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SCIENCE ADVANCES | RESEARCH ARTICLE

EVOLUTIONARY BIOLOGY

Bats without borders: Predators learn novel prey cues from other predatory species

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Learning from others allows individuals to adapt rapidly to environmental change. Although conspecifics tend to be reliable models, heterospecifics with similar resource requirements may be suitable surrogates when conspecifics are few or unfamiliar with recent changes in resource availability. We tested whether *Trachops cirrhosus*, a gleaning bat that localizes prey using their mating calls, can learn about novel prey from conspecifics and the sympatric bat *Lophostoma silvicolum*. Specifically, we compared the rate for naïve *T. cirrhosus* to learn an unfamiliar tone from either a trained conspecific or heterospecific alone through trial and error or through social facilitation. *T. cirrhosus* learned this novel cue from *L. silvicolum* as quickly as from conspecifics. This demonstrates social learning of a novel acoustic cue and suggests that heterospecific learning in bats may occur in nature. We propose that auditory-based social learning may help bats learn about unfamiliar prey and facilitate their adaptive radiation.

INTRODUCTION

Learning new behaviors allows individuals to expand their behavioral repertoire and respond adaptively to environmental change (*1*). Learning from others can be especially beneficial because it can save time and energy otherwise spent on trial-and-error learning and reduce the odds of making costly mistakes (*2*). Social learning, which differs from simple information transfer in that learned behaviors persist and modify an individual's future decision-making (*1*), is most beneficial when information is relevant and reliable (*1*, *3*). Conspecifics therefore often make good models because of similar resource requirements (*3*), as evidenced by examples of conspecific social learning in a wide range of taxa from insects to mammals (*4*, *5*).

Heterospecifics with overlapping resource requirements may also prove useful models, particularly if they attend to different cues or exploit novel but otherwise suitable resources (*5*). Lizards, for example, can learn to associate the presence of ripe figs with the presence of birds that also eat figs (*5*). However, evidence that individuals can learn novel sensory cues to later identify new food, rather than simply the presence of familiar food, has not been well documented (*5*).

Bats are well suited to benefit from social learning. Most species are gregarious, long-lived (up to 40+ years), and invest heavily in offspring (*6*, *7*). Known examples of social learning in bats include vocal learning and many forms of social enhancement via acoustic and chemical cues regarding roosts and food (*8*). Although many bats roost and forage in mixed-species groups, the only two studies investigating heterospecific social learning in bats yielded inconclusive results (*9*, *10*). Because there are >1300 bat species distributed globally, with considerable species overlap in range and resource use (*6*), heterospecific learning in bats warrants more careful investigation.

We first examined whether the fringe-lipped bat, *Trachops cirrhosus*, can learn to associate a novel, but biologically relevant, acoustic cue with food from conspecifics. It was previously established that *T. cirrhosus* can learn from conspecifics to associate the mating calls of cane toads, *Rhinella marina*, which are unpalatable and often too large for consumption, with a palatable food reward (*11*). However, *T. cirrhosus* likely had prior experience with cane toads in the wild where they are prevalent and likely learn through experience to avoid these calls (*12*). Thus, to ensure that the bats had no prior experience with the acoustic stimuli in this experiment, following Jones *et al.* (*13*) we tested social learning in *T. cirrhosus* with an artificial acoustic stimulus.

We then tested whether *T. cirrhosus* can learn a novel acoustic cue from another species, the sympatric white-throated round-eared bat, *Lophostoma silvicolum*. We predicted that *T. cirrhosus* would readily learn from conspecifics and heterospecifics given its ability to learn from conspecifics (*11*, *13*). Moreover, *T. cirrhosus* can be found in sympatry with as many as 15 other predatory gleaning species, including *L. silvicolum* (*14*). Both species belong to the family Phyllostomidae (~200 species), are of similar size (*T. cirrhosus*, 33 to 45 g; *L. silvicolum*, 21 to 38 g), and forage in forest understory where they hunt from perches (*15*) by listening to prey mating calls and gleaning prey from surfaces (*16*). *T. cirrhosus* prefers frogs when available (*16*) but also eats katydids, the preferred prey of *L. silvicolum*. However, the two bats target different katydid species based on different acoustic cues (*17*), providing the opportunity for *T. cirrhosus* to learn from *L. silvicolum* to attend to new cues to locate prey.

