

## Activity of aerial insectivorous bats in two rice fields in the northwestern Llanos of Venezuela

YARA AZOFEIFA<sup>1,2</sup>, SERGIO ESTRADA-VILLEGAS<sup>3,4,5</sup>, JESÚS MAVÁREZ<sup>6,7</sup>, and JAFET M. NASSAR<sup>1,8</sup>

<sup>1</sup>Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Aptdo. 20632, Carretera Panamericana km 11, Caracas 1020-A, Miranda, Venezuela

<sup>2</sup>Escuela de Ciencias Biológicas, Universidad Nacional, Heredia, Aptdo. 86-3000, Costa Rica

<sup>3</sup>Department of Biological Sciences, Marquette University, P.O. Box 1881, Milwaukee, Wisconsin, 53201-1881, USA

<sup>4</sup>Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama

<sup>5</sup>Programa para la Conservación de los Murciélagos de Colombia PCMCo. Carrera 10 # 65 - 63 - Oficina 201-3, Bogotá, Colombia

<sup>6</sup>Laboratoire d'Ecologie Alpine, UMR UGA-USMB-CNRS 5553 Université Grenoble Alpes, CS 40700 38058 Grenoble, cedex 9, France

<sup>7</sup>Departamento de Ciencias Biológicas y Ambientales, Universidad Jorge Tadeo Lozano, Carrera 4 #22-61, Bogotá, Colombia

<sup>8</sup>Corresponding author: E-mail: jafet.nassar@gmail.com

Even though agricultural lands provide abundant food to aerial insectivorous bats (AIB), our understanding of how spatio-temporal factors affect their foraging behavior in these habitats is limited and mostly restricted to temperate regions. In this study, we examined species richness, composition and patterns of activity of AIB in rice fields in the northwestern Llanos of Venezuela. Between 2013 and 2014, we conducted acoustic monitoring of AIB in two rice fields with contrasting forest cover, throughout three phases of the life cycle of this crop (vegetative, reproductive, and ripening), during the dry and rainy season. Out of 108 h recorded, we processed 12,630 files and identified 15 species and 10 sonotypes of AIB from families Molossidae, Mormoopidae, Vespertilionidae, Emballonuridae and Noctilionidae. *Molossus molossus* and *Myotis nigricans* showed the highest levels of feeding and general activity across species. The index of general activity (IGA) of AIB was higher above rice fields with more surrounding forest cover, during the dry season and throughout the entire life cycle of the plant. Relative feeding activity (RFA) did not change with respect to forest cover, season or crop phase, but a significant effect of the interaction of these factors was observed on this variable. The response of IGA and RFA to forest cover, season or crop phase was different between *M. molossus* and *M. nigricans* and among functional groups. Our results indicate that rice fields in the Venezuelan Llanos can be active feeding grounds for open space and edge-habitat foraging species of insect-feeding bats. Forest patches can promote AIB activity by favoring foraging of 'edge' species above rice fields. Higher general activity of most AIB species during the dry season suggests that rice fields are used more intensively when insect populations decrease in semi-deciduous forest patches around them. Overall, our results suggest that availability of abundant feeding areas to AIB, provided by the rice fields, together with presence of artificial and natural roosts to these bats, could ensure year-round permanence of a rich ensemble of AIB in the rice field-forest landscape in the northwestern Llanos of Venezuela. Some of these species could be the subject of field experiments to test their value in the control of rice's insect pest populations.

**Key words:** echolocation, rice, Venezuelan Llanos, insectivorous bats, *Molossus molossus*, *Myotis nigricans*, Neotropics

### INTRODUCTION

Aerial insectivorous bats (AIB) are one of the most important guilds of wildlife in agricultural landscapes, not only because they are resilient to habitat fragmentation, but because they can provide valuable ecosystem services to farmers (Kunz *et al.*, 2011; Williams-Guillén *et al.*, 2016). Aerial insectivorous bats can frequent a variety of crops across agricultural landscapes, where they seek

insects that depend on plants to complete their life cycle, and can help farmers by reducing the costs of food production (Wanger *et al.*, 2014; Maine and Boyles, 2015; Puig-Montserrat *et al.*, 2015). Crops such as rice, corn, cotton, sugar cane, coffee, and cocoa can function as habitats for AIB, and produce insect aggregations that bats can exploit (Leelapaibul *et al.*, 2005; McCracken *et al.*, 2012; Noer *et al.*, 2012; Heer *et al.*, 2015; Ongole *et al.*, 2018).

Different species of AIB show high activity levels across different agricultural landscapes and are able to track bursts of insect resources, even if these landscapes have moderate or high levels of forest conversion (Lentini *et al.*, 2012; Kalda *et al.*, 2014; Heer *et al.*, 2015; Crisol-Martínez *et al.*, 2016). Agricultural landscapes should not represent a perceptual challenge for these bats, and in fact may provide an opportunity to increase the rate of encounter with feeding patches (Schnitzler and Kalko, 2001; Jones and Rydell, 2003; Schnitzler *et al.*, 2003; Denzinger and Schnitzler, 2013). Indeed, there is now evidence that several Neotropical species of AIB (*Myotis nigricans*, *Eptesicus furi-nalis*, *Pteronotus paraguayensis*, *P. quadridens*, *P. davyi*, *Mormoops megalophylla*, and *M. blain-villei*) are consumers of pest insects in agricultural landscapes in the Brazilian Cerrado, Venezuela and Puerto Rico (Aguiar and Antonini, 2008; Molinari *et al.*, 2012; Rolfe *et al.*, 2014).

Even though there are several species of AIB that consume pest insects in agricultural landscapes, our understanding of the extrinsic and intrinsic factors that affect their activity levels and feeding behavior in these landscapes is quite limited (Maas *et al.*, 2015). For instance, it has been shown that gradients of forest cover in temperate agricultural landscapes could affect prey availability and therefore influence bat activity levels (Wickramasinghe *et al.*, 2003; Heim *et al.*, 2015; Rodríguez-San Pedro *et al.*, 2018). However, reduction in prey abundance caused by low forest cover, coupled with episodic supply of food resources in agricultural crops, could affect the insect pest suppression services that bats provide (Davidai *et al.*, 2015). Our understanding of the factors that affect feeding behavior of AIB is even more limited in tropical environments, and the few studies from temperate areas do not necessarily reflect the conditions of Neotropical agricultural landscapes. Overall, the ecology of AIB in Neotropical agricultural landscapes remains largely unknown, particularly in relation to spatio-temporal variation in species richness, functional composition and feeding activity, as well as the effect of forest cover, crop type, growth phase, and agricultural management practices on the activity of AIB.

A pilot study by Azofeifa and Nassar (2013) showed that rice fields in Venezuela could provide ample and constant resources for AIB. These authors reported that species from families Molossidae, Vespertilionidae, Emballonuridae, Mormoopidae and Noctilionidae flew frequently above

rice fields in the northwestern Llanos of Venezuela, suggesting that rice fields could attract a diverse ensemble of AIB. Based on their findings, we hypothesized that the mixed habitat composed of forests remnants and rice fields can function as feeding areas for AIB. Insects associated with rice fields, including pest species, could indeed represent an important food source for AIB commonly present in both disturbed and forested habitats. For instance, local farms usually produce rice during the rainy and dry season, thereby making possible a year-round presence of abundant insects used by AIB as food. Constant provision of insects could be particularly important to AIB in the Venezuelan Llanos, because many forest remnants in the region are seasonally semi-deciduous or totally deciduous from November to March (Gentry, 1995; Fajardo *et al.*, 2005; Andressen and López, 2015; Aymard, 2015). Loss of foliar biomass reduces the abundance of phytophagous insects (Richards and Winsor, 2007; Silva *et al.*, 2011), which in turn reduces food availability to AIB foraging inside the forest (Klingbeil and Willig, 2010; Barros *et al.*, 2014). Therefore, insects associated with rice fields, either harmful to the crop or not, could represent a key food source for AIB during the dry season in the region.

The foraging patterns of AIB associated with rice fields should also be influenced by the life cycle of this crop, as different species of herbivorous insects reach their peaks of abundance during different developmental phases of the rice plants (Meneses *et al.*, 2001). For example, larvae of some moths from families Crambidae (e.g., *Rupela albinella*, *Diatraea saccharalis*) and Noctuidae (e.g., *Spodoptera frugiperda*), and adults of some leafhoppers from families Delphacidae (e.g., *Tagosodes orizicolus*) and Cicadellidae (e.g., *Graminella* sp., *Hortensia* sp.) are more abundant in rice fields during the dry season, when they feed on tender leaves of young plants during the crop's vegetative phase and, occasionally, when they attack the panicles during the ripening phase (Cherry *et al.*, 1986; Vivas and Clavijo, 2000; Meneses *et al.*, 2001; Vivas *et al.*, 2009). Additionally, several species from families Curculionidae (e.g., *Lissorhoptus* sp.) and Pentatomidae (e.g., *Oebalus* sp.) show peaks of abundance during the rainy season, feeding preferentially during the vegetative and ripening phases of the plants, respectively (Páez, 2004; Vivas *et al.*, 2010). All these insects have a size range (3–35 mm) easily detectable by AIB (Schnitzler and Kalko, 2001; Jones and Rydell, 2003; Schnitzler *et al.*, 2003; Denzinger and Schnitzler, 2013).

The main goal of our study was to examine species richness, taxonomic composition, and levels of general and feeding activity of AIB in rice fields in the northwestern Llanos of Venezuela. We wanted to determine whether the amount of surrounding forest cover, climatic season, and stage of the rice's life cycle (crop phase) affect AIB's general and feeding activity levels. We predicted higher species richness of AIB and higher levels of general and feeding activity in rice fields with larger neighboring forest cover, because forest patches might provide a higher diversity and density of roosting sites for AIB. We also predicted that general and feeding activity of AIB above rice fields should be higher during the dry season, because in that period trees in the dry forest patches mixed with these crops shed their leaves, and rice plants become the most important source of food for many phytophagous insects. Finally, we expected to find higher general and feeding activity of AIB during the vegetative and ripening phases of rice, when rates of attack by pest insects reach their peak (Meneses *et al.*, 2001; Páez, 2004; Vivas *et al.*, 2010, 2011). We discuss our results in the context of the potential role of AIB as control agents of pest insects that affect rice production in the Venezuelan Llanos.

