Preliminary notes on bat activity and echolocation in northwestern Argentina

By: Matina C. Kalcounis-Rüppell, T.J. Brown, P.T. Handford, and R.A. Ojeda

Kalcounis-Rueppell MC, Brown TJ, Handford PT and Ojeda R. 2003. Preliminary notes on bat activity and echolocation in northwestern Argentina. Mastozoologia Neotropical 10(2):331-339.

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Abstract:

We recorded echolocation sequences to examine activity of bats in 4 biomes of northwestern Argentina during August 1997 (early southern spring). Our aims were to evaluate the level of bat activity among the four biomes and to preliminarily investigate whether the acoustic structure of echolocation signals conformed to general predictions. We sampled bat activity in sites representing high Andean Puna desert, lowland Chaco thornscrub, lowland Monte desert, montane Yungas forest and montane Chaco thornscrub. No bats were recorded in the Puna, while of the other biomes the least to the most active were: Monte desert, Yungas forest, lowland Chaco thornscrub and montane Chaco thornscrub. Our preliminary results suggest that echolocation signal structure differed among the biomes. In general, signals recorded from bats in Yungas forest were of relatively high frequency whereas signals recorded from bats in Monte desert were of relatively long duration. We show that bats in the less complex biomes tend to be less active. The results of this short-term, preliminary study highlight the high level of bat activity in the Chaco and the opportunity for further study of the bat community in northwestern Argentina.

Keywords: bats | bat detector | echolocation | Argentina | biomes | activity | Anabat | Chaco thornscrub | Puna | Yungas forest | Monte desert

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DISTRIBUCIÓN, HISTORIA NATURAL Y CONSERVACIÓN DE MAMÍFEROS NEOTROPICALES

DISTRIBUTION, NATURAL HISTORY AND CONSERVATION OF NEOTROPICAL MAMMALS

PRELIMINARY NOTES ON BAT ACTIVITY AND ECHOLOCATION IN NORTHWESTERN ARGENTINA

M.C. Kalcounis-Rüppell¹, T.J. Brown², P.T. Handford², and R.A. Ojeda³

¹ Department of Biology, University of North Carolina-Greensboro, PO Box 26170, Greensboro, NC, 27402-6170. <matina_kalcounis@uncg.edu>. ² Department of Biology, University of Western Ontario, London, Ontario, Canada, N6A 5B7. ³ GiB, I.A.D.I.Z.A-CONICET, Parque Gral. San Martin, 5500 Mendoza, Argentina

ABSTRACT. We recorded echolocation sequences to examine activity of bats in 4 biomes of northwestern Argentina during August 1997 (early southern spring). Our aims were to evaluate the level of bat activity among the four biomes and to preliminarily investigate whether the acoustic structure of echolocation signals conformed to general predictions. We sampled bat activity in sites representing high Andean Puna desert, lowland Chaco thornscrub, lowland Monte desert, montane Yungas forest and montane Chaco thornscrub. No bats were recorded in the Puna, while of the other biomes the least to the most active were: Monte desert, Yungas forest, lowland Chaco thornscrub and montane Chaco thornscrub. Our preliminary results suggest that echolocation signal structure differed among the biomes. In general, signals recorded from bats in Yungas forest were of relatively high frequency whereas signals recorded from bats in Monte desert were of relatively long duration. We show that bats in the less complex biomes tend to be less active. The results of this shortterm, preliminary study highlight the high level of bat activity in the Chaco and the opportunity for further study of the bat community in northwestern Argentina.

