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

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ABSTRACT

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 seasons. Out of 108 h recorded, we processed 12,630 files and identified 15 species and 10 sonotypes of AIB from the 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 RFA. 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 especially 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 rice fields. Overall, our results suggest that the 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.

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

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 provide habitats that are used by 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 speed 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 furinalis*, *Pteronotus paraguayensis*, *P. quadridens*, *P. davyi*, *Mormoops megalophylla*, and *M. blainvillei*) are consumers of pest insects in agricultural landscapes within 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 affect 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 the 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 might 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 provide 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 both in 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). The 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.

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 the 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 in 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 body length between 3 and 35 mm, a size range 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) affected 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 herbivorous 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). Finally, 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, Acarigua, 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

The 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 5 km (area 78.5 km²) superimposed to the center of each study location. For each habitat type, we measured the absolute area covered, the percentage in relation to the area of the circle, the number of patches, and the 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.) 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 2 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, pers. comm.). 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 SonoBat (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 x 3 crop phases x 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 $r = 0.2 - 0.94$, $N = 6$, $P = 0.02 - 0.71$; Acarigua: all comparisons with $r = 0.5 - 0.71$, $N = 6$, $P = 0.14 - 0.45$), 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; Ochoa *et al.*, 2000; Siemers *et al.*, 2001; Ibáñez *et al.*, 2002; Rydell *et al.*, 2002; Guillén-Servent and Ibáñez, 2007; Jung *et al.*, 2007; MacSwiney *et al.*, 2008; Surlykke and Kalko, 2008; Jung *et al.*, 2014). 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 the 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 1 min time blocks containing feeding buzzes divided by the sum of 1 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 these three variables 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 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 ($P \leq 0.05$), we conducted comparisons among the three levels of this variable using Student’s *t*-tests, with *P*-values estimated using 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 variable.

RESULTS

Composition and configuration of the landscape

In both farms, crops dominate the landscape (Table 1): 47.29 km² (60.23 %) in Turén, 41.94 km² (53.42 %) in Acarigua. The forest habitat represents a much larger fraction of the area studied in Acarigua –16.82 km² (21.43 %), than in Turén –3.45 km² (4.39 %), which is evidenced by more forest patches in Acarigua than in Turén (443 vs. 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 km² (14.74 %), than in Acarigua –7.43 km² (9.46 %). Finally, bodies of water occupied similar small areas in both farms: 2.73 km² (3.48 %) in Turén, 2.47 km² (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, start frequency, end frequency, and band-width. We identified fifteen species of AIB from the families Molossidae, Vespertilionidae, Emballonuridae, Mormoopidae and Noctilionidae. In addition, we identified ten sonotypes that belong to Molossidae and Emballonuridae (Table 3). We assigned the fifteen species and ten 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 and *Eumops* sp2 (probably *Eumops glaucinus* and *E. auripendulus*, respectively), *Cynomops* sp1 and *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.*

