Original Article

Flexible use of visual and acoustic cues during roost finding in Spix's disc-winged bat (*Thyroptera tricolor*)

Miriam Gioiosa,[a,b,] Marcelo Araya-Salas,[c,d,e] Christian Castillo-Salazar,[e] Silvia Chaves-Ramírez,[e] Maurizio Gioiosa,[b,f] Nazareth Rojas,[g] Mariela Sánchez-Chavarría,[d] Dino Scaravelli,[h] and Gloriana Chaverri[d,i,]

[a]Centro Studi Naturalistici, Foggia, Italy, [b]Regional Museum of Natural History, Foggia, Italy, [c]Centro de Investigación en Neurociencias, Universidad de Costa Rica, San Pedro, Costa Rica, [d]Sede del Sur, Universidad de Costa Rica, Golfito, Costa Rica, [e]Escuela de Biología, Universidad de Costa Rica, San Pedro, Costa Rica, [f]Department of Agriculture, Food, Natural Science and Engineering, University of Foggia, 71122 Foggia, Italy, [g]Escuela de Ciencias de la Computación e Informática, Universidad de Costa Rica, San Pedro, Costa Rica, [h]Department of Biological, Geological, and Environmental Sciences, University of Bologna, Bologna, Italy, and [i]Smithsonian Tropical Research Institute, Balboa, Ancón, Panamá

The ability of an animal to detect environmental cues is crucial for its survival and fitness. In bats, sound certainly plays a significant role in the search for food, spatial navigation, and social communication. Yet, the efficiency of bat's echolocation could be limited by atmospheric attenuation and background clutter. In this context, sound can be complemented by other sensory modalities, like smell or vision. Spix's disc-winged bat (*Thyroptera tricolor*) uses acoustic cues from other group members to locate the roost (tubular unfurled leaves of plants in the order Zingiberales). Our research focused on how individuals find a roost that has not been yet occupied, considering the urge to find a suitable leaf approximately every day, during nighttime or in daylight. We observed the process of roost finding in *T. tricolor* in a flight cage, manipulating the audio/visual sensory input available for each trial. A broadband noise was broadcast in order to mask echolocation, while experiments conducted at night reduced significantly the amount of light. We measured the time needed to locate the roost under these different conditions. Results show that with limited visual and acoustic cues, search time increases significantly. In contrast bats seemed capable of using acoustic and visual cues in a similarly efficient manner, since roost search showed no strong differences in duration when bats could use only sound, only vision, or both senses at the same time. Our results show that non-acoustic inputs can still be an important source of information for finding critical resources in bats.

Key words: **cues, echolocation, finding resources, roosting ecology, *Thyroptera tricolor*, vision.**

INTRODUCTION

Finding resources is an essential task for the growth, reproduction, and development of every organism. Therefore, the efficiency of an animal's searching behavior is fundamental to its survival and fitness. There are multiple morphological, physiological, and behavioral adaptations that allow individuals to efficiently locate resources like food, mates, or refugia, among others. But first and foremost, animals must be able to detect cues that will allow them to pinpoint the location of potential resources through various sensory modalities (Bell 2012). Vision, for example, is used by female zebra fishes (*Danio rerio*) to recognize their conspecifics, with whom they tend to aggregate and form shoals, which provides mating opportunities, protection from predators, and access to food (Pitcher 1986; Engeszer et al. 2007; Gerlai 2014; Dreosti et al. 2015; Nunes et al. 2020) . Crayfish, on the other hand, rely on chemical signals for mating and locating shelter (Moore 2019). In most cases, however, animals might use cues from various sensory modalities to search for and locate resources. For example, octopuses can integrate information from both chemical and visual cues during food search and selection (e.g., while chasing prey; Maselli et al. 2020).

Address correspondence to M. Gioiosa. E-mail: mi.gioiosa@gmail.com.

In bats, finding resources is often linked with the use of sound in the form of echoes from self-produced vocalizations (i.e., echolocation), which is often considered as their most important sensory modality (Griffin 1958; Dechmann and Safi 2005; Gillam and Fenton 2016). Echolocation certainly plays a role in searching for food, especially in insect-hunting bats (Thies et al. 1998; Schnitzler and Kalko 2001) but is also very relevant for spatial navigation and orientation (Griffin 1958; Neuweiler 2000; Schnitzler and Kalko 2001; Schnitzler et al. 2003; Thomas, Moss, and Vater 2004; Nelson and MacIver 2006). Sound is also known to greatly aid during the location of roost-sites, but primarily in the form of acoustic cues or signals emitted by conspecifics which have already located a suitable roost-site (Vaughan and O'Shea 1976; Ruczyński et al. 2007; Ruczyński et al. 2009; Chaverri and Gillam, 2010). Even echolocation alone can be used by bats for the location of roosts (Ruczyński et al. 2007). In fact, bats can use sound to identify the location of objects by comparing outgoing signals to the returning echoes (Jones 2005) and to recognize patterns by sampling multiple echoes (Ruczyński et al. 2007). Yet, bats' detection range based on echolocation can be limited given the high attenuation rates of the high-frequency calls typically used by bats (Eklöf 2003; Bradbury and Vehrencamp 2011). Therefore, other senses or sensory cues may complement echolocation in the detection of suitable resources, like vision (Eklöf 2003; Ruczyński et al. 2007; Ruczyński et al. 2011; McGowan and Kloepper 2020) or smell (Hessel and Schmidt 1994; Kalko et al. 1996; Von Helversen et al. 2000), given the relatively large areas over which bats must locate roosts. The combination of cues from different sensory modalities may increase the bats' success in finding roosts.

