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Original Article

Spatial learning overshadows learning novel odors and sounds in both predatory and frugivorous bats

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To forage efficiently, animals should selectively attend to and remember the cues of food that best predict future meals. One hypothesis is that animals with different foraging strategies should vary in their reliance on spatial versus feature cues. Specifically, animals that store food in dispersed caches or that feed on spatially stable food, such as fruits or flowers, should be relatively biased towards learning a meal's location, whereas predators that hunt mobile prey should instead be relatively biased towards learning feature cues such as odor or sound. Several authors have predicted that nectar-feeding and fruit-feeding bats would rely relatively more on spatial cues, whereas closely related predatory bats would rely more on feature cues, yet no experiment has compared these two foraging strategies under the same conditions. To test this hypothesis, we compared learning in the frugivorous bat, *Artibeus jamaicensis*, and the predatory bat, *Lophostoma silvicolum,* which hunts katydids using acoustic cues. We trained bats to find food paired with a unique and novel odor, sound, and location. To assess which cues each bat had learned, we then dissociated these cues to create conflicting information. Rather than finding that the frugivore and predator clearly differ in their relative reliance on spatial versus feature cues, we found that both species used spatial cues over sounds or odors in subsequent foraging decisions. We interpret these results alongside past findings on how foraging animals use spatial cues versus feature cues, and explore why spatial cues may be fundamentally more rich, salient, or memorable.

Key words: **adaptive specializations, bat, belongingness, cue reliance, domain-specific learning, feature cues, modality, object cues, prepared learning, spatial cues.**

INTRODUCTION

Diet shapes the evolution of almost every aspect of an animal's biology, including sensory and cognitive systems (MacLean et al. 2012; Stevens 2014; Rosati 2017; Amodio et al. 2019). If an animal can reliably find or evaluate the quality of food using a particular sensory modality, such as smell, then selection may favor enhanced sensitivity in that modality (Warrant 2016). There may also be selection to attend to and learn associations between food and odor, rather than cues in other sensory modalities (Garcia and Koelling 1966; Dunlap and Stephens 2014). For example, fruit flies can evolve to learn odor associations better than color associations when odor is a more reliable indicator of a safe place to lay eggs (Dunlap and Stephens 2014).

Strong evidence suggests that natural selection shapes which cues animals learn. Most evidence comes from comparing species that do or do not need to remember the location of hidden food. Scatter-hoarding species rely more on spatial cues (e.g., absolute position in space) than object-specific "feature" cues (e.g., shape or color) as compared with related species that do not scatter hoard (Sherry et al. 1992; Shettleworth 2003; Barkley and Jacobs 2007; Pravosudov and Roth II 2013; Supplementary Table S1). For example, when black-capped chickadees, *Poecile atricapillus*, were trained to find food which was simultaneously associated with a color pattern, a relative spatial position, and an absolute location in a room, this food-caching species preferentially relied on absolute location, whereas non-caching dark-eyed juncos, *Junco hyemalis*, showed no clear preference (Brodbeck 1994). Absolute location provides arguably the most reliable information for refinding hidden food after time has passed, because local spatial

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and feature cues are more susceptible to change. Location may also be the most reliable cue for animals that frequently return to a spatially predictable resource, such as nectivores that revisit flowers (Healy and Hurly 1998; Hurly and Healy 1996; Supplementary Table S1).

Although many studies show that animals that forage on spatially predictable food prefer using spatial cues (Supplementary Table S1), there has been less attention on animals with spatially *unpredictable* food. For these species, such as predators that hunt mobile prey, feature cues are more predictive of a future meal than spatial cues. As expected, studies of the European greenfinches (*Chloris chloris*) (Herborn et al. 2011), domestic chicks (*Gallus gallus*) (Vallortigara 1996), and humans (*Homo sapiens*) (Haun et al. 2006), each found preferences for feature cues in some treatments.

The New World leaf-nosed bats (Phyllostomidae) rapidly evolved diverse diets, including nectar, fruits, insects, and other small animals. Stich and Winter (2006) proposed that phyllostomid bat species vary in their reliance on spatial versus feature cues based on the extent to which their food is spatially stable ("niche-specific cognitive strategies"). On one end are nectar bats that have to remember and refind multiple flowers dispersed in the jungle (Stich and Winter 2006). In the middle are frugivorous bats which can benefit from remembering the locations of profitable trees, but once at a tree, detect ripe fruit using odor. On the other end are predatory bats predicted to rely relatively less on spatial associations and relatively more on feature cues such as prey shapes and sounds (Stich and Winter 2006; Hulgard and Ratcliffe 2014).