RESULTS

Treatment had a significant effect on learning rate of the novel cue [analysis of variance (ANOVA) $F_3 = 14.98$, $P < 0.0001$; Fig. 1 and table S1). On average, *T. cirrhosus* learned the novel cue from conspecifics [$n = 7$, 18.29 ± 9.19 (means ± SEM); Fig. 1 and table S1] significantly faster than through trial and error [$n = 6$, 88.33 ± 9.93; Tukey honestly significant difference (HSD) post hoc comparisons, $P < 0.0001$; Fig. 1 and table S1] or through social facilitation [$n = 6$, 86.67 ± 9.93; Tukey HSD, $P < 0.0001$; Fig. 1 and table S1]. All bats learned the cue from conspecifics, and there was no significant degradation in the rate of learning across the transmission chain (Pearson product-moment correlation, $r = -0.54$; $P = 0.22$; Fig. 2). Two individuals learned the novel cue in both the trial-and-error (56 and 74 trials) and social facilitation (43 and 77 trials) treatments. The learning rate of the novel cue from conspecifics (18.29 ± 4.35) was significantly slower ($t_7 = -2.88$, $P = 0.02$) than that of the cane toad call from conspecifics [$n = 10$, 5.30 ± 1.16; from the study of Page and Ryan (*11*); Fig. 1 and table S1].

Supporting our hypothesis, *T. cirrhosus* also learned to associate the novel cue with food significantly faster from the heterospecific

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L. silvicolum (n = 7, 29.57 ± 9.19; Fig. 1 and movie S1) than through trial and error (n = 6, 88.33 ± 9.93; Tukey HSD, P = 0.001; Fig. 1 and table S1) and social facilitation (n = 6, 86.67 ± 9.93; Tukey HSD, P = 0.002; Fig. 1 and table S1). Although at first glance there is an apparent trend toward a faster learning rate for *T. cirrhosus* learning from conspecifics compared to heterospecifics, the difference was not significant (P = 0.82; Fig. 1). If we exclude the one individual in our study who failed to learn by trial 100 from observing an *L. silvicolum* model, the apparent difference between conspecific and heterospecific treatments is no longer evident (18.3 ± 9.2 trials versus 17.8 ± 7.6 trials).

DISCUSSION

Our findings demonstrate that *T. cirrhosus* is a consummate learner, capable of acquiring new information about novel, potential prey from conspecifics and heterospecifics alike. The bats that successfully learned from heterospecifics did so as quickly as from conspecifics (Fig. 1). Our results corroborate previous work that, using a different methodology, shows *T. cirrhosus* can learn from conspecifics to associate artificial ringtones with a palatable food reward (*13*). In both studies, learning was likely facilitated by cues generated by the trained bat attacking and/or consuming the prey reward as bats are readily drawn to foraging behavior of conspecifics and heterospecifics (*18*, *19*). Although it is possible that naïve bats respond indiscriminately to trained individuals regardless of species, at least two studies suggest that several bat species preferentially respond to conspecific cues (search calls and feeding buzzes) (*18*, *20*). Here, *T. cirrhosus* would have had an opportunity to differentiate between conspecific and heterospecific models during the acclimation period and throughout trials, through species-specific sensory and behavioral cues, as observed in other bat species (*21*). For example, *T. cirrhosus* did not hang near *L. silvicolum* during the day in the flight room but did with the other *T. cirrhosus*, which is consistent with observations in the wild. Although their roosts can be found in close proximity to one another, the two species have yet to be documented roosting together in the same structure in more than 15 years of monitoring Neotropical bat roosts. As such, we suggest that *T. cirrhosus* are capable of discriminating between their own species and *L. silvicolum*. However, it is interesting to consider whether this discrimination would be relevant to the acquisition of socially learned behaviors in nature. The echolocation calls, especially those produced in the terminal phase of attack, are similar across most phyllostomid species (*22*). Thus, at foraging sites, *T. cirrhosus* may have its auditory attention drawn to novel prey by the successful attacks of conspecifics and heterospecific bats alike and thereby learn to associate novel prey sounds with unfamiliar, yet palatable food rewards.

