Effect of Light Intensity on Echolocation Behavior in Phyllostomid Bats

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Abstract

Echolocation is the dominant sensory modality for three-dimensional orientation in bats. However, bats also integrate different additional sensory modes such as olfaction and vision during flight, and especially during foraging. Studies in nectar-feeding bats have shown that they integrate olfaction to improve maneuvering in flight. But the extent to which bats use vision as a compensatory mechanism to echolocate is unknown. The objective of this study is to determine how behavior changes when both visual and echolocation information is available for orientation. The bat species *Glossophaga soricina* and *Leptonycteris yerbabuenae* were chosen for this study due to their distinct foraging behaviors. The difference in their dependency on vision and echolocation makes them ideal models. The prediction was that with lower light intensity, echolocation calls will be more frequent during approach towards an object and with more light available, the call sequences should be less frequent, indicating more reliance on visual cues. Since echolocation is an active and energy-consuming sense, using passive visual perception when available would be a more cost-effective approach. Although it seems that more light availability and visual cues encourage the bats to forage, operating in light environments jeopardizes their survival from natural predators. Navigating between more energy-effective foraging and less protection from predators is a challenge and no obvious approach prevails.

Introduction

New world leaf-nosed bats (Phyllostomidae) are found in Central and South America. They have a large variety of food sources, comprising of insects, fruits, nectar, and small vertebrates. A recent study on nectar-feeding bats showed that different modalities like olfaction and echolocation are integrated to improve maneuvering in flight (1). But how echolocation and vision work together under different light conditions has not been previously studied.

Phyllostomid bats are generally narrow-space gleaners and use a multitude of sensory cues while foraging. Their passive sense of olfaction is usually used for long distance orientation, for example to locate a flowering or fruiting tree. Their active sense of echolocation is used for collision avoidance and close distance orientation. For example, the acoustic properties of flower structures can provide more detailed information about the flower position on the plant for nectarivorous bats (1). Muchhala & Serrano show that nectarivorous bats rely on certain sensory methods during foraging depending on the complexity of the background (2). They presented two nectar bats, *Anoura caudifer* and *A. geoffroyi*, with scented and unscented flowers in simple and complex environments. They found that in a simple environment, the bats chose flowers indiscriminately. However, in a complex environment, the scented flowers were located first. This suggests that for exposed flowers, vision and echolocation are sufficient for detection, but when they are concealed, the bats rely on olfaction to locate them.

Another example of a multimodal sensory system is found in *Leptonycteris yerbabuenae*. Here a combination of olfaction and echolocation cues elicited a higher approach response than each individual cue, suggesting that nectar bats integrate various sensory modes to detect and precisely localize open flowers (1). On the other hand, insectivorous bats may utilize vision to locate large objects, such as vegetation, and echolocation to target small prey. Vision distinguishes faraway landscapes while echolocation can classify and precisely locate an object, making it important for close-range localization of targets (3). This creates a multimodal sensory system of echolocation (active hearing), scent, passive hearing, and vision, which contributes both to orientation and to the detection and localization of food items.

Experiments in Old World bats show that they use echolocation in both light and dark conditions (4). Individuals of the migratory flower-visiting bat species *Leptonycteris yerbabuenae* often fly in open habitats with relatively high light availability from moonlight (5). By contrast, individuals of *Glossophaga soricina* forage for flowers in narrow spaces inside the forest where vegetation eliminates most light (6). Interestingly, these bats are color-blind but capable of ultraviolet light perception, possibly as an adaptive function to enhance the contrast of ultraviolet-light-reflecting flowers during low light, thereby increasing flower search efficiency (7). Echolocation was refined to detect small targets in conjunction with using vision, revealing a nocturnal niche for bats and inciting diversification in echolocation and foraging tactics (3). Because echolocation is a strategy for close-distance orientation and not suitable for long-distance orientation, individuals of the migrating *L. yerbabuenae* presumably rely more on vision than other phyllostomid species (such as *G. soricina*), which could result in a better flight performance in more complex environments when light is available.

Echolocation is the dominant sensory modality for three-dimensional orientation in bats. However, bats also integrate different additional sensory modes such as olfaction and vision during flight and especially during foraging. Echolocation is constrained by the attenuation of high-frequency sounds and echoes from the background, called clutter. Therefore, echolocating bats must rely on other sensory cues in many situations where more clutter is present.