Studies on bat species predicted to rely more on spatial cues have supported the hypothesis of niche-specific cognitive strategies (Thiele and Winter 2005; Stich and Winter 2006; Carter et al. 2010; Henry and Stoner 2011). Phyllostomid bats that have morphological adaptations for feeding on flowers and fruits all relied overwhelmingly on spatial cues in the captive tests (Thiele and Winter 2005; Stich and Winter 2006; Carter et al. 2010). A problem, however, is that the hypothesis of niche-specific cognitive strategies has not been tested using bats that are predicted to rely strongly on feature cues.

The logical next step is to compare use of spatial and feature cues in bat species that vary in their foraging mode, and thus in their predicted cue use. Here, we compare cue selection in a frugivorous and a predatory phyllostomid bat. We chose a fruit-eating species, *Artibeus jamaicensis*, because it specializes on figs (Ortega and Castro-Arellano 2001) and finds them primarily using scent (Kalko et al. 1996), and we chose the predatory bat, *Lophostoma silvicolum*, because it finds katydids by listening to their mating calls (Tuttle et al. 1985; Belwood 1988; Falk et al. 2015). Notably, predatory acoustic eavesdroppers are expected to rely on feature cues even at a distance, because they may eavesdrop on the sexual advertisement calls of their prey from afar (Page et al. 2012; Jordan and Ryan 2015). To test which cues the bats would associate with food, we first allowed the subjects to learn to forage at one rewarded feeder in an array of four feeders, each with its own unique combination of odor, sound, and location. Next, we separated two of the rewarded cues (such as sound and location) and removed the third (such as odor), and then observed which feeder the bats chose. If the spatial stability of their natural food predicts how much a species relies on spatial versus feature cues, then we predicted that the insectivore would rely relatively more on sound cues and that the frugivore would rely relatively more on spatial and odor cues.

METHODS

Capture and care

We trained and tested 12 male, *Artibeus jamaicensis* and 10 male, *Lophostoma silvicolum*, caught from Soberanía National Park, Panamá and the surrounding forest, in either mist nets at night or in their roosts during the day. Bats were trained in cohorts of two to six individuals. We maintained the bats in a large open-air flight room (5 m × 5 m × 2.5 m) with a cloth roost in the corner. They were kept in small tents (~ 1.2 m × 0.75 m × 1 m) on the night they were captured and briefly during the nights of testing. Water was provided ad libitum from trays on the floor. *A. jamaicensis* were fed a mix of banana, papaya, and melon. *L. silvicolum* ate thawed katydids. At the end of the experiment, all the bats were injected with PIT tags (Biomark APT12, Idaho, USA) to prevent re-testing and returned to the wild.

Experimental apparatus and stimulus generation

Food was presented to bats on wood platform feeders that were 40 cm × 29 cm and 90 cm tall, with holes at the top to allow odor and sound cues to pass from a compartment below (Figure 1). The four odor cues were ultra-concentrated candy oils (cinnamon, anise, almond, or sassafras; LorAnn Oils, Michigan, USA) (O'Mara et al. 2014), placed in 1.5 mL plastic vials with a cotton wick. Previous experiments confirm that related frugivorous phyllostomids can detect and discriminate these odors (Ratcliffe and ter Hofstede 2005; O'Mara et al. 2014; Ramakers et al. 2016), and a pilot test showed

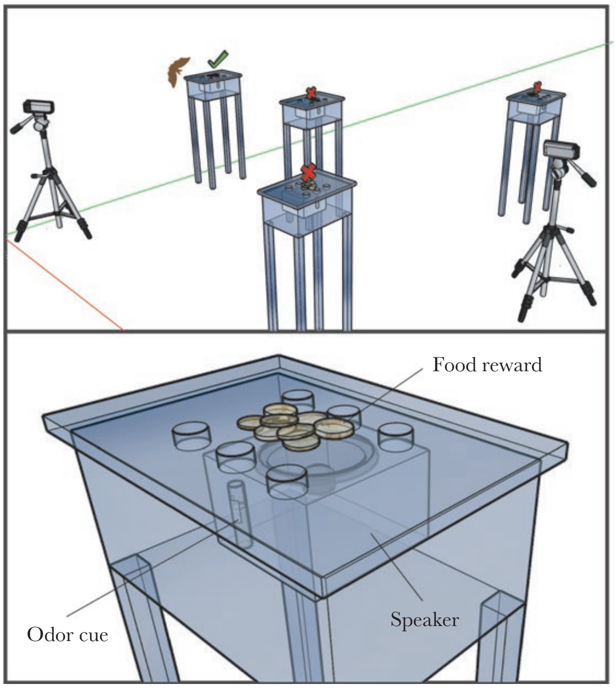

Figure 1.
Diagram of the experimental feeders and set-up. Top: Experimental set-up. Feeders were positioned in unique locations in the flight cage, and food was placed on top. Only one feeder was rewarded (indicated by green check), while the food on the other feeders was rendered inedible with ascorbic acid (indicated by red crosses). Bottom: Experimental feeder. Feeder platforms were each equipped with a speaker that played a unique sound and a vial containing fragrant candy oil. Food was either pieces of banana (pictured), or katydids.

that another predatory bat *Trachops cirrhosus*, which is closely related to *L. silvicolum*, can perform olfactory learning using only a candy oil odor cue (See Supplementary Material for details).