## MATERIALS AND METHODS

### *Study Sites*

The study region is located in an alluvial plain composed by a mixture of semi-deciduous forests, gallery forests and wooded savannas in the northwestern Llanos of Venezuela (Chacón *et al.*, 2015). Large tracts of the original ecosystems have been replaced by sizeable areas of corn, rice, sugarcane, cotton, sorghum, and sunflower crops, which are surrounded by scattered forest fragments (Aymard, 2015). During our study period (November 2013–October 2014), the average monthly temperature was 27.3°C (1.64 SD) and total annual rainfall was 1,262 mm.

We monitored bat activity through acoustic sampling in three rice plots located at two farms: (1) one plot of 8.3 ha at Parcela #551, Colonia Agrícola Turén, Portuguesa State (UTM 0486554 E, 1018625 N; 140 m a.s.l.; hereafter 'Turén') and (2) two rice plots, of 20 and 28 ha, respectively, at Agropecuaria Durigua, Portuguesa State (UTM 0487325 E, 1054836 N; 180 m a.s.l.; hereafter 'Acarigua'). A distance of 45.6 km separates the two farms, while the two rice plots in Acarigua are adjacent to one another. Given the proximity of the two farms, we assumed that temperature and rainfall would be very similar between localities.

### *Landscape Analysis*

Landscape analysis of the study locations was carried out using Landsat images (PATH 005/ROW 054 and PATH

005/ROW 053) from March 2014. In order to examine the possible effect of local landscape features on the activity of AIB, we determined the major habitat types (i.e., crop, forest, urban, and water bodies) present in a circle with a radius of five km (area 78.5 km<sup>2</sup>) superimposed to the center of each study location. For each habitat type, we measured absolute area covered, percentage in relation to the area of the circle, number of patches, and average minimum distance between patches of the same habitat type (i.e., Euclidean distance of the nearest neighbor). We performed the landscape analyses with the software Fragstats 4.2.1 (McGarigal *et al.*, 2012) and ArcGIS 10.0 (ESRI, 2011).

### *Acoustic Sampling of Bat Calls*

We recorded bat calls with two Echo Meter 3+ bat detectors (Wildlife Acoustics, Inc., 2013) programmed as follows: real time, sampling rate of 256 kHz, sound detection interval between 12 kHz and 128 kHz, intensity above 18 dB SPL (sound pressure level), and recording time of each sound sequence 1.5–3 s (Wildlife Acoustics, 2013). We placed the detectors vertically and tied to two m posts, allowing us to record at a maximum reach of 30 m and an optimum direction of  $\pm 30^\circ$  (J. King, Customer Service Manager, Wildlife Acoustics, Inc. USA, personal communication). We recorded bat activity between 18:30 and 21:00 h, the time interval at which AIB display the highest levels of activity (Anthony and Kunz, 1977; Chase *et al.*, 1991; Esbérard and Bergallo, 2010; Estrada-Villegas *et al.*, 2010). Finally, we processed all sound files (WAV format) with the SonoBat software (v. 2.9.7, DNDesign, Arcata, CA) and obtained sonograms at a sampling rate of 44 kHz (44,000 samples per second, de facto standard), using the FFT algorithm of 882 points.

We recorded bat calls simultaneously at two sites per night per locality, and at two different sites the following night in the same locality. Recording sites were separated by 150 m from one another, and were more than 100 m away from the edge of the rice field. We performed recordings at the same four sites during each of the three crop phases (vegetative, reproductive and ripening) of each climatic season (dry and rainy). Overall, for each locality, we obtained 24 activity records (4 sites  $\times$  3 crop phases  $\times$  2 seasons), of which three (one from Turén and two from Acarigua) were not used in the analyses due to their low call to noise ratio. The exploratory analysis of the data indicated that at each locality the activity of AIB showed low correlations between sampling sites (Turén: all comparisons with Pearson's  $r = 0.2\text{--}0.94$ ,  $n = 6$ ,  $P = 0.02\text{--}0.71$ ; Acarigua: all comparisons with  $r = 0.50\text{--}0.71$ ,  $n = 6$ ,  $P = 0.14\text{--}0.45$ ), therefore we assumed statistical independence of bat activity among sites for each locality.

### *Identification of AIB Species*

We identified sonograms up to species-level following Gardner (2007), or to 'sonotype' by comparing manually the spectral and temporal parameters of calls in search phase with a database of Neotropical bat calls (Kalko *et al.*, 1998; Ibáñez *et al.*, 1999, 2002; Ochoa *et al.*, 2000; Siemers *et al.*, 2001; Rydell *et al.*, 2002; Guillén-Servent and Ibáñez, 2007; Jung *et al.*, 2007, 2014; MacSwiney *et al.*, 2008; Surlykke and Kalko, 2008). All bats were assigned to a functional group according to definitions in Schnitzler and Kalko (2001) and Siemers *et al.* (2001).

### General Activity, Feeding Activity and Relative Feeding Activity of AIB

Due to variation in duration of sampling time between localities (Turén = 53 h, Acarigua = 55 h), we used Miller's (2001) index of general activity (IGA) modified to include sampling effort. This index is calculated as the sum of time blocks (1 block = 1 min) in which a bat is detected divided by total sampling time. It provides a standardized method to compare the relative contribution of activity time of all bats (ensemble), functional groups or particular species recorded between localities, seasons, or crop phases (Miller, 2001; Skalak *et al.*, 2012). Additionally, we quantified the number of capture attempts ('feeding buzzes') and standardized them as an index of feeding activity (IFA), calculated as the sum of time blocks in which a feeding buzz was detected divided by total sampling time. Furthermore, we estimated the index of relative feeding activity (RFA) as the sum of one min time blocks containing feeding buzzes divided by the sum of one min time blocks containing bat passes (Wickramasinghe *et al.*, 2003). The three indexes range between 0 (minimal activity) and 1 (maximal activity).

### Statistical Analysis

Given that IGA and IFA were correlated (see Results), we only evaluated the effects of locality (Turén, Acarigua), season (dry, rainy), and crop phase (vegetative, reproductive and ripening) on IGA and RFA. After verification of multivariate homogeneity of group dispersions with PERMDISP2 (Clarke and Gorley, 2015), the main effects of the three factors and their interactions on IGA and RFA were evaluated using three-way PerMANOVA tests (PRIMER v7). Overall, we conducted two PerMANOVAs to examine how IGA and RFA responded to all three explanatory variables for all species (ensemble), then four PerMANOVAs to examine how IGA and RFA responded to the three explanatory variables for the two most active functional groups, Aerial Insectivores in Uncluttered Space (AI-US) and Aerial Insectivores in Background-Cluttered Space (AI-BCS), and four PerMANOVAs to analyze the same explanatory variables for the most active species in the dataset, *Molossus molossus* and *Myotis nigricans*. All PerMANOVA tests were based on 'Bray-Curtis' distances, and *P*-values were determined using 999 permutations. When significant differences between crop phases were detected ( $P < 0.05$ ), we conducted multiple comparison tests among the three levels of this variable using a non-parametric statistic analogous to *t*-tests for multivariate analyses (pseudo-*t*) with Monte-Carlo permutations due to the low number of samples (Anderson *et al.*, 2008). Finally, we used

box plots to visualize differences among treatments of each factor for each dependent variable.

## RESULTS

### Composition and Configuration of the Landscape

In both farms, crops dominate the landscape (Table 1): 47.29 km<sup>2</sup> (60.23%) in Turén, 41.94 km<sup>2</sup> (53.42%) in Acarigua. The forest habitat represents a much larger fraction of the area studied in Acarigua, 16.82 km<sup>2</sup> (21.43%), than in Turén, 3.45 km<sup>2</sup> (4.39%); which is evidenced by more forest patches in Acarigua than in Turén (443 versus 205). As a consequence, the average minimum distance between forest patches is smaller in Acarigua (73.87 m ± 65.44) than in Turén (109.09 m ± 97.85). The opposite pattern was observed for urban habitats, which represent a larger fraction in Turén, 11.58 km<sup>2</sup> (14.74%), than in Acarigua, 7.43 km<sup>2</sup> (9.46%). Finally, bodies of water occupied similar small areas in both farms: 2.73 km<sup>2</sup> (3.48%) in Turén and 2.47 km<sup>2</sup> (3.15%) in Acarigua.

### Species Identification of AIB and Classification into Functional Groups

In total, we analyzed 23 activity records (4,751 sound files) from Turén and 22 activity records (7,898 sound files) from Acarigua (Table 2). Overall, 7,666 files (2,476 in Turén, 5,190 in Acarigua) and 4,983 files (2,275 in Turén, 2,708 in Acarigua) were obtained during the dry and rainy seasons, respectively. With regards to crop phase and season, we obtained 1.7 less sounds files in Turén compared to Acarigua across the vegetative, reproductive and ripening phases, and between dry and wet seasons combined (Table 2). The identification of species and sonotypes of AIB was possible using six temporal and spectral parameters: pulse interval, pulse duration, maximum power frequency,

TABLE 1. Spatial composition and configuration of landscapes at Turén and Acarigua. CA — class area, PL — percentage of landscape, NP — number of patches, and ED-NN — Euclidean distance from nearest neighbor (m)

Coverage	Turén				Acarigua			
	Composition		NP	Configuration	Composition		NP	Configuration
	CA (km <sup>2</sup> )	PL (%)			CA (km <sup>2</sup> )	PL (%)		
Forest	3.45	4.39	205	109.09 (97.85)	16.82	21.43	443	73.87 (65.44)
Crops	47.29	60.23	617	49.30 (12.84)	41.94	53.42	623	52.69 (16.11)
Urban	11.58	14.74	1,622	59.06 (29.28)	7.43	9.46	1,305	63.95 (36.51)
Water bodies	2.73	3.48	132	67.65 (76.71)	2.47	3.15	160	106.30 (186.94)
Clouds	1.18	1.50	311	86.69 (106.38)	0.84	1.06	198	116.08 (153.67)
Fire smokes	12.29	15.65	1,693	57.37 (31.61)	9.01	11.48	925	68.82 (65.29)

TABLE 2. Recording minutes (number of processed files) of AIB echolocation calls at each recording site (1–4) during two seasons (dry and rainy) and three crop phases (Vegetative, Reproductive, and Ripening; approximate age of rice plants in days) at Turén and Acarigua

