

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

FACULTY OF ENVIRONMENTAL SCIENCES



MASTER THESIS

The role of temporal lakes and ponds for bat conservation in the Neotropical rainforests

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Prague 2017

DIPLOMA THESIS ASSIGNMENT

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Nature Conservation

Thesis title

The role of temporal lakes and ponds for bat conservation in the Neotropical rainforests

Objectives of thesis

To conduct a field investigation exploring the ecosystem services provided by temporal ponds and lakes for aerial insectivorous bats in the Central Amazon. The specific aims of the project would be: a) Determine the effect of habitat structure (forest or lakes) and seasonality (dry and rainy) on bat richness and relative abundance of bats (in total and also at species level); b) Identify species specific dependence towards temporary lakes; and c) Detect shift of activity patterns along the night for several species within the pristine forest and the temporary lakes.

Methodology

Literature to begin reviewing:

Almeida, M. H., Ditchfield, A. D. & Tokumar, R. S. (2014) Habitat characteristics and insectivorous bat activity. *Chiroptera Neotropical* 20(2): 1264-1270.

Bader, E., Acácio, M. & Monadjem, A. (2015) The importance of water bodies for insectivorous bats in a Malagasy dry deciduous forest: A case example from Kirindy (CNFEREF). *Malagasy Nature*, 9: 88-96.

Castro, I.J. de & Michalski, F. (2015) Bats of a varzea forest in the estuary of the Amazon River, state of Amapá, Northern Brazil. *Biota Neotropica*, 15(2). DOI: <http://dx.doi.org/10.1590/1676-06032015016814>.

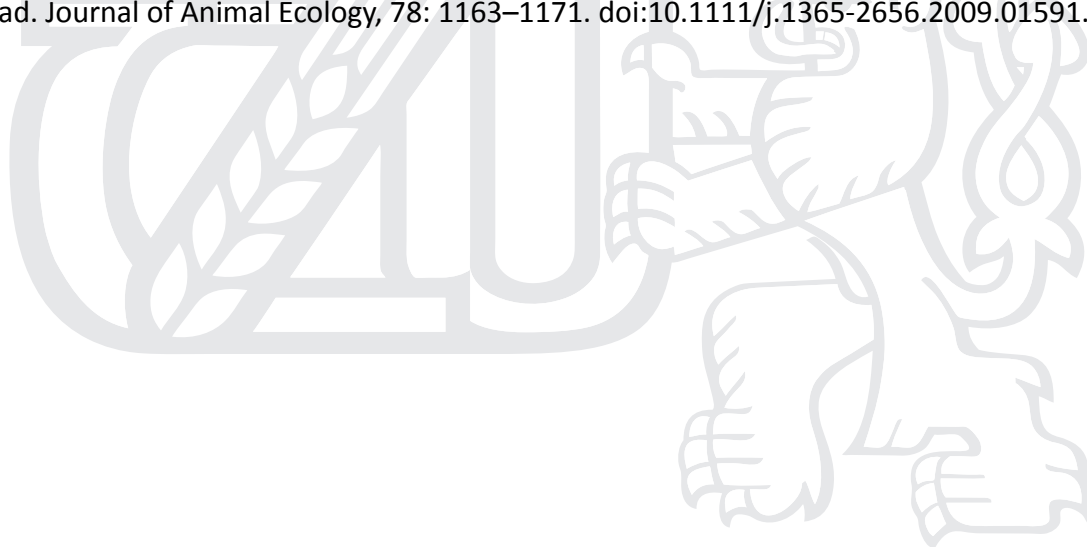
Korine, C., Adams, R., Russo, D., Fisher-Phelps, M. & Jacobs, D. (2016) Bats and Water: Anthropogenic Alterations Threaten Global Bat Populations. In: C.C. Voigt and T. Kingston (eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World*, DOI: 10.1007/978-3-319-25220-9_4, pp 215 – 241.

MacSwiney, M. C. et al. (2009) Insectivorous bat activity at cenotes in the Yucatan Peninsula, Mexico. – *Acta Chiropt.* 11: 139-147.

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Pereira, M. J. R., Marques, J. T., Santana, J., Santos, C. D., Valsecchi, J., De Queiroz, H. L., Beja, P. & Palmeirim, J. M. (2009) Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. *Journal of Animal Ecology*, 78: 1163–1171. doi:10.1111/j.1365-2656.2009.01591.x



The proposed extent of the thesis

100 pages

Keywords

Insectivorous bats, acoustic monitoring, temporary water bodies, Amazon, climate change

Recommended information sources

- Almeida, M. H., Ditchfield, A. D. & Tokumar, R. S. (2014) Habitat characteristics and insectivorous bat activity. *Chiroptera Neotropical* 20(2): 1264-1270.
- Bader, E., Acácio, M. & Monadjem, A. (2015) The importance of water bodies for insectivorous bats in a Malagasy dry deciduous forest: A case example from Kirindy (CNFEREF). *Malagasy Nature*, 9: 88-96.
- Pereira, M. J. R., Marques, J. T., Santana, J., Santos, C. D., Valsecchi, J., De Queiroz, H. L., Beja, P. & Palmeirim, J. M. (2009) Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. *Journal of Animal Ecology*, 78: 1163–1171.
doi:10.1111/j.1365-2656.2009.01591.x

Expected date of thesis defence

2016/17 SS – FES

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Declaration

I hereby declare that I am the sole author of the thesis entitled: “The role of temporal lakes and ponds for bat conservation in the Neotropical rainforests”. I duly marked out all quotations. The used literature and sources are stated in the attached list of references.

In Prague on 18.04.2017

Laura Torrent Alsina

Acknowledgments

I especially wish to express my greatest appreciation and gratitude to my supervisor and friend Adrià López Baucells for all his unconditional help, advices and moral support; to my supervisor Dr. Christoph Meyer for all his excellent guidance in the statistical analysis and crucial comments on earlies versions of this manuscript; and to my CULS supervisor doc. Peter Kumble, Ph.D. for his supervision on the final stages of the thesis.

I would like to thank Ricardo Rocha, Oriol Massana, Diogo Ferreira, Marta Acácio and Fabio Farneda for their fieldwork assistance and the Instituto Nacional de Pesquisas da Amazonia (INPA) and the Biological Dynamics of Forest Fragments Project (BDFFP), especially to José Luis Camargo, Rosely Hipólito and Ary Jorge Ferreira for their logistical support. This work was supported by the Portuguese Foundation for Science and Technology under Grant PTDC/BIABIC/111184/2009 (C.F.J.M.), SFRH/BD/80488/2011 (R.R.) and PD/BD/52597/2014 (A.L.B.). Research was conducted under the permit (26877-2) issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). I am also grateful to Johanna Blöcher for her support on statistical matters and to doc. Ing. Jiří Vojar, Ph.D. for his translation of the abstract.

Finally, I would like to deeply thank my family, Sergio and Kristýna for their incessant encouragement to write this diploma thesis.

In Prague on 18.04.2017

Laura Torrent Alsina

Abstract

The rise of temperatures in the Tropics due to climate change are predicted to be less important than those at higher latitudes or in arid regions. However, recent studies predict a future decrease in precipitation over the Amazon rainforest, causing harsh droughts and thus, a diminution of freshwater biomes, especially temporary flooded areas. Immediate consequences on terrestrial fauna associated to tropical temporary waters are mostly unknown as the vast majority of the studies come from temperate regions. While few studies are focused on the Tropics, mostly of them are focused on the amphibians and none on bats. Moreover, specifically, amongst all bat related studies conducted in the Neotropics, very few have focused on aerial insectivorous bats due to methodological bias and the misuse of bioacoustics. I studied the ecological role of temporary lakes surrounded by primary rainforest in Central Amazon for aerial insectivorous bats. Richness, species-specific activity and feeding activity was analyzed at ensemble and species level during both dry and rainy season. Generalized Linear Mixed Model results indicated 18 of 21 species were significantly more active over the temporary ponds while only 3 were significantly more active inside the continuous rainforest. While richness and 5 species-specific activity were significantly higher during the rainy season, for 2 species it was in the dry season. Lake size influence on richness, total and species-specific activity and was tested with multi comparison Kruskal Wallis test. Species richness and total activity were significantly higher over large ponds. Temporary lake size had a significant but differential effect on the species activity: 6 were positively more active on the largest lakes, while another 4 species more often in small waterbodies. In terms of activity patterns, most of the recorded bat families had the highest activity peak the first two hours of the night, with the exception of all mormoopid bats, which had it around midnight. My findings suggest that all the aerial insectivorous bats, even the cluttered specialists, use the temporary lakes to forage and drink. The recorded molossid bats were all significantly more active over the waterbodies and vespertilionid bats spend most of the night foraging over the water surfaces. More studies should be focused on tropical temporary ecosystems to obtain new information about the most elusive aerial insectivorous bats (e.g. *S. leptura*, *C. maximiliani*, *P. gymnonotus*, *P. personatus* and *F. horrens*). Finally, I suggest that by creating temporary ponds with a surface area between 200 m² and 3000 m², and preserving the existent ones, we can provide suitable foraging and drinking habitats for all aerial insectivorous bats.

Keywords: Acoustic monitoring, insectivorous bats, temporary water bodies, Amazon, Climate Change

Abstrakt

Očekávané zvýšení teplot v důsledku globálních klimatických změn by se tropů mělo dotknout méně než jiných oblastí. Poslední studie nicméně ukazují, že pokles srážek v amazonských pralesech může způsobit významná sucha a výrazný úbytek zejména dočasných vodních biotopů. Důsledky tohoto jevu na terestrické živočichy vázané na periodické vodní biotopy v tropech jsou velkou neznámou, neboť pozornost byla v tomto ohledu doposud věnována spíše mírnému klimatickému pásmu. Nepočtené studie v tropech se zaměřují spíše na obojživelníky, potenciální vliv na netopýry (Chiroptera) doposud zkoumán nebyl. Ze všech studií věnovaných obecně netopýrům v Neotropické oblasti se pouze malá část zabývala hmyzožravými druhy, zejména díky metodickým nejasnostem a problematickému využití bioakustických metod. Ve své diplomové práci se zabývám ekologickým významem dočasných vodních biotopů v tropických deštných pralesích centrální Amazonie pro hmyzožravé netopýry. Druhovú diverzitu společenstva netopýrů i aktivitu jednotlivých druhů, včetně potravní aktivity, byla sledována v různých částech roku lišících se množstvím srážek. Pomocí zobecněných lineárních modelů (GLM) bylo prokázáno, že 18 z 21 sledovaných druhů bylo více aktivních v oblastech s dočasnými vodními plochami a pouze 3 druhy byly aktivnější mimo tyto oblasti v zapojených porostech. Vyšší druhová diverzita, a také aktivita pěti druhů, byla zaznamenána během srážkového období, zatímco v období beze srážek vykazovaly vyšší aktivitu pouze dva druhy. Velikost vodní plochy pozitivně korelovala s druhovou bohatostí netopýrů, nicméně její vliv na aktivitu netopýrů byl druhově specifický – šest druhů vykazovalo průkazně vyšší aktivitu u větších vodních ploch, čtyři druhy naopak u menších. Co se týče rozložení aktivity netopýrů v průběhu noci, většina skupin netopýrů byla nejvíce aktivních v prvních dvou nočních hodinách, resp. po soumraku; pouze zástupci čeledi Mormoopidae byli nejaktivnější kolem půlnoci. Na základě dosažených výsledků předpokládám, že většina druhů loví v blízkosti vodních ploch a využívá je i k napájení. Všichni zástupci čeledi Molossidae byli aktivnější nad vodními plochami, podobně jedinci druhů z čeledi Vespertilionidae trávili v průběhu noci v rámci lovu více času nad vodními plochami. Bylo by vhodné provést více podobných studií zabývajících se dočasnými biotopy a poměrně obtížně sledovanými druhy netopýrů, jako např. *S. leptura*, *C. maximiliani*, *P. gymnotus*, *P. personatus* and *F. horrens*. Tvorba nových vodních biotopů o velikostech 200–3000 m², společně s důslednou ochranou těch existujících, může zajistit vhodné podmínky pro lov potravy i napájení všech druhů insektivorních netopýrů Neotropické oblasti.