The four sound cues were created from four different cell phone ringtones that were modified using Audacity V2.1.3 software to have peaks in frequencies at 5, 18, and 20 kHz (Supplementary Audio; Supplementary Figure S1), near the peak hearing sensitivities for both *A. jamaicensis* (Heffner et al. 2003) and *L. silvicolum* (Geipel et al. 2021). Although the different sounds had similar overall frequencies, they had different spectrotemporal structures. They were broadcast at 65 dB sound pressure level (SPL) (re 20 μPa) at 10 cm through full range speakers (Fostex P650k, Tokyo, Japan). We knew that all sound cues were audible to the bats at this amplitude, because in pilot studies both species oriented their bodies toward the speaker when each of the sound cues was played. The speaker cables ran from the platform feeders through a port in the wall to the next room, where they were controlled via Blu Touchbook M7 tablets (Blu Products, Florida, USA) running the Android V5.1.1 music app, and amplified by the stereo power amplifiers (Pyle PCA2, New York, USA).

To create unique spatial locations, we marked a 4 m × 4 m grid on the floor and used a random number generator to assign the feeders to coordinates with the condition that feeders could not be within a meter of one another. Sounds and odors were also randomly assigned to each feeder. The flight room was illuminated with a 25 W red light bulb and at least four infrared lights (Clover Electronics IR045, CA). Tests were filmed with two Sony Handycam DCR-SR45 cameras placed in corners of the flight room.

Pre-training

The multiple night pre-training period was designed to acclimate the bats to captivity and to train them to eat from the feeders. On the night of capture, bats were fed by hand inside a small tent. On the second night, they were trained to eat food from the feeders (without the experimental cues) inside the tent. We placed both fruits and katydids on the speakers during this phase and played a *Eubliastes pollonerae* katydid call at 65 dB SPL at intervals of 15 s until all the bats retrieved food from the feeder. To further entice *L. silvicolum* to the feeder, we played "calling songs" of different katydid species (e.g., *Docidocercus gigliotosi, Anapolisia colosseum*) which we knew elicit approaches (Falk et al. 2015), until all bats retrieved food. When bats were flying consistently to the feeders, we released them into the larger flight room, and started the training period.

Training

The multiple night training period was designed to teach bats the experimental association between food and the experimental cues. In this phase, bats learned to fly to a rewarded feeder with its unique odor, sound, and location, while avoiding the other feeders with their own unique cues. To elicit successful feeding, on the first night in the flight room we only set out the rewarded target feeder, in the rewarded location with the rewarded odor and sound cues. This set-up was sufficient to elicit-feeding visits from all the *A. jamaicensis*. For some of the *L. silvicolum*, we had to additionally broadcast low-amplitude calling songs of the aforementioned katydid species to coax the bats to the target feeder initially.

The following night, we placed all four feeders in the room, each with their respective sounds, odors, and locations (with no additional acoustic cues). To control for the effect of the food scent, we placed food on top of all feeders but rendered the food on the non-rewarded feeders inedible by coating it with ascorbic acid (vitamin C; bulksupplements.com, Nevada, USA, 1.25 g per 20 g of food). In pilot tests, we determined that this concentration of ascorbic acid, though harmless, is sour and aversive to the bats. We periodically replenished the food to ensure it was present at all feeders. To allow the bats to learn which feeder was rewarded, they foraged ad libitum in this set-up for 1 week. On the following night, we ran the cue learning test.

Cue learning test

This 1-h test was an experimental control designed to ensure that each bat had learned the target feeder, and that it was not finding this feeder using social cues or cues from the ascorbic acid. All the bats were moved to a holding tent in an adjacent room and each bat was tested individually in the flight room. The set-up was the same as in training except that all the feeders were rewarded (no ascorbic acid). Each feeder had 10 small (<0.5 g) pieces of food (katydids or banana), with more added if the feeder neared depletion. To proceed to the cue dissociation tests, bats had to fly to the target feeder at least 5 times and make no more than 2 incorrect choices (probability of passing by chance is ~1% and pilot trials showed bats would typically visit feeders more than 5 times per h). After all tests were run each evening, all the bats were returned to the flight room with the training set-up to feed to satiation and to reinforce the association with the target feeder. If a bat did not pass the cue learning test, it received the same test on the following night. When a bat did pass, it started cue dissociation testing on the following night.