Some Old-World fruit bats have practically lost echolocation as an orienting sense, mainly relying on vision for orientation

and foraging (8). Microchiropteran bats are known to use vision for long-range orientation, when echolocation is not very effective. Past experiments with the brown long-eared bat have shown that they preferred putting more importance on visual information rather than sonar cues when both sonar cues and visual cues are available (9). Recent experiments also show that bats usually do not echolocate when leaving their roost but rather use vision, avoiding obstacles like mist nets during highly moonlit nights (10).

Study aims

Bats play a critical role in pollen distribution, seed dispersal, and pest control, but it is not clear how they integrate visual information in their foraging behaviors. Bats primarily orient themselves by echolocation, but evidence suggests that they also utilize vision when light is available, regulating their biosonar based on the availability of visual information as a method of energy conservation (11). The extent to which bats use vision as a compensatory mechanism to echolocation is unknown. In their natural habitat, the primary light source is the moon, and light intensities vary depending on the moon cycle and vegetation cover. Understanding how light availability and intensity alters the bats' behavior can give insight into how different parameters of the environment are integrated into a multimodal sensory system.

The objective of this study was to determine how behavior changes when both visual and echolocation information is available for orientation. To investigate whether vision affects echolocation, I tested the hypothesis that with enough light available, nectar-feeding bats will rely both on vision and echolocation to improve foraging efficiency. Since vision is a passive form of orientation, it will reduce the effort spent on the active (energy-consuming) echolocation sense, changing the amount of echolocation calls per time unit. When maneuvering in a more complex arrangement, light availability could influence flight performance. The bat species *Glossophaga soricina* and *Leptonycteris yerbabuenae* were chosen for this study due to their distinct foraging behaviors. The difference in their dependency on vision and echolocation makes them ideal models. I tested their ability to orient to their environment under various simulated moonlight intensities and in total darkness. From the acoustic data, I calculated temporal call parameters. The prediction was that with lower light intensity, echolocation calls during approach will be more frequent; with more light available, the call sequence should be less frequent. The results will determine whether bats' vision influences echolocation behavior and facilitate a more in-depth understanding of their multimodal sensory system.

Methods

Study species

The small nectar-feeding bat *Glossophaga soricina* ranges from northern Mexico to Paraguay and northern Argentina. It lives in a wide variety of habitats, including tropical rainforests and savannas. This species feeds mainly on nectar but can include insects, fruits, and pollen in its diet (12). The medium-sized *Leptonycteris yerbabuenae*, another nectar-feeding bat, ranges from southern Arizona and New Mexico to Honduras and El Salvador. They live in thorn scrub and deciduous forests, and their range corresponds closely to the distribution of the mezcal plant (Agave angustifolia) in Mexico (13). Bats involved in this study were held in a species-appropriate husbandry at Ulm University (Ulm, Germany) and fed a honey-water and pollen diet. Typical day and night rhythm were simulated in the husbandry, using a time switch to adjust their activity rhythm to more common working hours.

Experimental setup

To test the bats' echolocation behavior during foraging under different light conditions, individuals were isolated from the colony, three or four at a time, and placed in a climate chamber measuring 4 m x 2.4 m x 2 m including resting places (two inversely hanging buckets with a rough cloth) and feeders. Room conditions were adjusted to about 24°C and 80–90% relative humidity. In total, 20 bats were tested: 5 adult females and 5 adult males of the species *G. soricina* and 5 adult females and 5 adult males of the species L. yerbabuenae. One additional female *G. soricina* was included in the study but performed only the simple environment experiments. After the animals were captured, they were transferred in a cotton bag into the climate chamber and given 24 hours to habituate prior to experiments. The chamber was completely dark. To apply different light conditions, 6 small 10-watt halogen lamps (Goobay: 10W/12V, G4, 2000h,140 lumens, 8x31, 2650k warm white) in parallel circuit were connected to a voltmeter that allowed voltages of 0 V, 10 V, 15 V, and 20 V to be set. Due to these three voltages, various light conditions during dusk or dawn could be simulated.