Klíčová slova: Akustický monitoring, hmyzožraví netopýři, dočasné vodní plochy, Amazonie, Klimatické Změny

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1. Literature review

1.1. The impact of global change on biodiversity

It has already been predicted that anthropogenic global changes are having and will continue to have serious effects on biodiversity at global, regional and local scales being its principal threats climate change, habitat loss and risk of extinction (e.g. Brown, 1968; Tittensor *et al.*, 2014). Accelerated climate change due to massive human exploitation of natural resources, habitats and ecosystems is severely disturbing the Earth's biota. Since the beginning of the twenty first century, predicting biodiversity and ecosystem responses to climate change has become a very productive subject of investigation. Research is being carried out at the scales of individuals, populations, species, communities, ecosystems and biomes (Dillon *et al.*, 2010; Gilman *et al.*, 2010; Pereira *et al.*, 2010; Salamin *et al.*, 2010; Beaumont *et al.*, 2011; Dawson *et al.*, 2011; McMahon *et al.*, 2011) and its impacts have already been described in the form of cascade repercussions. Such cascading effects due to climate change influence species extinction rates; cause the redistribution of species which could create environmental and human health issues; and entire communities will potentially modify their roles associated with ecosystem functions, such as pollination or pest control, on which humans rely (Angert *et al.*, 2013).

Whereas a direct precursor of climate change is global warming, its effects on species are expected to vary latitudinally and geographically (Thomas *et al.*, 2004; Parmesan, 2007). Climate change impacts related to the increase of temperatures in the Tropics are always predicted to be less important than those in Boreal and Arctic zones (Sala *et al.*, 2000; Solomon, 2007) and temperate or arid regions (Root *et al.*, 2003; Parmesan, 2007). Tropical ecosystems already have higher absolute temperatures and severe episodic droughts, like the El Niño Southern Oscillation (Trenberth & Hoar, 1996) which exert a regular influence on these regions. Therefore, it is generally accepted that within a safe threshold, tropical ecosystems will be less sensitive to future climatic changes and that is why we can see a bibliographic bias towards studies on higher latitudes. A solution to avoid this latitudinal bias is to use data of temperatures that have a wider topographical coverage and that focus on the biological consequences of global warming (Deutsch *et al.*, 2008).

An increase of temperatures cause biotic impacts and by studying the metabolic rate, fundamentally measured by physiological activity, it has been proven that metabolic rate rises exponentially with temperature in terrestrial ectotherms (Gillooly *et al.*, 2001).

Hence, metabolic rate can be used to predict latitudinal patterns of global warming related alterations in terrestrial ectotherm organisms (Dillon *et al.*, 2010).

Recent studies suggest that global warming within the past three decades has had greater influences on metabolic rates of ectotherm species from tropical regions than from Arctic regions (Dillon *et al.*, 2010). Therefore, tropical species, which have evolved within limited thermal ranges (low inter- and intra-annual weather variability) might have more restricted physiological tolerance and consequently could be more sensitive to global warming than others (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Corlett, 2011; Huey *et al.*, 2012; Şekercioğlu *et al.*, 2012). Thus, Tropical and subtropical ecoregions may be especially susceptible to climate warming. Using climate variability data from 1962 – 1990 as a baseline period, Beaumont *et al.* (2011) predicted that the average monthly temperature in the Tropics will become extreme with a relatively small increase in local temperatures.

Some climate models predict a precipitation decrease and more harsh drought during the dry season (June/July to October/November) over the Amazonian rainforest (Beaumont *et al.*, 2011), especially in the eastern Amazon Basin (Malhi *et al.*, 2009a; Shiogama *et al.*, 2011). Temperature rises in the Tropics can also cause greater vapor pressure deficits (VPD) and evaporation, decreasing soil moisture (Cisneros *et al.*, 2015), plant growth and net primary productivity (Zhao & Running, 2010; Beaumont *et al.*, 2011) due to the lack of water availability. Hence, we can foresee a reduction of freshwater biomes – streams, lakes, floodplains, temporary ponds – that will take place more and more often over tropical ecoregions with still little known consequences for the dependent terrestrial fauna to these aquatic systems.

1.2. The role of temporary lakes in ecosystems in the context of climate change

Almost all of Earth's water is saline (97.5%), found in the oceans, and only a relatively small portion of it is freshwater (1 %) – e.g. rivers, lakes, groundwater and temporary waterbodies – which, however, is able to sustain a large fraction of the world's animals (Gleick, 1993). Despite still being incompletely surveyed, Balian *et al.* (2008) estimated freshwater ecosystems provide suitable habitats for approximately 126,000 species of animals which represents 7% of all the species currently described (~ 1.8 million). From this number, the majority of species dependent on freshwater habitats are insects (60.4%) and only 14.5% are vertebrates, which are highly species-rich in the Tropics, sustaining the highest value of endemism, mainly fish (Balian *et al.*, 2008).

A substantial number of papers have been published studying biotic diversity in freshwater across the globe, mainly ichthyofauna, based on riparian and permanent water bodies (e.g. Heino *et al.*, 2002; Pearson & Boyero, 2009; Collen *et al.*, 2014) while a less proportion have been published focusing on temporary lakes. A great proportion of the studies specifically in temporary waterbodies are focus on zooplankton (e.g. Serrano & Fahd, 2005; Florencio *et al.*, 2014) and amphibians (Gómez-Rodríguez *et al.*, 2009). Thus, in general temporary waterbodies are understudied habitats for most taxa that it is not strictly dependent of the water (e.g. terrestrial reptiles, birds and mammals).

Blaustein and Schwartz (2001) defined a temporary pond as “any habitat that intermittently has standing water and that, once inundated, holds water long enough on occasion for some species to complete aquatic phases of their life cycle”. Temporary lakes can be easily formed nearly at any place, as long as there is water, a depression in the ground and a type of soil that prevents water drainage (Williams *et al.*, 2001). Moreover, temporary ponds can persist for longer periods than permanent lakes because they do not have a sedimentation process going on at the bottom of the waterbody (Williams *et al.*, 2001). Nonetheless temporary lakes also face a series of risks due to a) lack of common agreement on their classification and management; b) continued human population growth; c) demand and contamination of the waters; and d) climate change. However, a major threat is the absence of awareness of their presence, usually eclipsed by permanent waterbodies, like rivers and lakes, by conservationists, local authorities and the general public.

Human-driven expansion of agriculture and urbanization without proper directives on how to manage temporary freshwater habitats, characterized by their ephemerality and shallowness, is causing their rapid degradation and disappearance as well as increasing their tendency of becoming polluted (Williams *et al.*, 1998). However, very little is known about the potential effects of climate change upon these fragile ecosystems and consequently the terrestrial species that they will be able to sustain in the future. Evaluating and predicting the ecological impacts as well as the physiological and behavioral sensitivity of organisms to the climate change-driven variation in temperature would be essential in order to minimize anthropic impacts on biodiversity and to implement future mitigation actions.

Ectotherm fauna comprise the greater part of terrestrial biodiversity (Wilson, 1992) and are particularly expected to be susceptible to climate warming because their essential physiological functions like growth, locomotion, and reproduction are intensely influenced by the temperature of the environment (Deutsch *et al.*, 2008). However, the

vast majority of studies related to ephemeral waters and their associated species come from temperate habitats distributed across the globe: Europe (Zacharias *et al.*, 2007), Australia (Warwick & Brock, 2003), Western USA (Kneitel & Lessin, 2010) and South and North Africa (Rhazi *et al.*, 2006; Rhazi *et al.*, 2009), mainly focusing on amphibians (Rowe & Dunson, 1995; Smith *et al.*, 2003; Moreira *et al.*, 2007; Fonseca *et al.*, 2008; Gómez-Rodríguez *et al.*, 2009; Ferreira & Beja, 2013). Only few studies have been conducted in tropical regions regardless species dependence, assemblages and diversity in inundated Amazon areas, for instance for birds (Haugaasen & Peres, 2007) and non-flying mammals (Haugaasen & Peres, 2005b). However, none exclusively focusing on temporal waterbodies and none of them have addressed the impacts on aerial insectivorous bats.

1.3. Bats in Neotropical temporary lakes

Many studies have highlighted the importance of several types of water bodies – rivers, lakes, riparian and swampy regions, natural and artificial ponds – as they provide bats key habitats for their reproductive cycles (McLean & Speakman, 1999; Adams & Thibault, 2006; Adams & Hayes, 2008) and drinking and/or foraging (Vaughan *et al.*, 1996; Grindal *et al.*, 1999; Holloway & Barclay, 2000; Wickramasinghe *et al.*, 2003; Seibold *et al.*, 2013) in both temperate (Barclay, 1991; Rydell *et al.*, 1994; Mickevičienė & Mickevičius, 2001; Akasaka *et al.*, 2009; Scott *et al.*, 2010) and semi-arid regions (Warren *et al.*, 2000; Young & Ford, 2000; Russo & Jones, 2003; Rainho, 2007; Davie *et al.*, 2012; Monamy *et al.*, 2013).

Recently, a compilation of the key interactions between bats and open water bodies in semi-arid and arid environments was published by Korine *et al.* (2016). They review the existing knowledge about bats inhabiting semi-arid and arid habitats across the world and discuss the factors influencing their richness, phenology and activity linked to both natural and anthropogenic waterbodies. Insectivorous bats from arid and semi-arid regions commute to waterbodies to forage on aquatic insects and to drink, specially to supply internal water expenses from the flight and the roosting time. Although several studies from the Neotropics have analyzed the responses of aerial insectivorous bats to global change drivers such as habitat fragmentation, logging and deforestation (Estrada-Villegas *et al.*, 2010; Bader *et al.*, 2015; Meyer *et al.*, 2016), only a few have been carried out in fragmented systems with a water matrix (e.g. Meyer & Kalko, 2008a; Meyer & Kalko, 2008b). Unfortunately, none has exclusively focused on aerial insectivorous bat interactions with temporary freshwater habitats considering climate change effects.

Additionally, even during regional inventory studies, waterbodies tend to be generally left aside and thus, they are still widely under-explored. These sites are also mainly studied using more common capturing techniques (e.g. Pereira *et al.*, 2009; Costa *et al.*, 2012) rather than bioacoustics, leaving a poorly explored niche of knowledge to be filled in. Therefore, the full potential of bioacoustics has not been exploited for the study of aerial insectivorous bats in tropical habitats.

To conclude, despite the improvement of bioacoustics techniques within the last decade, only some studies have been performed on Neotropical bats over open water surfaces with bat detectors (e.g. Kalko *et al.*, 1998; Rydell *et al.*, 2002; Jung *et al.*, 2007; Kalko *et al.*, 2008) and even fewer entirely focus on aerial insectivorous bats (e.g. MacSwiney *et al.*, 2008; Almeida *et al.*, 2014; Marques *et al.*, 2015).

2. Aims of the project

The overarching aim of the project was to identify if temporary lakes and ponds play an important role for aerial insectivorous bats in tropical rainforest habitats and which conservation measures we could pinpoint to preserve them. Due to climate change, tropical regions will potentially undergo important drought problems; directly reducing the number of temporary lakes and ponds; and indirectly threatening many terrestrial species that depend on these waterbodies in ways we have not properly predicted yet. To test it, the main aim of this project was to identify the ecological facilities that temporal waterbodies can provide for aerial insectivorous bats in a Neotropical rainforest in the Central Amazon.