Cue dissociation tests

These 1-h trials were the main tests, designed to probe *how* the bats had learned to find the food by putting the previously rewarded cues into conflict (Brodbeck 1994). To assess if each cue was learned and its relevant salience to the bat, we tested each bat with only two of the three cues present simultaneously, following Carter et al. (2010). Each bat experienced all three cue combinations (location vs sound, location vs odor, and sound vs odor) one time in random order, with one test per night for three consecutive nights. In each test, one of the cue types was removed entirely (e.g., all sound cues) and the remaining cues were switched between the remaining three feeders, so that the previously rewarded cues were at different feeders (Figure 2). None of the feeders were rewarded; they all had 10 pieces of food (bananas or katydids) rendered unpalatable by coating in ascorbic acid. This encouraged the bats to switch feeders to increase our ability to detect if they had learned other rewarded cues. All the tests were recorded with video cameras placed in the corners of the flight room.

Location versus odor tests

Location versus odor tests were designed to test if bats prioritized location or odor cues in the absence of sound cues. In these tests, we removed all sound cues and one of the non-rewarded feeders. The three remaining odors were switched at random but in a way that the previously rewarded odor was in a new position. Bats then chose between the previously rewarded location with an unrewarded odor, the previously rewarded odor in an unrewarded location, and a control feeder with a location and odor that had never been rewarded.

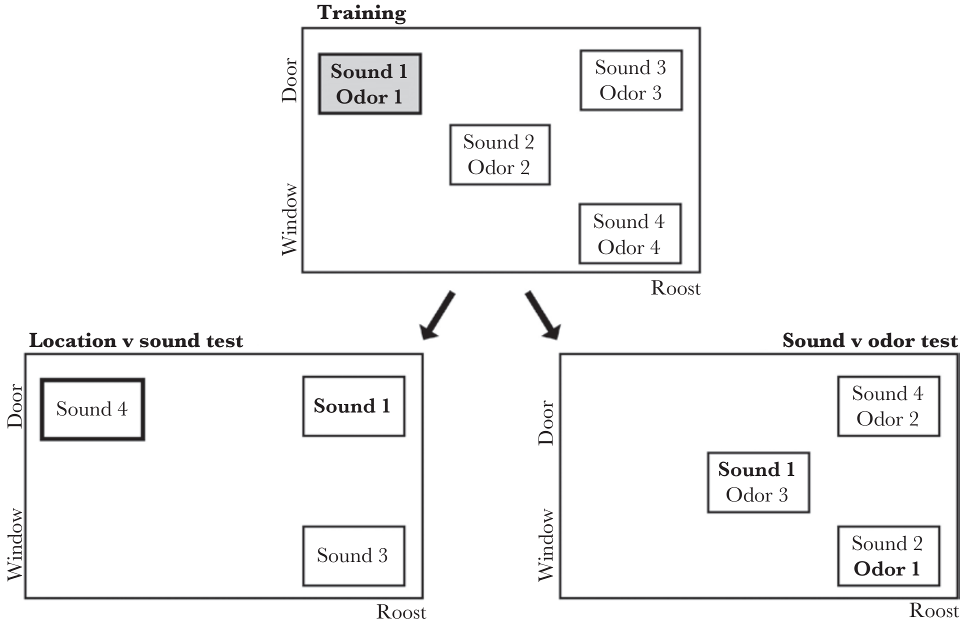

Figure 2.
Experimental setup. Panels show examples of how cues were arranged in the flight cage, as seen from above, during training and cue dissociation tests. Small rectangles represent the feeders, each with their own unique sound, odor, and location in the room. During training (top) one feeder was rewarded (shaded rectangle, bold font, bold border), and the food in the other feeders was distasteful. In location versus sound tests (bottom left), no feeders were rewarded, and bats could choose between a feeder with previously rewarded location (bold border), a feeder with previously rewarded sound (bold font), and a feeder with no previously rewarded cues. Location versus odor tests (not shown) were similar but with odors, not sounds. In sound versus odor tests (bottom right), no feeders were rewarded, and bats could choose between a feeder with a previously rewarded sound (bold), a feeder with previously rewarded odor (bold font), or a feeder with no previously rewarded cues. Figure not to scale.

Location versus sound tests

Location versus sound tests were designed to test if the bats prioritized location or sound cues in the absence of odor cues. We removed all the odor cues and one of the three non-rewarded feeders. The three remaining sound stimuli were switched at random such that the previously rewarded sound was in a new position. Bats then chose between the feeder in the previously rewarded location broadcasting a previously unrewarded sound, the feeder with the previously rewarded sound in a previously unrewarded location, and a control feeder with a location and sound that had never been rewarded.

Sound versus odor tests

Sound versus odor tests were designed to test if bats prioritized sound or odor cues in the absence of the rewarded locations. In these tests, we removed the feeder at the previously rewarded location and we removed a random non-rewarded odor and sound. The six remaining sounds and odors were switched at random such that bats chose between the previously rewarded sound, the previously rewarded odor, and a control feeder with a sound, odor, and location that had never been rewarded.