A feeder on a stand offered a solution of Alete® milk powder and honey water (with a sugar content of 18%) to *L. yerbabuenae* and a Nektar-Plus (17% sugar concentration, Nekton®) solution to *G. soricina*. Respectively, these were their preferred diet in the husbandry. The bats could feed ad libitum. To record the echolocation calls, a custom-made ultrasound microphone with a flat frequency response (±3dB between 18 and 100 kHz) was connected to an Avisoft-UltraSoundGate. Recordings of a minimum of 10 seconds were made using a pre-trigger of 5 seconds and a hold time of 5 seconds, and a sampling rate of 480 kHz. The ultrasound microphone was fixed to a tripod above the feeder as parallel as possible to the direction of the feeder. This captured the calls sent out when approaching the feeder. To avoid spatial learning, the feeder tripod was presented in four different positions in random sequence (Figure 1). The positions were

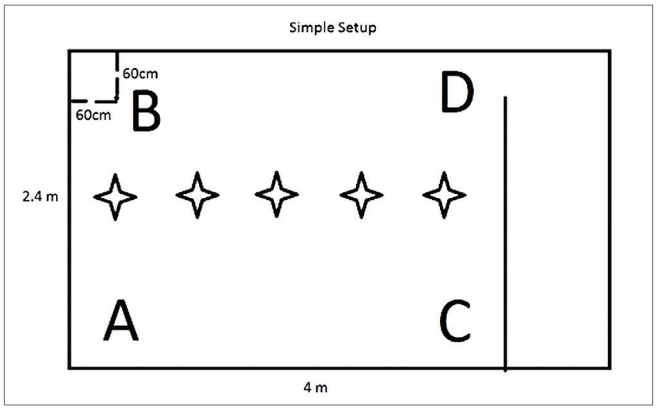

Figure 1. Simple environment setup.

changed so that the height of the feeder above ground was consistent and kept the same distance to the halogen lamps. The distance between the microphone and the feeder remained unchanged. An infrared-sensitive video camera (SONY Handycam, Japan) was set on a tripod directed at the feeder to monitor the bat approaching, hovering, or drinking. Cables of the camera and the microphone were led outside the room through a hole in one wall which was clogged by a big piece of cloth to prevent the diffusion of external light. To simulate a cluttered environment, two plastic garbage bags were cut into 30 strips of 5cm wide strips, roughly 50 cm long, and hung parallel to the corner 10 cm apart from each other and offset by 5 cm (Figure 2).

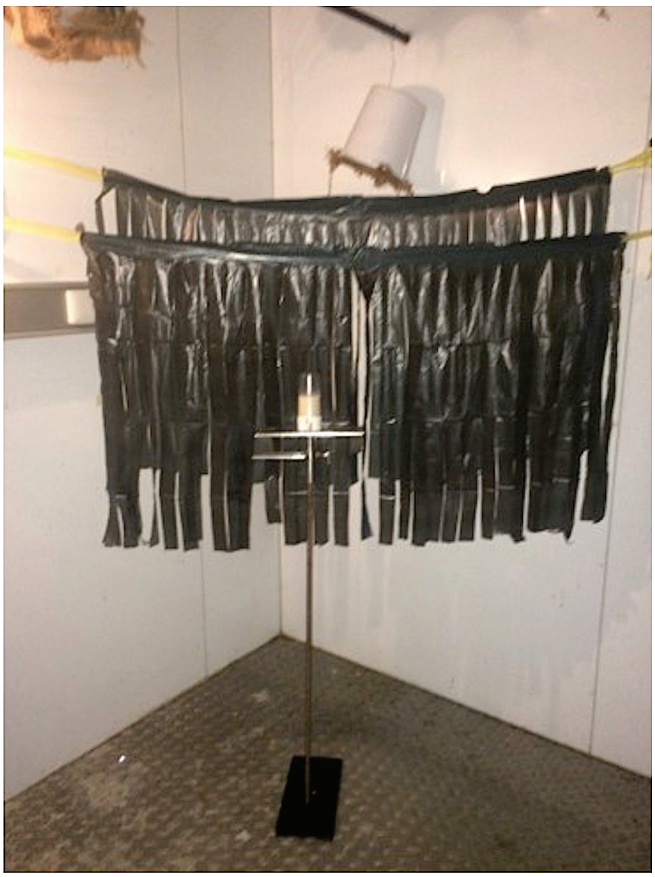

Figure 2. Cluttered environment setup.