RESUMEN. Notas preliminares sobre actividad y ecolocación en murciélagos del Noroeste argentino. Examinamos secuencias de ecolocación en murciélagos de 4 biomas del Noroeste de Argentina durante el mes de Agosto de 1997 (primavera temprana). Nuestros objetivos fueron evaluar el grado de actividad entre los cuatro biomas e investigar, de modo preliminar, la correspondencia de la estructura acústica de las señales de ecolocación con las predicciones generales. Registramos la actividad de murciélagos en sitios representativos del desierto de altura de la Puna, el Desierto del Monte, el Chaco arbustivo, la selva de las Yungas y el Chaco serrano. A excepción de la Puna, donde no obtuvimos registros, la actividad de los distintos sitios fue, de menor a mayor: Desierto del Monte, Selva de Yungas, Chaco arbustivo y Chaco montano. Nuestros resultados preliminares sugieren que la estructura de las señales de ecolocación difieren entre los biomas. En general, las señales registradas en murciélagos de las Yungas fueron de alta frecuencia, mientras que las señales registradas en murciélagos del Chaco y Desierto del Monte fueron de larga duración relativa. Los murciélagos de los biomas menos complejos tienden a mostrar menor actividad. Los resultados de este estudio preliminar resaltan el alto nivel de actividad de los murciélagos del Chaco y la oportunidad para continuar investigando la comunidad de guirópteros del Noroeste de Argentina.

Key words: bats, bat detector, echolocation, Argentina, biomes, activity, Anabat, Chaco thornscrub, Puna, Yungas forest, Monte desert

Palabras clave: murciélagos, detector de murciélagos, ecolocación, Argentina, biomas, Anabat, Chaco, Puna, Yungas, Monte

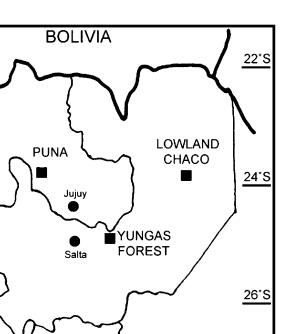
INTRODUCTION

In the northwestern region of Argentina, several important South American biomes meet. The northwestern region of Argentina is a tropical-temperate major interface between lowland forests and arid land biotas, with marked topographic and climatic gradients and a rich mammalian fauna (Ojeda and Mares, 1989). The South American biomes that meet in northwestern Argentina are the lowland Monte desert, the montane Yungas forest, the Chaco thornscrub forest, and the high Andean Puna desert. Although field research on bats in Argentina is increasing, our knowledge of bat activity and echolocation call structure is limited (Barquez et al. 1993 and references therein).

The echolocation demands of navigation and prey detection vary among habitats with different physical structures. Clearly, the challenge of prey capture in a cluttered forest habitat is different from that in an open grassland environment. Simmons et al. (1979) studied bat echolocation behaviour among bat species that typically forage in open, moderately open, and densely cluttered habitats and defined three different pursuit strategies which they termed the basic, the obstacle-monitoring, and the high resolution clutter rejecting pursuit strategies, respectively. In all three kinds of habitat the approach and terminal phases of the bat hunting behaviour were found to be characterized by broadband signals that increased in repetition rate, and decreased in inter-signal interval, as the bat neared the prey item. However, the typical signals of the search phase differed among habitats. From bats typical of foraging in open, moderately open, and cluttered habitats, the search phase signals were long narrow band, long broad band combined with a short narrow band, and broad band, respectively. Aldridge and Rautenbach (1987) also found differences in the structure of echolocation sequences among habitat types. They demonstrated that less maneuverable, open habitat, bats tended to have sequences composed of narrow band signals of lower frequencies relative to the sequence structure of more maneuverable, closed habitat, species.

In general, open habitat echolocation sequences should tend to be narrow banded and of relatively low frequency, because the lack of clutter permits these bats to utilize a sequence structure that maximizes prey detection at rather large distances. Once a prey item or obstacle has been detected, the bat may adjust its echolocation call structure to increase its ability to localize the object. In contrast, closed habitat echolocation sequences should tend to be broadband and of a relatively high repetition rate. The preponderance of obstacles in a cluttered closed habitat requires that a bat constantly localize obstacles while at the same time searching for prey. Broadband high frequency sequences, while having a decreased effective range due to increased attenuation, provide the maximum resolution of the immediate cluttered environment.