Behavioral analysis

Observers that were blind to which cues had been rewarded watched videos of the 1-h trials (in VLC media player) and recorded which feeder a bat chose first in a trial and the total number of choices to each feeder during the trial. Choices were counted if the bat hovered within 1 body length (about 7 cm) from the top of a feeder for more than 0.1 s (3 video frames) or if they touched down atop a feeder.

Statistical analysis

To determine whether bats of each species first chose any of the three cues in a test more than expected by chance (33%), we first used an exact multinomial test. If a deviation from chance was detected, we then used a binomial test to test if the most preferred cue was selected more than expected by chance.

As a measure of preference for each cue in a trial, we took the number of choices to each cue and subtracted the mean number of choices (i.e., the difference between the observed and expected values). To estimate the 95% confidence interval around the mean preference for each cue by species, we used nonparametric bootstrapping with 5000 permutations (boot package in *R* (Canty and Ripley 2021)).

To test whether *A. jamaicensis* and *L. silvicolum* differed in their preferences for the three cues in each test, we used a permutation test. To do this, we first found the mean number of choices to each cue across all the trials and calculated the species difference (*S*) as the mean choices by *A. jamaicensis* minus the mean choices by *L. silvicolum*. To create a null distribution of species differences (*S*) under the null hypothesis of random choices, we randomized the number of choices to each cue within each bat and test and calculated *S*, repeating this 5000 times. These permutations do not change the total number of choices per test and species, only the distribution of choices within each test, so differences between observed and expected values imply nonrandom choices by the bats. To get two-tailed *P* values, we calculated the proportion of expected *S* values that were equal to or more extreme than the observed *S* value. All code and data used in this study are publicly available at Dixon et al. (2022).

RESULTS

Frugivorous *Artibeus jamaicensis*

Location versus odor tests

In tests where bats could choose between the previously rewarded location, the previously rewarded odor, and a control feeder, *A. jamaicensis* did not make first choices randomly ($\alpha = 0.05$, $N = 9$, $P = 0.014$; Figure 3a); seven of nine bats chose the location feeder first (versus 3 bats expected by chance, $P = 0.008$). Over the trials, *A. jamaicensis* repeatedly chose the location feeder more often than odor and the control (Figure 3b).

Location versus sound tests

In tests where bats could choose between the previously rewarded location, the previously rewarded sound, and a control feeder, 8 of 11 *A. jamaicensis* first chose location (versus 3.7 bats expected by chance, $P = 0.009$), one chose sound, and two chose the control, suggesting non-random first choices ($\alpha = 0.05$, $P = 0.053$; Figure 3a). Over the trials, *A. jamaicensis* repeatedly chose location more often than sound and the control (Figure 3b).

Sound versus odor tests

In tests where bats could choose between the previously rewarded sound, the previously rewarded odor, and a control feeder, *A. jamaicensis* first choices were equal across the cues and consistent with random choices ($\alpha = 0.05$, $N = 12$, $P > 0.9$; Figure 3b). Over the trials, *A. jamaicensis* did not repeatedly choose any feeder more often than expected by chance, although they tended to choose sound more often than the control (Figure 3b).

Predatory *Lophostoma silvicolum*

Location versus odor tests

The predatory bat, *L. silvicolum*, chose feeders non-randomly ($\alpha = 0.05$, $N = 10$, $P = 0.006$; Figure 4a). In total, 8 of 10 bats chose location first (versus 3.3 expected by chance, $P = 0.003$), 0 chose odor, and 2 chose the control feeder. Over the trials, *L. silvicolum* repeatedly chose location relatively more often than odor and the control (Figure 4b).

Location versus sound tests

First choices by *L. silvicolum* did not deviate from random chance expectations ($\alpha = 0.05$, $N = 9$, $P > 0.3$; Figure 4a): five of eight chose location first, one sound, and three the control. Over the trials, *L. silvicolum* repeatedly chose location significantly more often than sound or the control (Figure 4b).

Sound versus odor tests

First choices did not deviate from random chance expectations ($\alpha = 0.05$, $N = 10$, $P > 0.6$; Figure 4a). In total, five flew first to sound, two to odor, and three to the control feeder. Over the trials, *L. silvicolum* did not repeatedly choose the sound feeders more often than the others (Figure 4b).