The specific aims of the project were to: a) Determine the effect of habitat structure (forest or lake) and season (dry and rainy) on aerial insectivorous bat species richness and activity (at both ensemble or total and species-specific level); b) Identify species dependence on temporary lakes; c) Identify if the size of the temporary ponds influences species richness and total and species-specific activity; and d) Determine nightly activity patterns of aerial insectivorous bat species within the continuous forest and over temporary lakes. Finally, I discuss how these findings could be used to improve and develop conservation and management strategies for bats and other terrestrial taxa under accelerating climate change.

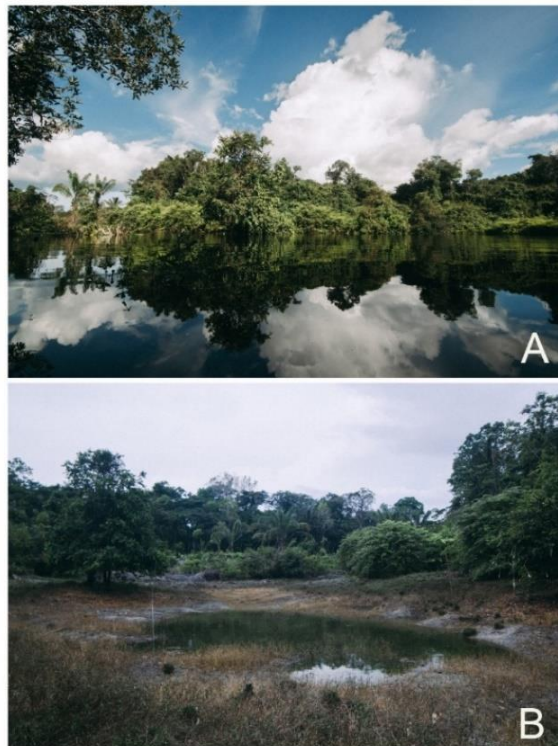


Figure 1. Water levels in Lake E (Porto Alegre reserve) in the A) rainy and B) dry season.

3. Materials and methods

3.1. Study area

The project was carried out in the Biological Dynamics of Forest Fragments Project (BDFFP), 80 km north of Manaus, in the Brazilian Amazon rainforest (Figure 2), an extensive reserve where since the 70s studies have been carried out to understand the consequences of habitat fragmentation on tropical rainforest biota. It is considered the world's largest ongoing fragmentation experiment. The BDFFP was born from a cooperative project between the U.S. Smithsonian Tropical Research Institute (STRI) and the Brazil's Instituto Nacional de Pesquisas da Amazônia (INPA).

The experimental area embraces an area of approximately 1000 km² of rainforest (Lovejoy & Bierregaard, 1990; Laurance *et al.*, 2011) and it is a mosaic of usually nutrient-poor, continuous unflooded upland or *terra firme* forest (De Oliveira & Mori, 1999), surrounded by a current matrix of secondary forest patches (~8325 ha) and forest fragments (~245 ha), isolated during the period 1980 – 1984 (Laurance *et al.*, 2011).

The average local temperature is 25.8 °C and the annual average precipitation in the area is 2547 mm per year (Kunert *et al.*, 2017). The precipitation attains its maximum, with more than 300 mm/month, during the months of March and April, and its lowest values, less than 100 mm/month, in August (Kunert *et al.*, 2017). Monthly precipitation can reach values lower than 100 mm/month, during the month of June to October, if it is an unusually dry year (Kunert *et al.*, 2015).

The topography is relatively flat (80 – 160 m.a.s.l.) divided by many small streams; and large rivers and waterbodies are almost completely absent. The primary forest canopy ranges between 30 – 37 m tall with emergent trees reaching up to 55 m of height (Sampaio *et al.*, 2003; Laurance *et al.*, 2011).

The sampled sites include seven points in primary forest - five locations (Forest 1 - 3 and 6 – 7) in continuous forest (located in the Cabo Frio and Km 41 reserves within the BDFFP area) - and two locations (Forest 4 – 5) inside 100 Ha forest fragments (situated in Dimona and Porto Alegre reserves) - and eleven lakes/ponds - one in Dimona (Lake G); one in Colosso (Lake F); two in Porto Alegre (Lake D and Lake E); three in Km 41 (Lake A, Lake C and Lake H) and another one close to the main road (Lake B) (Figure 2 and Table 1).

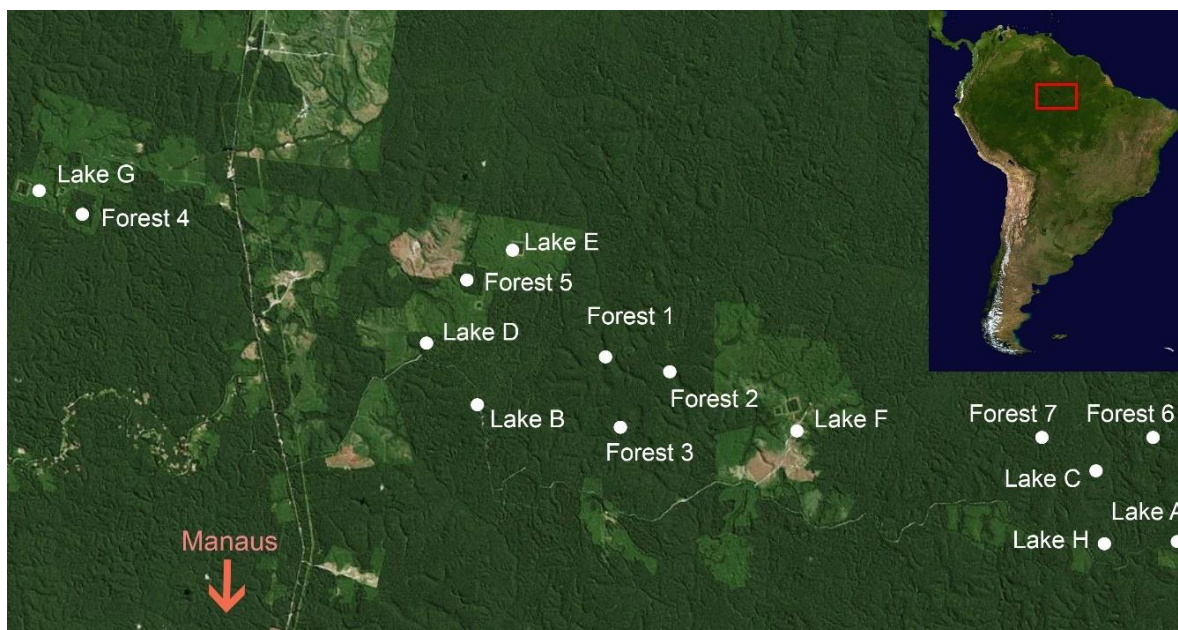


Figure 2. Geographical situation of the BDFFP area and the sampled temporary ponds (Lake A to H) and primary forests (Forest 1 to 7). Dark green areas: primary rainforest; light green: secondary regrowth forest and pastures. **Source:** Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

Table 1. General information about the surveyed temporary lakes (including the reserve name, the oscillation of the water level between the rainy and dry seasons and the geographical location).

Name	Reserve	Size in rainy season (m ²)	Size in dry season (m ²)	Geographical coordinates
Lake A	Km 41	9740	2446	-02.4476869°, -059.7505882°
Lake B	Km 21	9611	9611	-02.4051716°, -059.9704628°
Lake C	Km 41	2902	855	-02.4305276°, -059.7741627°
Lake D	Porto Alegre	2316	1294	-02.3851464°, -059.9841295°
Lake E	Porto Alegre	2527	395	-02.3574670°, -059.9593178°
Lake F	Colosso	2099	437	-02.4109754°, -059.8690231°
Lake G	Dimona	200	200	-02.3398381°, -060.1016720°
Lake H	Km 41	61	61	-02.4492385°, -059.7701420°
Forest 1	Cabo Frio	-	-	-02.380979°, -059.928022°
Forest 2	Cabo Frio	-	-	-02.399757°, -059.900202°
Forest 3	Cabo Frio	-	-	-02.416985°, -059.926773°
Forest 4	Dimona	-	-	-02.343255°, -060.095072°
Forest 5	Porto Alegre	-	-	-02.363252°, -059.975384°
Forest 6	Km 41	-	-	-02.427005°, -059.749305°
Forest 7	Km 41	-	-	-02.416634°, -059.780269°

Lake A and Lake B were the biggest of the sampled lakes, with an area of more than 9000 m² during the rainy season (Table 1). Whereas Lake A reduced its area considerable, to approximately 2000 m² in the dry season, Lake B only slightly reduced

its surface cover because it was partially connected to a stream (López-Baucells *pers. comm.*). Lake C - F had from 2000 to 3000 m² in the rainy season, but showed different levels of decrease in size during the dry season. Lake D kept its size the whole year as it was also connected to a stream. However, Lake E and Lake F oscillated considerably between seasons, reducing their areas to less than 500 m² and sometimes dried out completely (López-Baucells *pers. comm.*) (Figure 1). Lake G was the smallest and the most cluttered lake with foliage, with an area of approximately 200 m² and connected to a narrow stream. Finally, a pool (Lake H) nearby one of the camp sites was also sampled with an area of approximately 60 m² (Figure 3).

Whereas most of the lakes were situated in open areas without any vegetation or vertical structures over the water, due to the small size, Lake G was almost completely covered by the surrounding flora and embedded inside the rainforest (López-Baucells, *pers. comm.*).



Figure 3. Types of temporary lakes and ponds surveyed for this study.

3.2. Acoustic surveys

In each locality, a Song Meter Bat Recorder (SM2Bat+) with an omnidirectional ultrasonic SMX-US microphone (Wildlife Acoustics, In. Maynard, Massachusetts, USA) was installed at 1 - 2 m height (Figure 4). Each site was sampled twice per season and acoustic surveys were conducted during both the dry season (June, October and November) in 2013 and the rainy season (April, May, September) in 2014.

During each sampling session, the detectors were programmed to passively and continuously record from 18:00 to 06:00 in real time with a full spectrum resolution of 16-bit, with a high pass filter set at $f_s/32$ (12 kHz) and the trigger level 18SNR, for the period of 3 consecutive nights. The total amount of acoustic surveys was 70 nights in the temporary lakes and 79 nights in the primary forest.

3.3. Sound analysis

Kaleidoscope Pro Software (version 4.0.4.) (Wildlife Acoustics, In. Maynard, Massachusetts, USA) was used to analyze the recordings and identify them to species level whenever possible. The acoustic files, compressed in .wac format by the recorders, were uncompressed and split into shorter .wav files to sequences of a maximum length of five seconds'.

Due to the impossibility to count individuals using acoustic data (or absolute bat abundance) (Wickramasinghe *et al.*, 2003), my sample unit was defined as a “bat pass” and it was used as a surrogate of activity levels. I defined a “bat pass” as an echolocation sequence with a minimum of two recognizable echolocation pulses per species emitted by a flying bat within a five second file (Azam *et al.*, 2015; Millon *et al.*, 2015). I quantified “species-specific activity” as the number of bat passes per night recorded for each species (or sonotypes – which include several species) and “total activity” as the sum of all bat passes per night. I also quantified foraging activity as the number of feeding buzzes detected per species (Kalko & Schnitzler, 1989).

Call sequences were identified to species level or left as mixed-species groups, i.e. sonotypes, when it was not possible to clearly assign a call to a particular species (

Table 2). Classification was undertaken following López-Baucells *et al.* (2016), and comparing my recordings with a local reference call library compiled in the same study area during the period 2011 – 2014 by López-Baucells *et al.* (unpublished). Species were

identified taking into consideration a series of acoustic features and standard measurements: shape of the calls, harmonic with the frequency of maximum energy (FME), start, end, maximum and minimum frequency and duration (Appendix 1). For the identification of doubtful sequences and pulses the measurements were taken from the harmonic with the most energy and from the more defined pulses within a sequence. If bat sequences or pulses were too faint (< 10 dB of difference from the background noise), to obtain the needed information for species identification, they were discarded from the analysis.

