Traffic noise affects foraging behavior and echolocation in the Lesser Bulldog Bat, *Noctilio albiventris* (Chiroptera: Noctilionidae)

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**A B S T R A C T**

Urban noise, such as that of traffic, can affect the sensory capabilities in animals. Foragers acting optimally are expected to exploit feeding patches depending on the cost/benefit ratio, and some noises can cause increased foraging costs. We hypothesized that traffic noise affects foraging patch quality for aerial-insectivorous bats and predicted that there are measurable differences in their foraging activity and in their echolocation signals between nights with or without traffic noise. We tested these predictions in the Lesser Bulldog Bat, *Noctilio albiventris*, foraging over aquaculture fishponds, by recording bat activity on nights playing traffic noise and on traffic-sound free control nights. We measured foraging activity by counting the number of search passes and feeding buzzes made by the bats and measured several characteristics of echolocation signals. Foraging activity was higher during noisy nights than during control ones, probably due to the need of more time to obtain information about prey under noisy conditions. When exposed to traffic noise, the bats changed the spectral and temporal characteristics of echolocation signals. We suggest that exposure to traffic noise increases foraging costs for *N. albiventris* and posit that these bats continue foraging under noisy conditions because they can modulate their echolocation signals to obtain enough information.

1. Introduction

Anthropogenic noise production is closely linked to urban activity, exploitation of natural resources, and development of transport networks (Russo and Ancillotto, 2015). Three mechanisms may explain the effects of noise on bats in urban areas: 1) acoustic masking, which occurs due to a spectral and temporal overlap between the target sound and the noise, hindering the detection or recognition of the target sound (Farina, 2014; Bunkley and Barber, 2015; Bunkley et al., 2015), 2) attention decline, where the processing of the limited resources is filled by a distracting stimulus linked to the noise (Bunkley and Barber, 2015), and 3) noise avoidance, where foraging animals abandon a feeding patch due to acoustic disturbance (Bennett and Zurcher, 2013; Luo et al., 2015). Thus, animals that forage in urban environments and that rely on acoustic signals to communicate or detect predators, may be affected by stimuli associated with these environments such as traffic noise.

Sounds are fundamental in the life of bats since they use ultrasonic signals emitted specifically to obtain echoes to build a 3D “image” of their surroundings and to obtain information about the environment they are in (Griffin, 1958; Simmons and Stein, 1980). The frequency of the pulses used by bats to echolocate is generally between 16 and 120 kHz, and they have ears sensitive enough to detect even weak echoes generated by potential prey and other objects (Schnitzler and Kalko, 1998; Simmons and Stein, 1980). Consequently, bats are sensitive to acoustic perturbations such as cluttered backgrounds, insect noise or even echolocation signals of conspecifics (Arlettaz et al., 2001; Corcoran and Moss, 2017; Ulanovsky et al., 2004), and it has been indicated that they are also sensitive to urban noise (Francis and Barber, 2013). Indeed, urban noises can cause bats, such as *Myotis myotis* and *Antrozous pallidus* to lower their activity because such noises interfere with the bats’ efficiency to find food (Schaub et al., 2009; Bunkley and Barber, 2015). Since foraging under noisy conditions may affect bat activity, there are potentially missed foraging opportunities when bats decide to abandon feeding patches due to frequent or chronic noise that interferes with the

*Abbreviations:* CF, Constant frequency; FM, Frequency modulated; CF-FM, Constant frequency-frequency modulated; MaxFreq, Maximum frequency; MinFreq, Minimum frequency; FME, Frequency with most energy; BW, Bandwidth; PD, Pulse Duration; IPI, Interpulse interval; GLM, Generalized Linear Model; r_b, Rank-biserial correlation coefficient.

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Several aerial insectivorous bat species persist in urban environments and appear to have mechanisms to deal with acoustic perturbations typical of these settings. *Tadarida brasiliensis* modifies bandwidth and duration of ultrasonic pulses, improving the signal-noise ratio and, thereby, the detectability of prey under noisy conditions (Bunkley et al., 2015). *Rhinolophus ferrumequinum* increases pulse frequency when the frequencies of noisy background sounds are close to its own (Hage et al., 2013). *Molossus sinaloae* changes the spectral and temporal characteristics of its pulses, including increased pulse frequency, between urban and natural habitats (Lara-Nunez et al., 2022). In contrast, *Mormops megalophyllus* makes only minor changes in the initial and final frequencies of its pulses (Lara-Nunez et al., 2022). Thus, some bats modify their echolocation signals in response to urban noises, but the responses of species are not the same.

