found in starlings (Kacelnik & Marsh, 2002; Pompilio & Kacelnik, 2005), locusts (Pompilio et al., 2006), fish

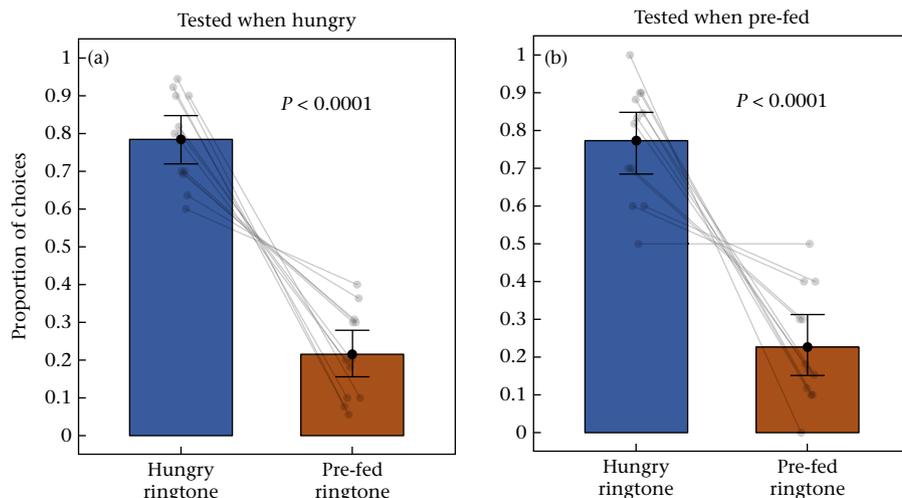


Figure 3. Mean proportion of choices for ringtones experienced when hungry and pre-fed during training. Bars represent 95% bootstrapped confidence intervals. Each subject was tested in both a (a) hungry state and (b) pre-fed state.

(Aw, Holbrook, Burt de Perera, & Kacelnik, 2009) and pigeons (Vasconcelos & Uruioli, 2008), and now for the first time in a wild mammal (although one could debate whether humans should be considered wild). Such findings support the notion that these behaviours have adaptive advantages (Pompilio et al., 2006).

For animals that forage in spatially or temporally heterogeneous environments, it may be particularly adaptive for the animal to base its decisions upon approximate cues that are available, such as their own internal reserves (McNamara et al., 2012). Because rewards are more likely in a food-rich environment, an animal's internal reserves can serve as an indication of whether any given environment is sparse or rich. Low reserves most likely indicate that the environment is food-poor, whereas high reserves correspond to food-rich environments. In changing and uncertain environments, state-dependent valuation can be favoured by natural selection: individuals should allow their hunger to affect learning for future decisions. Indeed, through a series of evolutionary simulations, McNamara et al. (2012) showed that under most moderate environmental conditions, it is adaptive for animals to place a higher value on food rewards obtained when they have low reserves. This makes intuitive sense as rewards that provide a benefit when food is generally less available may be more important to learn and place a higher value on (Aw, Vasconcelos, & Kacelnik, 2011; McNamara et al., 2012). Such behaviours can appear irrational in an economic sense; however, these state-dependent learning mechanisms are probably adaptive in most environments, making them ecologically rational (McNamara et al., 2012).

For frog-eating bats, these behaviours make ecological sense. These bats eavesdrop on multiple species of frogs and are able to discriminate between palatable and poisonous species based on the preys' mating calls (Tuttle & Ryan, 1981). In addition to frogs, these bats consume a wide variety of invertebrates such as beetles and katydids (Giannini & Kalko, 2005) and other small vertebrates such as lizards, birds, and even other bats (Bonato & Fature, 2000). Their diet is also seasonally diverse and varies quite remarkably between wet and dry seasons each year (Jones et al., 2014). As a result, these bats must associate different calls with what is edible and seasonally available, while integrating information about the energetic rewards they received from each prey type. Flight cage experiments have shown that these bats do in fact differ in their responsiveness to the calls of different prey types depending on the current season (Jones et al., 2014). If these predators acquire experience hunting for one species when experiencing greater energetic need (e.g. during the dry season) and for another species in a richer context (e.g. during the wet season), captures will cause different improvements in fitness in spite of delivering similar energetic gains (McNamara et al., 2012). In such cases, these gains most likely cause differences in the value placed on different prey items.

In this experiment, the deprivation periods were very mild; however, we still think that we captured a realistic fluctuation of internal state in these animals. These bats weigh around 35 g and in captivity typically eat around 15 g per night (~45% of their body weight). The hunger states of the bats during training and testing probably closely matched the hunger states that they experience throughout the night in the wild. Telemetry data have shown that, in the wild, these animals will forage in these discrete bouts throughout the night (Jones, Hämsch, Page, Kalko, & O'Mara, 2017; Kalko et al., 1999), suggesting that they cycle through similar periods of hunger in a single night as we used in this experiment. Although these behaviors appear to be widespread taxonomically, the strength of these effects could differ depending on how dynamic fluctuations in hunger state are over time. For these bats, such dramatic fluctuations in hunger state within a single night might contribute to the magnitude of these biases. Future studies

testing animals that vary in their energy requirements and metabolic rates could be done to disentangle the role that either may potentially play in these behaviours.

Although these behaviours appear to be quite common and taxonomically widespread, there is evidence to suggest that different taxa arrive at these behaviours through two different mechanisms. One is 'perceptual distortion', in which the animal's energetic state influences sensory perception in ways that alter memory properties. There is some evidence for this mechanism in desert locusts, *Schistocerca gregaria*. Mouthparts in these insects become increasingly more sensitive as nutrient reserves drop, indicating that, neurologically, these animals most likely receive greater stimulation when experiencing hunger (Pompilio et al., 2006; Simpson & Raubenheimer, 2000). Indeed, these locusts prefer options that they learn about when in a state of low reserves (Pompilio et al., 2006). The other mechanism is 'remembered value', which states that the memory for the magnitude is accurate, but the animal attaches subjective attractiveness to each option, depending on its state while learning (Pompilio et al., 2006). This appears to drive state-dependent behaviours in starlings, as individuals can accurately encode information about delays to food rewards in different energetic states (Pompilio & Kacelnik, 2005). Whether frog-eating bats attached subjective value to the food rewards in our experiment or experienced shifts in their perceptual systems that influenced their memory formation is subject to further investigation. There is some evidence in other mammals for nutritional-dependent modulation in perceptual systems (rats: Giza, Scott, & Vanderweele, 1992; primates: Rølls, 1999).

In some circumstances, it may be adaptive for the perceived rewards to correspond to current fitness benefits. Both empirical data (Aw et al., 2009; Pompilio & Kacelnik, 2005; Pompilio et al., 2006) and theoretical models (McNamara et al., 2012) suggest that this type of learning is both common and adaptive in most environments. As a result, behaviours that appear economically irrational in the laboratory can be considered ecologically rational once we take into consideration the ecological setting in which they have evolved (Dukas, 2004).

Data Availability

Our data set and code are publicly available on figshare (<https://figshare.com/account/home#/projects/56810>).

Author Contributions

C.T.H. conceived the study, conducted the experiments and analysed the data. M.R. and R.P. supervised the study. All authors contributed to writing the manuscript.

Conflict of Interest

We have no competing interests.

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