A bat species that is required to constantly locate new roost-sites is Spix's disc-winged bat *Thyroptera tricolor*, an insectivorous bat occurring in lowland Neotropical forests from southern Mexico to southeastern Brazil (Wilson and Findley 1977) that forms very stable social groups of 2–12 individuals (Vonhof and Fenton 2004). This species roosts in the unfurled leaves of plants in the order Zingiberales that typically grow in secondary forests and clearings (Stiles 1975; Seifert 1982; Dobkin 1984; Horvitz and Schemske 1994; Vonhof and Fenton, 2004). Leaves remain in their ideal tubular shape for bat roosting for very short periods of time (approximately one day), which means that *T. tricolor* probably also needs to change roosts during the day (Findley and Wilson 1974; Vonhof and Fenton 2004). Therefore, individuals must constantly locate new roost-sites in areas that span approximately 0.19 ha (Vonhof et al. 2004). Several studies show that an exchange of social calls is critical for rapid location of new roost-sites when a group member has already found and occupied a suitable tubular leaf (Chaverri and Gillam 2010; Chaverri et al. 2010, 2013; Gillam et al. 2013; Sagot et al. 2018); however, how individuals locate new roosts without the aid of conspecifics is unknown. *T. tricolor* emits low-intensity echolocation calls of dominant frequencies ranging from 45 to 70 kHz, which are barely detected with a microphone at a distance of 1 m from the bat (Fenton et al. 2000). Hence, echolocation can effectively aid in roost location on an extremely short range. This, coupled with the further challenge represented by the background clutter from other plants and leaves all around the roost (Eklöf 2003), makes it possible that visual cues may be important for *T. tricolor* when searching for roosts.

In this study, we aim to understand the relative role of different sensory modalities in the roost-finding behavior of bats, using *T. tricolor* as a model. Roosts provide critically important resources for bats, including protection from predators. *Thyroptera tricolor* faces an important constant challenge as the tubular leaves they use for roosting may fully open during the daytime, rendering group members vulnerable to predation. Finding a new roost thus becomes extremely urgent, particularly during the daytime when bats are approximately 10 times more likely to be hunted by diurnal predatory birds (Speakman et al. 1994). In this situation, echolocation calls might not provide enough information over longer distances and in a timely manner. We evaluated the hypothesis that *T. tricolor* uses stimuli from different sensory modalities for finding roosts and predicted that bats will primarily rely on vision for this task. We tested our hypothesis by experimentally manipulating the acoustic and visual stimuli available when searching for a roost.

METHODS
Field methods

The use of vision in *T. tricolor* for roost finding was investigated based on a set of experiments performed both in daylight and during nighttime. The daylight experiments took place in a 5-week period, from 6 November to 7 December 2019, in La Cherenga Field Station (8°38′N, 83°05′W; 93.6 ha) on road 14 Golfito-Rio Claro, in southwestern Costa Rica. This site consists of a farm surrounded by a matrix of primary and secondary wet tropical forest and agricultural lands. *Heliconia imbricata* and *Calathea lutea* are abundant in the understory, being the main roosting resource for *T. tricolor* in the site (Buchalski et al. 2014). The nighttime experiments took place between the 24 and 29 January 2020 in Barú Biological Station, Puntarenas Province, a private 320 ha coastal lowland of the Pacific slope in Costa Rica (9°81′N, 84°81′W) (Johnson 2005). We searched for groups of *T. tricolor* in areas with high abundance of plants used as roosts. In order to capture a group of bats, all the potential leaves that were in the furled stage were examined with a telescopic mirror. If a group of bats was detected, the top of the leaf was pinched and closed, so that the animals could not fly away. Then the leaf was inserted into a plastic bag (20 cm × 1 m) and the bats were gently directed out by gradually closing the leaf behind them. All bats inside the leaf were promptly transferred from the plastic bag to a cloth bag and taken back to the field station. All the individuals found in the same leaf were considered to be part of the same group (Vonhof et al. 2004; Chaverri 2010). All bats were marked with transponders (Mini HPT8 Transponder; Biomark Inc., ID) and scanned using Biomark's HPR Lite reader to individually identify them. Transponders were injected subcutaneously in the mid-dorsal area after cleaning the needle, the transponder and the injection area and its surroundings with an antiseptic (Chlorhexidine Gluconate).