Given the high energy demands of flight and their small size, bats, especially, are expected to behave according to the predictions of optimal foraging theory (Norberg and Rayner, 1987; Sánchez, 2006). Optimal patch use models predict that foragers that behave optimally will abandon a feeding patch when the costs of exploiting it are higher than the benefits received from it (Brown, 1988; Charnov, 1976). As indicated above, in urban environments or in environments in transition toward urbanization, many animals face potential costs related to urban noise, which may negatively affect the value of foraging sites. Therefore, we hypothesized that acoustic contamination affects foraging behavior and echolocation by Lesser Bulldog Bat *Noctilio albiventris* while searching for food, as in other species of aerial-insectivorous bats (Bunkley et al., 2015; Bunkley and Barber, 2015; Schaub et al., 2009).

The Lesser Bulldog Bat feeds mainly on insects flying around water bodies, but may also include in its diet small fish and even fruit (*Ara* spp.). This species is characterized by using a variety of foraging behaviors while foraging on insects and have highly versatile echolocation signals, which can change in their spectral and temporal characteristics depending on context (Kalko et al., 1998). In addition, *Noctilio* bats are able to tolerate human-dominated areas and have been recorded using ponds in wildlife refuges and in urban areas (Jung and Kalko, 2010; Tavares et al., 2010). Consequently, we expected to find measurable differences in the foraging activity of *N. albiventris* and in its echolocation signals between nights with or without traffic noise.

2. Materials and methods

2.1. Study site

We did this study on the Campus Sede Barcelona of the Universidad de los Llanos in the exurban area of Villavicencio in the Andean foothills of Colombia, Orinoco region; 4°04’29”N to 73°34.56’W, ~ 400 m above sea level. The campus is a mosaic of environments, which includes crops, pastures and open areas, small forest fragments, secondary forests, fishponds, buildings and roads. Average annual precipitation is 3515 mm, with a rainy season between April and October, and a dry season between November and March, annual average air temperature is 25.3 °C (IDEAM, 2005).

We obtained sound recordings of *N. albiventris* while they foraged over ponds, some with fish in them and others without. The fishponds were of different sizes and contained different fish species. We had previously captured the bats and noted their morphometric details. There are 15 rectangular fishponds on campus, which are 36 ± 0.74 m (mean ± 1 SD) long, 14.1 ± 0.31 m wide, and 0.88 ± 0.13 m deep. Corn and cacao crops, a forest remnant, and one-story buildings surround the fishponds. Some of the buildings have lamps directed toward the fishponds and are turned on around 18:00 h and stay on throughout the night. This probably helps attract the bats, since *N. albiventris* is known to commute between streetlights and their roost in other Neotropical areas (Jung and Kalko, 2010).

2.2. Study animals

The genus *Noctilio* currently includes two piscivorous species: *N. albiventris* Desmarest, 1818, and *N. leporinus* Linnaeus, 1758. They have evolved mechanisms for the search and capture of prey on and near water surfaces, but *N. leporinus* hunts and trawls for fish more frequently than do *N. albiventris* (Schnitzler et al., 1994; Kalko et al., 1998). Indeed, *N. albiventris* feeds mainly on insects, and complement its diet with fish and fruit (Fenton et al., 1993; Schnitzler et al., 1994; Aranguren et al., 2011). Both *Noctilio* species produce quasi-constant frequency (qCF), frequency modulated (FM) and constant frequency- modulated frequency (CF-FM) echolocation pulses. The pulses of the two species can be easily distinguished because the qCF pulses in the search phase of *N. albiventris* are between 67 and 72 kHz, whereas in *N. leporinus* are between 53 and 61 kHz (Kalko et al., 1998; López-Baucells et al., 2016; Schnitzler et al., 1994). qCF pulses begin with a short, upward modulation followed by a constant frequency segment and end with a short downward modulation. The long FM pulses begin with a short and steep downward sweep, followed by a segment with shallow modulation, and end with another steep FM downward sweep. In the CF-FM pulses, the CF segment is similar to the qCF pulses, but these pulses end with a long FM downward sweep (Brown et al., 1983; Roverud and Grinnell, 1985a, 1985b; Kalko et al., 1998).