Species differences

In location versus odor tests, *L. silvicolum* chose location relatively more often than *A. jamaicensis* (mean proportion of choices = 82% vs 57%, respectively; $S = -19$, $P = 0.0014$; Supplementary Figure S2a), and odor relatively less often than *A. jamaicensis*

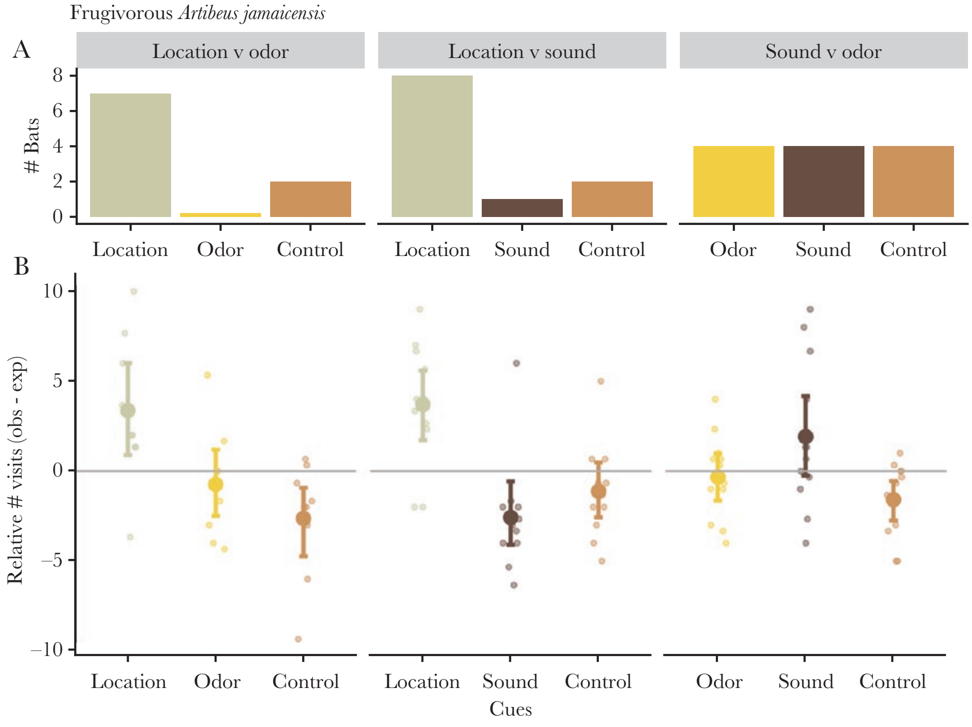

Figure 3.
Artibeus jamaicensis choices to the cues in each of the three test types. a) The cue each bat chose first in a trial. b) The relative number of choices (choices to cue minus mean choices) that bats made to each cue over 1 h. Small points represent individual bats, large points and error bars represent means and 95% confidence intervals.

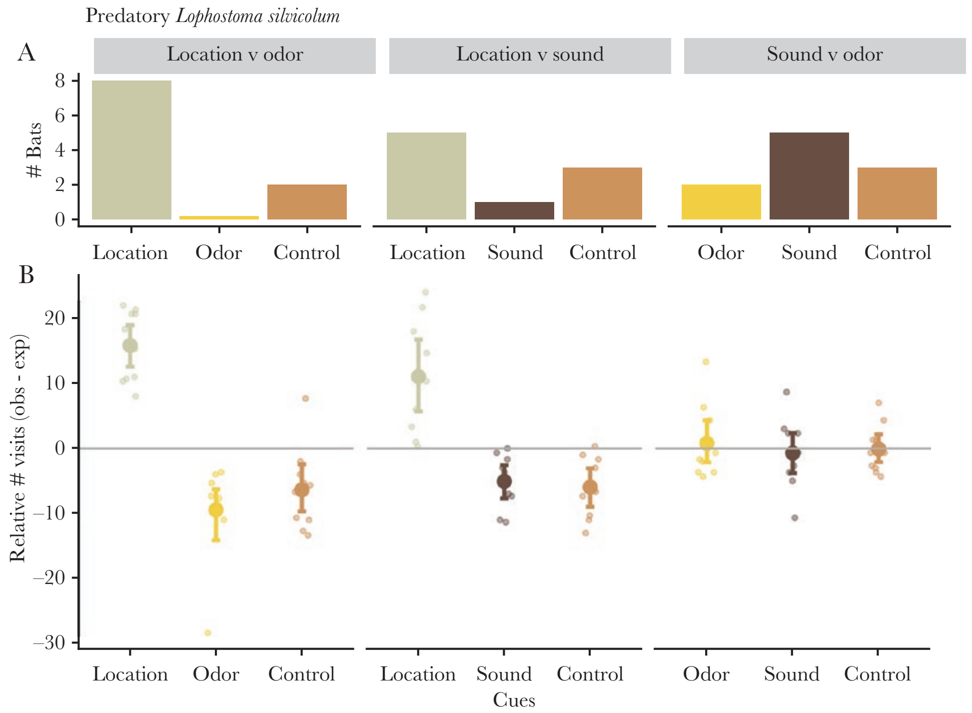

Figure 4.
Lophostoma silvicolum choices to the cues in each of the three test types. a) The cue each bat chose first in a trial. b) The relative number of choices (choices to cue minus mean choices) that bats made to each cue over 1 h. Small points represent individual bats, large points and error bars represent means and 95% confidence intervals.