I used a total of 21 sonotypes from which 14 were classified to species level and 7 sonotypes grouped several species, from the families *Emballonuridae*, *Furipteridae*, *Molossidae*, *Mormoopidae* and *Vespertilionidae* (

Table 2).

Table 2. Sonotypes and their ranges of frequencies. Parts of a pulse: SF – start frequency; EF – end frequency; FME – frequency of maximum energy; lp – lower pulse; mp – middle pulse; hp – high pulse (López-Baucells *et al.*, 2016).

Sonotype	Included species	Range of FME (kHz)
Emballonuridae		
<i>Rhynchonycteris naso</i>	<i>Rhynchonycteris naso</i>	98 – 105
<i>Saccopteryx leptura</i>	<i>Saccopteryx leptura</i>	lp: 46 – 49 and hp: 43 – 46
<i>Saccopteryx bilineata</i>	<i>Saccopteryx bilineata</i>	lp: 41 – 43 and hp: 44 – 46
<i>Centronycteris maximiliani</i>	<i>Centronycteris centralis</i> / <i>maximiliani</i>	39 – 41
<i>Peropteryx macrotis</i>	<i>Peropteryx macrotis</i>	37 – 39
<i>Peropteryx kappleri</i>	<i>Peropteryx kappleri</i>	29 – 33
<i>Cormura brevirostris</i>	<i>Cormura brevirostris</i>	lp: 23 – 25, mp: 26 – 28 and hp: 29 – 33
<i>Emballonuridae</i> 1	<i>Saccopteryx gymnura</i> / <i>canescens</i>	54 -55
Furipteridae		
<i>Furipterus horrens</i>	<i>Furipterus horrens</i>	117 - 122
Molossidae		
<i>Molossidae</i> I	<i>Molossus molossus</i>	lp 33 - 35, mp 35 – 40 and hp 40 - 45
<i>Molossidae</i> II	<i>Molossus sinaloae</i> / <i>currentium</i> / <i>rufus</i>	lp 25 – 30, mp 30 – 35 and hp 35 - 40
<i>Molossidae</i> III	<i>Cynomops planirostris</i> / <i>paranus</i> , <i>Cynomops greenhalli</i> / <i>abrasus</i> , <i>Eumops auripendulus</i> / <i>glaucus</i> / <i>dabbeni</i> / <i>hansae</i> / <i>maurus</i> , <i>Nyctinomops laticaudatus</i> , <i>Tadarida brasiliensis</i>	lp EF: 17 – 21 and hp EF: 21 - 24
<i>Molossops</i> 1	<i>Molossops neglectus</i> , <i>Molossops temminckii</i>	lp EF: 44 – 54 and hp EF: 46 – 55
<i>Promops</i> 1	<i>Promops centralis</i> , <i>Promops nasutus</i>	lp EF: 28 – 34 and hp EF: 30 – 37
Mormoopidae		
<i>Pteronotus personatus</i>	<i>Pteronotus personatus</i>	SF: 60 – 69
<i>Pteronotus</i> sp1	<i>Pteronotus</i> sp1	59 – 61
<i>Pteronotus gymnonotus</i>	<i>Pteronotus gymnonotus</i>	45 – 60
<i>Pteronotus rubiginosus</i>	<i>Pteronotus rubiginosus</i>	54 – 56
Vespertilionidae		
<i>Vespertilionidae</i> 1	<i>Eptesicus brasiliensis</i> / <i>chiriquinus</i>	EF: 25 - 45

	<i>Eptesicus furinalis</i> / <i>Lasiurus</i> sp. /	
	<i>Roghessa io</i>	
<i>Myotis riparius</i>	<i>Myotis riparius</i> / <i>Thyroptera tricolor</i>	EF: 55 – 65
<i>Myotis nigricans</i>	<i>Myotis nigricans</i>	EF: 45 - 50



Figure 4. SM2Bat+ recorder set in Lake E.

3.4. Statistical analysis

Normalization tests were performed to check if my variables (richness and total activity, buzz sequences and social calls) were normally distributed. Shapiro-Wilk and the Kolmogorov-Smirnov tests were used from the “stats” package for R (Team, 2013). Since none of my response variables were normally distributed, they were log-transformed but all variables still violated the assumption of normal distribution, even after applying log transformation.

In order to test if I could use “total activity” as a surrogate for foraging activity (based on feeding sequences) and social activity (based on social calls) in further models, Pearson correlation was tested between total bat passes and total buzz sequences and between total bat passes and total social calls. Whereas a strong positive correlation was found between number of bat passes and buzz sequences (Pearson’s correlation, $R^2 = 0.89$) (Figure 5), low correlation was found between number of bat passes and social calls (Pearson’s correlation, $R^2 = 0.14$). Therefore, I could confirm that while I could use bat passes as a surrogate of bat foraging activity, I could not extrapolate social activity.

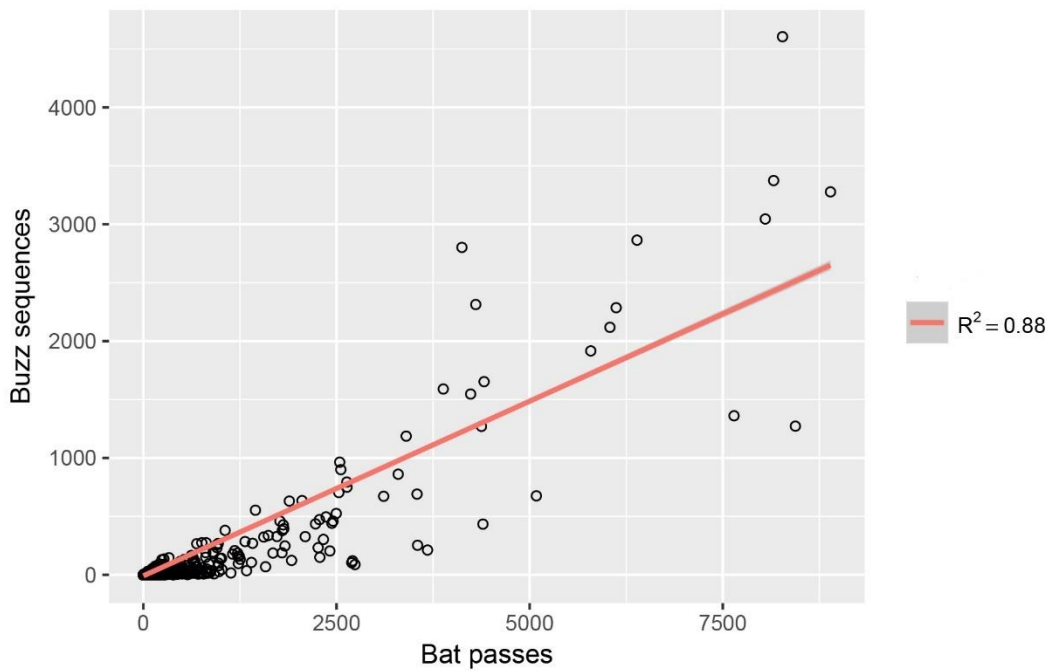


Figure 5. Correlation between bat passes and buzz sequences considering all the sonotypes.

“Richness” was defined as the total number of sonotypes registered in a single night. Both rarefaction and extrapolation are considered suitable techniques used to compensate the differences of the n^0 of individuals (in my case, bat passes) captured in each site. Rarefaction is used to calculate the expected species richness from a random subsample of n samples (minimum samples recorded in all sites) created from the original sample of N samples (Simberloff, 1978). Rarefied species was calculated using the function “rarefy” (Hurlbert, 1971; Heck *et al.*, 1975) from the package “vegan” (Oksanen *et al.*, 2008). On the other site, extrapolation is a non-parametric technique that estimates individual-based rarefaction curves ahead of the reference sample size (Colwell *et al.*, 2012). I used extrapolation in my dataset using the “iNEXT” – iNterpolation and EXTrapolation package (Hsieh *et al.*, 2016). Neither one or the other were suitable for my datasets due to the overdispersed nature of the acoustic data (with some sites where only some tens of bats were recorded and others where I got thousands).

3.4.1. Comparison of bat activity between temporary ponds and primary forest

In order to visualize and compare general activity for each bat species between habitat types (temporary lake vs primary forest), the percentage of bat passes per species recorded in each habitat was computed and plotted using a double bar plot.

3.4.2. Effect of habitat type and season on richness and total and species-specific activity

In order to study the effect of habitat type (temporary lakes vs primary forest) and season (dry vs rainy) on total activity and richness I used a Generalized Linear Mixed-effect Model (GLMM) with a Poisson distribution, fitted in a Bayesian framework using Markov chain Monte Carlo method (MCMC). Bolker *et al.* (2009) recommended GLMMs as the best tool for analyzing non-normal sets of data with random effects and also recommended to use the Poisson distribution with a log-link when the response variable consists of count data. My response variables were richness (total number of species) and activity (both total and species-specific). The fixed effects were habitat type (temporary ponds and primary forest) and season (dry and rainy) and the random factor was the sampling locality (Dimona, Porto Alegre, Km 21, Km 41, Colosso and Cabo Frio). In the models, I also considered the interaction between both fixed-effect variables to test the influence of each variable in the response independently. Models were built with the “MCMCglmm” R package (Hadfield, 2010), and the interaction plotted with the “effects” package in the R software (Fox, 2003).

3.4.3. Effect of lake size on richness and total and species-specific activity

As lake size did not vary continuously, I grouped them into three categories: “Small” (up to 200 m²); “Medium” (between 2000 and 3000 m²); and “Large” (more than 9000 m²). As my data were not normally distributed, I applied the non-parametric Kruskal-Wallis test to analyze the effect of the temporary lake size on the number of bat passes per species. For a multiple comparison between size categories I used the function “kruskal” (Conover, 1999) from the “agricolae” R package (de Mendiburu, 2016). Only for these analyses, all the species from the family Molossidae were discarded as they are known to not forage in cluttered environments and small lakes (Mora *et al.*, 2004; Kalko *et al.*, 2008).

3.4.4. Nightly activity patterns

For each recorded species, activity patterns along the night were quantified and plotted for both habitat types using polynomial regression curves with 95% confidence intervals. Species-specific activity patterns for both habitats were computed using the percentage of the activity per species per hour across the night using the following formula:

$$N^{\circ} \text{ of "Bat passes" per Species per Hour} / N^{\circ} \text{ of "Bat passes" per Night} * 100$$

All plots were built using the package “ggplot2” in R (Wickham, 2009) and all statistical analyses were conducted in the program R studio version 0.99.902 and the R version 3.3.2 for Windows (R Core Team, 2013).

4. Results

From a total of 290.899 files I identified 353.099 bat passes, 69.454 buzz sequences and 542 social calls.

4.1. Species percentage of occurrence in temporary ponds and primary forest

Whereas the majority of the recorded species and sonotypes was mostly recorded at the temporary lakes, several (*Furipterus horrens*, *Cormura brevirostris*, *Centronycteris maximiliani*, *Myotis riparius*, *Pteronotus sp1*, *Pteronotus rubiginosus*, *Saccopteryx bilineata*, *Saccopteryx leptura* and *Vespertilionidae 1*) were also present in primary forest (Figure 6). Specifically, only *Pteronotus sp1*, *Pteronotus rubiginosus* and *Furipterus horrens* were more often recorded in the primary forest than in the temporary lakes (Figure 6).