gymnonotus, 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 $r = 0.77$, $N = 22$, $P < 0.0001$ in Acarigua; $r = 0.79$, $N = 23$, $P < 0.0001$ in Turén) and relative feeding activity (RFA; Pearson's $r = 0.95$, $N = 22$, $P < 0.0001$ 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 ($r = 0.57$, $N = 22$, $P = 0.01$). 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 ($IGA_{(Acarigua)} = 0.72 \pm 0.15$, $IGA_{(Turén)} = 0.60 \pm 0.19$; $F_{1,33} = 12.34$, $P = 0.003$; Fig. 1A), higher during the dry season ($IGA_{(Dry)} = 0.71 \pm 0.18$, $IGA_{(Rainy)} = 0.62 \pm 0.18$; $F_{1,33} = 5.99$, $P = 0.014$; Fig. 1B), and higher during the vegetative phase of the crop's cycle ($IGA_{(Veg)} = 0.78 \pm 0.17$, $IGA_{(Rep)} = 0.65 \pm 0.17$, $IGA_{(Rip)} = 0.56 \pm 0.17$; $F_{2,33} = 9.33$, $P = 0.001$; $IGA_{(Veg)}$ vs. $IGA_{(Rep)}$, $t = 2.40$, $P = 0.025$; $IGA_{(Veg)}$ vs. $IGA_{(Rip)}$, $t = 4.69$, $P = 0.001$; 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 ($F_{2,33} = 4.14$, $P = 0.019$). At Turén, during the dry season, RFA was significantly lower in the reproductive phase (0.33 ± 0.04) compared to the vegetative phase (0.57 ± 0.16 ; $t = 3.02$, $P = 0.014$) and ripening phase (0.52 ± 0.08 ; $t = 4.34$, $P = 0.006$; Table 3). During the rainy season, RFA values did not differ significantly across the three crop phases ($RFA_{(Veg)} = 0.51 \pm 0.22$, $RFA_{(Rep)} = 0.50 \pm 0.17$, $RFA_{(Rip)} = 0.51 \pm 0.08$; Table 3). At Acarigua, during the dry season, RFA reached the highest average values during the vegetative (0.59 ± 0.07) and reproductive phases (0.54 ± 0.30), and then markedly dropped during the ripening phase (0.27 ± 0.06 ; Table 3). Only the vegetative and ripening phases were significantly different ($t = 4.57$, $P = 0.009$). During the rainy season, RFA showed similar values during the three phases of the crop cycle ($RFA_{(Veg)} = 0.51 \pm 0.07$, $RFA_{(Rep)} = 0.40 \pm 0.05$, $RFA_{(Rip)} = 0.48 \pm 0.05$; Table 3).

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 ($F_{2,33} = 9.93$, $P = 0.001$). During the dry season, IGA values did not differ significantly across the three crop phases (IGA_(veg) = 0.49 ± 0.25 , IGA_(Rep) = 0.47 ± 0.18 , IGA_(Rip) = 0.44 ± 0.09 ; Fig. 2A). During the rainy season, IGA reached the highest average values during the vegetative and ripening phases (IGA_(veg) = 0.48 ± 0.19 , IGA_(Rep) = 0.16 ± 0.04 , IGA_(Rip) = 0.22 ± 0.03 ; Fig. 2B). In this season, the three pairs of comparisons were significant (IGA_(veg) vs. IGA_(Rep), $t = 6.98$, $P = 0.001$; IGA_(veg) vs. IGA_(Rip), $t = 6.27$, $P = 0.001$; IGA_(Rep) vs. IGA_(Rip), $t = 3.56$, $P = 0.001$). With regards to RFA, we found significant interactions between locality, season and crop phase ($F_{2,33} = 3.76$, $P = 0.018$). At Turén, during the dry season, RFA reached the highest average values during the vegetative and ripening phases (RFA_(veg) = 0.50 ± 0.20 , RFA_(Rep) = 0.28 ± 0.05 , RFA_(Rip) = 0.51 ± 0.09 ; Table 3). Only RFA estimates during the reproductive and ripening phases were significantly different ($t = 4.24$, $P = 0.007$). During the rainy season, RFA values did not differ significantly across the three crop phases (RFA_(veg) = 0.36 ± 0.20 , RFA_(Rep) = 0.42 ± 0.15 , RFA_(Rip) = 0.50 ± 0.17 ; Table 3). At Acarigua, during the dry season, RFA reached the highest average values during the vegetative (0.48 ± 0.23) and reproductive phases (0.57 ± 0.20), and then markedly dropped during the ripening phase (0.28 ± 0.09 ; Table 3). Only the reproductive and ripening phases were significantly different ($t = 2.81$, $P = 0.027$). During the rainy season, RFA showed similar values during the three phases of the crop cycle (RFA_(veg) = 0.52 ± 0.18 , RFA_(Rep) = 0.32 ± 0.21 , RFA_(Rip) = 0.49 ± 0.13 ; Table 3).