Data sampling

Video recordings

Videos were taken alongside audio recordings and ranged from 10 minutes to over an hour, depending on the bat's motivation. The visual information from the cameras verified that an approach was successful (when the bat's tongue or snout was inserted into the feeder), giving the cue to manually trigger the audio. The videos themselves were not analyzed for data.

Audio recordings

To observe the bats' echolocation behavior, an audio recording was triggered when the bat was seen on a monitor connected to the SONY camera, inserting its snout into the feeder. This was categorized as a drinking event. At least 5 successful feeding events were recorded for every light condition, environment type, and feeder position for each bat.

The sequences were divided into orientation and search events before drinking. The decrease of echolocation calls per time unit and their decrease in intensity were defined as search sequences. The less organized sequences of the call were classified as orientation. The more organized and patterned sequences were classified as search. Approach calls of different light conditions were compared among each other.

Data analysis

Measuring sequence parameters

Recordings were analyzed with the software Avisoft SASLAB PRO v. 5.2.07 (R. Specht, Avisoft Bioacoustics, Glienicke, Germany) using Window Hamming, FFT 256, y-scale enlargement 2, frame % 100, resolution 1953 Hz (Figure 3).

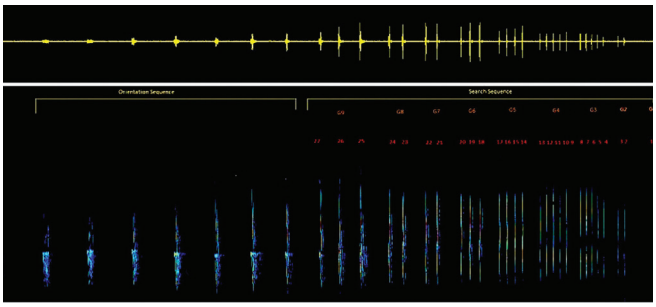

Figure 3. FB CALL2017-12-15_17-21-47_545 20V: Call example traversing the simple environment.

All temporal parameters were measured from the oscillogram to improve accuracy and precision, and checked using the spectrogram with a magnification window of about 5 seconds. The call sequences were analyzed starting from the end of the sequence (last call) toward the beginning to avoid echoes and increase measurement accuracy and precision. Measurements were taken from the beginning of the first pulse of a group to the beginning of the first pulse of the following group. Any pulse or group number is counted from the terminal pulse or group as the starting point. Measurements were taken from the audio files recorded using the parameters below:

- *Approach* was defined as a successful drinking attempt towards the feeder.
- *Sequence Start Time* (seconds) was defined as the apparent start of the approach toward the feeder, distinguished from the waveform, either by the appearance of pulses or, if connected to a longer burst of calls, to the first clear pulse shown on the spectrogram that looks as if it relates to the other calls in an orientation effort.
- *Orientation Sequences* were defined as when the distance of the groups is visually different from the search calls and usually consistently spaced with each other.
- *Search Sequences* were defined from when the group becomes distinguished from previous groups by spacing or grouping (G9).

- *Time Spent Orienting* (seconds) was defined as the distance from the start of sequence to where the pulse splits (sequence from left to Pulse 27).
- *Search Sequence Time* (seconds) was defined from where the pulse split appears to the end of the sequence (Pulse 27–1)
- *Pulse Interval* (seconds) was defined as the distance from the previous pulse.
- The *Group Interval* (seconds) was defined as the distance from the previous group.
- *Pulse Split* demarcates the beginning of the search phase and was defined as the point at which the group becomes distinguished from previous groups by a few characteristics varying between individuals: whenever a hooked call appears (90% of sequences), the second harmonic elongates and becomes wavy, the harmonics overlap more, or there is a single isolated pulse (Pulse 27/Group 9). This term was also interpreted as the bat's intent to attempt a drinking event.
- *Pulse ID* was the number of the pulse within the group.
- *Number of Pulses* is defined as the total amount of pulses between where the pulse split occurs and the end of the sequence (Pulse 27-1).
- *Group ID* was the number of the group starting from the terminal group.
- *Number of Groups* was counted from the terminal group to where the pulse split appears.
- *Feeding Buzz* (Figure 4) was defined as any sequence that ended with a group containing 6 or more pulses with pulse intervals below 015s.