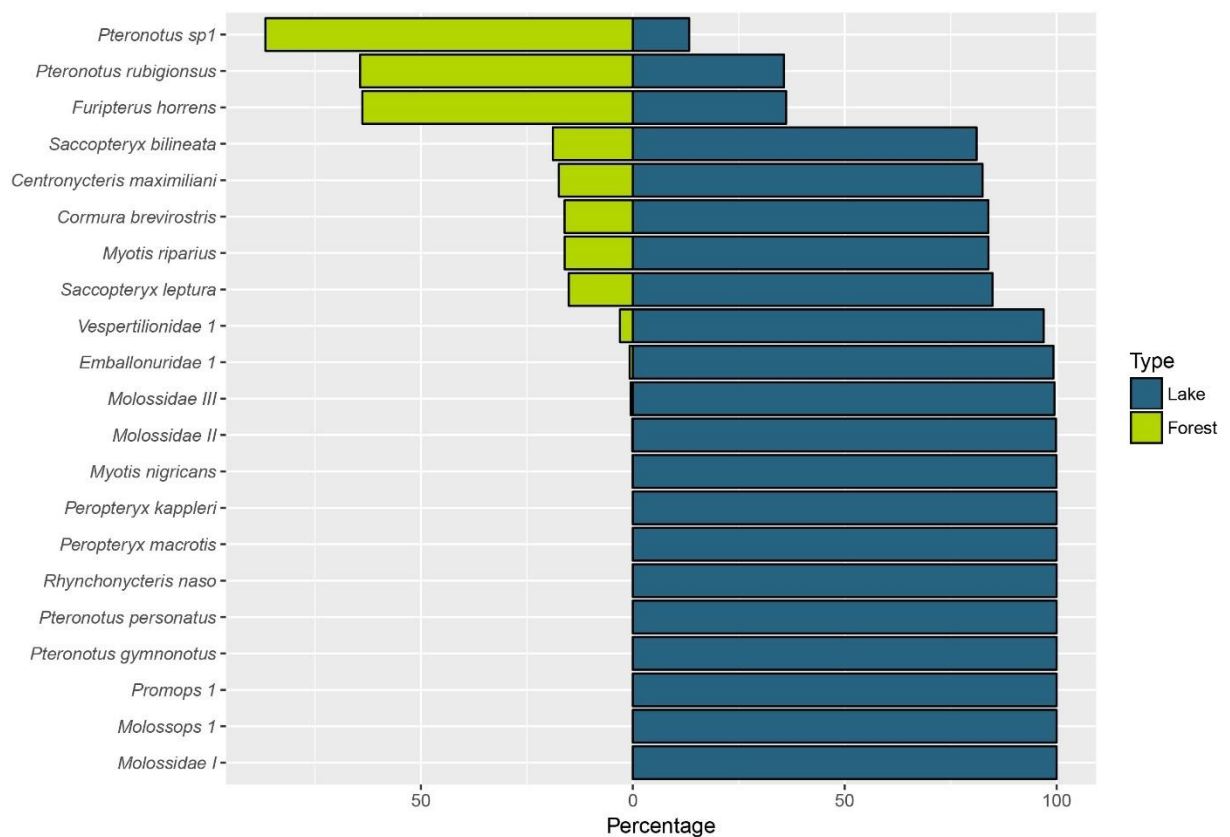


Figure 6. Percentage of species occurrence in temporary lakes and rainforest.

4.2. Effect of habitat type and season on aerial insectivorous bats

4.2.1. Richness and total activity

Richness and total activity were significantly higher in the temporary ponds than in the rainforest (Table 3, Figure 6, Figure 8 and Figure 7). Richness was also significantly higher in the rainy season than in the dry season (Table 3 and Figure 9). I also found significantly more buzz sequences and social calls in the temporary lakes (Table 3 and Figure 7). Moreover, while richness significantly increased in the rainy season in the primary forest, it decreased in the temporary lakes (Figure 8).

Table 3. Summary of the MCMC-GLMM testing the effect of habitat type and season on richness and total activity. Significant p-values (<0.05) are marked in bold. The independent variable “Type” indicates the habitat type; “Season” indicates the season; “Interaction” indicates the interaction between both fixed-effect variables with each response variable; and “Locality” indicates the sampling sites.

Model: Y ~ Season * Type+ (1 Locality)					
Richness					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.15	0.06	0.26	8.96	p<0.05
Habitat type	0.85	0.72	0.98	5.06	p<0.05
Intercept	-0.19	-0.35	-0.07	4.69	p<0.05
Total activity					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.14	-0.20	0.48	1000	0.42
Habitat type	2.96	2.55	3.32	1000	p<0.05
Intercept	-0.02	-0.49	0.56	1000	0.94
Buzz sequences					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.14	-0.44	0.77	420.3	0.62
Habitat type	4.04	3.22	4.64	838.9	p<0.05
Intercept	0.33	-0.45	1.22	485.1	0.47
Social calls					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.91	-1.02	2.97	151.4	0.38
Habitat type	4.54	2.51	6.53	124.2	p<0.05
Intercept	-0.38	-2.80	1.61	158.5	0.75

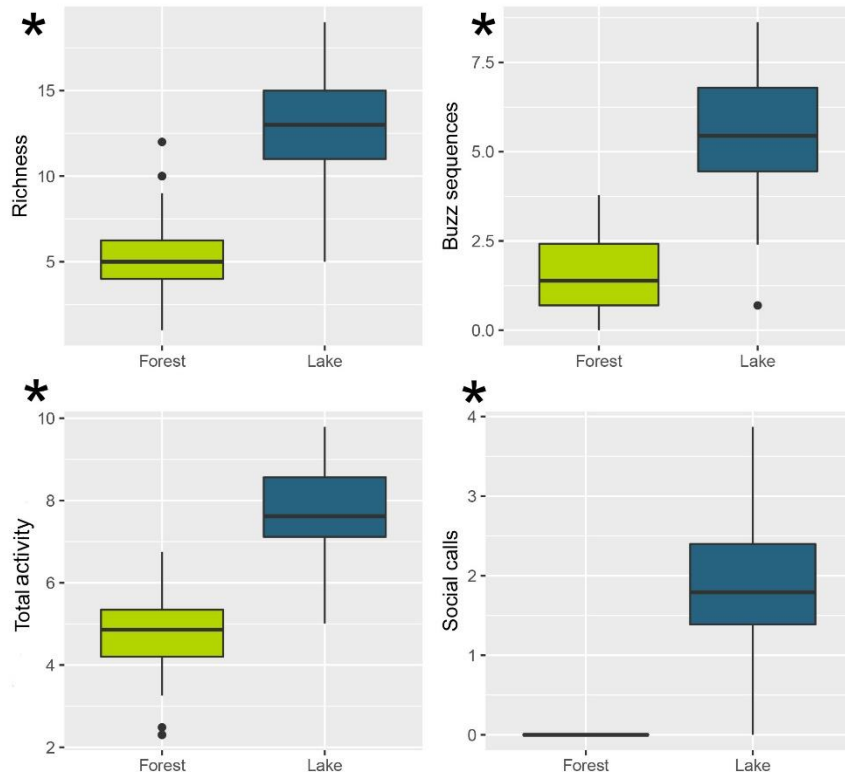


Figure 7. Richness, total activity and number of buzz and social call sequences per night in primary forest and temporary lakes. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

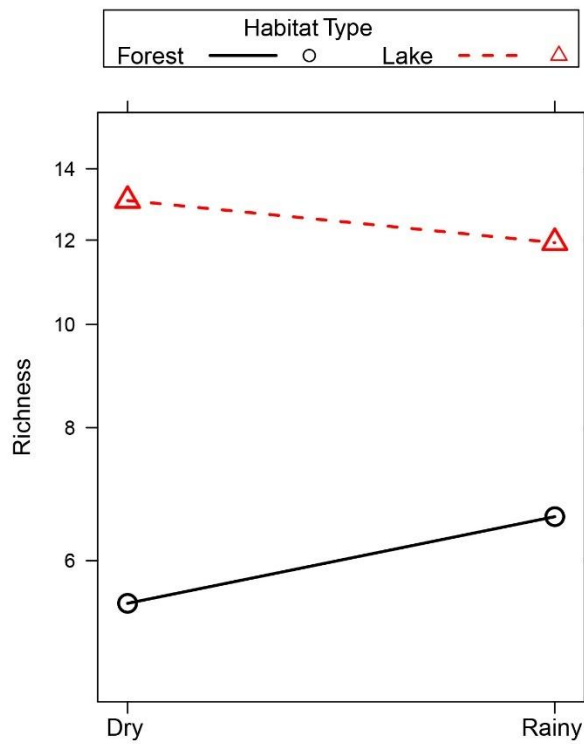


Figure 8. Interaction plots for richness between habitat type (forest and lake) and season (dry and rainy).

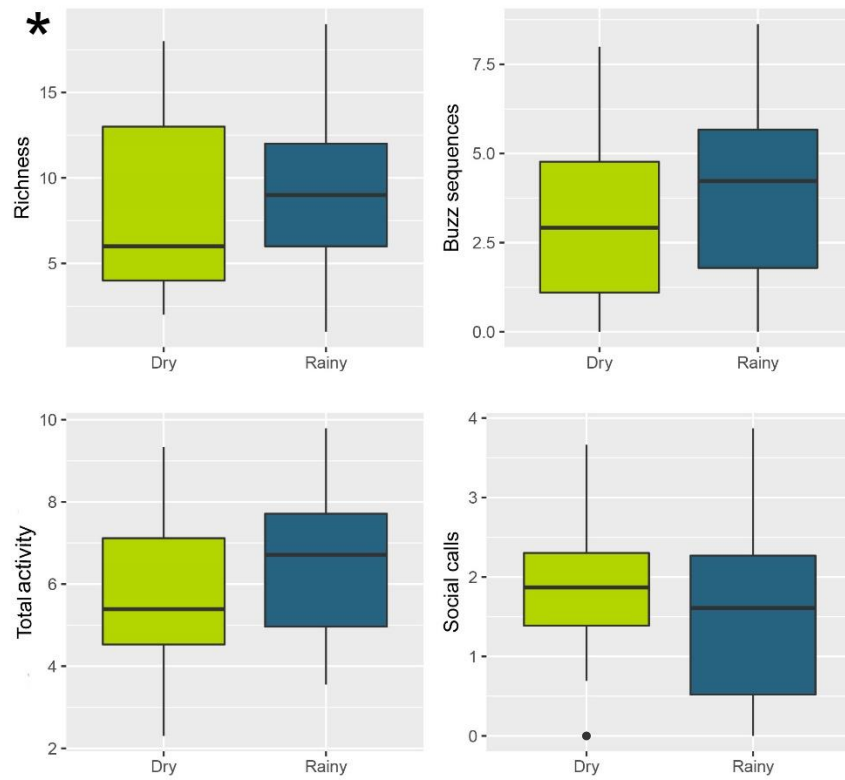


Figure 9. Richness, total activity and number of buzz and social call sequences per night in the dry and rainy season. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

4.2.2. Species-specific responses

Cormura brevirostris, *Centronycteris maximiliani*, *Myotis nigricans*, *Myotis riparius*, *Peropteryx kappleri*, *Peropteryx macrotis*, *Pteronotus gymnonotus*, *Pteronotus personatus*, *Rhynchonycteris naso*, *Saccopteryx bilineata* and *Saccopteryx leptura* and the sonotypes *Emballonuridae 1*, *Molossidae I*, *Molossidae II*, *Molossidae III*, *Molossops 1*, *Promops 1* and *Vespertilionidae 1* were significantly more detected in temporary ponds than in rainforest (Figure 10, Figure 11, Figure 12 and Table 6 in Appendix 2). On the other hand, only *Furipterus horrens* and *Pteronotus sp1* had significantly higher relative abundances in the primary forest (Figure 11, Figure 12 and Table 6 in Appendix 2). **Error! Reference source not found.**

In terms of seasonality, whereas the species-specific activity of *Cormura brevirostris*, *Centronycteris maximiliani*, *Myotis nigricans* and *Saccopteryx leptura* and the sonotype *Molossidae III* was significantly higher in the rainy season (Figure 13 and Figure 15), for the sonotypes *Molossops 1*, *Promops 1* and *Vespertilionidae 1* it was higher in the dry season (Figure 14, Figure 15 and Table 6 in Appendix 2).