(mean proportion of choices = 7% vs 25%; $S = 2$, $P = 0.041$; Supplementary Figure S2b), but had similar proportion of choices to the control feeder (mean proportion of choices = 11% vs 18%; $S = -3$, $P > 0.3$; Supplementary Figure S2c). In location versus sound tests, *L. silvicolum* chose location relatively more often than *A. jamaicensis* (mean proportion of choices = 81% vs 60%; $S = -8$, $P = 0.029$; Supplementary Figure S2d), but did not clearly choose the sound or control feeders more or less often (sound: mean proportion of choices = 10% vs 16%; $S = 2$, $P > 0.4$; Supplementary Figure S2e; control: mean proportion of choices = 9% vs 24%; $S = 4$, $P > 0.1$; Supplementary Figure S2f). In sound versus odor tests, we saw no clear differences between species in the relative amount that they chose the three feeder types (mean proportion of choices were between 22% and 41%, $S = -3$ to 1, $P > 0.1$ for each; Supplementary Figure S2g–i).

DISCUSSION

A goal of cognitive ecology is to understand how natural selection shapes the process of associative learning. In this experiment, we tested whether two bats with different foraging strategies would rely on cues differently when learning about a novel food item. Specifically, we predicted that the acoustic eavesdropping predator *L. silvicolum* would rely relatively more on sound cues than spatial cues, compared with the frugivorous *A. jamaicensis*, which is predicted to rely relatively more on spatial cues, followed by odor cues. However, we did not detect this pattern. Instead, both species used spatial cues more than the feature cues (Figures 3 and 4), which is consistent with spatial memory overshadowing the learning of novel sounds and odors. Indeed, there was no clear evidence that either species relied on the odor or the sound cues, even when the rewarded location was unavailable. Contrary to predictions, the predatory *L. silvicolum* appeared to rely on spatial cues more than the frugivore (Supplementary Figure S2).

This result does not support the hypothesis that foraging predatory bats are cognitively specialized to rely relatively less on spatial cues than foraging frugivorous bats (Stich and Winter 2006; Carter et al. 2010; Hulgard and Ratcliffe 2014), but it has two main interpretations. First, it is possible that phyllostomid bat species do not have clear diet-based cognitive specializations for learning the kinds of cues we tested. They might all flexibly shift their use of different cue types as the context changes, or they might all rely first on spatial cues. These bats diversified ~18–25 MYA (Monteiro and Nogueira 2011; Baker et al. 2012), and these cognitive specializations might require more evolutionary time than their obvious morphological divergences (e.g., Santana and Cheung 2016; Arbour et al. 2019). However, we do not think this is the most likely explanation.

The other interpretation is that any species differences in preferences for acoustic or odor cues were overshadowed by an overwhelming preference for use of spatial cues. This interpretation is consistent with two lines of evidence from past work. First, when reliable spatial cues are never available, we do see evidence for species differences between phyllostomids in preference for different feature cues. For instance, when learning in the absence of rewarded locations, the blood-feeding phyllostomid bat *Desmodus rotundus* preferred to use an acoustic cue, whereas the omnivorous *Phyllostomus discolor* preferred to use a visual cue (Schmidt et al. 1988). However, when spatial cues are available, all five phyllostomid bat species that have been tested in this paradigm preferred spatial cues (Table 1).

Second, there are more examples in the literature of animals preferring spatial cues (Supplementary Table S1), and several species predicted to use feature cues were found to instead use spatial cues (Williams 1967a, 1967b; Hodgson and Healy 2005; Daneri et al. 2011). The three opportunistic foragers mentioned in the introduction that preferred feature cues in some treatments (domestic chicks, European greenfinches, and humans) all preferred spatial cues in other treatments (Vallortigara 1996; Haun et al. 2006; Herborn et al. 2011). For instance, while 3-year-old humans relied on feature cues, 1-year-old humans, orangutans, gorillas, bonobos, and chimpanzees all relied more on spatial cues (Haun et al. 2006).

We know that each of the bat species in Table 1 can and does learn feature cues when foraging for food, including odors, echoacoustic shapes, and sounds (Lemke 1984; Belwood 1988; Kalko et al. 1996; Thies et al. 1998; Patriquin et al. 2018; Brokaw et al. 2021). Why then were spatial cues so dominant in this experimental paradigm? Below, we consider five non-mutually exclusive factors.