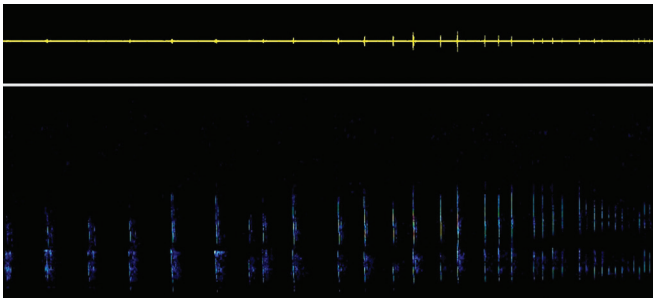

Figure 4. FB CALL2017-12-13_18-32-12_486 20V: Call example traversing the cluttered environment

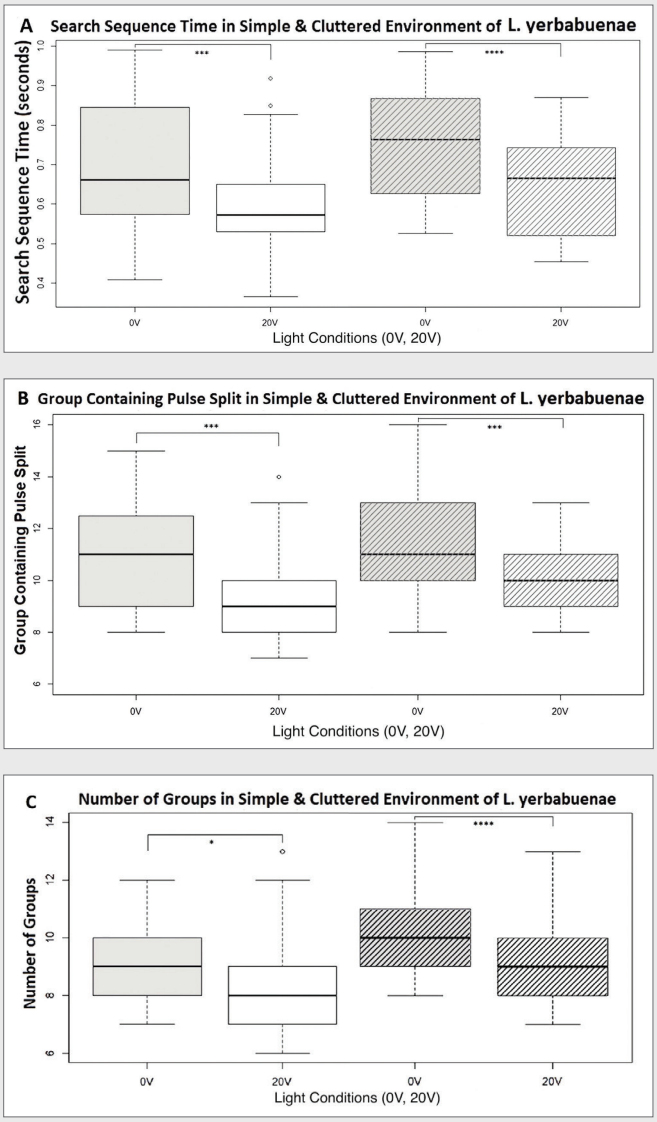

Figure 5. Sequences (N~100 sequences) between two light conditions (0 V, shaded gray, and 20 V) and two environments (left simple, right/patterned cluttered) were compared from the same 10 individuals (5 male, 5 female) of L. yerbabuenae. The data was collected from 05/12/17 to05/02/18 at Ulm University. Three parameters were measured: Duration of Search Sequence, Location of the group containing the Pulse Split, and number of groups. Paired T-ttst determined significance: A) Simple (t = 3.04, df = 32, p-value = 0.0047) versus Cluttered (t = 4.02, df = 32, p-value = 0.0003). B) Simple (t = 3.0, df = 31, p-value = 0.005) versus Cluttered (t = 3.44, df = 32, p-value = 0.0017). C) Simple (t = 2.22, df = 31, p-value = 0.03354) versus Cluttered (t = 3.90, df = 32, p-value = 0.0005).

Statistical analysis

The program R was used to perform statistical analysis. The first 7 or 8 approaches were used to determine statistical significance, excluding any feeding buzzes to create consistency and improve accuracy. I used a paired t-test to determine a significant p-value and a Welch's two sample t-test to confirm significance and account for any variance in the population.