Given 1) the need for research on bat activity and echolocation and 2) the diversity of habitats and biomes available in northwestern Argentina, we were interested in recording echolocation sequences in northwestern Argentina for a short-term, preliminary study. The main purpose of our study was to evaluate the level of bat activity among four different biomes in northwestern Argentina during the early southern spring. A secondary purpose was to investigate whether echolocation sequence structure characteristics were associated with biome type in a manner consistent with the general open habitat vs. closed habitat predictions outlined above. CHILE



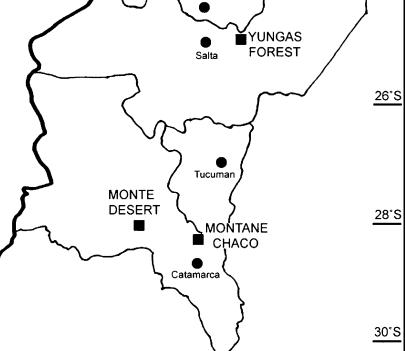


Fig. 1. Map of study area. Sampling sites in each biome are indicated by the square.

MATERIALS AND METHODS

Our study was conducted during August 1997 (early southern spring) in the provinces of Jujuy, Salta, Tucumán and Catamarca (**Fig. 1; Appendix 1**). We determined bat activity by monitoring echolocation sequences using the Anabat system (Titley Electronics, Ballina, Australia; O'Farrell et al., 1999), which is specifically designed to facilitate identification of free-flying bats by producing frequencytime graphs of echolocation sequences. The battery-powered system can be deployed remotely while it records echolocation sequences to audiotapes for later transcription and computer analysis. The detectors were placed ca. 3-4 m high with the microphone of the detector pointed toward the middle of the habitat and directed at an angle of 45° from the ground (sensu Kalcounis et al., 1999). The detector system was connected to a timer with a light sensor that turned the system on at dusk and off at dawn. A voice-activated recorder was used so that the system was recording only when incoming echolocation sequences were detected.

We sampled bat activity in four biomes: Puna, Chaco thornscrub, Monte desert and Yungas forest (Cabrera, 1976; Handford, 1988; see **Appendix 1** for site names and characteristics). We had two sites in the Chaco thornscrub, one was a riparian site in montane Chaco while the other was a site in lowland Chaco forest. We treat these two sites separately in the analysis because they were sufficiently different (high elevation riparian Chaco vs. lowland dry Chaco) even though they represent the same biome. Because of distances between biomes, only one site was sampled on any given night. Where possible, a site was sampled for up to 3 consecutive nights. All biomes were not sampled equally: Puna 3 nights, lowland Chaco 3 nights, Yungas forest 2 nights, Monte desert 3 nights and montane Chaco 1 night.

Due to differing levels of sound attenuation in open versus structured areas, one constraint that may affect the volume of space sampled by detectors is whether detectors are placed in open or structured habitats within a biome (Weller and Zabel, 2002). We dealt with this by simultaneously sampling with one bat detector in open and another bat detector in structured habitat within a biome on each night. We pooled the sequences recorded. Echolocation sequences were analyzed using Anabat5 software (O'Farrell et al., 1999). We counted the number of echolocation sequences per night to obtain an index of bat activity. We defined a sequence as two or more echolocation signals separated by at least a 1-s pause before the next sequence. For each recorded sequence, the following measurements were obtained: maximum and minimum frequencies of signals, modal frequency of signals, mean duration of signals within a sequence, and mean time between signals (repetition rate) of a sequence. Because we did not have reference echolocation sequences of bats in the areas that we were sampling and because of problems inherent in identifying individuals echolocation sequences to a particular species (Barclay, 1999; O'Farrell and Gannon, 1999; Fenton et al., 2001), we did not attempt to identify echolocation sequences to species or any other taxonomic group - we simply sampled bat echolocation activity and signal types.