Experiments

In order to test the relative importance of two sensory modalities for roost finding, sound, and vision, we conducted experiments with individuals of *T. tricolor* under different conditions related to the availability of sensory inputs: 1) sound and visual input (hereafter "sound and vision"), 2) only sound input ("sound"), 3) only visual input ("vision"), and 4) no (or very limited) sound and visual input ("lessen input"). The sound and vision condition was recreated by running experiments during daylight without any acoustic interference. The sound condition was conducted at nighttime also in the absence of acoustic interference, while the vision condition involved broadcasting a broadband noise within the frequency range of the echolocation calls during daylight. The lessen input

condition consisted in broadcasting the same broadband noise as the latter, but with experiments run during nighttime. Finally, we included an additional condition in which we broadcast a broadband noise that did not overlap in frequency with *T. tricolor* echolocation calls. This fifth condition ("noise control") was conducted as an experimental control to determine if the behavior of bats during experiments involving broadband noise was affected by bats being disturbed by the emission of sound by itself or if it was only due to acoustic masking. We conducted experiments within a flight cage (2.5 × 3.5 × 5.5 m), one made of saran shade cloth, which was used during the daytime, and another made of double-walled cloth to reduce the amount of artificial light for our nocturnal experiments.

Two Ultrasonic Omnidirectional Dynamic Speakers (Vifa, Avisoft Bioacoustics, Glienike/Nordbahn, Germany) were positioned inside the flight cage on tripods at 2 m distance one from each other. A furled leaf of *Heliconia* sp. or *C. lutea*, taped on a tripod, was then placed between the two speakers. The leaf was replaced every day with a new one. An UltraSoundGate Player 216H (Avisoft Bioacoustics), controlled by Avisoft Recorder software (Avisoft Bioacoustics), was used to broadcast sounds that would allow us to mask calls from bats or to create a noisy environment around the roost. In order to reach maximum sound levels (according to the manufacturer's specifications), the UltraSoundGate Player was attached to an external power supply, consisting of a set of three batteries of 12 V each connected in series (36 V total).

In both daylight and nighttime experiments, each trial had a maximum duration of 5 min. However, the first, explorative trial (hereafter "Exploration") could last 1–2 min longer. Each trial began when the bat started to fly and ended when the bat entered the leaf or when the maximum time of 5 min was reached. After every experiment, the time (in seconds) required for the bat to enter the leaf was registered. For trials in which bats did not enter the leaf we registered a time of 300 s (maximum duration of trial). The first trial, Exploration, always consisted of the bat flying without the researcher broadcasting any sound. Its purpose was to let the bat become familiar with the flight cage, in addition to identifying the presence of a suitable roost-site. The order of following trials was randomized to minimize the effect of trial order on the bat's behavior. Only bats who entered the leaf during the Exploration trial were used in subsequent experiments. When flights exceeded the 5-min limit, the bat was captured with a hand net.

For each bat, a total of four trials, including Exploration and three experimental trials, were performed during the daylight experiments. These trials consisted of Vision, Noise Control and Sound and Vision trials (Figure 1). For the Noise Control trial, we broadcast white noise not masking echolocation (range 0–45 kHz). For the Vision trial we broadcast white noise that would mask echolocation (range 45–500 kHz). No sounds were broadcast in the Sound and Vision trial. We also conducted experiments during the night to determine if a bat's roost-location abilities would suffer when visual stimuli were limited. These experiments consisted of only three trials: the first was always Exploration and was followed by either Sound (no sounds were broadcast) or Lessen Input (broadcast white noise that would mask echolocation; Figure 1), in random order. We used an infrared camera (HD Pan/Tilt Wi-Fi Camera NC450) located within the flight cage to determine when the bat entered the roost, as the amount of light available precluded us from observing this directly.