2.3. Experimental protocol

We recorded the foraging activity of the bats using an ultrasound microphone (Model M500, Pettersson Elektronik AB, Uppsala, Sweden) connected to a portable computer with Windows 10 and used BatSound Touch Lite (Pettersson Elektronik) to obtain high-quality recordings at a sampling rate of 500 kHz and a resolution of 16 bits. We saved all files in .wav format without compression. We used the unidirectional option of the microphone, 1 m above the water surface, aimed parallel to it, to record foraging bats (Fig. 1), thus minimizing recording redundancies which sometimes take place while using omnidirectional microphones (Darras et al., 2018).

We made 5 min recordings with 1 min between recordings, from 18:00 h to 20:00 h, since these species are most active soon after sunset (Brown, 1968; Schnitzler et al., 1994; Kalko et al., 1998). On 40 rainless nights, we made recordings: 20 nights while playing-back recordings of
urban traffic noise and 20 control nights without the noise. On noise treatment nights, we placed a loudspeaker (TOP SONIC, model TS PF77BT, Guangdong, China) between fishponds and set the speaker to reproduce the recording at 80 dB from their source because traffic sounds are regularly at an intensity of 80–90 dB (West, 2016). Sound pressure level (SPL) was measured using the application Sonometro version 2.12 for Android, and the noise of city traffic was obtained from the Internet site https://mixkit.co/free-sound-effects/traffic/. Based on our recordings (Supplementary material 1), we determined that the traffic noises played for the bats had their highest frequencies between 22.07 and 23.74 kHz (95% confidence interval; n = 100).

Since air temperature may affect the foraging activity of Neotropical insectivorous bats (Appel et al., 2019), we obtained air temperature data from a meteorological station on campus and less than 400 m from the fishponds (IDEAM station, code 35035070). In addition, on every experimental night, we recorded the time when the bats appeared at the fishponds as the time between the sunset and the detection of the first N. albiventris at the fishponds. We obtained the time of sunset from www.timeanddate.com.

2.4. Sound analysis

Search passes and feeding buzzes provide information about the foraging activity of aerial-insectivorous bats (Fenton, 1970; Kalcounis et al., 1999). To determine the potential effects of urban noise on the foraging activity of the bats, we counted the number of search passes and feeding buzzes in recorded spectrograms. Following Fenton et al. (1998), we considered a search pass as a regular succession of echolocation pulses produced by a bat while flying through the space sampled by the microphone. We considered two consecutive passes as different when the pulse sequences were separated by three times or more the interval of time between pulses (Estrada-Villegas et al., 2010). Feeding buzzes were considered as a series of short-duration pulses emitted at a very high repetition rate (Kalko and Schnitzler, 1998); these indicate attempts to capture prey, but it is not possible to know whether the attempts was successful (Griffin et al., 1960). Noctilio albiventris produces only short FM pulses at high repetition rates during a feeding buzz, and it does not emit qCF pulses. After an attempt to capture prey, N. albiventris stops producing echolocation pulses for 90.2 ± 64.4 ms and then resumes searching (Kalko et al., 1998).

We used BatSound Pro 4.2 to visualize and analyze the echolocation pulses in 500 ms Hamming windows type (threshold 11, amplitude contrast 2), 1024 samples Fast Fourier Transformation (FFT) and overlap of 80%. We measured the following spectral and temporal variables: frequency with most energy (FME); minimum and maximum frequencies (MinFreq, MaxFreq), as well as the interpulse interval (IPI); and pulse duration (PD) (Avila-Flores and Fenton, 2005; Bunkley et al., 2015). We measured the FME in power spectra, from which we extracted the frequency with the highest intensity in the pulse, and calculated bandwidth (BW) as the difference between maximum and minimum frequency. The IPI was measured as the time from the beginning of one pulse to the beginning of the next one (Jung et al., 2007) (Supplementary material 1, Fig. A1). We only measured pulses from search passes, since their spectral and temporal characteristics are far less variable than those of pulses emitted during the approach phase or during feeding buzzes (Fenton et al., 1998; Bunkley et al., 2015). In order to reduce the likelihood of pseudoreplication, the number of individuals recorded is more important than the total number of pulses recorded (Jones et al., 2002; Waters and Gannon, 2002). Therefore, from different sequences of pulses we measured one qCF pulse, one CF-FM pulse and an FM pulse; we took care to select pulses with intensities greater than −45 dB, without overlapping noises or echoes (Kalko et al., 1998; Zurc et al., 2017). We made 30 measurements from each sampling night until we obtained 600 measurements with traffic noise present and 600 measurements without noise; each one of those groups of measurements consisted of 200 qCF pulses, 200 CF-FM pulses, and 200 FM pulses.