First, spatial learning is arguably fundamentally different from learning to associate specific sensory cues with a target object, because spatial cues can be perceived in multiple senses (e.g., smell, vision, echolocation), and represented in multiple ways (e.g., through egocentric, geometric, or landmark cues). "Locations" are not single "cues" but rather a collection of many possible cues, and as such may be more salient than any one type of cue (Gibbs et al. 2007). Animals may therefore have a general bias towards using "spatial cues" whenever they are reliable (Day et al. 2003). Our study and several others used repeated training trials (e.g., Williams 1967a, 1967b; Hodgson and Healy 2005; Carter et al. 2010; Herborn et al. 2011); extended training periods like these switched European greenfinches from relying on feature cues to spatial cues (Herborn et al. 2011), and affected rats in a similar fashion (Packard and McGaugh 1996). These results are consistent with the idea that even animals that do not otherwise rely on spatial cues may switch strategies and flexibly use them when they experience that a location is reliable.

A second related idea is that cue selection depends on perceptual salience and context. For example, mountain chickadees normally rely primarily on spatial cues when finding food, but relied first on visual cues and secondarily on spatial cues when the visual task was much easier (2 colors vs 16 closely spaced locations) (LaDage et al. 2009; see also Kanngiesser and Call 2010). Discriminating the four locations may have been much easier for the bats in this study than discriminating the four experimental sounds and odors. If so, the strong preference for spatial cues found in this and other experiments may represent a ceiling effect that prevents the detection of differences between species.

Third, foraging frugivores and nectivores might not actually rely on spatial cues much more than foraging predatory bats do. Predatory bats might use spatial memory extensively to return to previously profitable prey patches or hunting perches (Ratcliffe 2009). For instance, another predatory bat, *Megaderma lyra*, appears to use spatial memory to assess familiar hunting grounds, which may reduce the need to echolocate when hunting (Ratcliffe et al. 2005), and harbor seals use spatial memory to remember hunting grounds (Iorio-Merlo et al. 2022).

A fourth consideration is that spatial learning is critically important in these animals' lives in contexts beyond foraging. The species in Table 1 all forage in the rainforest interior, navigating nightly through dense, cluttered jungle to find food and then returning to their roosts. Bechstein's bat, *Myotis bechsteinii*, feeds on flying insects but preferentially relied on spatial cues over feature cues to relocate suitable day roosts (Hernández-Montero et al. 2020). Bats may be biased towards learning spatial cues if they have experienced spatial cues as being more reliable signals than feature cues in their lives overall (McLinn and Stephens 2006). If selection for spatial memory for homing or navigation generalizes to learning about food, then many species might preferentially rely on spatial cues in novel tasks, even when spatial associations are not good predictors of food in the wild. If so, foraging habitat may be a better predictor of cue reliance than foraging guild (Odling-Smee and Braithwaite 2003; Cheng et al. 2014). There is some evidence that foraging in cluttered space versus open space predicts bat spatial cognition (Clarin et al. 2013) and brain size (Safi and Dechmann 2005; Dechmann and Safi 2009). It would, therefore, be interesting to compare spatial and feature learning between closely related bat species that forage in the forest interior versus open space.

Finally, bats might have cognitive specializations that take a different form than the one we tested. We considered how bats choose which novel cues to associate with food, but specializations may occur at other stages of cognition. For example, species have different "sensory filters" that constrain what they can perceive (Geipel et al. 2021) and different innate preferences that determine what stimuli are attractive (Saumweber et al. 2011). Even if two species prefer to associate the same type of cue with food, they might differ in how quickly they can form associations, or how many associations they can learn.

We suggest that future experiments could assess variation in ability to learn cues between bats with different foraging strategies by comparing rates of learning of single cue types in different modalities. To test the relative use of sound versus odor between species, investigators could repeat this experiment but make the spatial cue unreliable from the start (e.g., Schmidt et al. 1988; Muchhala and Serrano 2015). Larger sample sizes are necessary to measure subtle differences in cue salience, and much clarity would come from increasing the scope and scale of these experiments (e.g., MacLean et al. 2014).

In conclusion, we detected no pronounced difference in cue salience between a bat expected to primarily use odor and spatial cues

Table 1

Bat species tested in foraging cue dissociation experiments with spatial cues

Guild	Species	Cues tested	Primary cue used	Secondary cue	Citation
Nectivore	*Glossophaga commissarisi*	Location (absolute), location (relative position), shape	Location (absolute)	Shape	(Thiele and Winter 2005)
	Glossophaga soricina	Location, odor, shape	Location	Shape/odor possibly	(Carter et al. 2010)
Frugivore	*Carollia perspicillata*	Location, odor, shape	Location	Shape/odor possibly	(Carter et al. 2010)
	Artibeus jamaicensis	Location, odor, sound	Location	None detected	Current study
Insectivore	*Lophostoma silvicolum*	Location, odor, sound	Location	None detected	Current study

and a close relative expected to overwhelmingly use acoustic cues. Although there may be differences in cue learning between bat species that we did not detect, our findings show that surrounding spatial cues can easily overshadow more local features associated with a food source, even in species that feed on mobile prey found in unpredictable locations.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

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ETHICAL APPROVAL

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