White noise audios used for playback during the experiments were created with the R package seewave (version 2.1.6; Sueur et al. 2008), with a duration of 30 s, sampling rate of 1 million hertz and depth of 16 bits. When played, each sound was put in a loop mode so that it could last for the entire duration of the test. Furthermore, sound intensity was set to approximately 80 dB, measured at 1-m distance from each speaker (i.e., the distance at which the leaf was positioned) using a sound level meter (Extech Instruments, New Hampshire). As mentioned above, two types of playback files were used in our experiments. During the Noise Control trials we broadcast white noise within a frequency range from 0 to 45 kHz. It creates a noisy environment without masking the bat's echolocation calls (Figure 1). The goal was to remove the interference to echolocation calls while keeping the potential acoustic disturbance of a loud sound in the hearing range of the species and close to the roost. During Vision and Lessen input trials (Figure 1), a white noise with frequencies ranging from 45 to 500 kHz was broadcast. This would allow us to mask *T. tricolor*'s echolocation calls, whose frequencies range between 45 and 100 kHz, with the energy peak at about 47 kHz (Fenton et al. 2000). While Vision trials were performed when light was available, Lessen Input treatments took place at night. Playback started a few seconds before the bat was released and lasted the entire experiment. Since each bat performed the trials in sequence, the position of the roost was moved about 1 m after each trial, in order to prevent the bat from finding the roost using spatial memory. Also, bats were promptly removed from the roost once they had entered it, to preclude roost localization in subsequent trials to be influenced by olfactory cues. Despite this, we cannot unambiguously discard the role of odor in roost localization.

After each experiment, we provided water and mealworms (*Tenebrio molitor*) to all individuals (Chaverri et al. 2013). Also, during the nighttime experiments, the bats were abundantly fed before they were tested in order to prevent them from searching for food instead of searching for a roost. All the bats were released after each session of experiments (4–5 h after the capture). After daylight
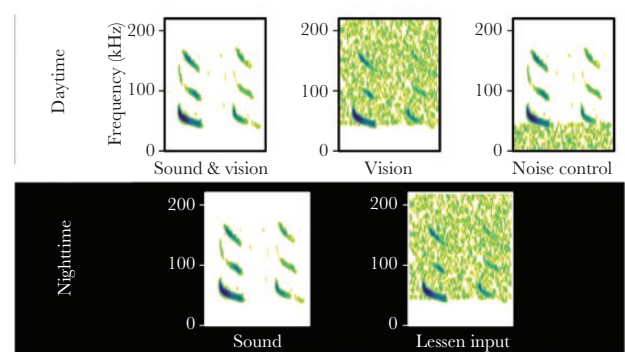
Figure 1

Experiments conducted during the daytime (top) and nighttime (bottom). For each experiment we show in the spectrogram not only the echolocation calls of *Thyroptera tricolor*, but also which sound (if any) was broadcast from the speaker. For the Noise Control trial we broadcast white noise not masking echolocation (range 0–45 kHz). For the Vision and Lessen Input we broadcast white noise that would mask echolocation (range 45–500 kHz—the maximum frequency shown in spectrogram has been set to 200 kHz for illustrative purposes). No sounds were broadcast in the Sound and Vision and Sound trials. All daytime and nighttime experiments included the initial Exploration trial (not shown).
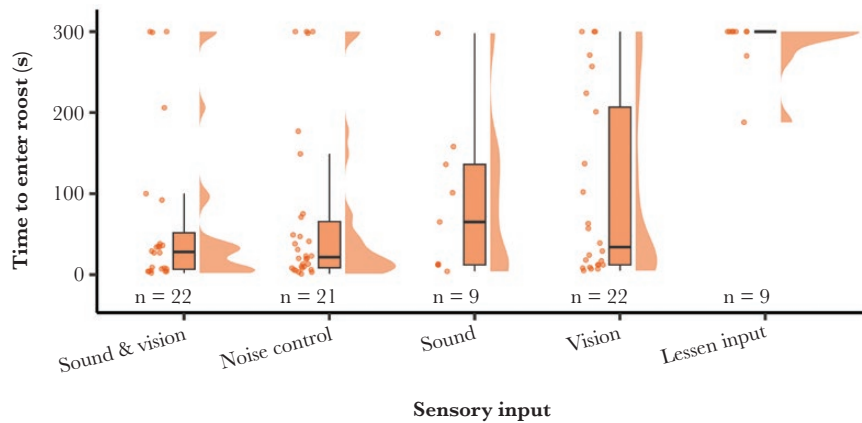
Figure 2

Raincloud plot showing the jittered individual data points, boxplots (median, interquartile range and overall range) and half violin plots of time to enter the roost by Spix's disc-winged bats under five different treatments: Noise Control, Sound and Vision (daylight without acoustic interference), Sound (night without acoustic interference), Vision (daylight with acoustic interference), and Lessen Input (night experiments with acoustic interference).

experiments, the bats were gently released within the same leaf in which they were captured, or in a new one nearby. Bats from nighttime experiments were released from the cloth bag near the capturing site. We ran experiments on 33 individuals. However, two individuals were excluded as only one treatment was properly assessed on them. For the remaining individuals, 9 were tested in 2 treatments at nighttime and 22 in 3 treatments in daylight (Supplementary Material 1).