2.5. Statistical analyses

Initially, we applied independent analyses using general linear models with the number of search passes or feeding buzzes per night as dependent variables, traffic noise as a fixed factor and air temperature or the time of arrival to the fishponds as covariates (Quinn and Keough, 2002). However, the data did not meet the criteria of normality and homoscedasticity. Therefore, we applied generalized linear models with a Poisson probability distribution and a logarithmic link function (Zuur et al., 2007). We ran all tests using IBM SPSS 22.

Given the non-parametric nature of the data, we compared the temporal and spectral characteristics of the echolocation pulses from nights with and without traffic noise using Mann-Whitney tests (Zar, 2013). We then used the software JASP v. 0.13.1 to obtain rank-biserial correlations (r) as a measurement of the size of the effect; values lower than 0.1 indicate negligible effects, values between 0.3 and 0.5 indicate intermediate effects, and values greater than 0.5 indicate large effects (Goss, 2019). In all tests, we included in the final models only independent variables with significant effects and used α = 0.05 as the acceptable level of significance.

3. Results

3.1. Traffic noise and foraging activity of bats

We recorded a total of 22,097 search passes and 4431 feeding buzzes of N. albiventris. These were made up of 16,777 search passes and 3783 feeding buzzes under the traffic noise treatment, and 5320 search passes and 640 feeding buzzes without the noise. In all the analyzes, time of arrival had no effect (all p > 0.05) and therefore, we did not include this factor in the final statistical models. The number of passes and the number of feeding buzzes increased significantly in the presence of traffic noise over no-noise conditions (Wald χ² = 5394.992, p < 0.01 and Wald χ² = 1558.165, p < 0.01, respectively; Fig. 2). Air temperature also had a significant effect on the number of search passes (Wald χ² = 253.575, p < 0.01) and the number of feeding buzzes (Wald χ² = 5.239, p < 0.05). There was a negative correlation between both the number of passes and the number of feeding buzzes and air temperature (Spearman correlation coefficient ρ = −0.350; p = 0.031, and ρ = −0.395; p = 0.014, respectively).

During twenty nights without traffic noise, bat activity began between 18:20 h and 18:30 h; on average the bats arrived at the fishponds 21 ± 9 min (n = 20) after sunset. During twenty nights with noise, activity began between 18:27 h and 18:34 h; on average the bats arrived at the fishponds 23 ± 7 min (n = 20) after sunset. There was no significant difference between mean times of arrival at the fishponds between nights with or without traffic noise (tSB = −1.131; p = 0.265).

3.2. Traffic noise and the echolocation signals of bats

There were significant differences in qCF pulses between nights with noise and the nights without noise in several spectral and temporal variables (Fig. 3): FME (U = 15,779; p < 0.001); MaxFreq (U = 15,704; p < 0.001) and PD (U = 16,657; p < 0.01) increased significantly, whereas IPI decreased significantly (U = 23,869; p < 0.001). Further, the noise treatment was correlated with differences in FM pulses in the following variables (Fig. 2): MaxFreq (U = 15,117; p < 0.001), BW (U = 13,359; p < 0.001), and PD (U = 13,582; p < 0.001) significantly increased, whereas MinFreq decreased (U = 23,644; p < 0.01). There were also differences in CF-FM pulses associated to the noise treatment, and particularly affected the following variables (Fig. 3): MaxFreq (U = 13,496; p < 0.001), BW (U = 14,080; p < 0.001) and IPI (U = 23,530; p < 0.01) significantly increased, whereas MinFreq decreased (U = 22,814; p < 0.05).
search time increases, and capture success is reduced when they are exposed to noisy conditions (Siemers and Schaub, 2011; Bunkley and Barber, 2015). Also, field studies with free-ranging insectivorous bats show that they decrease foraging activity and feeding buzzes in the presence of noise with frequencies audible to humans (Domer et al., 2021; Finch et al., 2020). Since feeding buzzes indicate attempts to capture prey but are no proof of successful captures, our results may indicate that *N. albiventris* may invest more time searching for prey and might have to get closer to their prey to obtain enough information to detect and locate insects under noisy conditions. We feel that this explanation is the most plausible and is consistent with our results from the changes in the echolocation signals found under noisy conditions explained in the next section.

Increased night air temperature (reduced air density) may correspond with increases in foraging activity by Neotropical insectivorous bats, but for several species this effect has not been recognized and this is probably due to the low variation of the temperature throughout the night (Meyer et al., 2004; Dias-Silva et al., 2018; Appel et al., 2019). We found that the higher, the air temperature the lower the number of search passes and feeding buzzes by *N. albiventris*, which suggest that there may not be a single relationship between air temperature and the activity of Neotropical insectivorous bats, and future studies should explore the different patterns.