Results

To study whether *L. yerbabuenae* and *G. soricina* change their echolocation behavior while foraging, calls of the feeding events were recorded under different light conditions. Several variables suggest that when *L. yerbabuenae* and *G. soricina* can use vision in foraging, they adjust their echolocation both in time and composition.

Both species take significantly longer to search for the feeder when approaching in the dark versus the lighter environment (Figure 5A, Figure 7A). *L. yerbabuenae* show a statistical difference of a t-value of 3.04 with a degree of freedom of

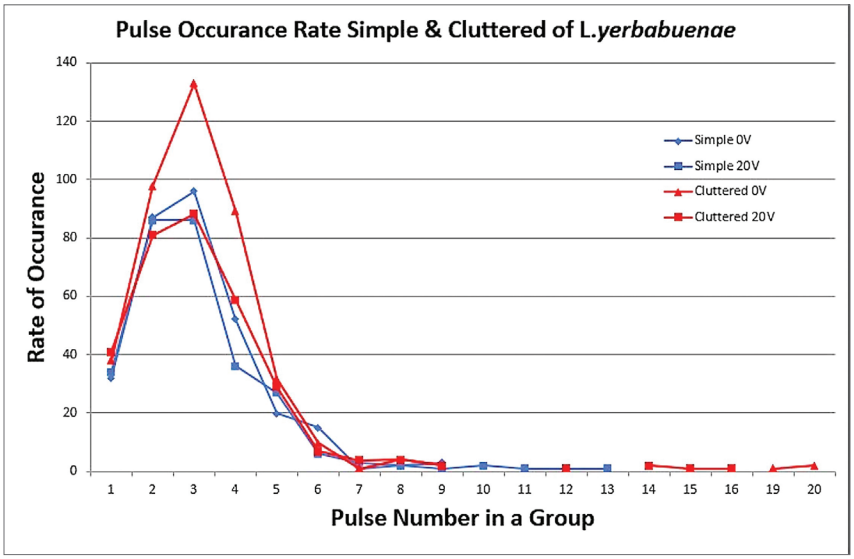

Figure 6. Five female and 5 male L. yerbabuenae were tested from 05/12/17 to 05/02/18 at Ulm University under two conditions (0V and 20V). The types of groups and their occurrence from the first 5 approaches were compared (30,34 sequences under 0V and 38,36 sequences under 20V) between the simple condition (t = 1.2451, df = 8, p-value = 0.2483) and the cluttered condition (t = 1.7802, df = 9, p-value = 0.1087).

32 and a p-value of 0.0047 in the simple environment and a t-value of 4.02 with a degree of freedom of 32 and a p-value of 0.0003 in the cluttered environment. *G. soricina* show a statistical difference of a t value of 4.8013 with a degree of freedom of 52 and a p-value of 0.00001375 in the simple environment and a t-value of 4.6392 with degree of freedom of 50 and p-value of 0.00002551 in the cluttered environment.

Both species produce more groups during their approaches in the dark, and significantly less groups when there is more light available (Figure 5B, Figure 7B). This is true both in the simple and cluttered environment. In the simple environment, *L. yerbabuenae* has a t-value of 3 with a degree of freedom of 31 and a p-value of 0.005, and in the cluttered environment has a t-value of 3.44 with a degree of freedom of 32 and a p-value of 0.0017. *G. soricina* show a statistical difference of a t-value of 6.9223 with a degree of freedom of 52 and a p-value of 0.000000006583 in the simple environment and a t-value of 3.3061 with a degree of freedom of 50 and a p-value of 0.001756 in the cluttered environment.

The sizes of the groups do not seem to show significance and remain the same (Figure 6, Figure 8). This suggests that when the bat can use more of its vision, it does not need to search as much with echolocation, at least initially.

Both species begin their search call echolocation (or change their call types) significantly earlier in the approach during a dark environment versus a lighter environment (Figure 5C, Figure 7C). *L. yerbabuenae* show a statistical difference of a t-value of 2.22 with a degree of freedom of 31 and a p-value of 0.03354 in the simple environment and a t-value of 3.90 with a degree of freedom of 32 and a p-value of 0.0005 in the cluttered environment. *G. soricina* show a statistical difference of a t-value of 5.2764 with a degree of freedom of 49 and a p-value of 0.000002978 in the simple environment and a t-value of 4.1611 with degree of freedom of 49 and p-value of 0.0001274 in the cluttered environment.