Statistical analysis

We used Bayesian regression models to evaluate the effect of the different sensory inputs (categorical predictor) in the time required for the bat to enter the roost (response, modeled with a lognormal function), including individual as random effect (varying intercept). The regression models included the observations for individuals that were tested more than once in the same experimental condition. Regressions were run in Stan (Stan Development Team 2021) through the R package brms (Bürkner 2017; R Core Team 2021). Effect sizes are presented as median posterior estimates and 95% credibility intervals as the highest posterior density interval. We compared the model with an intercept-only model (null model) using the Bayesian leave-one-out information criterion (LOOIC, Vehtari et al. 2017) with the R package loo (Vehtari et al. 2020). We conducted multiple comparisons of sensory input treatments (similar to post hoc tests in frequentist statistics) using the joint posterior distribution of the model parameters with the function *hypothesis* from the package brms (Bürkner 2017).

Models were run on four chains for 5000 iterations, following a warm-up of 2500 iterations. The effective sample size was kept above 3000 for all parameters. Performance was checked visually by plotting the trace and distribution of posterior estimates for all chains. We also plotted the autocorrelation of successive sampled values to evaluate the independence of posterior samples. A potential scale reduction factor was used to assess model convergence and kept below 1.05 for all parameter estimates.

ETHICS

All sampling protocols followed guidelines approved by the American Society of Mammalogists for capture, handling and care

of mammals (Sikes et al. 2016) and the ASAB/ABS Guidelines for the use of animals in research. This study was conducted in accordance with the ethical standards for animal welfare of the Costa Rican Ministry of Environment and Energy, Sistema Nacional de Áreas de Conservación, permit no. SINAC-ACOPAC-RES-INV-008-2017 (Decree No. 32553-MINAE). Protocols were also approved by the University of Costa Rica's Institutional Animal Care and Use Committee (CICUA-42-2018).

RESULTS

When evaluating the effect of sensory input on the time to enter roosts, only the Lessen Input treatment had a strong difference compared to other treatments. The model indicates that finding the roost took longer during the Lessen Input treatment compared to treatments with presence of any sensory input (effect size and 95% CrI: Lessen Input vs. Noise Control = 2.19 (1.079–3.26); Lessen Input vs. Sound and Vision = 2.41 (1.28–3.53), Lessen Input vs. Sound = 1.93 (0.81–3.06), Lessen Input vs. Vision = 1.80 (0.67–2.91); Figures 2 and 3). All other treatment pairwise differences were small (Figure 3). This model had stronger support than the null (intercept only) model (Supplementary Material 2). Results remained qualitatively equivalent when excluding individuals that did not enter the roost during the time of the experiment, for which the entry time registered was the maximum duration of trials (Supplementary Material 2).

DISCUSSION

Recent studies show that acoustic signals from other group members can help *T. tricolor* locate the leaves that they use for roosting (e.g., Chaverri et al. 2010; Sagot et al. 2018). No research to date, however, had determined how these bats find a roost-site that had not been previously discovered by other individuals. The results of our study show that this species relies on both visual and acoustic cues to find the ephemeral furled leaves that it uses as diurnal roosts, adding to our growing understanding of the multiple ways in which nocturnal animals find essential resources and how this specialist bat in particular is able to constantly locate a unique but patchy-distributed and often rare roost-site (Chaverri and Kunz 2011).

Since the integration of various sensory modalities is known to decrease search time in other species, we expected bats to find roosts faster when both visual and acoustic cues were available to them. Desert ants, *Cataglyphis fortis*, benefit from the combined use of visual and olfactory cues, reaching nest entrance in shorter times (Steck et al. 2011). Similarly, the integration of vision and olfaction increases the chances of finding prey in *Octopus vulgaris* (Maselli et al. 2020). However, our results suggest that bats released in a flight cage can quickly find the roost regardless of the type of sensory input available: the most marked increases in search time when comparing treatments were observed when no clear sensory input was supplied (lessen input vs all other treatments; Figure 3). The results also suggest more subtle differences between treatments. Particularly noteworthy is the increase in search time when only one sensory modality input was available (vision or sound) compared to inputs from two modalities (sound and vision; Figure 3), which may indicate integration from different sensory modalities. Nonetheless, our results only provide weak support to this pattern, given the large uncertainty around this estimate. A potential explanation for the apparent little sensory integration could be that *T. tricolor* can adapt its searching strategy depending on the environmental context. A similar strategy has been observed in other species. For example, great tits, *Parus major*, have been observed to prefer visual cues over acoustic cues for vigilance when their hearing was impaired by a loud noise (Klett-Mingo et al. 2016). Also solitary bees, *Centris analis*, can use different cues in the process of nest location. Even though spatial and visual information hierarchically overtake odor in terms of better performance, *C. analis* showed high adaptability in learning how to reach the nest in different contexts (Antunes et al. 2021). Analogue experiments showed that different sensory modalities as vision and olfaction are equally used by Long-Evens rats during homeward trips after food search. In fact, blindfolded rats could easily find their way using olfactory cues. Furthermore, during some trials rats were clearly switching among different sensory modalities depending on the distance to the nest. Cues could then be used concurrently, in sequence or flexibly (Maaswinkel and Whishaw 1999). In *T. tricolor*, this flexibility could be driven from the complexity of its environmental background that must be adequately perceived either when light is available or in conditions of complete darkness.