To describe sequence and signal characteristics among biomes we used univariate parametric statistics (ANOVA). Characteristic variables were tested for assumptions of normality using the Shapiro-Wilk test and all variables were transformed with the square root + 1 transformation.

RESULTS

Over the 12 nights of sampling we recorded 1067 echolocation sequences. We did not record any sequences in the Puna over the 3 sampling nights. We recorded 46.4, 39.9, 9.1, and 4.6 percent of all echolocation sequences in montane Chaco, lowland Chaco, Yungas

forest and Monte desert, respectively. On a per night basis, we recorded 46.4, 13.3, 4.5, and 1.53 percent of all echolocation sequences in montane Chaco, lowland Chaco, forest and Monte desert, respectively. In all biomes except Monte desert the bat detector placed in the open habitat recorded more sequences (**Table 1**).

The three frequency variables were correlated (all correlation coefficients significant at p<0.001), therefore we used only modal frequency of sequences in our ANOVA. Echolocation sequences recorded from the Yungas forest had a relatively high modal frequency compared to sequences recorded in the Monte desert and montane Chaco (ANOVA $F_{3, 1063}$ =14.52, p<0.001; **Fig. 2**). The repetition rate of signals was relatively high in the montane Chaco thornscrub ($F_{3, 1063}$ =11.46, p<0.001; **Fig. 3**). The signals of the longest duration were recorded in the Monte desert ($F_{3, 1063}$ =8.01, p<0.001; **Fig. 4**).

DISCUSSION

Using ground based Anabat detectors, we attempted to record microchiropteran echolocation sequences to assess activity in four biomes in northwestern Argentina during the early southern spring. No bats were recorded in the Puna, while of the remaining sites, the least to the most active were: Monte desert, Yungas forest, lowland Chaco thornscrub and the riparian site in montane Chaco thornscrub. Our results show that the two least active biomes are the least complex, both structurally and floristically (Puna and Monte desert). No records of bats were reported for the Puna in Argentina (Ojeda and Mares, 1989). The lack of structural complexity in the Puna biome would provide little diversity of roosting and foraging sites for bats. Furthermore, limited food supply at high elevations, cold nights, and a limited capacity to regulate body temperature may contribute to the lack of bat activity found in the Puna (McNab, 1983). The high level of activity recorded in the open montane Chaco thornscrub most likely reflects the atypical nature of our sampling site that was situated near a river.

Table 1

Total number of sequences recorded from open vs. structured habitat within each biome sampled in northwestern Argentina.

	Bat detector placed in open habitat	Bat detector placed in structured habitat
Lowland chaco	242	184
Monte desert	14	35
montane Chaco	482	13
Yungas forest	85	12
Puna	0	0

Our finding that the lowland Chaco thornscrub is more active than Yungas forest sites may seem counterintuitive, but may not be unusual. In terms of bat species richness, regions of the Neotropical rain forest have been described as the richest areas on earth (Findley, 1993), however 80 % of the species found in Argentina occur in the Chaco thornscrub biome (Barquez and Ojeda, 1992). Barquez (1987, from Barquez and Ojeda, 1992) found that of all of the phytogeographic provinces in Argentina, lowland Chaco thornscrub had the greatest number of bat species. Insectivorous mammal species and adaptations towards insectivory are apparent in the Chaco biome. The ecotonal region between deciduous lowland forest and Chaco thornscrub has the richest assemblage of insectivorous (vespertilionid and molossid) bat species (Ojeda and Mares, 1989). It is likely that the richness and abundance of the insect