Crop phase (plant age)	<i>n</i>	Recording sites				Total
		1	2	3	4	
Turén						
Dry season						
Vegetative	9	116 (123)	179 (282)	21(122)	116 (201)	432 (728)
Reproductive	66	168 (176)	172 (368)	168 (316)	172 (237)	680 (1,097)
Ripening	86	149 (160)	159 (348)	156 (143)	LQ	464 (651)
Rainy season						
Vegetative	33	49 (78)	56 (128)	150 (192)	148 (486)	403 (884)
Reproductive	76	150 (281)	150 (353)	149 (107)	150 (116)	599 (857)
Ripening	111	151 (72)	152 (88)	154 (106)	150 (268)	607 (534)
Total		783 (890)	868 (1,567)	798 (986)	736 (1,308)	3,185 (4,751)
Acarigua						
Dry season						
Vegetative	17	151 (653)	150 (718)	LQ	LQ	301 (1,371)
Reproductive	81	149 (1,211)	151 (406)	151 (317)	153(396)	604 (2,330)
Ripening	118	150 (353)	150 (266)	151 (438)	150 (432)	601 (1,489)
Rainy season						
Vegetative	25	150 (271)	151 (352)	151 (288)	149 (262)	601 (1,173)
Reproductive	65	150 (103)	151 (117)	150 (244)	164 (188)	615 (652)
Ripening	102	147 (216)	151 (171)	160 (225)	150 (271)	608 (883)
Total		897 (2,807)	904 (2,030)	763 (1,512)	766 (1,549)	3,330 (7,898)

LQ: low quality (low call to noise ratio)

start frequency, end frequency, and band-width. We identified 15 species of AIB from families Molossidae, Vespertilionidae, Emballonuridae, Mormoopidae, and Noctilionidae. In addition, we identified 10 sonotypes that belong to Molossidae and Emballonuridae (Supplementary Table S1). We assigned the 15 species and 10 sonotypes to three functional groups: a) Aerial Insectivores in Uncluttered Space (AI-US): *M. molossus*, *Molossus* sp1, *Molossus* sp2, *Molossidae* sp3 (probably *Nyctinomops* sp.), *Eumops* sp1 (probably *E. glaucinus*), *Eumops* sp2 (probably *E. auripendulus*), *Cynomops* sp1, *Cynomops* sp2, *Peropteryx macrotis*, and Emballonuridae sp1; b) Aerial Insectivores in Background-Cluttered Space (AI-BCS): *Myotis nigricans*, *Molossops temminckii*, *Saccopteryx bilineata*, *S. leptura*, *Rhynchonycteris naso*, Emballonuridae sp2, Emballonuridae sp3, *Eptesicus furinalis*, *Lasiurus ega*, *Mormoops megalophylla*, *Pteronotus personatus*, *P. davyi*, and *P. gymnotus*; and c) Background-cluttered space trawling insectivores/piscivores (AI-BCS-T): *Noctilio albiventris* and *N. leporinus*.

#### General Activity, Feeding Activity, and Relative Feeding Activity of AIB

The index of feeding activity (IFA) was tightly correlated with both the index of general activity

(IGA) (Pearson's  $r = 0.77$ ,  $N = 22$ ,  $P < 0.001$  in Acarigua;  $r = 0.79$ ,  $N = 23$ ,  $P < 0.001$  in Turén) and relative feeding activity (RFA) (Pearson's  $r = 0.95$ ,  $N = 22$ ,  $P < 0.001$  in Acarigua;  $r = 0.78$ ,  $N = 23$ ,  $P < 0.001$  in Turén). Contrary to these results, IGA and RFA showed either no correlation in Turén ( $r = 0.28$ ,  $N = 23$ ,  $P = 0.19$ ) or a moderate correlation in Acarigua ( $r = 0.57$ ,  $N = 22$ ,  $P < 0.05$ ). Therefore, we restricted our analyses to the effects of locality, season and crop phase on IGA and RFA.

IGA was significantly higher in Acarigua than in Turén ( $IGA_{Acarigua} = 0.72 \pm 0.15$ ,  $IGA_{Turén} = 0.60 \pm 0.19$ ;  $F_{1, 33} = 12.34$ ,  $P < 0.01$  — Fig. 1A), higher during the dry season ( $IGA_{Dry} = 0.71 \pm 0.18$ ,  $IGA_{Rainy} = 0.62 \pm 0.18$ ;  $F_{1, 33} = 5.99$ ,  $P < 0.05$  — Fig. 1B), and higher during the vegetative phase of the crop's cycle ( $IGA_{Veg} = 0.78 \pm 0.17$ ;  $IGA_{Rep} = 0.65 \pm 0.17$ ;  $IGA_{Rip} = 0.56 \pm 0.17$ ;  $F_{2, 33} = 9.33$ ,  $P < 0.01$ ;  $IGA_{Veg}$  versus  $IGA_{Rep}$ ;  $t = 2.40$ ,  $P < 0.05$ ;  $IGA_{Veg}$  versus  $IGA_{Rip}$ ;  $t = 4.69$ ,  $P < 0.01$  — Fig. 1C). No significant interactions between locality, season, and crop phase were detected for IGA for the whole ensemble of species.

For RFA, we found significant interactions between locality, season and crop phase ( $F_{2, 33} = 4.14$ ,  $P < 0.05$ ). At Turén, during the dry season, RFA was significantly lower in the reproductive phase ( $0.33 \pm 0.04$ ) compared to the vegetative phase

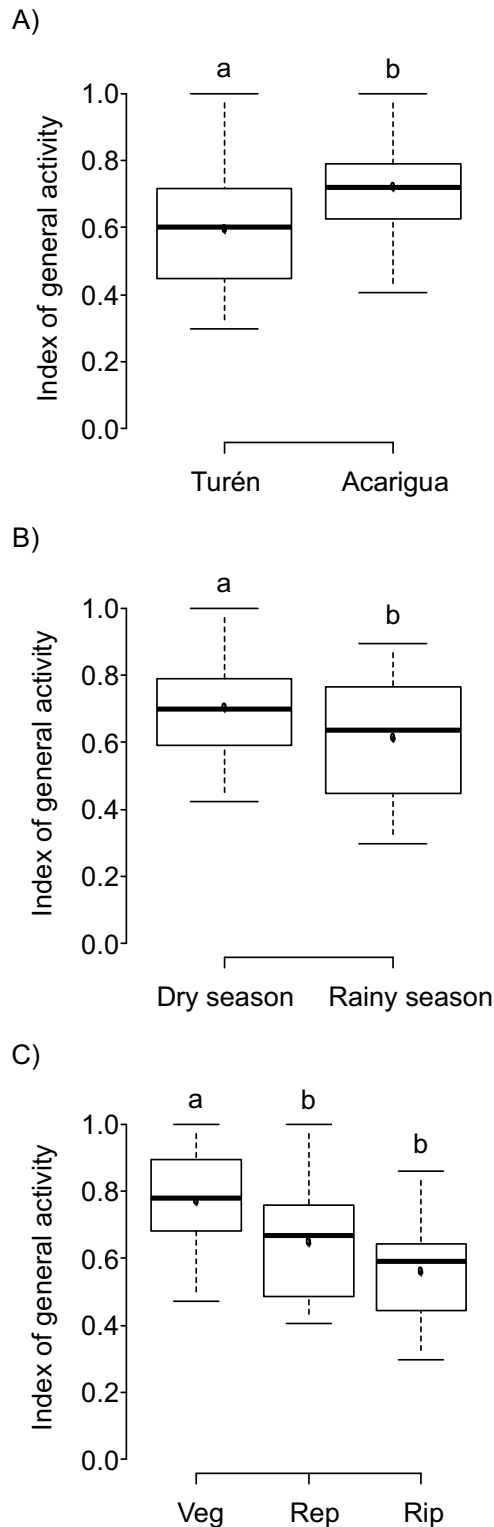


FIG. 1. Index of general activity (IGA) of AIB based on total calls recorded by (A) locality, (B) season, and (C) phases of the rice's life cycle (Veg: vegetative, Rep: reproductive, and Rip: ripening) in the northwestern Venezuelan Llanos. Box-plots show minimum and maximum values, average value (black dot), and inter-quartile range (top line: 75% of data, intermediate line: median, bottom line: 25% of data). Significant differences between levels of a variable are indicated with different lowercase letters (Student's *t*-test,  $P < 0.05$ )

( $0.57 \pm 0.16$ ;  $t = 3.02$ ,  $P < 0.05$ ) and ripening phase ( $0.52 \pm 0.08$ ;  $t = 4.34$ ,  $P < 0.01$ ). During the rainy season, RFA values did not differ significantly across the three crop phases ( $RFA_{Veg} = 0.51 \pm 0.22$ ;  $RFA_{Rep} = 0.50 \pm 0.17$ ;  $RFA_{Rip} = 0.51 \pm 0.08$  — Supplementary Table S1). At Acarigua, during the dry season, RFA reached the highest average values during the vegetative ( $0.59 \pm 0.07$ ) and reproductive phases ( $0.54 \pm 0.30$ ), and then markedly dropped during the ripening phase ( $0.27 \pm 0.06$ ). Only the vegetative and ripening phases were significantly different ( $t = 4.57$ ,  $P < 0.01$ ). During the rainy season, RFA showed similar values during the three phases of the crop cycle ( $RFA_{Veg} = 0.51 \pm 0.07$ ;  $RFA_{Rep} = 0.40 \pm 0.05$ ;  $RFA_{Rip} = 0.48 \pm 0.05$  — Supplementary Table S1).

#### *General Activity and Relative Feeding Activity of Aerial Insectivores in Uncluttered Space (AI-US)*

Interactions between season and crop phase produced significant effects on IGA ( $F_{2, 33} = 9.93$ ,  $P < 0.01$ ). During the dry season, IGA values did not differ significantly across the three crop phases ( $IGA_{Veg} = 0.49 \pm 0.25$ ;  $IGA_{Rep} = 0.47 \pm 0.18$ ;  $IGA_{Rip} = 0.44 \pm 0.09$  — Fig. 2A). During the rainy season, IGA reached the highest average values during the vegetative and ripening phases ( $IGA_{Veg} = 0.48 \pm 0.19$ ;  $IGA_{Rep} = 0.16 \pm 0.04$ ;  $IGA_{Rip} = 0.22 \pm 0.03$  — Fig. 2B). In this season, the three pairs of comparisons were significant ( $IGA_{Veg}$  versus  $IGA_{Rep}$ ,  $t = 6.98$ ,  $P < 0.01$ ;  $IGA_{Veg}$  versus  $IGA_{Rip}$ ,  $t = 6.27$ ,  $P < 0.01$ ;  $IGA_{Rep}$  versus  $IGA_{Rip}$ ,  $t = 3.56$ ,  $P < 0.01$ ).