Nevertheless, although we found that *T. cirrhosus* learned as quickly from heterospecifics as from conspecifics, one individual *T. cirrhosus* failed to learn from *L. silvicolum*, suggesting that *T. cirrhosus* may not learn as consistently from heterospecifics as conspecifics. In addition, we found that at least some bats can learn about new prey on their own. A third of the bats learned the novel cue without trained models via trial and error and social facilitation, albeit considerably more slowly (62 trials, on average) than under social learning conditions (18 trials, on average) (Fig. 1 and table S1).

Our results also suggest that learning about a new prey cue may be more difficult than learning new information about a previously familiar call from an unpalatable anuran. *T. cirrhosus* took an average of three times longer to learn the novel cue compared to learning to respond to cane toad calls, although the same palatable food rewards (fish) were used in both studies (*11*). Consisting of a long-duration, amplitude-modulated trill, the structure of cane toad calls is quite different from most anuran prey species in this Neotropical community, but these calls would have presumably been familiar to *T. cirrhosus* because cane toads are prevalent in the wild. By contrast, the structure and periodicity of the novel cue would have been unfamiliar but consisted of biologically relevant elements. Several katydids in our study area produce pure tones at or above 13 kHz (*17*), which is well within the hearing range of *T. cirrhosus* (*23*), but *T. cirrhosus* is generally more responsive to frequency-modulated cues that contain multiple harmonics (*17*). The pulse duration and rate differed from typical katydid mating calls but were similar to anuran calls preferred by *T. cirrhosus* (*17*). Thus, bats in our study had to learn to associate the novel cue with potential prey,

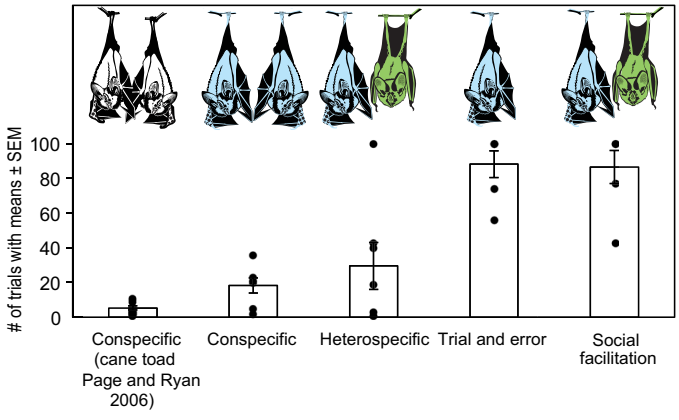

Fig. 1. Rates for *T. cirrhosus* to learn a familiar, unpalatable cane toad call from conspecifics compared to learning a novel acoustic prey cue under four treatments. Number of trials to learn from conspecifics to associate an unpalatable cane toad call with a palatable food reward (gray icon, far left) compared to number of trials to learn a 13-kHz pure-tone novel cue with food under four treatments (colored icons) (histograms display means ± SEM): (i) conspecific (conspecific model present), (ii) heterospecific (heterospecific model present), (iii) trial and error (naïve *T. cirrhosus*, no model), and (iv) social facilitation (naïve *T. cirrhosus* and naïve *L. silvicolum*, no model).

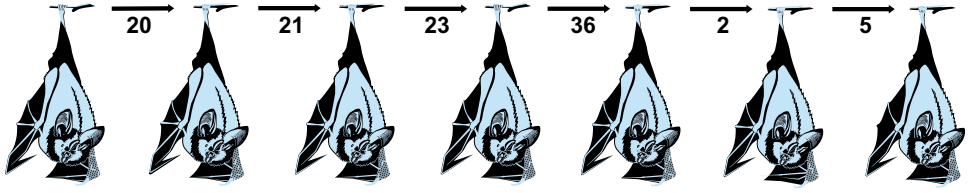

Fig. 2. Transmission chain for *T. cirrhosus* to learn a novel acoustic prey cue from one initially trained conspecific. Number of trials to learn to associate food with a 13-kHz pure-tone novel cue.