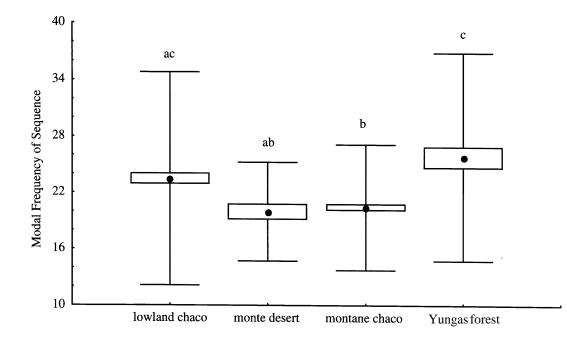


Fig. 2. Box and whisker plots (mean-standard error-standard deviation) for modal frequency of echolocation sequences. Biomes with the same letter are not significantly different from one another. Actual data are presented however the statistics were performed on the transformed data.

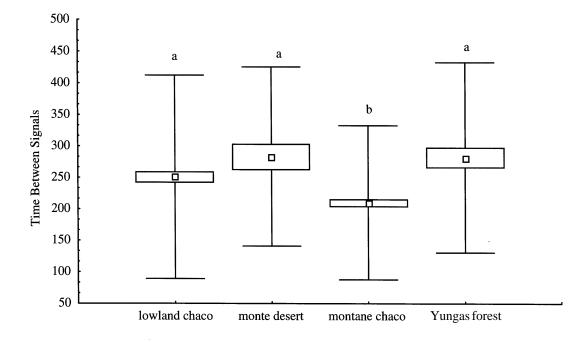


Fig. 3. Box and whisker plots (mean-standard error-standard deviation) for time between signals. Biomes with the same letter are not significantly different from one another. Actual data are presented however the statistics were performed on the transformed data.

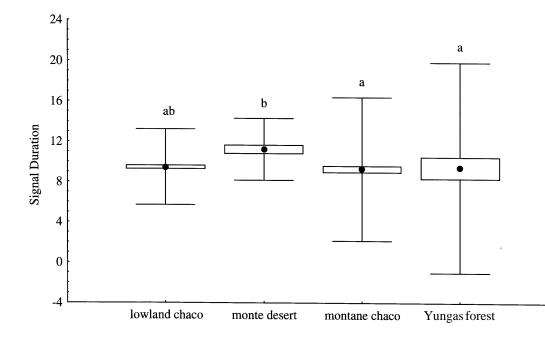


Fig. 4. Box and whisker plots (mean-standard error-standard deviation) for signal duration. Biomes with the same letter are not significantly different from one another. Actual data are presented however the statistics were performed on the transformed data.

resource base in the Chaco biome (Bucher, 1982) is the basis for the activity patterns we observed.

Alternatively sampling biases may exist in our study that would favor Anabat detection of activity in the lowland Chaco thornscrub relative to the Yungas forest. One bias concerns the fact that, for reasons of signal attenuation, the effective sampling area of the Anabat detectors is greater in the lowland Chaco thornscrub than it is in the Yungas forest. Another bias stems from the fact that the data collected by our ground based detection equipment more closely represents the true activity in the lowland Chaco thornscrub than it does the true activity in the structured Yungas forest. Acoustic sampling through the canopy of structured forest has revealed considerable amounts of activity within and above the canopy (e.g., Kalcounis et al., 1999). A final bias relates to the among biome differences in species composition. Phyllostomidae (whispering bats) emit echolocation signals that are lower in intensity than those of most other bats (Dusenbury, 1992). Barquez et al. (1993) describe 11 Phyllostomid species as being distributed in the regions of our field work. All 11 of these species may be found in Yungas forest habitat while only 5 of them may be found in the lowland Chaco scrub. Thus, the greater proportion of the whispering bats found in the Yungas forest, relative to the lowland Chaco thornscrub, may underestimate the degree of activity recorded for the Yungas forest (e.g., Johnston et al., 2002).