With regards to RFA, we found significant interactions between locality, season and crop phase ( $F_{2, 33} = 3.76$ ,  $P < 0.05$ ). At Turén, during the dry season, RFA reached the highest average values during the vegetative and ripening phases ( $RFA_{Veg} = 0.50 \pm 0.20$ ;  $RFA_{Rep} = 0.28 \pm 0.05$ ;  $RFA_{Rip} = 0.51 \pm 0.09$ ). Only RFA estimates during the reproductive and ripening phases were significantly different ( $t = 4.24$ ,  $P < 0.01$ ). During the rainy season, RFA values did not differ significantly across the three crop phases ( $RFA_{Veg} = 0.36 \pm 0.20$ ;  $RFA_{Rep} = 0.42 \pm 0.15$ ;  $RFA_{Rip} = 0.50 \pm 0.17$  — Supplementary Table S1). At Acarigua, during the dry season, RFA reached the highest average values during the vegetative ( $0.48 \pm 0.23$ ) and reproductive phases ( $0.57 \pm 0.20$ ), and then markedly dropped during the ripening phase ( $0.28 \pm 0.09$ ). Only the reproductive and ripening phases were significantly different ( $t = 2.81$ ,  $P < 0.05$ ). During the rainy season, RFA showed similar values during the three phases of

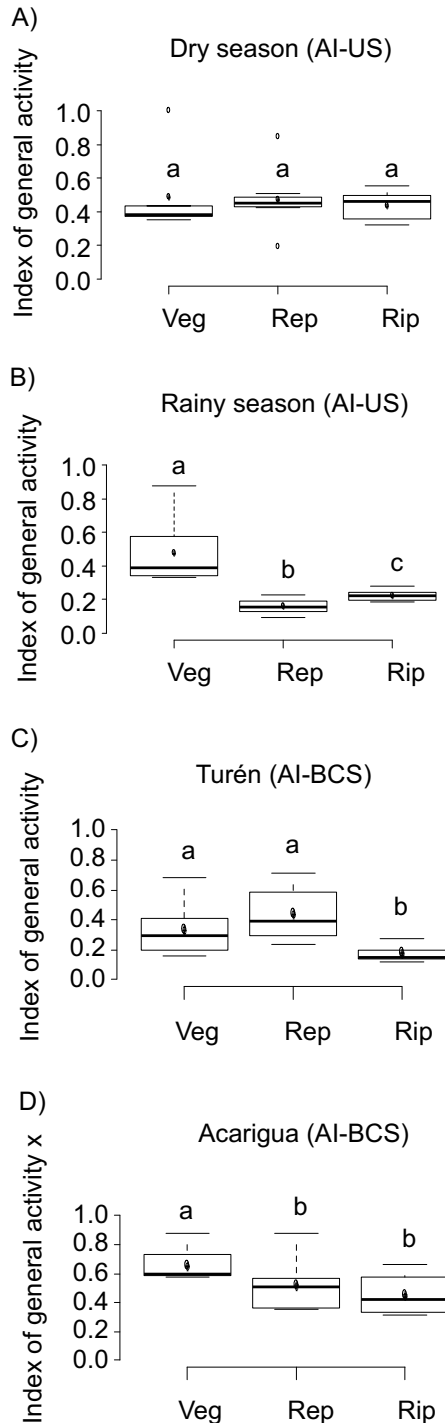


FIG. 2. Index of general activity (IGA) of AIB in Uncluttered Space (AI-US) and AIB in Background-Cluttered Space (AI-BCS) in the northwestern Venezuelan Llanos. IGA of AI-US as a function of total calls recorded for each phase of the rice's life cycle phases (Veg: vegetative, Rep: reproductive, and Rip: ripening) at each season (A–B). IGA of AI-BCS as a function of total calls recorded for each phase of rice's life cycle at each locality (C–D). Box-plots show minimum and maximum values, average value (black dot), and inter-quartile range (top line: 75% of data, intermediate line: median, bottom line: 25% of data). Significant differences between levels of a variable are indicated with different lowercase letters (Student's  $t$ -test,  $P < 0.05$ )

the crop cycle ( $RFA_{Veg} = 0.52 \pm 0.18$ ;  $RFA_{Rep} = 0.32 \pm 0.21$ ;  $RFA_{Rip} = 0.49 \pm 0.13$  — Supplementary Table S1).

#### General Activity and Relative Feeding Activity of Aerial Insectivores in Background-Cluttered Space (AI-BCS)

Interactions between locality and crop phase produced significant effects on IGA ( $F_{2, 33} = 5.09$ ,  $P < 0.01$ ). At Turén, IGA was significantly lower in the ripening phase ( $0.17 \pm 0.06$ ) compared to the vegetative phase ( $0.33 \pm 0.17$ ;  $t = 2.38$ ,  $P < 0.05$ ) and reproductive phase ( $0.44 \pm 0.18$ ;  $t = 4.05$ ,  $P < 0.01$  — Fig. 2C). At Acarigua, IGA was significantly higher in the vegetative phase ( $0.66 \pm 0.12$ ) compared to the reproductive phase ( $0.51 \pm 0.17$ ;  $t = 2.31$ ,  $P < 0.05$ ) and ripening phase ( $0.45 \pm 0.14$ ;  $t = 3.30$ ,  $P < 0.05$  — Fig. 2D).

For RFA, we found significant interactions between locality, season and crop phase ( $F_{2, 33} = 3.10$ ,  $P < 0.05$ ). At Turén, during the dry season, RFA values did not differ significantly across the three crop phases ( $RFA_{Veg} = 0.46 \pm 0.20$ ;  $RFA_{Rep} = 0.31 \pm 0.07$ ;  $RFA_{Rip} = 0.50 \pm 0.17$ ). During the rainy season, RFA reached the highest value during the vegetative phase, and then decreased in the following crop phases ( $RFA_{Veg} = 0.62 \pm 0.09$ ;  $RFA_{Rep} = 0.44 \pm 0.26$ ;  $RFA_{Rip} = 0.46 \pm 0.05$  — Supplementary Table S1). Only the vegetative and ripening phases were significantly different ( $t = 2.96$ ,  $P < 0.05$ ). At Acarigua, during the dry season, RFA reached the highest average values during the vegetative, and then gradually decreased in the following phases of the crop ( $RFA_{Veg} = 0.57 \pm 0.03$ ;  $RFA_{Rep} = 0.39 \pm 0.38$ ;  $RFA_{Rip} = 0.16 \pm 0.03$ ). Only the vegetative and ripening phases were significantly different ( $t = 8.14$ ,  $P < 0.01$ ). During the rainy season, RFA showed similar values during the three phases of the crop cycle ( $RFA_{Veg} = 0.48 \pm 0.02$ ;  $RFA_{Rep} = 0.41 \pm 0.07$ ;  $RFA_{Rip} = 0.42 \pm 0.10$  — Supplementary Table S1).

#### General Activity and Relative Feeding Activity of *M. molossus*

The index of general activity (IGA) for *M. molossus* varied in response to the combined effects of locality, season and crop phase ( $F_{2, 33} = 8.32$ ,  $P < 0.01$ ). At Turén, during the dry season, IGA presented similar average values in the three cultivation phases ( $IGA_{Veg} = 0.33 \pm 0.22$ ;  $IGA_{Rep} = 0.26 \pm 0.09$ ;  $IGA_{Rip} = 0.34 \pm 0.13$ ). During the rainy season, IGA was significantly higher in the vegetative phase

( $IGA_{Veg} = 0.40 \pm 0.15$ ) than in the reproductive ( $IGA_{Rep} = 0.13 \pm 0.05$ ;  $t = 3.84$ ,  $P < 0.01$ ) and ripening phase ( $IGA_{Rip} = 0.13 \pm 0.03$ ;  $t = 4.30$ ,  $P < 0.01$  — Supplementary Table S1). At Acarigua, during the dry season, IGA reached similar average values in the three cultivation phases ( $IGA_{Veg} = 0.30 \pm 0.12$ ;  $IGA_{Rep} = 0.30 \pm 0.06$ ),  $IGA_{Rip} = 0.24 \pm 0.03$ ). During the rainy season, average IGA in the reproductive phase ( $IGA_{Rep} = 0.02 \pm 0.01$ ) was significantly lower than during the vegetative phase ( $IGA_{Veg} = 0.19 \pm 0.01$ ;  $t = 5.95$ ,  $P < 0.01$ ) and ripening phase ( $IGA_{Rip} = 0.18 \pm 0.03$ ;  $t = 5.63$ ,  $P < 0.01$  — Supplementary Table S1).

Relative feeding activity (RFA) of *M. molossus* varied in response to the significant interaction between locality and crop phase ( $F_{2, 32} = 3.23$ ,  $P < 0.05$ ). At Turén, RFA values were higher during the vegetative ( $RFA_{Veg} = 0.44 \pm 0.18$ ) and ripening ( $RFA_{Rip} = 0.52 \pm 0.12$ ) phases than in the reproductive phase ( $RFA_{Rep} = 0.33 \pm 0.13$  — Fig. 3A). Nevertheless, a significant difference was observed only between the reproductive and ripening phases ( $t = 2.85$ ,  $P < 0.05$ ). At Acarigua, RFA reached similar average values in the three cultivation phases ( $RFA_{Veg} = 0.60 \pm 0.16$ ;  $RFA_{Rep} = 0.57 \pm 0.32$ ;  $RFA_{Rip} = 0.49 \pm 0.17$  — Fig. 3B).