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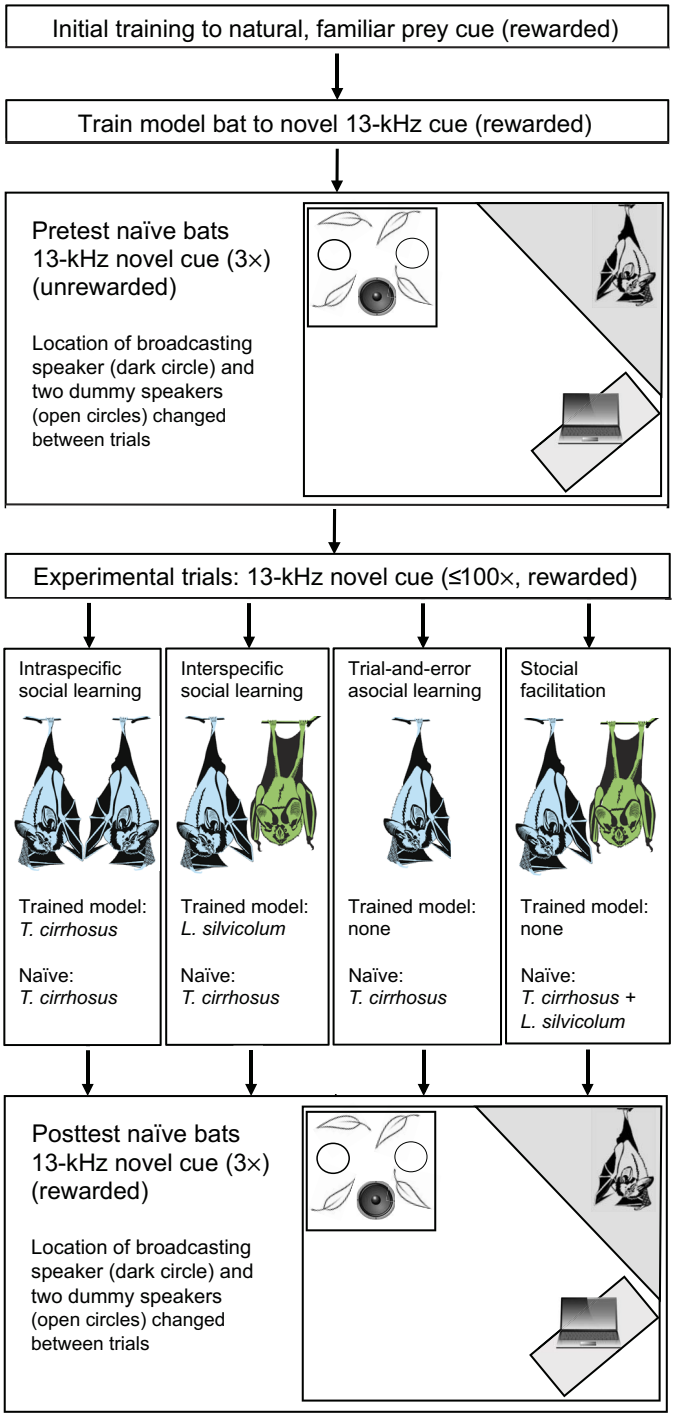

Fig. 3. Protocol overview. Diagram is not to scale. Adapted from Jones et al. (*13*).

learn that this new prey is palatable, and overcome potential challenges in localizing the cue due to its relatively high, constant frequency. Future work should be conducted to parse out the importance of the echolocation behavior that directly precedes a model's attack and the chewing sounds produced thereafter.

Unlike previous studies investigating heterospecific learning in bats (*9*, *10*), we used a biologically relevant task, perhaps explaining why we are the first to find clear-cut evidence of this behavior. Gleaning bats may also be better suited than other species to learn from heterospecifics. *T. cirrhosus* and *L. silvicolum* are both perch-hunting gleaners; nearby observers can eavesdrop on the echolocation calls and chewing noises of successful hunters, perhaps facilitating the connection between novel prey-generated cues and palatable prey. Consequently, individuals learn more reliable information about food, including location, type, and palatability, compared to simply learning potential prey locations based on feeding buzzes (*18*, *20*, *24*) or availability based on odor on breath and fur (*25*, *26*).

Our findings offer insight into the historical adaptive radiation of bats. Bats are found nearly everywhere, except north of the tree line, Antarctica, and a handful of oceanic islands (*27*). This wide distribution is attributed to flight and bats' ability to occupy a nocturnal niche through echolocation (*27*). Once in a new environment, however, bats may have persisted through a combination of individual and social learning, taking cues from heterospecifics already familiar with available food in new environments (*28*). As evidenced by the transmission chains demonstrated here (Fig. 2) and elsewhere (*11*), new behaviors could then spread rapidly and faithfully across individuals.