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 ($F_{2,33} = 5.09$, $P = 0.005$). At Turén, IGA was significantly lower in the ripening phase (0.17 ± 0.06) compared to the vegetative phase (0.33 ± 0.17 ; $t = 2.38$, $P = 0.027$) and reproductive phase (0.44 ± 0.18 ; $t = 4.05$, $P = 0.002$; Fig. 2C). At Acarigua, IGA was significantly higher in the vegetative phase (0.66 ± 0.12) compared to the reproductive phase (0.51 ± 0.17 ; $t = 2.31$, $P = 0.039$) and ripening phase (0.45 ± 0.14 ; $t = 3.30$, $P = 0.013$; Fig. 2D). For RFA, we found significant interactions between locality, season and

crop phase ($F_{2, 33} = 3.10$, $P = 0.033$). At Turén, during the dry season, RFA values did not differ significantly across the three crop phases ($\text{RFA}_{(\text{Veg})} = 0.46 \pm 0.20$, $\text{RFA}_{(\text{Rep})} = 0.31 \pm 0.07$, $\text{RFA}_{(\text{Rip})} = 0.50 \pm 0.17$; Table 3). During the rainy season, RFA reached the highest value during the vegetative phase, and then decreased in the following crop phases ($\text{RFA}_{(\text{Veg})} = 0.62 \pm 0.09$, $\text{RFA}_{(\text{Rep})} = 0.44 \pm 0.26$, $\text{RFA}_{(\text{Rip})} = 0.46 \pm 0.05$; Table 3). Only the vegetative and ripening phases were significantly different ($t = 2.96$, $P = 0.026$). 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 ($\text{RFA}_{(\text{Veg})} = 0.57 \pm 0.03$, $\text{RFA}_{(\text{Rep})} = 0.39 \pm 0.38$, $\text{RFA}_{(\text{Rip})} = 0.16 \pm 0.03$; Table 3). Only the vegetative and ripening phases were significantly different ($t = 8.14$, $P = 0.001$). During the rainy season, RFA showed similar values during the three phases of the crop cycle ($\text{RFA}_{(\text{Veg})} = 0.48 \pm 0.02$, $\text{RFA}_{(\text{Rep})} = 0.41 \pm 0.07$, $\text{RFA}_{(\text{Rip})} = 0.42 \pm 0.10$; Table 3).

General activity and relative feeding activity of Molossus molossus

The index of general activity (IGA) for *M. molossus* varied in response to the combined effects of locality, season and crop phase ($F_{2, 33} = 8.32$, $P = 0.001$). At Turén, during the dry season, IGA presented similar average values in the three cultivation phases ($\text{IGA}_{(\text{Veg})} = 0.33 \pm 0.22$, $\text{IGA}_{(\text{Rep})} = 0.26 \pm 0.09$, $\text{IGA}_{(\text{Rip})} = 0.34 \pm 0.13$; Table 3). During the rainy season, IGA was significantly higher in the vegetative phase ($\text{IGA}_{(\text{Veg})} = 0.40 \pm 0.15$) than in the reproductive ($\text{IGA}_{(\text{Rep})} = 0.13 \pm 0.05$; $t = 3.84$, $P = 0.006$) and ripening phase ($\text{IGA}_{(\text{Rip})} = 0.13 \pm 0.03$, $t = 4.30$, $P = 0.003$; Table 3). At Acarigua, during the dry season, IGA reached similar average values in the three cultivation phases ($\text{IGA}_{(\text{Veg})} = 0.30 \pm 0.12$, $\text{IGA}_{(\text{Rep})} = 0.30 \pm 0.06$, $\text{IGA}_{(\text{Rip})} = 0.24 \pm 0.03$; Table 3). During the rainy season, average IGA in the reproductive phase ($\text{IGA}_{(\text{Rep})} = 0.02 \pm 0.01$) was significantly lower than during the vegetative phase ($\text{IGA}_{(\text{Veg})} = 0.19 \pm 0.01$; $t = 5.95$, $P = 0.001$) and ripening phase ($\text{IGA}_{(\text{Rip})} = 0.18 \pm 0.03$; $t = 5.63$, $P = 0.001$; Table 3).