#### General Activity and Relative Feeding Activity of *M. nigricans*

The index of general activity (IGA) of *M. nigricans* only varied in response to crop phase ( $F_{2, 33} = 8.54$ ,  $P < 0.01$ ), with the ripening phase ( $IGA_{Rip} = 0.10 \pm 0.05$ ) showing significantly lower values than the vegetative phase ( $IGA_{Veg} = 0.24 \pm 0.17$ ;  $t = 3.21$ ,  $P < 0.01$ ) and reproductive phase ( $IGA_{Rep} = 0.29 \pm 0.19$ ;  $t = 4.23$ ,  $P < 0.01$  — Fig. 3C). Relative feeding activity (RFA) varied in this species as a function of the interaction between locality and season ( $F_{1, 33} = 5.55$ ,  $P < 0.05$ ). At both sites, the highest RFA values were observed in the rainy season ( $RFA_{Turén-Dry} = 0.44 \pm 0.25$ ;  $RFA_{Turén-Rainy} = 0.51 \pm 0.22$ ;  $RFA_{Acarigua-Dry} = 0.22 \pm 0.17$ ;  $RFA_{Acarigua-Rainy} = 0.46 \pm 0.09$  — Supplementary Table S1). However, those seasonal differences in RFA were significant only at Acarigua ( $t = 4.33$ ,  $P < 0.01$ ).

#### DISCUSSION

We used acoustic monitoring techniques to document for the first time in the Neotropics the richness, composition, and activity of aerial

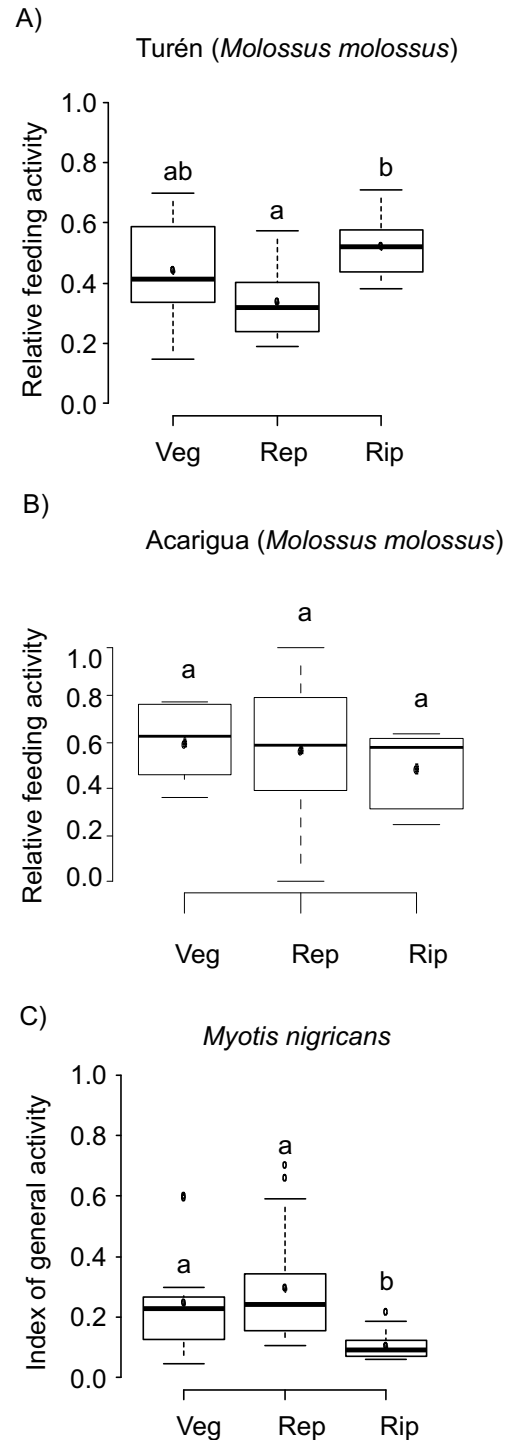


FIG. 3. Index of relative feeding activity (RFA) of *M. molossus* and index of general activity (IGA) of *M. nigricans* in the northwestern Venezuelan Llanos. RFA of *M. molossus* as a function of total calls recorded for each phase of rice's life cycle at each locality (A and B). IGA of *M. nigricans* as a function of total calls recorded for each phase of rice's life cycle (C). Box-plots show minimum and maximum values, average value (black dot), and inter-quartile range (top line: 75% of data, intermediate line: median, bottom line: 25% of data). Significant differences between levels of a variable are indicated with different lowercase letters (Student's  $t$ -test,  $P < 0.05$ )



insectivorous bats (AIB) associated with rice fields. We identified 25 different species/sonotypes, and determined the general activity, feeding activity, and relative feeding activity for the ensemble of AIB, two functional groups, and two of the most frequently detected species of AIB in the cultivated areas. Our results support the prediction that forest patches favor AIB activity, although background-cluttered space bats (AI-BCS) seem to be more affected by forest reduction than uncluttered space bats (AI-US). Rice fields were used more intensively by most bat species during the dry season, which may reflect a reduction of food resources in neighboring forest patches during this period. Bat activity remained relatively high during the three phases of rice cultivation throughout the year, suggesting high concentration of high-quality feeding patches as a result of irrigation of agricultural lands. Overall, these findings represent an opportunity to promote bat conservation in agricultural habitats in the Neotropics and to test management practices of the most common and active AIB species (*M. molossus* and *M. nigricans*) to help control insect pests of crops in the region.

#### *Species Composition of AIB in Rice Fields*

We found a rich ensemble of AIB across the rice fields we studied in the northwestern Llanos of Venezuela. The species of AIB we detected have also been recorded in other agricultural settings in the Neotropics. For example, several molossid bats, which were the most active and showed high number of feeding buzzes in our study, have also been found foraging in cocoa (*M. molossus*, *M. temminckii*, *Cynomops* sp. and *Eumops* sp.), coffee (*M. molossus*, *Eumops* sp. and *Cynomops* sp.), pineapple, and banana plantations (*M. molossus* and *Eumops* sp.) in Brazil, Mexico, and Costa Rica (Faria and Baumgarten, 2007; Williams-Guillén and Perfecto, 2011; Alpizar, 2014; Heer *et al.*, 2015). Among Vespertilionidae, three species detected in our study (*M. nigricans*, *Eptesicus furinalis* and *Lasiurus ega*) were also observed foraging in the aforementioned crops (Williams-Guillén and Perfecto, 2011; Alpizar, 2014; Heer *et al.*, 2015). Several species of Emballonuridae detected in our rice fields have also been recorded in cocoa (*Peropteryx macrotis*, *Saccopteryx bilineata* and *Rhynchonycteris naso*), coffee (*P. macrotis* and *S. bilineata*), pineapple, and banana plantations (*P. macrotis*, *S. bilineata* and *S. leptura* — Faria and Baumgarten, 2007; Williams-Guillén and Perfecto,

2011; Alpizar, 2014; Heer *et al.*, 2015). Several species of Mormoopidae have also been reported in coffee (*Mormoops megalophylla* and *Pteronotus davyi*), banana, and pineapple plantations (*Pteronotus gymnonotus* and *P. davyi* — Williams-Guillén and Perfecto, 2011; Alpizar, 2014). Our study is the first to report presence of the mormoopid *P. personatus* and two species of noctilionids, *Noctilio albiventris* and *N. leporinus*, in agricultural fields in the Neotropics. Overall, our results are indicative that AIB are able to tolerate the spatio-temporal dynamics that characterize certain crop-forest mosaics in the Llanos ecosystem of northern South America. These mixed habitats may function as year-round reliable sources of food for a significant proportion of AIB, but in particular, for those species resilient to anthropogenic modifications of natural habitats (Mendenhall *et al.*, 2014, 2016).

*Molossus molossus* and *M. nigricans* showed the highest levels of general activity and relative feeding activity of all AIB identified. This is not surprising, given that both species are broadly distributed in Venezuela and are common in open vegetation, savannas with solitary trees or tree patches, forest gaps, and areas close to water bodies (Linares, 1998). Additionally, both species are gregarious, highly resilient to anthropogenic activity, and form large colonies (several thousand individuals) with quite flexible roosting habits (e.g., caves, tree holes, buildings, bridges and house roofs; Linares, 1998). For example, we identified roosting sites shared by *M. molossus* and *M. nigricans* close to the rice fields. We observed them roosting underneath houses with thin roofs and under thatched roofs made of palm leaves and supported by wood poles (locally known as ‘caney’). We estimated (visual observations) more than 100 bats roosting underneath these roofs. The caney was also used by *E. furinalis* and *L. ega*. Based on our observations, we believe that *M. molossus* and *M. nigricans* are opportunistic species that live near areas cultivated with rice, where they are supplied with a safe and abundant source of food. Part of this food supply could include rice pests. According to Páez (2004) and Vivas *et al.* (2010), pest insects associated with rice fields in Venezuela belong to four insect orders (Coleoptera, Lepidoptera, Orthoptera and Hemiptera) and 11 families in them. These four orders of insects, and several of the families in them (Curculionidae, Chrysomelidae, and Pentatomidae), have been reported as part of the recorded diets for *M. nigricans* (Aguiar and Antonini, 2008) and *M. molossus* (Muñoz-Romo, 1996; Ramírez-Chaves *et al.*, 2008).

Other bat species were actively feeding above the rice fields, but probably also depend on the forest as a source of food and roof or as flight route. For example, we observed *S. bilineata* and *S. leptura* in a hollow trunk of a jabillo (*Hura crepitans*) and *R. naso* on low branches of trees (unidentified) in patches of forest near the rice fields. In addition, Azofeifa and Nassar (2013) reported catches of other bat species (*N. albiventris*, *P. personatus*, *P. davyi*, *P. gymnonotus*, *M. megalophylla*, *M. temminckii* and *M. nigricans*) in the ecotone located in front of the same rice fields considered in this studio. Mormoopids usually roost during the day in deep and dark galleries of caves and abandoned mines (Linares, 1998; Gardner, 2007), but interestingly, these structures have not been described in the studied region (Galán and Herrera, 2017).