Learning from heterospecifics may also help individuals adapt to contemporary in situ changes. Human development and climate change alter prey availability through habitat loss, range shifts, and asynchronous timing of emergence or migration, mismatching spatial and temporal distribution of predators and their prey (*29*). As former prey disappear and/or new prey become available, individuals must learn to hunt a new prey. These same forces may also result in geographic isolation of conspecifics so that there may be too few to act as reliable models. Heterospecifics may then serve as surrogates, such as when birds copy the choices of heterospecifics during migration or when establishing nesting sites upon returning to breeding grounds (*30*, *31*).

More broadly, our findings have important theoretical implications. Models predict that individual learning is favored over social learning when the costs of copying potentially maladaptive behaviors of inexperienced conspecifics or those with outdated information are high (*1*, *32*). These models, however, overlook the potential role of experienced heterospecifics—that is, social learning could persist even in the absence of reliable conspecifics if individuals can instead learn from heterospecifics. Also of theoretical interest is that the role of heterospecifics may play as sources of putatively innovative behavior arising in conspecific social groups, which is central to questions around animal culture (*4*) within which the role of learning from heterospecifics has been largely ignored.

MATERIALS AND METHODS

General methods

We conducted our study at the Smithsonian Tropical Research Institute in Gamboa, Panamá, following all the Institutional Animal Care and Use Committee guidelines. We captured bats in mist nets and tested them in an outdoor flight cage (5 m × 5 m × 2.5 m) exposed to ambient conditions but protected from rain. To observe bats during experiments, we illuminated the cage with a 25-W red light bulb, which was within normal light levels experienced by bats foraging in the wild (*33*), and three infrared lights (IR Illuminator CM-IR100B). We recorded behavior using two Sony NightShot Plus camcorders (DCR-SR45). One camcorder was focused on the experimental arena to record approaches to the novel cue, and the other was focused on the test bat to document its behavior. To ensure that bats were not tested in more than

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one treatment, all bats were marked with a passive integrated transponder (PIT) tag before release at site of capture.

To ensure that bats had no prior experience with our novel cue, we generated a 13-kHz pure-tone artificial call consisting of six 1.5-s pure-tone pulses with 1-s interpulse intervals (that is, 2.5-s period). This frequency is within the range of many katydid species and the hearing ranges of both bat species (*17*, *23*). All cues were broadcast through a Fostex speaker (FE103En) via a Lenovo ThinkPad laptop, together with a Pyle PCA2 stereo power amplifier. All cues were broadcast at 75-dB sound pressure level (1 m from the speaker) to approximate intensities characteristic of prey in the wild (*33*).

To ensure that test bats were responding to the playback cue and not to other acoustic, visual, or olfactory cues, we also included two dummy speakers from which no sound was broadcast. The speaker and two dummy speakers were placed below a screen (1.5 m × 1.5 m) covered in leaf litter to further ensure that bats were localizing food using the playback cue and not other sensory cues (Fig. 3). We also arbitrarily moved the speakers to different locations under the screen for each trial to prevent spatial bias. The speakers and screen were placed above ground level (1.5 m) on top of a table to reflect foraging heights when gleaning for katydids.

Training

We first ensured that all bats would approach playback calls in our captive setting by broadcasting a prey call (a frog call for *T. cirrhosus* or a katydid call for *L. silvicolum*) through a speaker with a food reward on the screen above the speaker. Because frogs are protected in Gamboa, we used small bait fish as a reward for *T. cirrhosus*, which they readily consumed. We provided katydids as a reward for *L. silvicolum* because they primarily consume katydids (*17*). Both food types were made available during trials when both species were present. We therefore ensured that both species were not deterred by the presence of the alternate food reward during initial training by placing both food types on the speakers in the final stages of training. We provided multiple pieces of each reward type during trials to ensure that both model and test bat had access to a reward.

For the conspecific and heterospecific social learning treatments (see below), we trained either a *T. cirrhosus* or *L. silvicolum* to obtain a food reward in response to the novel cue to serve as models for test (naïve) bats. To do this, we broadcast the prey cue and then systematically increased the intensity of the novel cue while simultaneously decreasing the prey cue in five steps, following Page and Ryan (*33*):

(i) prey cue at 100% amplitude, 13-kHz tone at 0% amplitude;
(ii) prey cue at 75% amplitude, 13-kHz tone at 25% amplitude;
(iii) prey cue at 50% amplitude, 13-kHz tone at 50% amplitude;
(iv) prey cue at 25% amplitude, 13-kHz tone at 75% amplitude;
(v) prey cue at 0% amplitude, 13-kHz tone at 100% amplitude.