However, for some species the differences between temporary ponds and forests significantly differed depending on the season, i.e. there was a significant interaction effect. While the species-specific activity of *Centronycteris maximiliani* and *Peropteryx kappleri* and the sonotype *Vespertilionidae 1* significantly increased in the rainy season in primary forest, it was almost constant along the year in the temporary lakes. While the species-specific activity of *Myotis nigricans* and the sonotypes *Molossops 1* and *Promops 1* significantly increased in the rainy season in temporary lakes, for all it decreased in primary forest. The species-specific activity of *Pteronotus rubiginosus* and sonotype *Molossidae III* decreased between seasons in both habitats but more drastically in the temporary ponds (Table 6 and plots in Appendix 2).

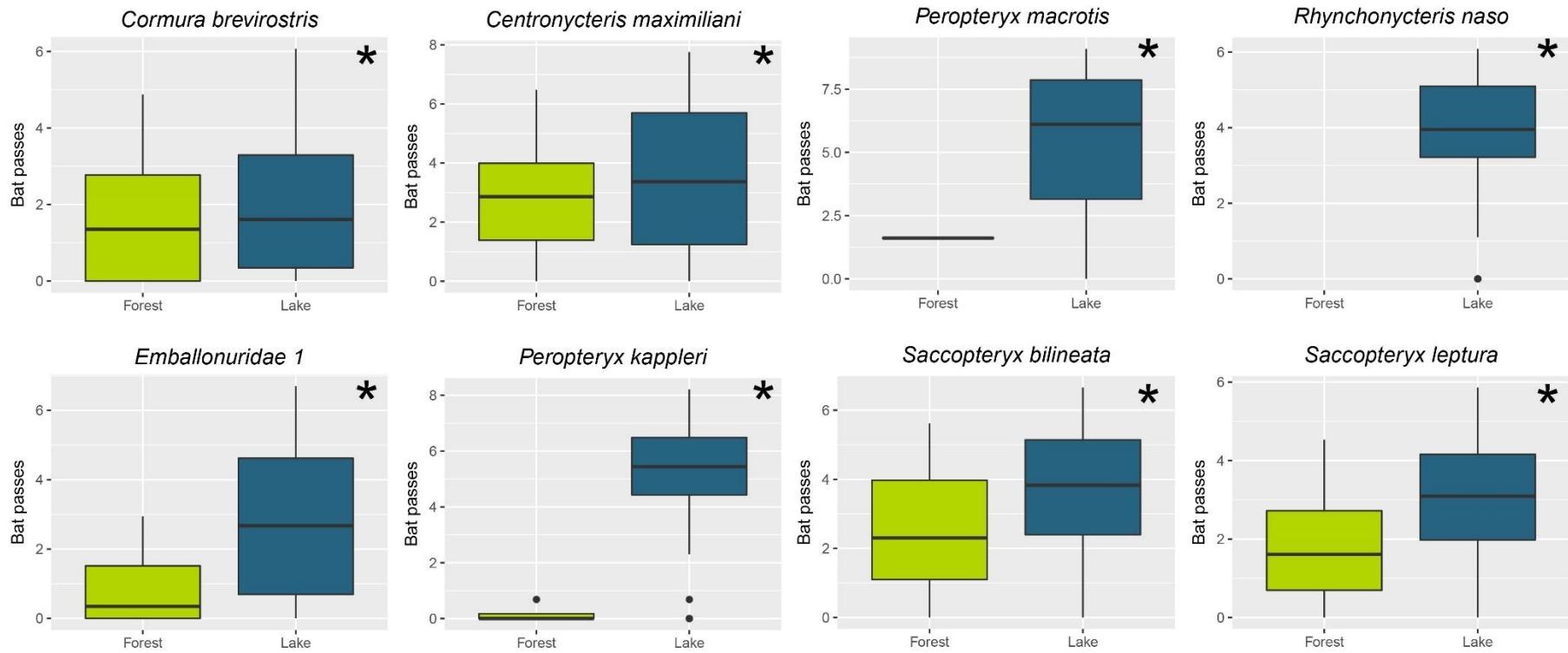


Figure 10. Total number of bat passes per species per night between primary forest and temporary lakes in emballonurid bats. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

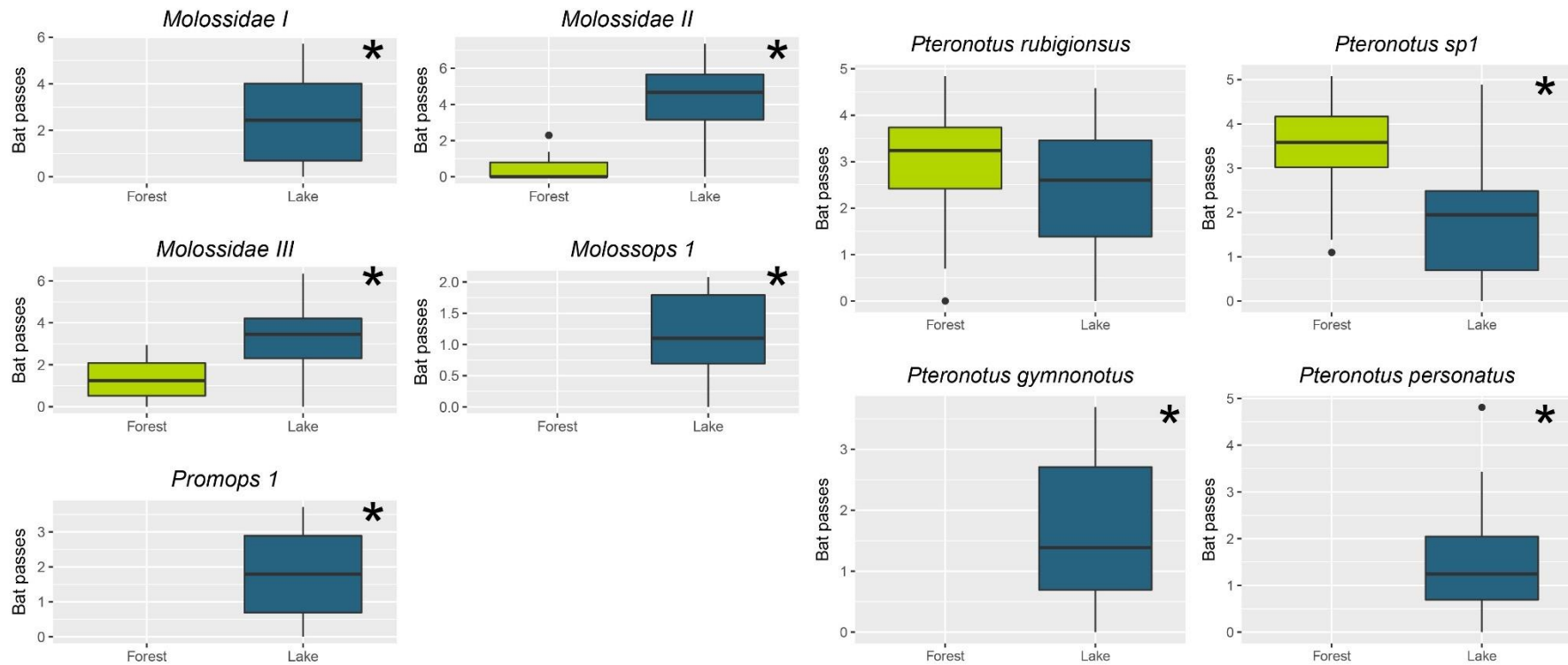


Figure 11. Total number of bat passes per species per night between primary forest and temporary lakes in molossid and mormoopid bats. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

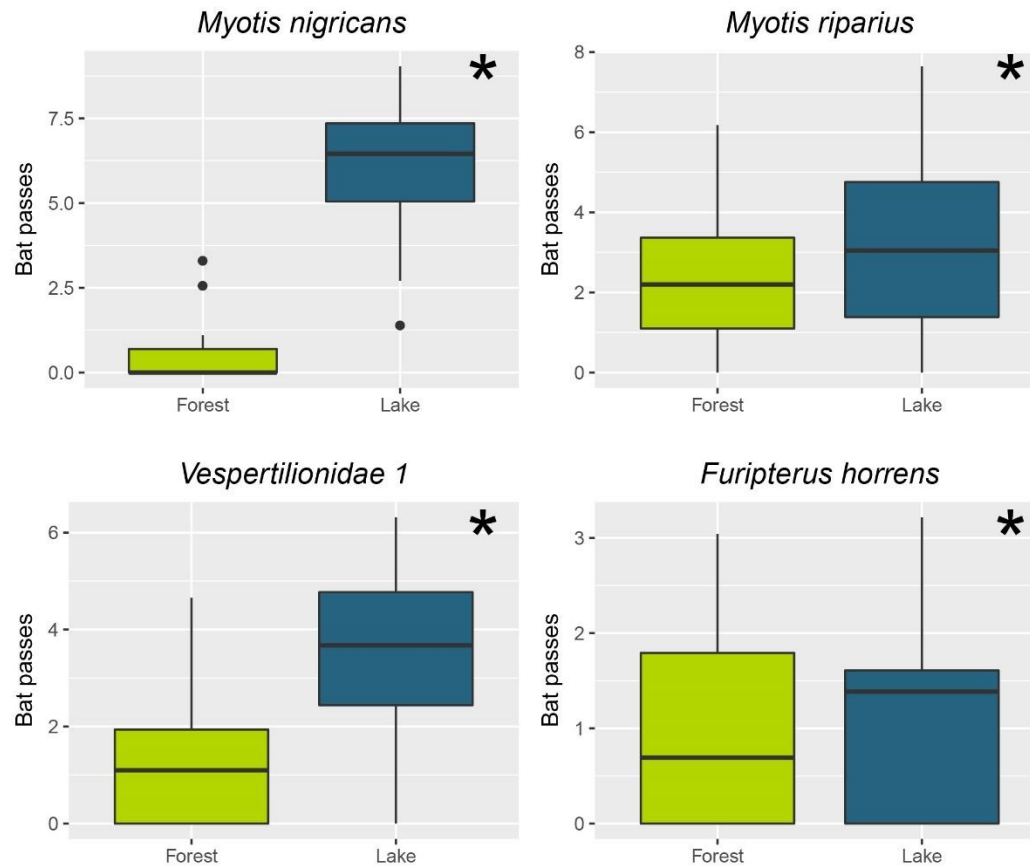


Figure 12. Total number of bat passes per species per night between primary forest and temporary lakes in vespertilionid and furipterid bats. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