The results of our study strongly suggest that *T. tricolor* may significantly rely on vision when the ability to echolocate, the sensory modality which is most commonly used by bats for locating resources at night, is hampered by noise that masks the returning echoes. The latter may be explained by the fact that bats seemed equally efficient at locating roosts when only vision or only sound were available as sensory cues. The ability of *T. tricolor* to facultatively exploit a particular sense depending on the environmental conditions may be especially important in this species because its echolocation range is relatively limited (Fenton et al. 2000), and the background clutter (Eklöf 2003) significantly high in *Heliconia* and *Calathea* patches where this bat locates its roosts (Chaverri et al. 2022). Moreover, location of roosts may be necessary during the day if bats are flushed or evicted from their current roost and urgently need to find a new one. In this context, the ability to use another sensory modality such as vision may be vital for locating a suitable roosting resource faster, which is particularly urgent to bats as these mammals are known to suffer great levels of predation during the daytime (Speakman et al. 1994).

The findings also demonstrate the effectiveness of our experimental manipulation of sensory inputs available to bats in the different treatments. We showed that the Lessen Input treatment significantly increases searching time, indicating that the white noise playback masking their echolocation signals did affect the level of acoustic input available for roost finding. The fact that the playback broadcast during Noise Control treatment (white noise not masking echolocation) did not trigger a similar response indicates that the effect observed in the Lessen Input treatment is the result of effective acoustic masking rather than a response to the disturbance of a noisy environment. However, a potential drawback of our study is that we could not conduct the daytime and nighttime experiments on the same individuals since we lacked the necessary equipment and infrastructure to conduct the latter at the start of our experiments. Despite this, we believe our results provide unambiguous evidence of the role of both vision and sound for roost finding in *T. tricolor*.

In conclusion, given the patchy nature of roosting resources, the short range over which their echolocation calls travel, and the need to have some light available to locate new roost-sites (precluding their location at night), *T. tricolor* may rely on other means to constantly discover new suitable leaves. In our study, we found that
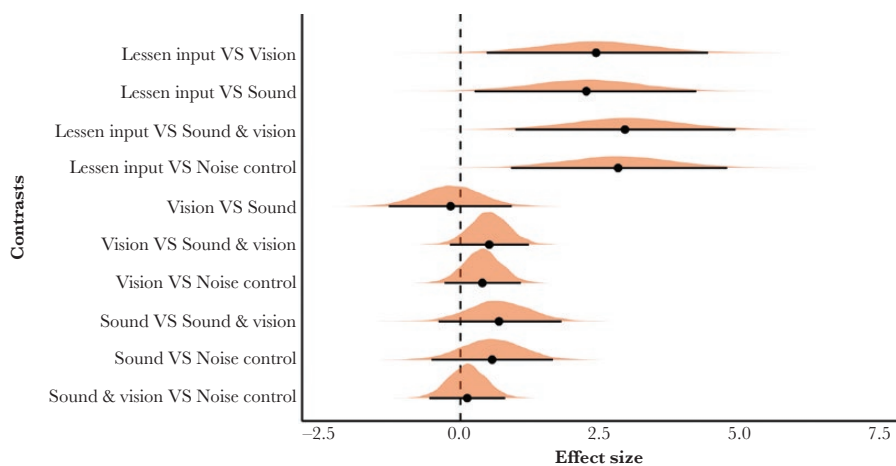
Figure 3
Posterior distribution of the differences in time (in standard deviation units) to enter the roost between all pairwise treatment comparisons. Black dots and error bars show the median and 95% credibility interval of the posterior distributions.

both visual and acoustic cues, when available, are efficiently used in locating a new tubular leaf. Hearing and vision could also hypothetically help bats keep track of leaf development within the bats' territory, facilitating rapid location of new roosts at a later moment. Overall, our research indicates that despite the complex adaptations for low light environments found in bats, non-acoustic inputs can still be an important source of information for finding critical resources.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

Data Availability: Analyses reported in this article can be reproduced using the data provided by Gioiosa et al. (2023).