Relative feeding activity (RFA) of *M. molossus* varied in response to the significant interaction between locality and crop phase ($F_{2, 32} = 3.23$, $P = 0.041$). At Turén, RFA values were higher during the vegetative ($\text{RFA}_{(\text{Veg})} = 0.44 \pm 0.18$) and ripening ($\text{RFA}_{(\text{Rip})} = 0.52 \pm 0.12$) phases than in the reproductive phase ($\text{RFA}_{(\text{Rep})} = 0.33 \pm 0.13$; Fig. 3A). Nevertheless, a significant difference was observed only between the reproductive and ripening phases ($t = 2.85$, $P = 0.01$). 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 Myotis nigricans

The index of general activity (IGA) of *M. nigricans* only varied in response to crop phase ($F_{2, 33} = 8.54$, $P = 0.001$), with the ripening phase ($IGA_{(Rip)} = 0.10 \pm 0.05$) showing significantly lower values than the vegetative phase ($IGA_{(Veg)} = 0.24 \pm 0.17$; $t = 3.21$, $P = 0.004$) and reproductive phase ($IGA_{(Rep)} = 0.29 \pm 0.19$; $t = 4.23$; $P = 0.001$; Fig. 3C). Relative feeding activity (RFA) varied in this species as a function of the interaction between locality and season ($F_{1, 33} = 5.55$, $P = 0.011$). At both sites, the highest RFA values were observed in the rainy season ($RFA_{(Turén-Dry)} = 0.44 \pm 0.25$, $RFA_{(Turén-Rainy)} = 0.51 \pm 0.22$, $RFA_{(Acarigua-Dry)} = 0.22 \pm 0.17$, $RFA_{(Acarigua-Rainy)} = 0.46 \pm 0.09$; Table 3). However, those seasonal differences in RFA were significant only at Acarigua ($t = 4.33$, $P = 0.002$).

DISCUSSION

We used acoustic monitoring techniques to document for the first time in the Neotropics the richness, composition, and activity of aerial 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 common 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 conservation of bats in agricultural habitats in the Neotropics and to test management practices of populations of the most common and active bat species (*Molossus molossus* and *Myotis nigricans*) to 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 detected 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 (*Peropterys 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 *Pteronotus 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.

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 study. 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; Estrada and Coates-Estrada, 2001, 2002; Estrada *et al.*, 2004; 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; Fuentes-Montemayor *et al.*, 2017). We found that AI-BCS species were more sensitive to changes in forest cover than AI-US species. 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 may indicate 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 both functional groups, which suggests that we require information on activity and diet of bats and prey availability at the landscape level to fully understand the processes behind the patterns we 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 space as much as it forages in background clutter space, 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* show higher 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. furinalis*, *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; Pérez, 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 in 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.

Concluding remarks

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 activity 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, and (4) use of artificial roosts. 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, probably other designs could offer optimal 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.

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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).

Turén				
Coverage	Composition			Configuration
	CA (km ²)	PL (%)	NP	ED-NN (1 SD)
Forest	3.45	4.39	205	109.09 (97.85)
Crops	47.29	60.23	617	49.30 (12.84)
Urban	11.58	14.74	1,622	59.06 (29.28)
Water bodies	2.73	3.48	132	67.65 (76.71)
Clouds	1.18	1.50	311	86.69 (106.38)
Fire smokes	12.29	15.65	1,693	57.37 (31.61)
Acarigua				
Coverage	Composition			Configuration
	CA (km ²)	PL (%)	NP	ED-NN (1 SD)
Forest	16.82	21.43	443	73.87 (65.44)
Crops	41.94	53.42	623	52.69 (16.11)
Urban	7.43	9.46	1,305	63.95 (36.51)
Water bodies	2.47	3.15	160	106.3 (186.94)
Clouds	0.84	1.06	198	116.08 (153.67)
Fire smokes	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.

Turén					
Crop phase (plant age)	Recording sites				Total
	1	2	3	4	
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					
Crop phase (plant age)	Recording sites				Total
	1	2	3	4	
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)

^a No index due to low call to noise ratio and reduced number of sound sequences obtained (< 10). ^b Taxon includes two sonotypes that were difficult to discriminate. ^c The IAG and the RFA of AI-BCS-T are the same as those of *N. albiventris*.

FIGURE CAPTIONS

Figure 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, $P < 0.05$).

Figure 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, $P < 0.05$).

Figure 3. Index of relative feeding activity (RFA) of *Molossus molossus* and index of general activity (IGA) of *Myotis 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). IAG 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, $P < 0.05$).

A)

B)

C)

A)

B)

C)

D)

A)

Turén (*Molossus molossus*)

B)

Acarigua (*Molossus molossus*)

C)

Myotis nigricans