*Noctilio* bats emerge from their daily roost sites about 30 min after sunset (Fenton et al., 1993; Kalko et al., 1998). This concurs with what we found, since bats appeared at the fishponds 21 ± 9 min after sunset, independent of noise treatment. Thus, traffic noise does not appear to have an effect on foraging start-time at the fishponds or the onset of the activity of *N. albiventris*.

### 4.2. Traffic noise and the echolocation signals of bats

The echolocation signals of *Noctilio* bats differed between control and noise treatment nights; in the later FM and CF-FM pulses had increased BW; QCF and FM pulses increased PD; and QCF and CF-FM decreased IPI. Narrow band, CF pulses are adequate for target detection, but imprecise in locating such targets with precision because CF pulses activate few neuronal filters (Schnitzler and Kalko, 2001; Schnitzler et al., 2003). In contrast, FM pulses, which sweep through a wide range of frequencies in a short time, activate multiple neuronal filters producing the necessary time markers for an exact determination of the time delay that provides information on the range and angle of the target (Simmons and Stein, 1980; Schnitzler and Kalko, 2001; Schnitzler et al., 2003). When *N. albiventris* was experimentally exposed to white noise, it was harder for this bat to successfully discriminate prey, and it increased the number of successive pulses probably to integrate more information (Roverud and Grinnell, 1985a). Also, this bat increased the number of CF-FM pulses, probably because the FM component provides more information about the distance to targets, and the more frequencies they use, the more information they obtain from their environment (Roverud and Grinnell, 1985a, 1985b; Roverud, 1994). This response is similar to that in *R. ferrumequum*, which also increased bandwidth of CF and FM pulses when noise masked its echolocation signals (Hage et al., 2014). Thus, our results suggest that traffic noise does affect echolocation in *N. albiventris*, particularly increasing the need to obtain more information on the location of prey.

*Noctilio* bats regularly forage close to water, which acts as an acoustic mirror (Greif et al., 2017). When the axis of the echolocation beam crosses the water surface at an acute angle, most of the energy of the pulses is not reflected back to the bat (Greif and Siemens, 2010). This makes prey between the bat and the water surface more conspicuous since prey generate echoes with higher amplitudes than the same prey flying in the air away from the water (Siemers et al., 2003). During the traffic noise treatment, the bats received not only the echoes from the prey, but also the echoes generated by the noise. Therefore, increasing the BW in the FM and CF-FM pulses might help to: (1) improve temporal

### 4.1. Traffic noise and the foraging behavior of bats

Contrary to previous studies that reported that the foraging activity of aerial-insectivorous bats was negatively affected by traffic noise (Finch et al., 2020). The foraging activity of *N. albiventris* increased with traffic noise. We propose several possible explanations for our results. First, several species of insects rely on acoustic signals to communicate, locate, attract and court potential partners, and to evade predators (Morley et al., 2014; Corcoran and Moss, 2017). These insects, therefore, can be affected by anthropogenic noise (Lampe et al., 2012; Shieh et al., 2012) and noise may reduce their chances of survival when attacked by a predator (Morley et al., 2014). In addition, at our study site there are eight species of raptors (Avendano et al., 2018) which are potential bat predators (Mikula et al., 2016; Whitacre and Burnham, 2013) and for example the owls (*Athena cunicularia*, *Megascops choliba*), depend on acoustic cues to hunt their prey and for intraspecific communication (Speakman, 1991). Feeding efficiency and the ability to detect bats by *N. albiventris*, which suggest that there may not be a single relationship between air temperature and the activity of Neotropical insectivorous bats, and future studies should explore the different patterns.

*Noctilio* bats emerge from their daily roost sites about 30 min after sunset (Fenton et al., 1993; Kalko et al., 1998). This concurs with what we found, since bats appeared at the fishponds 21 ± 9 min after sunset, independent of noise treatment. Thus, traffic noise does not appear to have an effect on foraging start-time at the fishponds or the onset of the activity of *N. albiventris*.