#### *Species Richness, Bat Activity in Rice Fields, and Farm Forest Cover*

Based on the marked differences between the two localities in terms of forest cover, we expected to detect differences in species composition and richness, as it has been shown in other agricultural landscapes (Frey-Ehrenbold *et al.*, 2013; Heim *et al.*, 2015; Crisol-Martínez *et al.*, 2016); however, we did not observe such differences. Species inventories of AIB at Turén and Acarigua were very similar in terms of species composition and richness. The two localities belong to the same ecosystem type and are separated by ca. 46 km of relatively flat landscapes, which do not represent a spatial barrier to these bats. AIB are capable of flying between forest patches, across monocultures and open areas, as it has been shown in other agricultural landscapes with mixed habitats in the Neotropics (e.g., Estrada *et al.*, 1993, 2004; Estrada and Coates-Estrada, 2001, 2002; Faria and Baumgarten, 2007; Medina *et al.*, 2007; Heer *et al.*, 2015). On the other hand, the two study sites differed with respect to bat activity; AIB at Acarigua, which has larger forest patches close to the rice fields, had higher levels of general activity than AIB at Turén. On this regard, our results concur with our initial prediction and with other studies, indicating that larger forest cover contributes to higher levels of bat activity in the crop-forest mosaic (Wolcott and Vulinec, 2012; Frey-Ehrenbold *et al.*, 2013; Kalda *et al.*, 2014; Heim *et al.*, 2015; Crisol-Martínez *et al.*, 2016). This difference in bat activity could be explained by differences in population size of several of the species

present at both localities, with larger populations associated to higher availability of roosting sites in the forest remnants.

The amount of forest cover has a differential effect between functional groups (Frey-Ehrenbold *et al.*, 2013; Fuentes-Montemayor *et al.*, 2013, 2017). We found that species of aerial insectivores in background-cluttered spaces (AI-BCS) were more sensitive to changes in forest cover than species of aerial insectivores in uncluttered species (AI-US). For example, forest-sensitive AI-BCS species had an average IGA of 1.15–2.6 times higher throughout the rice's life cycle in the more forested Acarigua compared to Turén. On the contrary, general activity of relatively forest-insensitive AI-US species was not affected by locality but by the climatic season and crop phase. In general, these results could be indicative that forest cover in these forest-crop mixed habitats has a differential effect on general activity of these two functional groups. However, we recognize that bat's relative feeding activity responds to a greater number of factors (locality, season and crop phase) in the two functional groups, which suggests that we require additional information on activity and diet of bats and prey availability at the landscape level to fully understand the processes behind the patterns observed.

The relatively low activity levels of several species and sonotypes susceptible to forest degradation at Turén (e.g., *S. leptura*, *S. bilineata*, *R. naso*, Emballonuridae sp2, *M. megalophylla*, *P. personatus*, *P. davyi*, and *P. gymnonotus*) probably contributed to the observed differences in bat activity between sites. Even though *S. bilineata* does not seem to be affected by forest fragmentation on land bridge systems, or in other types of mixed-habitat landscapes with pastures (Estrada-Villegas *et al.*, 2010; Bader *et al.*, 2015), the presence of crop fields in our localities could have a negative effect on the activity of this species.

*Molossus molossus* and *M. nigricans*, two species tolerant to habitat fragmentation, had the highest levels of activity at both study sites. *Molossus molossus* had high levels of general activity at both localities, mainly during the dry season and throughout the life cycle of the crop, but the highest relative feeding activity was observed at Acarigua during most part of the crop's life cycle. On the other hand, general activity of *M. nigricans* did not vary between localities, but responded to the rice's life cycle. The highest relative feeding activity of *M. nigricans* was observed at Turén on both seasons. It is possible that *M. molossus* and

*M. nigricans* behave more opportunistically than species more dependent on forested habitats. *Molossus molossus* is a fast flier and can move considerable distances through open spaces at low energy cost (Voigt and Holderied, 2012; McCracken *et al.*, 2016). *Myotis nigricans* seems to forage in open spaces as much as it forages in background clutter spaces, despite its intermediate levels of mobility (Siemers *et al.*, 2001; Bader *et al.*, 2015). So, by reducing bandwidth and increasing call duration, *M. nigricans* can increase prey detectability and capture efficiency in open spaces (Siemers *et al.*, 2001). Thus, we propose that this vespertilionid has a plastic foraging strategy that allows it to hunt in intervened open spaces and also in areas with space cluttered background (Siemers *et al.*, 2001). It is necessary to study the foraging behavior of AIB across the agricultural landscape to understand under what circumstances species like *M. molossus* and *M. nigricans* display high activity levels and how this may impact pest consumption and crop protection.

#### *Activity of AIB through Seasons*

In agreement with our predictions, general activity of AIB in the rice fields was affected by seasonal conditions and the highest levels of activity occurred during the dry period. Rice fields are attractive food sources for phytophagous insects during the dry season, most likely because the deciduous trees of the surrounding forest patches shed their leaves, reducing their foliage cover, and abundance of phytophagous insects inside the forest declines. This boost of phytophagous insects in the rice fields attracts predators. Under this scenario, AIB should concentrate their general and feeding activity in the rice fields. As a consequence, it is possible that whatever the impact of the AIB is on pest insect populations, it should be greater during the dry season. However, the seasonal factor might be influenced by the relative importance of the forest cover around the crop. For example, high tree density could still have a positive effect on levels of hunting activity of AIB during the dry season in addition to presence of rice fields (Davidai *et al.*, 2015; Heim *et al.*, 2015). In our case, Turén, with relatively low forest cover, showed lower relative feeding activity than Acarigua during most of the dry season. Moreover, we detected lower activity of several species of the AI-BCS (*S. bilineata*, *R. naso*, *E. furi-nalis*, *P. personatus*, and *P. gymnonotus*) at Turén with respect to Acarigua. These species could play

a significant role as predators of rice pests at Turén during the rainy season, but a more detailed study on the seasonal behavior of this functional group would be necessary to confirm this insight. In contrast, *M. molossus* and *M. nigricans* maintained high activity levels throughout the dry season, although the most important increase in feeding activity for *M. nigricans* occurred during the rainy season. In sum, AIB, and particularly *M. molossus* and *M. nigricans*, could exert a higher pressure on insects in rice fields during the dry season.

#### *Activity of AIB through Phases of the Rice's Life Cycle*

The role of AIB as potential biological controllers of pest insects in rice fields should be directly associated with those stages of the life cycle at which pest insects are more abundant or when plants are more vulnerable to insect attacks. To identify those stages, we sampled general activity and feeding activity of AIB during the three phases of rice development across seasons. As predicted, our results indicated that activity of AIB in the rice fields increased significantly during the vegetative and ripening phases, when tender leaves and panicles are more vulnerable to insect attacks, and when crop yield is more susceptible to herbivory (Meneses *et al.*, 2001; Páez, 2004; Vivas *et al.*, 2010, 2011). Puig-Montserrat *et al.* (2015) also reported high activity of AIB consuming insects in rice fields in Spain during those two phases of the crop's life cycle. But contrary to their results, we also detected high activity, and even an increase of relative feeding activity, during the reproductive phase. Feeding activity of AIB in relation to the rice's life cycle was also influenced by locality and season. Relative feeding activity was comparatively higher at Acarigua than Turén, mainly during the vegetative and reproductive phases in the dry season. However, at both localities, feeding activity of bats remained relatively high during the vegetative and ripening phases during the rainy season. This confirms the importance of AIB as potential predators of pest insects in rice fields during two continuous crops within the same year.

In conclusion, we present evidence indicating that rice fields in the northwestern Llanos of Venezuela host a species-rich ensemble of AIB, and that this ensemble of bats shows high general and feeding activity in cultivated areas. We also showed that forest cover seems to promote general and feeding activity of AIB in the rice fields. In particular,

*M. molossus* and *M. nigricans* showed the highest levels of general and feeding activity among the AIB recorded. Consequently, these two species would be our primary candidates to conduct field experiments to evaluate their role as bio-controllers of pest insect populations in rice fields in the Venezuelan Llanos. Both species share several attributes that could facilitate such management plans: (1) high abundance and broad distribution in the Llanos region, (2) gregarious habits, (3) high tolerance to human activity, (4) use of artificial roosts, and (5) diets include several orders and families of insects also reported as containing pest species of rice in Venezuela. Installing artificial bat roosts adapted to the climatic conditions of the region seems like a promising strategy to boost bat activity in rice fields, and increase predation on pest insect populations. Bat boxes worked well in Spain according to Puig-Montserrat *et al.* (2015), but in the high temperatures of the Llanos region in northern South America other designs could offer better results. In any case, before a pest control program can be tested or implemented in agricultural areas in the Venezuelan Llanos, we must first examine the feeding habits of *M. molossus* and *M. nigricans* to determine to what extent these species include pest insects in their diets. Thanks to the versatile techniques currently available to infer diet of insect-feeding bats using molecular markers (Bohmann *et al.*, 2011; Pompanon *et al.*, 2012; Salinas-Ramos *et al.*, 2015), this is now a feasible task and it is the focus of a forthcoming investigation in our laboratory.

#### SUPPLEMENTARY INFORMATION

Contents: Supplementary Table S1. Index of general activity (IGA) and index of relative feeding activity (RFA) of species and sonotypes of AIB recorded at Acarigua and Turén, northwestern Venezuelan Llanos, during dry and rainy seasons and phases of the rice's life cycle. Supplementary Information is available exclusively on BioOne.

#### ACKNOWLEDGEMENTS

This study was funded by The Rufford Small Grants Foundation (grant # 12366-1) to the first author and Bat Conservation International to the first author. IDEA WILD provided an ultrasonic detector equipment to the first author. The research staff and students of Laboratorio de Biología de Organismos, Centro de Ecología (IVIC) provided research equipment and logistic support. Special thanks to José Antonio González-Carcacia and Grisel Velázquez for their invaluable help along this study with field assistance and spatial analyses, respectively. We also thank Brendan Pinto for kindly accepting to proofread a former version of this manuscript. Finally, we express our deep gratitude to the owners of the two rice farms where we conducted this study, Daniel Sánchez and José Luis Alvarez.