Discussion

Significant differences in the search sequence time, the time at which the bat starts searching (signified by the Pulse Split), and the number of groups in the search sequence show that the echolocation behavior during foraging in both *L. yerbabuenae* and *G. soricina* changes during an environment with light (20V) when compared to total darkness (0V), supporting the hypothesis that these bats rely more on vision when there is more light available while foraging. These results imply that visual cues during dusk or dawn might help the bats to localize flowers more quickly than with echolocation alone. Since echolocation is an active and energy-consuming sense, using passive visual perception when available would be a more cost-effective approach. For many animals, energy is a limiting factor. This is especially true for bats, as they do not build up fat tissue as energy reserve and their foraging flights are very energy-consuming.

Statistical significance found in the simple environment was often amplified in the cluttered environment. *L. yerbabuenae* exhibit a significant difference in the time spent during search flight both in the simple environment (p-value = 0.0047) and in the cluttered environment (p-value = 0.0003). Comparison in *G. soricina* also shows similar statistical significance in the simple environment (p-value = 0.00001375) and in the cluttered environment (p-value = 0.00002551). This demonstrates that the bats spent significantly more time in their search flight in a dark environment than in a light environment. The difference suggests that the bats were getting the required spatial information more quickly when visual cues were available.

The group in which the pulse type changes (Pulse Split) was compared showed statistical significance in *L. yerbabuenae* both in the simple environment (p-value = 0.005) and in the cluttered environment (p-value = 0.0017). Experiments with *G. soricina* also showed similar statistical significance both in the simple environment (p-value = 0.000000006583) and in the cluttered environment (p-value = 0.001756). The temporal location where this one pulse type splits into another pulse type was interpreted as where the bat had sufficient information to attempt to approach the target. The change in pulse type occurred significantly earlier when visual cues were available as opposed to when they were not. This could mean that the bats were sure of their target much earlier in the light environment, if this change in pulse type is interpreted as the start of a decisive approach.

The number of pulse groups that the bats produced during the search phase of their foraging flight shows a statistical significance in *L. yerbabuenae* both in the simple environment (p-value = 0.03354) and in the cluttered environment (p-value = 0.0005). Experiments with *G. soricina* also showed similar statistical significance in the simple environment (p-value =