#### 4.4. Discussion

**Fig. 2.** Foraging activity of *Noctilio albiventris*, indicated by the number of search passes (A) and feeding buzzes (B), was higher in nights with traffic noise (gray boxes) than in control nights (white boxes) (** indicate p < 0.01). The line inside the box is the median, the extremes of the box are the first and third quartile, and the whiskers indicate the percentiles 10 and 90, whereas the dots are outlier values.
resolution, making it possible for bats to differentiate among overlapped echoes from different objects, and (2) improve their capability to locate and recognize objects because broadband signals carry more spectral information than narrowband signals, providing more structural details of the target (Holderied et al., 2006; Boonman and Ostwald, 2007; Tressler and Smotherman, 2009).

We found that Noctilio bats increase pulse duration when exposed to traffic noise, which is similar to the response reported for other bats with short pulses such as Pipistrellus kuhlii (8–12 ms), when exposed to noisy conditions (Amichai et al., 2015). It has been argued that bats emitting short pulses can increase their detection capabilities by increasing pulse duration (Luo et al., 2015). When exposed to traffic noise, Noctilio albiventris also decreased IPL, a mechanism to obtain more information per unit time (Gomes et al., 2016). Consequently, the combination of increased pulse duration and pulse emission rate may improve the signal to noise ratio, improving the information obtained by the bats while...
In conclusion, the versatility in the use of different pulse types allows *N. albiventris* to exploit different types of prey around water bodies (Kalko et al., 1998), and this versatility becomes obvious when they are faced with noisy conditions. Foraging activity was greater during nights with noise than during control nights, and several spectral and temporal characteristics of echolocation pulses changed when the bats were exposed to traffic noise. We suggest that this is probably because the noise makes it more difficult for the bats to capture prey and they require more time to obtain sufficient information to either detect or locate prey. In sum, our results suggest that traffic noise can bring about increased foraging costs for piscivorous bats such as *N. albiventris* and the versatility of these bats’ echolocation signals allow them to obtain enough information to continue exploiting the feeding patches despite the noisy conditions.

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**Data Availability**

Data will be made available on request.

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**References**

Allen, L.C., Heist, N.J., Rubin, J.J., Lightsy, J.T., Barber, J.R., 2021. Noise distracts foraging bats. Proc. R. Soc. B: Biol. Sci. 288, 1–7. https://doi.org/10.1098/rspb.2020.2689.

Amichai, E., Blumrosen, G., Yovel, Y., 2015. Calling louder and longer: how bats use bioacoustic under severe acoustic interference from other bats. Proc. Roy. Soc. B, 282, 1–15. https://doi.org/10.1098/rspb.2015.2064.

Appel, G., López-Baucells, A., Magnussén, W.E., Bobrowiec, P.E.D., 2019. Temperature, rainfall, and moonlight intensity effects on activity of tropical insectivorous bats. J. Mammal. 100, 1889–1900. https://doi.org/10.1093/jmammal/gyz149.

Aranguren, C.J., González-Carcacía, J.A., Martínez, H., Nassar, J.M., 2011. *Noctilio albiventris* (Nocitiloidea), a potential seed disperser in disturbed tropical dry forest habitats. Acta Chiropterol. 13, 189–194. https://doi.org/10.3161/1508110115X79732.

Arlettaz, R., Jones, G., Racey, P.A., 2001. Effect of acoustic clutter on prey detection by foraging insectivorous desert bats. Mamm. Biol. 101, 497–501. https://doi.org/10.1016/s0025-0641(00)00021-x.

Avendaño, J.E., Tijerina-M, N., Díaz Cárdenas, J., Amaya-Burgas, J.J., Aponte, A.F., Gamboa, N., José Salcedo-Sarmiento, Y.E., Velañez-Suárez, Á.J., Morales-Rozo, A., 2018. Birds of Universidad de los Llanos (Villavicencio, Colombia): a rich community at the Andean foothills-savanna transition. Boletín Genti. Cent. Mus. 22, 51–75. https://doi.org/10.17151/bcm.2018.22.2.5.

Avilá-Flórez, R., Fenton, M.B., 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. J. Mammal. 86, 1193–1204. https://doi.org/10.1644/04-MAMMA-08851.1.

Bennett, V.I., Zurcher, A.A., 2013. When corridors collide: road-related disturbance in commuting bats. J. Wildl. Manag. 77, 93–101. https://doi.org/10.1002/jwmg.467.

Boonman, A., Ostwald, J., 2007. A modeling approach to explain pulse design in bats. Biol. Cybern. 97, 159–172. https://doi.org/10.1007/s00422-007-0164-2.

Brown, J.I.L., 1968. Activity patterns of some Neotropical bats. J. Mammal. 49, 754–757. https://doi.org/10.2307/1378737.

Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol. 22, 37–47. https://doi.org/10.1007/BF00995696.