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REFERENCES

Antunes PR, Telles FJ, Rodríguez-Gironés MA, Augusto SC. 2021. How does the solitary bee Centris (Heterocentris) analis (Fabricius) find its nest? Ecol Entomol. 46(5):1165–1176.

Bell WJ. 2012. Searching behaviour: the behavioural ecology of finding resources. Southport: Springer Science & Business Media.

Bradbury JW, Vehrencamp, SL. 2011. Principles of animal communication. Sunderland: Sinauer Associate.

Buchalski MR, Chaverri G, Vonhof MJ. 2014. When genes move farther than offspring: gene flow by male gamete dispersal in the highly philopatric bat species Thyroptera tricolor. Mol Ecol. 23(2):464–480.

Bürkner PC. 2017. Advanced Bayesian multilevel modeling with the R package brms. arXiv, preprint arXiv:1705.11123, preprint: not peer reviewed.

Chaverri G. 2010. Comparative social network analysis in a leaf-roosting bat. Behav Ecol Sociobiol. 64(10):1619–1630.

Chaverri G, Araya-Salas M, Barrantes JP, Uribe-Etxebarria T, Peña-Acuña M, Varela AL, Aihartza J. 2022. Landing manoeuvres predict roost-site preferences in bats. J Exp Biol. 225(21):jeb244267.

Chaverri G, Gillam EH. 2010. Cooperative signaling behavior of roost location in a leaf-roosting bat. Commun Integr Biol. 3(6):599–601.

Chaverri G, Gillam EH, Kunz TH. 2013. A call-and-response system facilitates group cohesion among disc-winged bats. Behav Ecol. 24(2):481–487.

Chaverri G, Gillam EH, Vonhof MJ. 2010. Social calls used by a leaf-roosting bat to signal location. Biol Lett. 6(4):441–444.

Chaverri G, Kunz TH. 2011. Response of a specialist bat to the loss of a critical resource. PLoS One. 6(12):e28821.

Dechmann DK, Safi K. 2005. Studying communication in bats. Cogn Brain, Behav. 9(3):479–496.

Dobkin DS. 1984. Flowering patterns of long-lived Heliconia inflorescences: implications for visiting and resident nectarivores. Oecologia. 64(2):245–254.

Dreosti E, Lopes G, Kampff AR, Wilson SW. 2015. Development of social behavior in young zebrafish. Front Neural Circuits. 9:39.

Eklöf J. 2003. Vision in echolocating bats. Sweden: Goteborg University.

Engeszer RE, Da Barbiano LA, Ryan MJ, Parichy DM. 2007. Timing and plasticity of shoaling behaviour in the zebrafish, Danio rerio. Anim Behav. 74(5):1269–1275.

Fenton MB, Rydell J, Vonhof MJ, Eklöf J, Lancaster WC. 2000. Constant-frequency and frequency-modulated components in the echolocation calls of three species of small bats (Emballonuridae, Thyropteridae, and Vespertilionidae). Can J Zool. 77(12):1891–1900.

Findley JS, Wilson DE. 1974. Observations on the neotropical disk-winged bat. Thyroptera tricolor Spix. J Mammal. 55(3):562–571.

Gerlai R. 2014. Social behavior of zebrafish: from synthetic images to biological mechanisms of shoaling. J Neurosci Methods. 234:59–65.

Gillam EH, Chaverri G, Montero K, Sagot M. 2013. Social calls produced within and near the roost in two species of tent-making bats, Dermanura watsoni and Ectophylla alba. PLoS One. 8(4):e61731.

Gillam E, Fenton MB. 2016. Roles of acoustic social communication in the lives of bats. In: Fenton M, Grinnel AD, Popper AN, Fay RR, editors. Bat bioacoustics. New York, NY: Springer. p. 117–139.

Gioiosa M, Araya-Salas M, Castillo-Salazar C, Chaves-Ramírez S, Gioiosa M, Rojas N, Sanchez M, Scaravelli D, Chaverri G. 2023. Data from: flexible use of visual and acoustic cues during roost finding in Spix's disc-winged bat. Behav Ecol. doi: 10.5061/dryad.rjdfn2zgt.

Griffin DR. 1958. Listening in the dark: the acoustic orientation of bats and men. New Haven, CT: Yale Univer. Press.

Hessel K, Schmidt U. 1994. Multimodal orientation in carollia-perspicillata (Phyllostomidae). Folia Zool. 43(4):339–346.

Horvitz CC, Schemske DW. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. Ecology. 75(7):1949–1958.

Johnson DM. 2005. Metapopulation models: an empirical test of model assumptions and evaluation methods. Ecology. 86(11):3088–3098.

Jones G. 2005. Echolocation. Curr Biol. 15(13):R484–R488.

Kalko EK, Herre EA, Handley CO Jr. 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old-World tropics. J Biogeogr. 23(4):565–576.

