Physical clutter affects the use of artificial ponds by the Lesser Bulldog Bat *Noctilio albiventris* (Chiroptera: Noctilionidae)

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**Abstract.** Bats frequently feed over water bodies, but the net value of the water bodies depends on characteristics such as the amount of physical clutter the water body has. More physical clutter may reduce the detection of prey by bats and may also increase energetic costs by increasing the number of obstacles to avoid. Consequently, we hypothesized that increasing physical clutter affected the use of an artificial pond where the Lesser Bulldog Bat *Noctilio albiventris*, a Neotropical fishing bat, forages regularly over water. We experimentally tested this idea recording the number of passes and feeding buzzes emitted by the bats on different nights when we added two levels of obstacles over the water and on control nights with no obstacles. We only found differences between the treatment with the highest obstacle density and the control; there were fewer passes and less feeding buzzes with more obstacles. Therefore, the addition of obstacles did affect the foraging behavior of *N. albiventris*. Furthermore, we suggest that increasing physical clutter, as in our experiments, may be a cost-effective way to reduce conflicts between local fisher farmers and fishing bats in Neotropical rural areas.

**Keywords.** Bats-humans conflict; Colombia; Echolocation; Fish-eating bats.

**INTRODUCTION**

Aquatic ecosystems are highly valuable for multiple species of Neotropical bats. Water streams are regularly used for commuting, and these water bodies, as well as lentic bodies, may be used as resource patches where flying insects are readily available (Fleming *et al.*, 1972; Bernard & Fenton, 2003; Medina *et al.*, 2007). These water bodies can be highly productive environments capable of sustaining large numbers of insects, which in turn may be highly attractive for bats (Siemers *et al.*, 2001). Studies on bats from temperate regions indicate that foraging over water bodies encompasses specific challenges depending on the characteristics of the site, such as water speed, turbulence, physical clutter, and occurrence of floating plants (von Frenckell & Barclay, 1987; Boonman *et al.*, 1998; Rydell *et al.*, 1999). These effects appear to be independent of the distribution and abundance of prey. Thus, the problem of detecting prey near the water becomes a problem of “acoustic visibility”, since prey positioned over objects near the water surface or flying near turbulent water may be masked by surrounding echoes (Rydell *et al.*, 1999). Also, some experiments have shown that insectivorous bats tend to avoid artificial cluttered areas, where a greater number of obstacles may make flight harder and the acoustic interference created by these obstacles may make echolocation more difficult (Mackey & Barclay, 1989; Brigham *et al.*, 1997; Grindal & Brigham, 1998). As far as we know, these ideas have not been tested in Neotropical species.

Water bodies are particularly important for bats of the genus *Noctilio*, which are adapted to exploiting different prey associated with water bodies (Pavan *et al.*, 2012). Currently there are two recognized species in the genus *Noctilio*: *N. albiventris*, the Lesser Bulldog Bat, and *N. leporinus*, the Greater Bulldog Bat. The two species differ in size, with *N. leporinus* being bigger (forearm longer than 73 mm; body mass 58.33-90 g) than *N. albiventris* (forearm shorter than 70 mm; body mass 18-45 g) (Linares, 1998). The two species are found in most of South and Central America, and they are regularly found in sympatry (Gardner, 2007). One of the suggested explanations for the coexistence of the *Noctilio* bats is their dietary differentiation. The bigger species appears to be more specialized on the consumption of fish, and complements its diet with insects, whereas the...
smaller species includes a wider variety of insects, but may also consume fish, and may complement its diet with fruits (Hooper & Brown, 1968; Gonçalves et al., 2011). Noctilio bats use echolocation to detect animal prey, and they are quite versatile at it. They may use quasi-constant frequency pulses (QCF), which may aid in the detection of moving prey in a cluttered environment while foraging near water or land (Schnitzler et al., 1994; Kalko et al., 1998). However, they may also add a broader range of frequencies, using pulses with a QCF component and a frequency-modulated component (FM) which may be more useful when they forage farther from the water. The difference in size between the Noctilio species is associated with differences in the characteristics of the echolocation pulses they use, and N. leporinus uses a lower frequency (53-61 kHz) than N. albiventris (68-76 kHz) (López-Baucells et al., 2016). Thus, the smaller species is better suited to detect smaller obstacles than the bigger one, and should be able to use environments with higher concentrations of physical clutter (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987).