Biomes are heterogeneous with respect to their degree of clutter. Echolocation signals are context specific, and bats alter their sequence patterns to suit the immediate demands (Simmons et al., 1979). From our preliminary analyses, echolocation sequences differed among the 4 biomes in which sequences were recorded. Signal structure varied according to biome complexity in the Yungas forest, lowland Chaco and Monte desert. The Yungas forest signals were of higher modal frequency relative to the signals recorded from the less complex biome types. Monte desert signals were long with a relatively low modal frequency. Sequences recorded from the lowland Chaco thornscrub were characterized by intermediate signals. Sequences recorded from montane Chaco thornscrub had a relatively high repetition rate of signals and were characterized by low frequency signals with modal frequency comparable to that found in the Monte desert. These results suggest that within each biome bat echolocation signals respond to the amount of clutter so as to minimize the effects of clutter on echolocation capabilities in a predictable manner. For example, modal frequency differed among these biomes, and it did so in a predictive manner. The lowest frequencies were typical of the least complex biomes (Monte desert), sequences of intermediate frequencies were found in the lowland Chaco thornscrub, while the highest modal frequencies were characteristic of the complex Yungas forest.

Surprisingly, sequences recorded from riparian montane Chaco had a relatively high repetition rate of signals and were characterized by relatively low frequency signals. This paradox is likely explained through the atypical nature of the montane Chaco sampling site and the high levels of feeding over the river. The high level of feeding at this site would decrease our sampling of true search phase signals as prey items would be detected almost continually. Thus, in relation to the other three biomes in which bats were recorded, sequences from the montane Chaco would tend to possess a lower proportion of search phase signals and a greater proportion of the more high repetition rate and lower frequency signals of the terminal end of the approach phase (Kalko and Schnitzler, 1998).

In terms of bat foraging activity, this study illustrates that the less complex biomes tend to be less active. Our finding of the lowland Chaco thornscrub to be the most active natural biome agrees with the finding of Barquez (1987) that it is also the most species rich. However, the magnitude of the difference in activity found between the lowland Chaco thornscrub and Yungas forest biomes may have been increased by several biases that favor the recording of echolocation sequences in the lowland Chaco thornscrub relative to the Yungas forest. Differences in echolocation sequence structure were found among the biomes in a predictive manner; signal structure varied according to biome complexity in the Yungas forest, lowland Chaco thornscrub and Monte desert.

Our preliminary, short-term, small-scale study that took place in the early southern spring, demonstrates high levels of bat activity in northwestern Argentina and suggests that this region offers opportunities for further study. Relatively close proximity of different biomes in this region and habitat heterogeneity within biomes allows for study of community-level and intraspecific variation in bat activity, habitat use, and echolocation call structure. We suggest that further study in the Chaco thornscrub would be particularly interesting with respect to the diverse community of insectivorous bat species and resource partitioning.

ACKNOWLEDGEMENTS

This study was conducted in association with the Neotropical Biodiversity field course offered by the Zoology Department, University of Western Ontario Ontario and the Biodiversity Research Group-CONICET, Mendoza, Argentina. Partial funding for the course was provided by the Zoology Department and the Fundación Antorchas. We thank the students of the course for assistance in the field. Diana Moreno assisted with the analysis of the echolocation sequences. We are grateful to Keith Hobson, Canadian Wildlife Service, for loan of the three Anabat detector systems. Three anonymous reviewers made thoughtful comments to an earlier draft of this manuscript.

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APPENDIX 1 Location of Study Sites

Puna. Saladillo, Jujuy province, near junction of RN 40 and RP 52. 3700m. 24° 34' 0S 66° 13' 0W

Lowland Chaco. Near La Union, eastern Salta province, n.w. of Rivadavia. 173m. 23° 52' 60S 63° 10' 0W

Rainforest. Parque Nacional El Rey, Salta province. 912m. 24° 40' 0S 64° 35' 60W Monte desert. Rio Amanao, west of Andalgalá, Catamarca province. 1059 m. 27° 33' 0S 66° 31' 0W

Montane Chaco. near La Viña, Catamarca province. 464m. 28° 1' 60S 65° 34' 0W