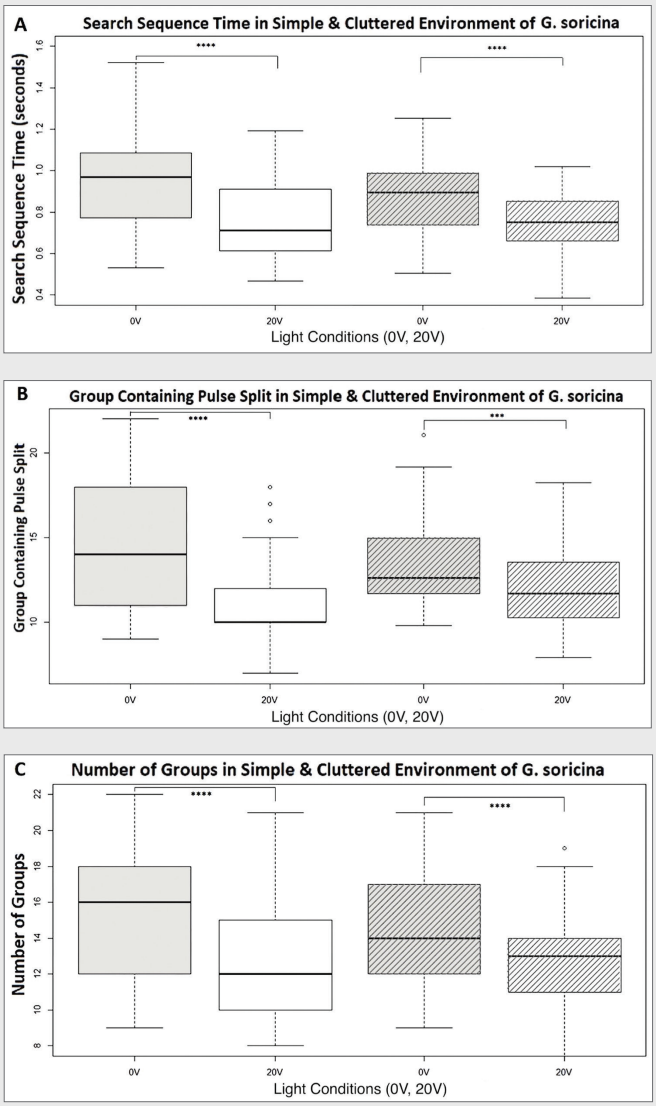

Figure 7. Sequences (N=100) between two light conditions (0 V, shaded gray, and 20 V) and two environments (left simple, right/patterned cluttered) were compared from the same 10 individuals (5 male, 5 female) of G. soricina (*6 females for the cluttered environment). The data was collected from 05/12/17 to05/02/18 at Ulm University. Three parameters were measured: Duration of Search Sequence, Location of the group containing the Pulse Split, and number of groups. Paired t-test determined significance: A) Simple (t = 4.8013, df = 52, p-value = 0.00001375) versus Cluttered (t = 4.6392, df = 50, p-value = 0.00002551). B) Simple (t = 6.9223, df = 52, p-value = 0.000000006583) versus Cluttered (t = 3.3061, df = 50, p-value = 0.001756). C) Simple (t = 5.2764, df = 49, p-value = 0.000002978) versus Cluttered (t = 4.1611, df = 49, p-value = 0.0001274).

0.000002978) and in the cluttered environment (p-value = 0.0001274). Their inclination to produce less groups and less ultrasound calls to locate a potential food source suggests that, even from a distance, they are acquiring enough visual cues to distinguish the location accurately. This accounts for their ability to spot obstacles like trees as potential food sources from a distance.

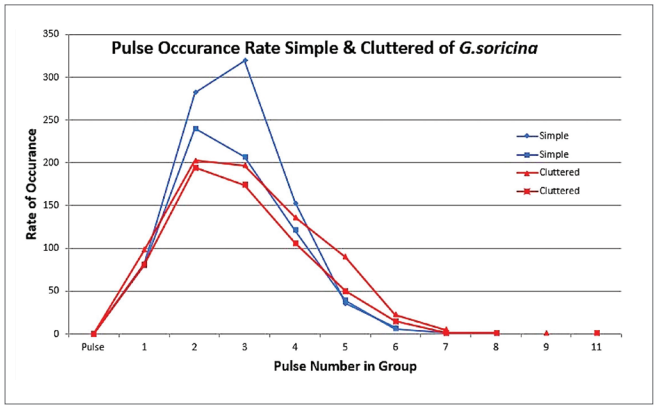

Figure 8. Five female and 5 male G. soricina were tested from 01/02/2018 to 01/24/2018 at Ulm University under two conditions (0V and 20V). The types of groups and their occurrence from the first 5 approaches were compared (30,34 sequences under 0V and 38,36 sequences under 20V) between the simple condition (t = 0.8353, df = 5, p-value = 0.4416) and the cluttered condition (t = 1.2585, df = 7, p-value = 0.2486).

Although it seems that more light availability and visual cues encourage the bats to forage, operating in light environments jeopardizes their survival from natural predators. The bats exhibited significant individual differences in their echolocation and foraging behavior, as exemplified by the large range in the data. Although significant results were shown despite this, a larger sample size of bats and species would illustrate a better picture of the data and behavior. To obtain distinct calls, further experiments should eliminate more variables such as directionality toward the feeder and microphone, since the subjects were untrained and allowed to fly and forage ad libitum. To improve precision and simplify data analysis, future experiments should record the approaches with a high-speed infrared camera. Additionally, studies involving the neurology of these bats would provide insight into their visual and echolocation perceptions. Light intensities of 10 V and 15 V were also tested but preliminary data analysis was not promising, and further analysis was not pursued. These lower light intensities might be under the neuronal potential threshold and not sufficient to elicit a response in the photoreceptors. Therefore, eliminating more variables could show differences even in lower intensity light.

Acknowledgments

I would like to thank my supervisor apl. Proffessor Dr. Marco Tschapka for his support throughout and constructive suggestions. I would like to thank Gloria Glücksklee for her guidance and unwavering patience throughout this project. I would also like to thank the staff, students, and educators at Ulm University Institute of Evolutionary Ecology and Conservation Genomics for welcoming me with warmth and allowing me to use their facilities.

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