Models were considered successfully trained when they obtained a food reward three times consecutively in response to the novel cue without any prey cue playback (*33*).

Learning tests

For all social learning and control treatments (Fig. 3), bats were subject to the following three sets of tests. The location of the broadcasting speaker was moved for each trial in each set of tests.

Pretest

Before beginning learning trials, we tested whether test (naïve) bats *T. cirrhosus* had innate responses to our novel cue by conducting three initial tests. In each test, we broadcast the novel cue from the speaker. No rewards were offered on the speaker. None of the test bats approached the speaker in response to our initial test. Model bats for conspecific and heterospecific social learning and social facilitation conditions were then placed in the room with test bats (one model bat and one test bat in each instance) and allowed to acclimate together overnight.

Experimental trials

We broadcast the novel cue and recorded the number of trials required for test bats to learn to associate the novel cue with food (learning rate). Learning criterion consisted of the bats landing on the broadcasting speaker (and not the dummy speakers) in three consecutive trials, at which point trials were stopped and model bats were removed. In learning trials, rewards were placed on the speaker and both dummy speakers in every trial. In the interest of balancing sample size and time, experiments were terminated if bats did not learn the cue after 100 trials, and a value of 100 was assigned for that sample.

Posttest

After we removed the model (if present), we broadcast the novel cue again in three final tests. We confirmed that the test bat learned the novel acoustic cue if it landed on the speaker in each of the three final tests without the model present. We also confirmed that the test bat learned to associate the food reward with the novel acoustic cue, and not some other acoustic, visual, olfactory, or spatial cues, by removing the model bat, providing food on two dummy speakers in addition to the broadcasting speaker, and by moving the location of the broadcasting speaker between each trial.

In all cases, trials were only conducted when model and test bats were motivated, which was assessed on the basis of behavior (for example, sleeping versus alert) and through periodically broadcasting a natural, familiar prey cue (that is, a common, sympatric, palatable frog or katydid mating call). If bats were not responsive to natural, familiar prey cues (that is, did not obtain a food reward from the speaker broadcasting a frog or katydid call), we stopped trials for an hour and then resumed or we stopped for the night and resumed the next night.

Treatments

Using the above protocol, we measured the learning rate (means ± SEM trials) for *T. cirrhosus* to associate the novel cue with palatable prey in four possible treatments. (i) Conspecific social learning: *T. cirrhosus* was trained to the novel cue to serve as a model for naïve test *T. cirrhosus*. Each test bat that successfully learned the novel cue became the model for the subsequent test bat, resulting in a transmission chain. (ii) Heterospecific social learning: *L. silvicolum* was trained to the novel cue to serve as a model for naïve test *T. cirrhosus*. We did not use transmission chains here due to space, time, and capture constraints. (iii) Trial-and-error control: A single naïve *T. cirrhosus* was present, but no trained model was present. This served as a control for the possibility that *T. cirrhosus* can learn novel cues through individual learning as readily as from conspecific or heterospecific models. (iv) Social facilitation control: Both *T. cirrhosus* and *L. silvicolum* were present and naïve. This served as a control for the possibility that the mere presence of conspecifics or heterospecifics, even if inexperienced, somehow motivates learning.

Analyses

We first tested whether learning rate differed among the four treatments using a one-way ANOVA ($\alpha = 0.05$). We then examined which treatments differed by performing post hoc pairwise comparisons using Tukey-Kramer HSD to correct for multiple comparisons. We also used

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a *t* test to compare the rate for conspecifics to learn the novel cue to the rate for conspecifics to learn to associate a familiar, but unpalatable, cane toad call with a palatable reward documented in the study of Page and Ryan (*11*) that used the same experimental design used here, thus facilitating comparison between studies. All tests were performed using JMP (v. 13, SAS Institute).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/3/eaaq0579/DC1

table S1. Number of trials to learn to associate food with either a cane toad call and a 13-kHz pure-tone novel cue or a cane toad call [from the study of Page and Ryan (*11*)].

movie S1. Video footage of trained and naive bat responses to novel prey cues.

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