Mackey & Barclay (1989) showed experimentally that increasing physical clutter and noise over water bodies reduces foraging activity by aerial insectivorous bats due to masking sounds. In one of their experiments they added obstacles over calm water to test the effect of clutter. In light of all the above, we proposed to test these ideas with the Neotropical N. albiventris, the most agile and maneuverable species of its genus, using an experimental protocol similar to the one used by Mackey & Barclay (1989). Particularly, we expected a decrease in the use of artificial ponds by N. albiventris due to the increase in the density of physical clutter.

**MATERIAL AND METHODS**

**Study site and the bats**

We did the experiments at the campus of Universidad de los Llanos in Villavicencio, Meta, Colombia; 04°04′N, 73°34′W, ~400 m a.s.l. (Alfonso & Sánchez, 2019). The campus is in the periurban area of the city, it includes buildings, roads, plantations, native rainforests in regeneration, and artificial ponds for aquaculture. The campus is surrounded by rural land, recreational farms, and a military base. There are 15 rectangular ponds on campus; width 36 ± 0,74 SE m; length 14,1 ± 0,31 SE m; depth 0,88 ± 0,13 SE m. The area with the ponds is surrounded by cornfields, a patch of secondary forest, a plantation of shade-grown coffee, a soursop crop and one-story buildings.

Noctilio albiventris inhabits most of South America, including Colombia, Venezuela, Trinidad Island, Guyana, Surinam, French Guiana, Brazil, Ecuador, Peru, Bolivia, Paraguay, and Argentina, and is present in Central America and southern Mexico too (Hood & Pitocchelli, 1983; Gardner, 2007). This versatile species is present in lowlands with tropical dry forests and rainforests, savannas, and rural and urban areas (Aguirre et al., 2003; Alberico et al., 2005; Calongue et al., 2010; Aranguren et al., 2011; Ballesteros & Racer-Casarrubia, 2012). We have previously captured this species and recorded its echolocation calls in the ponds of the campus.

**Experimental set-up**

To evaluate the effect of different levels of obstacle density, we used a control without obstacles, a treatment with one line of obstacles, and a treatment with two lines of obstacles (Fig. 1). Based on Mackey & Barclay (1989), we used as obstacles cuboids made of polystyrene, 70 × 50 × 2 cm in one of the ponds. We attached the cuboids to a rope, separating neighboring squares by 5 m. The obstacles were placed right above the water and along the pond’s longest diagonals; for the treatment with one line, we used one diagonal of the pond, and for the treatment with two lines, we used both diagonals. We recorded the echolocation pulses emitted by N. albiventris using an ultrasonic microphone Petterson M500® connected to a portable computer using the software Bat SoundPro, at a 500 kHz sampling rate, 16 bits resolution, and saved files in .WAV format. We did the recordings during 15 rainless nights in October and November of 2017; five nights per treatment, and we applied one treatment per night and the treatment for a particular night was randomly decided. During an experimental night, we did recordings of 5 minutes from 18:30 to 21:00 h, with intervals of 5 minutes between consecutive recordings. During the recordings, we directed the microphone toward the pond using its unidirectional mode to record the bats foraging above the water. We recognized the echolocation calls of N. albiventris by its characteristic QCF/FM shape, and because the frequency with the most energy was 67-72 kHz (Kalko et al., 1998). We measured activity in number of passes and number of feeding buzzes in the recordings. We counted the number of passes, i.e., sequences of consecutive pulses produced by a N. albiventris, and considered sequences separated by at least 100 ms to be different passes. In addition, we counted the number of feeding buzzes, i.e., sequences of pulses with extremely reduced times between consecutive pulses and pulse duration, which correspond to attempts to capture prey (Altringham, 2001). We did not record the number of at-
tempts to capture preys by trawling (Kalko et al., 1998), since they were very infrequent during the experiments.

**Statistical analyses**

We examined residuals of parametric analyses of variance and did tests of Levene, and found deviations from the assumption of homoscedasticity (Kuehl, 2000). Hence, we used the nonparametric option, a Kruskal-Wallis test (Zar, 2010) using either the number of passes or the number of feeding buzzes as dependent variables, and the density of physical clutter as the independent variable. After these analyses, we applied the Nemenyi test as method for multiple comparisons (Elliot & Hynan, 2011). We used SPSS v. 18 to run all tests, and used $\alpha = 0.05$ as level of significance.