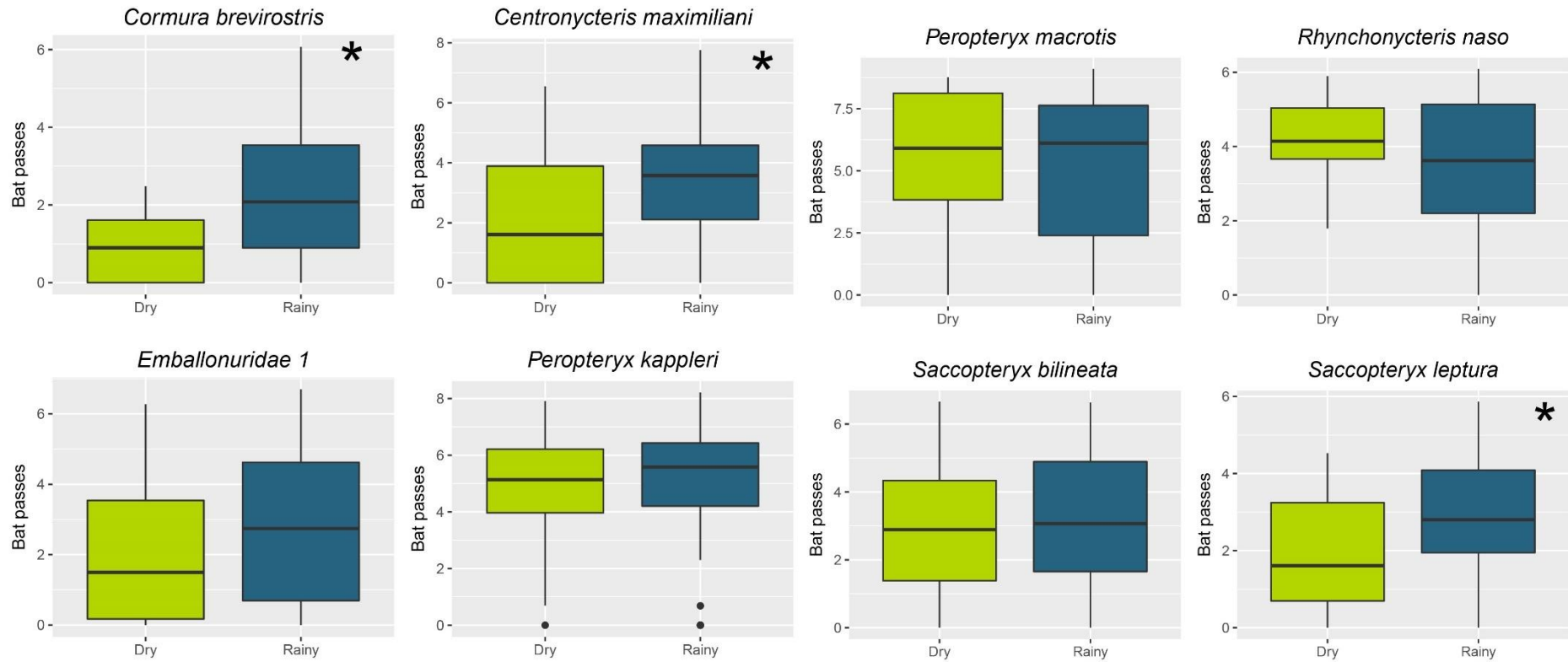


Figure 13. Total number of bat passes per species per night between dry and rainy season in emballonurid bats. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

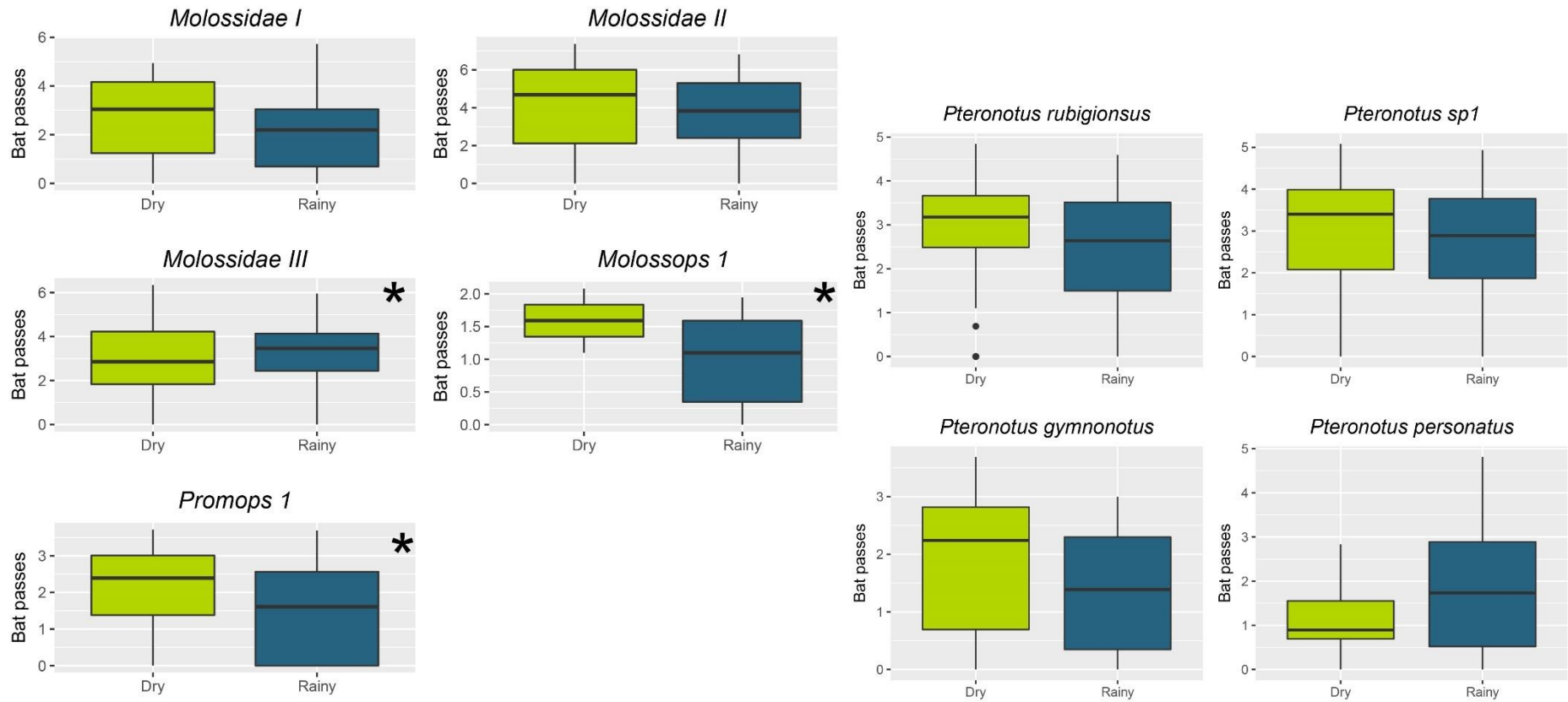


Figure 14. Total number of bat passes per species per night between dry and rainy season in molossid and mormoopid bats. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

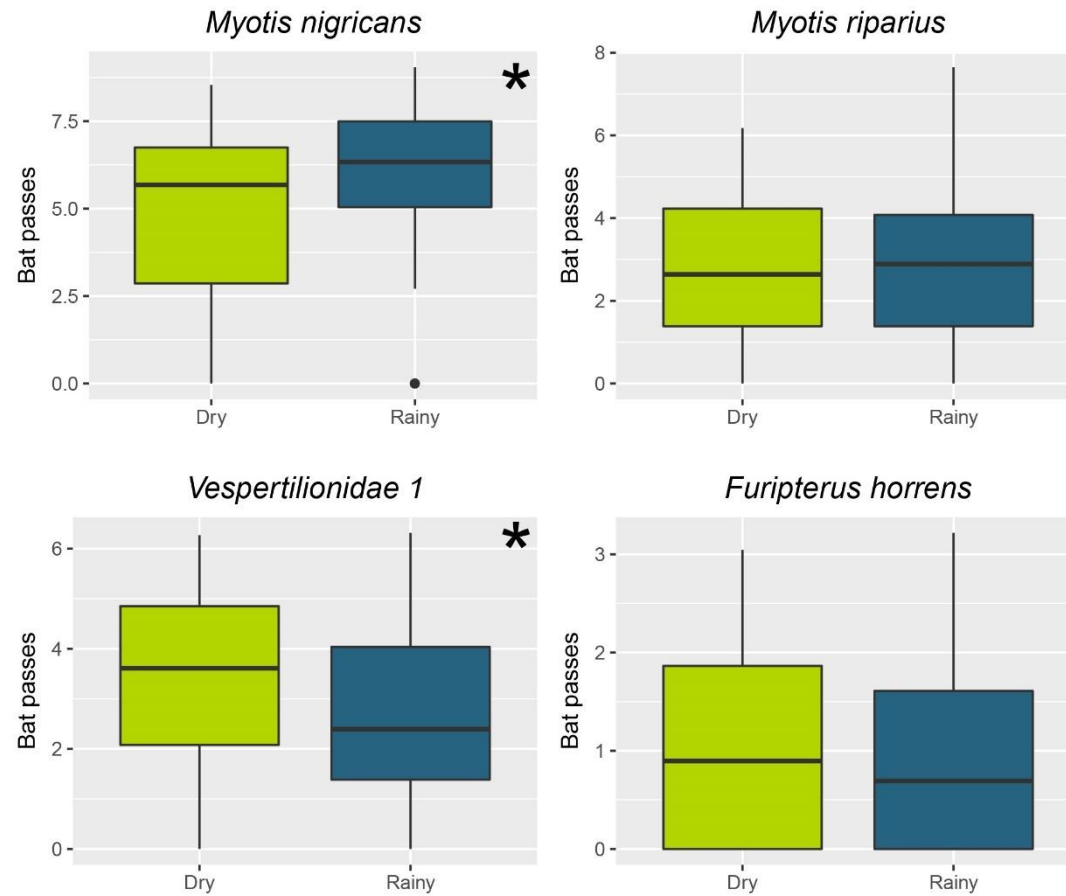


Figure 15. Total number of bat passes per species per night between dry and rainy season in vespertilionid and furipterid bats. Axis Y has been log-transformed. The * indicates significance ($p < 0.05$).

4.3. Effect of lake size

4.3.1. Richness and total activity

Temporary ponds size was simplified as a categorical variable (considering only the following groups: small, medium and large) and significant differences were found between richness for all the size categories and for total activity between the large lakes and the medium, large and small size categories (Table 4 and Figure 16). Richness and total activity values were significantly greater in the larger ponds than in the other two categories. Regardless buzz sequences, I found significant differences between size categories (Table 4 and Figure 16). Hence, in larger lakes there were significantly more feeding recordings than in the medium and small ones. Social call sequences had significant differences between large and small ponds but not between the other categories (Table 4 and Figure 16). Thus, the large and medium ponds had significantly more social call sequences recorded than the small ones.

Table 4. Results of the Kruskal-Wallis test for the relationship between richness, total activity, buzz and social call sequences and the three size categories of the temporary lakes. Significant p-values (<0.05) are marked in bold.

Richness				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	14.04	0.07	-0.71	28.78
Small-Large	38.48	p<0.05	22.47	54.49
Small-Medium	24.44	p<0.05	11.22	37.66
Total activity				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	24.42	p<0.05	8.98	39.85
Small-Large	36.71	p<0.05	19.95	53.46
Small-Medium	12.29	0.09	-1.55	26.12
Buzz sequences				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	19.91	p<0.05	4.39	35.44
Small-Large	36.23	p<0.05	19.37	53.08
Small-Medium	16.31	p<0.05	2.39	30.23
Social calls				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	5.68	0.93	-7.90	19.25
Small-Large	15.15	p<0.05	0.40	29.89
Small-Medium	9.47	0.18	-2.70	21.64