Klett-Mingo JI, Pavón I, Gil D. 2016. Great tits (Parus major) increase vigilance time and reduce feeding effort during peaks of aircraft noise. Anim Behav. 115:29–34.

Maaswinkel H, Whishaw IQ. 1999. Homing with locale, taxon, and dead reckoning strategies by foraging rats: sensory hierarchy in spatial navigation. Behav Brain Res. 99(2):143–152.

Maselli V, Al-Soudy AS, Buglione M, Aria M, Polese G, Di Cosmo A. 2020. Sensorial hierarchy in Octopus vulgaris's food choice: chemical vs. visual. Animals. 10(3):457.

McGowan KA, Kloepper LN. 2020. Different as night and day: wild bats modify echolocation in complex environments when visual cues are present. Anim Behav. 168:1–6.

Moore PA. 2019. Peering into the Darkness. In: Moore PA, editor. Into the illusive world. Cham: Springer. p. 49–54.

Nelson ME, MacIver MA. 2006. Sensory acquisition in active sensing systems. J Comp Physiol A. 192(6):573–586.

Neuweiler G. 2000. The biology of bats. New York, NY: Oxford University Press on Demand.

Nunes AR, Carreira L, Anbalagan S, Blechman J, Levkowitz G, Oliveira RF. 2020. Perceptual mechanisms of social affiliation in zebrafish. Sci Rep. 10(1):1–14.

Pitcher TJ. 1986. Functions of shoaling behaviour in teleosts. In: Pitcher, TJ, editor. The behaviour of teleost fishes. Boston, MA: Springer. p. 294–337.

R Core Team. 2021. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ruczyński I, Kalko EK, Siemers BM. 2007. The sensory basis of roost finding in a forest bat, Nyctalus noctula. J Exp Biol. 210(20):3607–3615.

Ruczyński I, Kalko EK, Siemers BM. 2009. Calls in the forest: a comparative approach to how bats find tree cavities. Ethology. 115(2):167–177.

Ruczyński I, Szarlik A, Siemers BM. 2011. Conspicuous visual cues can help bats to find tree cavities. Acta Chiropt. 13(2):385–389.

Sagot M, Schöner CR, Jago AJ, Razik I, Chaverri G. 2018. The importance of group vocal behaviour in roost finding. Anim Behav. 142:157–164.

Schnitzler HU, Kalko EK. 2001. Echolocation by Insect-Eating Bats: we define four distinct functional groups of bats and find differences in signal structure that correlate with the typical echolocation tasks faced by each group. Bioscience. 51(7):557–569.

Schnitzler HU, Moss CF, Denzinger A. 2003. From spatial orientation to food acquisition in echolocating bats. Trends Ecol Evol. 18(8):386–394.

Seifert RP. 1982. Neotropical Heliconia insect communities. Q Rev Biol. 57(1):1–28.

Sikes RS; Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J Mammal. 97(3):663–688.

Speakman JR, Lumsden LF, Hays GC. 1994. Predation rates on bats released to fly during daylight in south-eastern Australia. J Zool. 233(2):318–321.

Steck K, Hansson BS, Knaden M. 2011. Desert ants benefit from combining visual and olfactory landmarks. J Exp Biol. 214(8):1307–1312.

Stiles FG. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. Ecology. 56(2):285–301.

Sueur J, Aubin T, Simonis C. 2008. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics. 18(2):213–226.

Thies W, Kalko EK, Schnitzler HU. 1998. The roles of echolocation and olfaction in two Neotropical fruit-eating bats, Carollia perspicillata and C. castanea, feeding on Piper. Behav Ecol Sociobiol. 42(6):397–409.

Thomas JA, Moss CF, Vater M, editors. 2004. Echolocation in bats and dolphins. Chicago and London: University of Chicago press.

Vaughan TA, O'Shea TJ. 1976. Roosting ecology of the pallid bat, Antrozous pallidus. J Mammal. 57(1):19–42.

Vehtari A, Gabry J, Magnusson M, Yao Y, Bürkner P, Paananen T, Gelman A. 2020. loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.4.1.

Vehtari A, Gelman A, Gabry J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat Comput. 27(5):1413–1432.

Von Helversen O, Winkler L, Bestmann HJ. 2000. Sulphur-containing "perfumes" attract flower-visiting bats. J Comp Physiol A. 186(2):143–153.

Vonhof MJ, Fenton MB. 2004. Roost availability and population size of Thyroptera tricolor, a leaf-roosting bat, in north-eastern Costa Rica. J Trop Ecol. 20(3):291–305.

Vonhof MJ, Whitehead H, Fenton MB. 2004. Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. Anim Behav. 68(3):507–521.

Wilson DE, Findley JS. 1977. Thyroptera tricolor. Mamm Species. (71):1–3.