#### LITERATURE CITED

- AGUIAR, L. M. S., and Y. ANTONINI. 2008. Diet of two sympatric insectivorous bats (Chiroptera: Vespertilionidae) in the Cerrado of Central Brazil. *Revista Brasileira de Zoologia*, 25: 28–31.
- ALPIZAR, P. 2014. Murciélagos insectívoros aéreos en agroecosistemas: el caso piñeras y bananeras en Sarapiquí, Costa Rica. M.Sci. Thesis, Universidad de Costa Rica, San Jose, Costa Rica, 58 pp.
- ANDERSON, M. J., R. N. GORLEY, and R. CLARKE. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth, 214 pp.
- ANDRESEN, R., and J. LOPEZ. 2015. Características climáticas de las tierras llaneras. Pp. 40–62, in *Tierras Llaneras de Venezuela...tierras de buena esperanza* (R. LÓPEZ, J. M. HÉTIER, D. LÓPEZ, R. SCHARGEL, and A. ZINCK, eds.). Universidad de Los Andes, Mérida, Venezuela, 860 pp.
- ANTHONY, E. L. P., and T. H. KUNZ. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58: 775–786.
- AYMARD, G. A. 2015. Bosques de los Llanos de Venezuela: Composición florística, estructura, diversidad y estado actual de conservación. Pp. 241–268, in *Tierras Llaneras de Venezuela...tierras de buena esperanza* (R. LÓPEZ, J. M. HÉTIER, D. LÓPEZ, R. SCHARGEL, and A. ZINCK, eds.). Universidad de Los Andes, Mérida, Venezuela, 860 pp.
- AZOFEIFA, Y., and J. M. NASSAR. 2013. Murciélagos insectívoros aéreos como potenciales controladores de insectos plaga en arrozales de los Llanos Occidentales de Venezuela. *Boletín de la Red Latinoamericana y del Caribe para la Conservación de Murciélagos*, 4: 4–6.
- BADER, E., K. JUNG, E. K. V. KALKO, R. A. PAGE, R. RODRIGUEZ, and T. SATTLER. 2015. Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics. *Biological Conservation*, 186: 97–106.
- BARROS, M. A. S., D. M. A. PESSOA, and A. M. RUI. 2014. Habitat use and seasonal activity of insectivorous bats (Mammalia: Chiroptera) in the grasslands of southern Brazil. *Zoologia*, 31: 153–161.
- BOHMANN, K., A. MONADIEM, C. L. NOER, M. RASMUSSEN, M. R. K. ZEALE, E. CLARE, G. JONES, E. WILLERSLEV, and M. T. P. GILBERT. 2011. Molecular diet analysis of two African free-tailed bats (Molossidae) using high throughput sequencing. *PLoS ONE*, 6: e21441.
- CHACÓN, E., A. R. ULLOA, L. D. LLAMBÍ, D. ACEVEDO, and A. UTRERA. 2015. Paisajes y ecosistemas llaneros: ecología y conservación. Pp. 195–240, in *Tierras Llaneras de Venezuela...tierras de buena esperanza* (R. LÓPEZ, J. M. HÉTIER, D. LÓPEZ, R. SCHARGEL, and A. ZINCK, eds.). Universidad de Los Andes, Mérida, Venezuela, 860 pp.
- CHASE, J., M. Y. SMALL, E. A. WEISS, D. SHARMA, and S. SHARMA. 1991. Crepuscular activity of *Molossus molossus*. *Journal of Mammalogy*, 72: 414–418.
- CHERRY, R. H., D. B. JONES, P. O. DRAWER, and F. W. MEAD. 1986. Leafhoppers (Homoptera: Cicadellidae) and planthoppers (Homoptera: Delphacidae) in southern Florida rice fields. *Florida Entomologist*, 69: 180–184.
- CLARKE, K. R., and R. N. GORLEY. 2015. PRIMER v7: User manual/tutorial. PRIMER-E, Plymouth, 296 pp.
- CRISOL-MARTÍNEZ, E., G. FORD, F. G. HORGAN, P. H. BROWN, and K. R. WORMINGTON. 2016. Ecology and conservation of insectivorous bats in fragmented areas of macadamia

- production in eastern Australia. *Austral Ecology*, 42: 597–610.
- DAVIDAI, N., J. K. WESTBROOK, J.-P. LESSARD, T. G. HALLAM, and G. F. MCCracken. 2015. The importance of natural habitats to Brazilian free-tailed bats in intensive agricultural landscapes in the Winter Garden region of Texas, United States. *Biological Conservation*, 190: 107–114.
- DENZINGER, A., and H.-U. SCHNITZLER. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4: 1–5.
- ESBÉRARD, C. E. L., and H. G. BERGALLO. 2010. Foraging activity of the free-tailed bat *Molossus molossus* (Chiroptera; Molossidae) in southeastern Brazil. *Brazilian Journal of Biology*, 70: 1011–1014.
- ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, C.A.
- ESTRADA, A., and R. COATES-ESTRADA. 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography*, 24: 94–102.
- ESTRADA, A., and R. COATES-ESTRADA. 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biological Conservation*, 103: 237–245.
- ESTRADA, A., R. COATES-ESTRADA, and D. MERITT. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography*, 16: 309–318.
- ESTRADA, A., C. JIMÉNEZ, A. RIVERA, and E. FUENTES. 2004. General bat activity measured with an ultrasound detector in a fragmented tropical landscape in Los Tuxtlas, Mexico. *Animal Biodiversity and Conservation*, 27: 5–13.
- ESTRADA-VILLEGAS, S., C. F. J. MEYER, and E. K. V. KALKO. 2010. Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Biological Conservation*, 143: 597–608.
- FAJARDO, L., V. GONZÁLEZ, J. M. NASSAR, P. LACABANA, C. A. PORTILLO, F. CARRASQUEL, and J. P. RODRÍGUEZ. 2005. Tropical dry forests of Venezuela: characterization and current status. *Biotropica*, 37: 531–546.
- FARIA, D., and J. BAUMGARTEN. 2007. Shade cacao plantations (*Theobroma cacao*) and bat conservation in southern Bahia, Brazil. *Biodiversity and Conservation*, 16: 291–312.
- FREY-EHRENBOLD, A., F. BONTADINA, R. ARLETTAZ, and M. K. OBRIST. 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology*, 50: 252–261.
- FUENTES-MONTEMAYOR, E., D. GOULSON, L. CAVIN, J. M. WALLACE, and K. J. PARK. 2013. Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems and Environment*, 172: 6–15.
- FUENTES-MONTEMAYOR, E., K. WATTS, N. A. MACGREGOR, Z. LOPEZ-GALLEGO, and K. J. PARK. 2017. Species mobility and landscape context determine the importance of local and landscape-level attributes. *Ecological Applications*, 27: 1541–1554.
- GALÁN C., and F. F. HERRERA. 2017. Ríos subterráneos y acuíferos kársticos de Venezuela: inventario, situación y conservación. Pp. 153–171, in *Ríos en Riesgo de Venezuela* (D. RODRÍGUEZ-OLARTE, ed.). Universidad Centroccidental Lisandro Alvarado, Barquisimeto, Venezuela, 236 pp.
- GARDNER, A. (ed.). 2007. *Mammals of South América*. Volume 1. Marsupials, xenarthrans, shrews, and bats. University of Chicago Press, Chicago, 481 pp.
- GENTRY, A. H. 1995. Diversity and floristic composition of neotropical dry forests. Pp. 146–194, in *Seasonally dry tropical forests* (S. H. BULLOCK, H. A. MOONEY, and E. MEDINA, eds.). Cambridge University Press, Cambridge, 468 pp.
- GUILLÉN-SERVENT, A., and C. IBÁÑEZ. 2007. Unusual echolocation behavior in a small molossid bat, *Molossops temminckii*, that forages near background clutter. *Behavioral Ecology and Sociobiology*, 61: 1599–1613.
- HEER, K., M. HELBIG-BONITZ, R. G. FERNANDES, M. A. R. MELLO, and E. K. V. KALKO. 2015. Effects of land use on bat diversity in a complex plantation-forest landscape in north-eastern Brazil. *Journal of Mammalogy*, 96: 720–731.
- HEIM, O., J. T. TREITLER, M. TSCHAPKA, M. KNÖRNSCHILD, and K. JUNG. 2015. The importance of landscape elements for bat activity and species richness in agricultural areas. *PLoS ONE*, 10: e0134443.
- IBÁÑEZ, C., A. GUILLÉN, J. JUSTE, and J. L. PÉREZ-JORDÁ. 1999. Echolocation calls of *Pteronotus davyi* (Chiroptera: Mormoopidae) from Panamá. *Journal of Mammalogy*, 80: 924–928.
- IBÁÑEZ, C., J. JUSTE, R. LÓPEZ-WILCHIS, L. ALBUJA, and A. NÚÑEZ-GARDUÑO. 2002. Echolocation of three species of sac-winged bats (*Balantiopteryx*). *Journal of Mammalogy*, 83: 1049–1057.
- JONES, G., and J. RYDELL. 2003. Attack and defense: interactions between echolocating bats and their insect prey. Pp. 301–345, in *Bat ecology* (T. H. KUNZ and M. B. FENTON, eds.). University of Chicago Press, Chicago, 779 pp.
- JUNG, K., E. K. V. KALKO, and O. VON HELVERSEN. 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *Journal of Zoology* (London), 272: 125–137.
- JUNG, K., J. MOLINARI, and E. K. V. KALKO. 2014. Driving factors for the evolution of species-specific echolocation call design in new world free-tailed bats (Molossidae). *PLoS ONE*, 9: e85279.
- KALDA, O., R. KALDA, and J. LIIRA. 2014. Multi-scale ecology of insectivorous bats in agricultural landscapes. *Agriculture, Ecosystems and Environment*, 199: 105–113.
- KALKO, E. K. V., H.-U. SCHNITZLER, I. KAIPF, and A. D. GRINNELL. 1998. Echolocation and foraging behavior of the lesser bulldog bat, *Noctilio albiventris*: preadaptations for piscivory? *Behavioral Ecology and Sociobiology*, 42: 305–319.
- KLINGBEIL, B. T., and M. R. WILLIG. 2010. Seasonal differences in population-, ensemble- and community-level responses of bats to landscape structure in Amazonia. *Oikos*, 119: 1654–1664.
- KUNZ, T. H., E. BRAUN DE TORREZ, D. BAUER, T. LOBOVA, and T. H. FLEMING. 2011. Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, 1223: 1–38.
- LEELAPAIBUL, W., S. BUMRUNGSRI, and A. PATTANAWIBOON. 2005. Diet of wrinkled-lipped free tailed bat (*Tadarida plicata* Buchanan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica*, 7: 111–119.
- LENTINI, P. E., P. GIBBONS, J. FISCHER, B. LAW, J. HANSPACH, and T. G. MARTIN. 2012. Bats in a farming landscape benefit from linear remnants and unimproved pastures. *PLoS ONE*, 7: e48201.