**RESULTS**

The increase in clutter density did affect the use of the pond by *N. albiventris*, both in the number of passes ($H = 15.6, p < 0.01$) and the number of feeding buzzes ($H = 10.8, p < 0.01$). We found significantly fewer passes in the treatment with the highest density compared to the control but found no differences between the treatment with one line and the control (Fig. 2A). Furthermore, the density of physical clutter had a significantly negative effect on the number of feeding buzzes, but only at the highest density (Fig. 2B).

**DISCUSSION**

Our results supported our predictions, and increasing clutter did affect the activity of *N. albiventris*, but only at the highest density of obstacles. Thus, our results are in agreement with those from species in temperate regions that are capable of foraging near the water, and prefer water bodies with low densities of obstacles (Mackey & Barclay, 1989). Von Frenckell & Barclay (1987) hypothesized that bats such as *Myotis lucifugus*, which heavily rely on water bodies to obtain prey, use less frequently turbulent waters compared to calm waters, because the physical clutter adds echoes that mask the presence of prey, reducing the possibilities of the bats to capture flying insects. Rydell et al., (1999) did additional experiments showing that such masking effects can effectively reduce foraging efficiency in bats. In addition to the acoustical effects, clutter can also increase energetic costs of foraging, since bats have to invest more avoiding collisions with obstacles (Sleep & Brigham, 2003). Indeed, while foraging, aerial insectivorous bats require maneuvering and agility, including chasing and diving behind insect prey (Brigham et al., 1997). This implies that less spatially-complex habitats have lower energetic costs of flight and reduced difficulties of echolocation than more complex ones (Grindal & Brigham, 1998). Therefore, our results suggest that *N. albiventris* negatively reacts to the addition of high density of clutter because it probably interferes with the echolocation of the bats, and increases energetic costs of foraging.

One of the main consequences of the response of bats to physical clutter is related to habitat selection. Indeed, habitat selection is a hierarchical process in which organisms use the available information to estimate the contribution of different habitats to its reproductive success (Rosenzweig, 1981). Since one of the main sources of information for the bats is impaired by physical clutter over the water, the value of obstacle-rich spaces will be lower for the bats. Thus, as reported for several bats from temperate regions, our results suggest that *N. albiventris* should prefer calm waters over turbulent ones to forage. Also, *N. albiventris* should prefer calm water with enough space free of obstacles to forage efficiently.

These results may have a practical application, since currently there is a conflict between fish-eating bats and humans in Colombia. In Colombia, fish farming has been a traditional and widely spread practice to obtain fish for subsistence, as well as for commercial purposes and at different scales, for both ornamental fish and fish used as food (Merino et al., 2013). Fish farmers and
wildlife may enter in conflict when animals such as birds or otters remove fish from tanks, ponds or natural water bodies used to extract fish by humans (López-Arévalo et al., 2003; Andrade-Ponce & Angarita-Sierra, 2017). In the Colombian Orinooco local fish farmers have reported problems with young fish killed during the night by bats, very probably *N. leporinus*. Unfortunately, ignorance about bat diversity in rural areas of Latin America, leads to measures which may not be directed to the bats that cause the damage and may negatively affect other bat species (Aguirre et al., 2010; Tuttle, 2013). Thus, there is a need for specific management alternatives to reduce the conflict. Even though we did not study *N. leporinus*, our results point toward a practical and cost efficient solution to reduce the conflict between people and fish-eating bats. The addition of relative cheap obstacles significantly reduced the value of the pond where we did the experiments for *N. albiventris*. Both noctilionids have wings with high aspect ratios and rounded tips, particularly in *N. leporinus*, which are adaptations for slow and sustained flight away from clutter (Norberg & Rayner, 1987). Despite these adaptations, *N. leporinus* is much bigger than *N. albiventris* both in mass and wing span, and therefore it is less maneuverable (Alridge & Rautenbach, 1987). Thus, increasing physical clutter above fishing ponds or tanks, even with simple arrays, should considerably decrease the value of such environment and consequently the effect of fish-eating bats on the production of fish. This solution appears to be specific to the problem, cost-effective, and causes no damage to the bats. To test these ideas and defining the particular density of obstacles for specific water bodies is highly recommended.

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REFERENCES