- LINARES, O. 1998. Mamíferos de Venezuela. Sociedad Conservacionista Audubon de Venezuela, Caracas, Venezuela, 691 pp.
- MAAS, B., D. S. KARP, S. BUMRUNGSI, K. DARRAS, D. GONTHIER, J. C. C. HUANG, C. A. LINDELL, J. J. MAINE, L. MESTRE, N. L. MICHEL, *et al.* 2015. Bird and bat predation services in tropical forests and agroforestry landscapes: ecosystem services provided by tropical birds and bats. *Biological Reviews*, 91: 1081–1101.
- MACSWINEY, M. C., F. M. CLARKE, and P. A. RACEY. 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology*, 45: 1364–1371.
- MAINE, J. J., and J. G. BOYLES. 2015. Bats initiate vital agroecological interactions in corn. *Proceedings of the National Academy of Sciences*, 112: 12438–12443.
- MCCRACKEN, G. F., J. K. WESTBROOK, V. A. BROWN, M. ELDRIDGE, P. FEDERICO, and T. H. KUNZ. 2012. Bats track and exploit changes in insect pest populations. *PLoS ONE*, 7: e43839.
- MCCRACKEN, G. F., K. SAFI, T. H. KUNZ, D. K. N. DECHMANN, S. M. SWARTZ, and M. WIKELSKI. 2016. Airplane tracking documents the fastest flight speeds recorded for bats. *Royal Society Open Science*, 3: 160398.
- MCGARIGAL, K., S. A. CUSHMAN, and E. ENE. 2012. FRAGSTATS v4: spatial pattern analysis Program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at [umass.edu/landeco/research/fragstats](http://umass.edu/landeco/research/fragstats).
- MEDINA, A., C. A. HARVEY, D. SÁNCHEZ, S. VÍLCHEZ, and B. HERNÁNDEZ. 2007. Bat diversity and movement in an agricultural landscape in Matiguás, Nicaragua. *Biotropica*, 39: 120–128.
- MENDENHALL, C. D., D. S. KARP, C. F. J. MEYER, E. A. HADLY, and G. C. DAILY. 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, 509: 213–217.
- MENDENHALL, C. D., A. SHIELDS-ESTRADA, A. J. KRISHNASWAMI, and G. C. DAILY. 2016. Quantifying and sustaining biodiversity in tropical agricultural landscapes. *Proceedings of the National Academy of Sciences of the USA*, 113: 14544–14551.
- MENESES, R., A. GUTIÉRREZ, A. GARCÍA, G. ANTIGUA, J. GÓMEZ, F. CORREA, and L. CALVERT. 2001. Guía para el trabajo de campo en el manejo integrado de plagas del Arroz, 4th edition. Instituto de Investigaciones del Arroz, La Habana, Cuba, 71 pp.
- MILLER, B. W. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica*, 3: 93–105.
- MOLINARI, J., J. M. NASSAR, A. GARCÍA-RAWLINS, and R. J. MÁRQUEZ. 2012. Singularidad biológica e importancia socioeconómica de los murciélagos cavernícolas de la península de Paraguaná, Venezuela, con propuestas para su conservación. *Revista de Ecología Latino Americana*, 17: 1–40.
- MUÑOZ-ROMO, M. 1996. Ecomorfología y dieta en los murciélagos insectívoros de los géneros *Eumops* y *Molossus*. B.Sci. Tesis, Universidad de Los Andes, Mérida, 77 pp.
- NOER, C. L., T. DABELSTEEN, K. BOHMANN, and A. MONADJEM. 2012. Molossid bats in an African agro-ecosystem select sugarcane fields as foraging habitat. *African Zoology*, 47: 1–11.
- OCHOA J., M. J. O'FARRELL, and B. W. MILLER. 2000. Contribution of acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela. *Acta Chiropterologica*, 2: 171–183.
- ONGOLE, S., M. SANKARAN, and K. K. KARANTH. 2018. Responses of aerial insectivorous bats to local and landscape-level features of coffee agroforestry systems in Western Ghats, India. *PLoS ONE*, 13: e0201648.
- PÁEZ, O. 2004. El cultivo de arroz en Venezuela. Serie Manuales de Cultivo INIA, 1: 1–204.
- POMPANON, F., B. E. DEAGLE, W. O. C. SYMONDSON, D. S. BROWN, S. N. JARMAN, and P. TABERLET. 2012. Who is eating what: diet assessment using next generation sequencing. *Molecular Ecology*, 21: 1931–1950.
- PUIG-MONTSERRAT, X., I. TORRE, A. LÓPEZ-BAUCELLS, E. GUERRIERI, M. M. MONTI, R. RÁFOLS-GARCÍA, X. FERRER, D. GISBERT, and C. FLAQUER. 2015. Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. *Mammalian Biology*, 80: 237–245.
- RAMÍREZ-CHAVES, H. E., O. MEJÍA-EGAS, and G. ZAMBRANO-G. 2008. Anotaciones sobre dieta, estado reproductivo, actividad y tamaño de colonia del murciélago mastín común (*Molossus molossus*: Molossidae) en la zona urbana de Popayán, Departamento del Cauca, Colombia. *Chiroptera Neotropical*, 14: 384–390.
- RICHARDS, L. A., and D. M. WINDSOR. 2007. Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *Journal of Tropical Ecology*, 23: 169–176.
- RODRÍGUEZ-SAN PEDRO, A., P. N. CHAPERON, C. A. BELTRÁN, J. L. ALLENDES, F. I. ÁVILA, and A. A. GREZ. 2018. Influence of agricultural management on bat activity and species richness in vineyards of central Chile. *Journal of Mammalogy*, 99: 1495–1502.
- ROLFE, A. K., A. KURTA, and D. L. CLEMANS. 2014. Species-level analysis of diets of two mormoopid bats from Puerto Rico. *Journal of Mammalogy*, 95: 587–596.
- RYDELL, J., H. T. ARITA, M. SANTOS, and J. GRANADOS. 2002. Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. *Journal of Zoology (London)*, 257: 27–36.
- SALINAS-RAMOS, V. B., L. G. HERRERA, V. LEÓN-REGAGNON, A. ARRIZABALAGA-ESCUADERO, and E. L. CLARE. 2015. Dietary overlap and seasonality in three species of mormoopid bats from a tropical dry forest. *Molecular Ecology*, 24: 5296–5307.
- SCHNITZLER, H.-U., and E. K. V. KALKO. 2001. Echolocation by insect-eating bats. *BioScience*, 51: 557–569.
- SCHNITZLER, H.-U., C. F. MOSS, and A. DENZINGER. 2003. From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology and Evolution*, 18: 386–394.
- SIEMERS, B. M., E. K. V. KALKO, and H.-U. SCHNITZLER. 2001. Echolocation behavior and signal plasticity in the Neotropical bat *Myotis nigricans* (Schinz, 1821) (Vespertilionidae): a convergent case with European species of *Pipistrellus*? *Behavioral Ecology and Sociobiology*, 50: 317–328.
- SILVA, N. A. P., M. R. FRIZZAS, and C. M. OLIVEIRA. 2011. Seasonality in insect abundance in the 'Cerrado' of Goiás State, Brazil. *Revista Brasileira de Entomologia*, 55: 79–87.
- SKALAK, S. L., R. E. SHERWIN, and R. M. BRIGHAM. 2012. Sampling period, size and duration influence measures of

- bat species richness from acoustic surveys. *Methods in Ecology and Evolution*, 3: 490–502.
- SURLYKKE, A., and E. K. V. KALKO. 2008. Echolocating bats cry out loud to detect their prey. *PLoS ONE*, 3: e2036.
- VIVAS, L. E., and S. CLAVIJO. 2000. Fluctuación poblacional de *Tagosodes orizicolus* (Muir) 1926 (Homoptera: Delphacidae) en el sistema de riego Río Guárico, Calabozo, estado Guárico, Venezuela. *Boletín de Entomología Venezolana*, 15: 217–227.
- VIVAS, L. E., D. ASTUDILLO, and J. POLEO. 2009. Monitoreo de *Tagosodes orizicolus* M. e incidencia del virus de la hoja blanca 'VHB' en el cultivo del arroz en Calabozo, Estado Guárico, Venezuela. *Agronomía Tropical*, 59: 457–467.
- VIVAS, L. E., A. NOTZ, and D. ASTUDILLO. 2010. Fluctuación poblacional del chinche vaneadora en parcelas de arroz, Calabozo, Estado Guárico. *Agronomía Tropical*, 60: 61–73.
- VIVAS, L. E., D. ASTUDILLO, and C. J. POLEO. 2011. El taladrador (*Diatraea saccharalis* F.) y su manejo en el cultivo de Arroz. *INIA Divulga*, 84: 43–46.
- VOIGT, C. C., and M. W. HOLDERIED. 2012. High maneuvering costs force narrow-winged molossid bats to forage in open space. *Journal of Comparative Physiology*, 182B: 415–424.
- WANGER, T. C., K. DARRAS, S. BUMRUNGSRI, T. TSCHARNTKE, and A. M. KLEIN. 2014. Bat pest control contributes to food security in Thailand. *Biological Conservation*, 171: 220–223.
- WICKRAMASINGHE, L. P., S. HARRIS, G. JONES, and N. VAUGHAN. 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *Journal of Applied Ecology*, 40: 984–993.
- WILDLIFE ACOUSTICS, INC. 2013. Echo meter user manual. Concord, MA, USA, 41 p.
- WILLIAMS-GUILLÉN, K., and I. PERFECTO 2011. Ensemble composition and activity levels of insectivorous bats in response to management intensification in coffee agroforestry systems. *PLoS ONE*, 6: e16502.
- WILLIAMS-GUILLÉN, K., E. OLIMPI, B. MAAS, P. J. TAYLOR, and R. ARLETTAZ. 2016. Bats in the anthropogenic matrix: challenges and opportunities for the conservation of chiroptera and their ecosystem services in agricultural landscapes. Pp. 151–186, *in* *Bats in the Anthropocene: conservation of bats in a changing world* (C. C. VOIGT and T. KINGSTON, eds.). Springer International Publishing AG, Cham, Switzerland, 606 pp.
- WOLCOTT, K. A., and K. VULINEC. 2012. Bat activity at woodland/farmland interfaces in Central Delaware. *Northeastern Naturalist*, 19: 87–98.

Received 14 November 2017, accepted 10 March 2019

Associate Editor: Wiesław Bogdanowicz