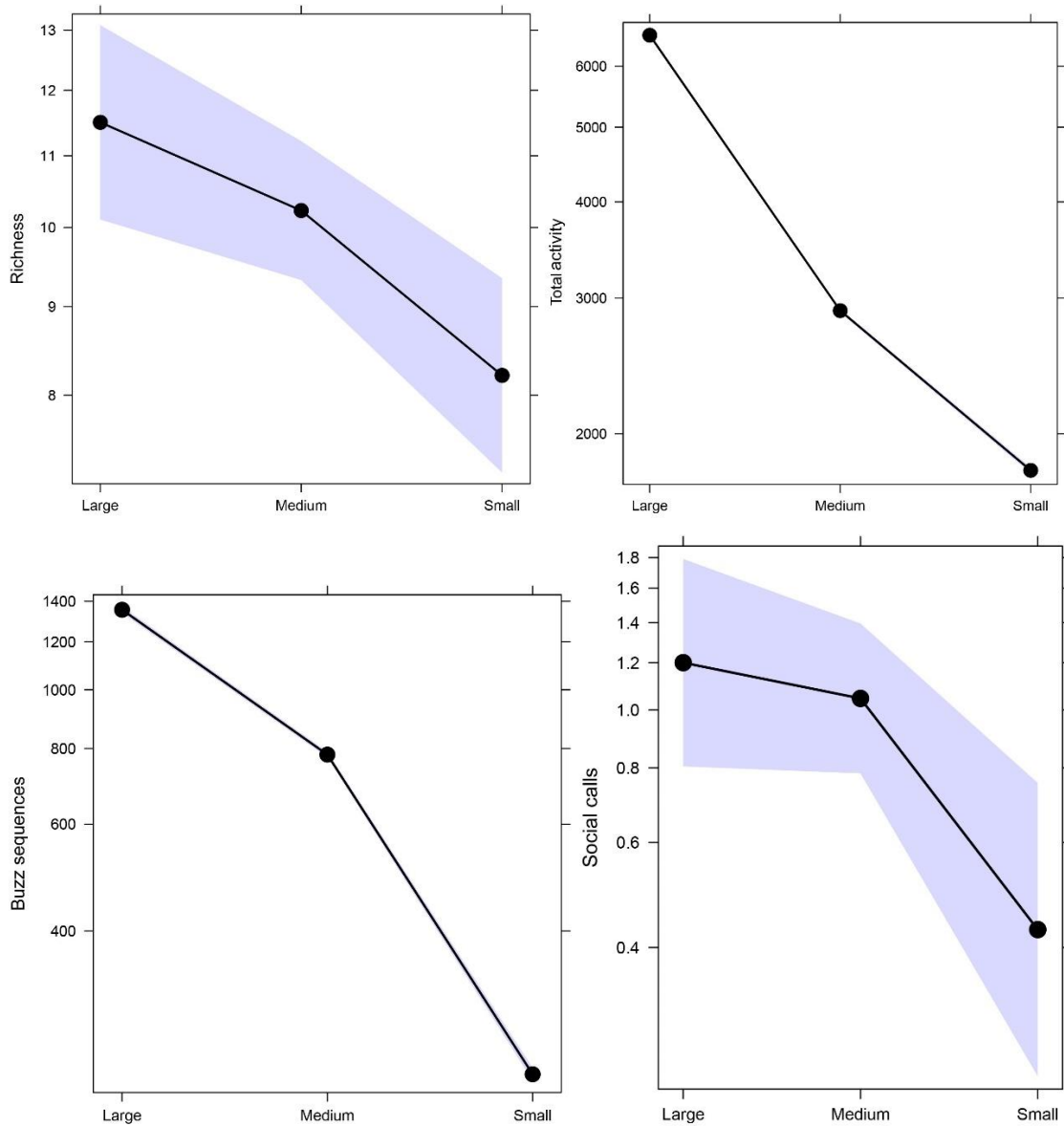


Figure 16. Comparison of richness, total activity, buzz and social call sequences (without molossid bats), per site per night between different size categories of temporary lakes. “Small” (up to 200 m²); “Medium” (between 2000 and 3000 m²); and “Large” (more than 9000 m²). Blue line indicates the confidence interval.

4.3.2. Species-specific responses to lake size

While some aerial insectivorous bat species tended to be significantly more detected over large size temporary ponds (> 9000 m²): the vespertilionid species *Myotis nigricans* and the furipterid *Furipterus horrens*; others were highly detected in both medium and large lakes: the emballonurid *Rhynchonycteris naso*, *Saccopteryx bilineata* and the sonotypes *Emballonuridae 1* and the mormoopid species *Peropteryx kappleri* and *Peropteryx macrotis* (Figure 17, Figure 18 and Table 7 in Appendix 2). The emballonurid species *Centronycteris maximiliani*, the mormoopid species *Pteronotus rubiginosus* and *Pteronotus sp1*, and the vespertilionid *Myotis riparius* were only significantly more detected in the small size temporary lakes (Figure 17, Figure 18 and Table 7 in Appendix 2).

Bat activity levels for the species *Cormura brevirostris*, *Pteronotus gymnonotus*, *Pteronotus personatus*, *Saccopteryx leptura* and the sonotype *Vespertilionidae 1* did not seem to be affected by the lake size (Figure 17, Figure 18 and Table 7 in Appendix 2).

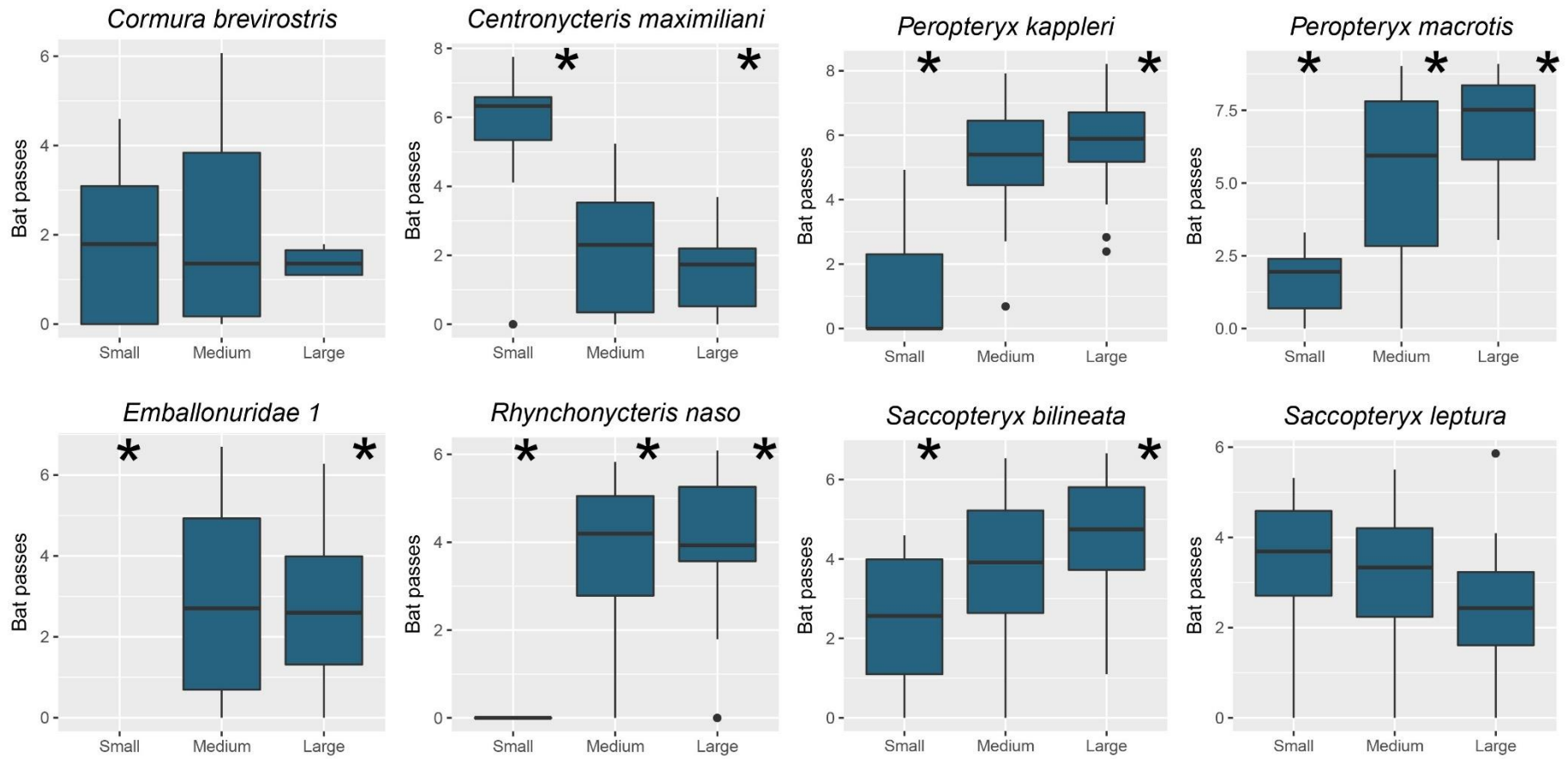


Figure 17. Species and sonotypes activity per site per night between temporary lake size in emballonurid bats. The * indicates significant interaction ($p < 0.05$) between temporary lake size (tested with a Kruskal-Wallis test). If * is at the right side of the box from “Large” category, it indicates significant interaction between small and large size categories.

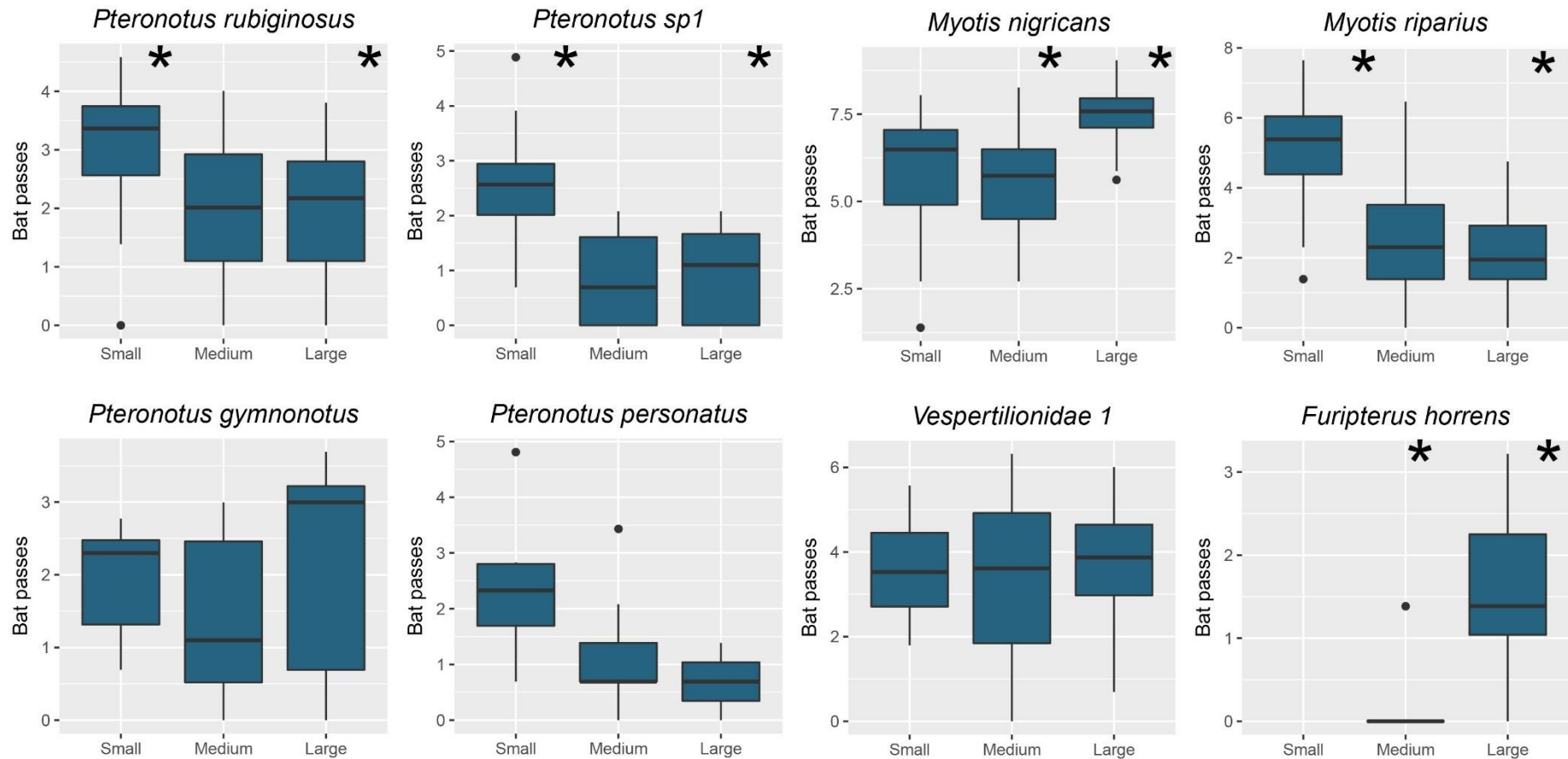


Figure 18. Species and sonotypes activity per site per night between temporary lake size in mormoopid, vespertilionid and furipterid bats. The * indicates significant interaction ($p < 0.05$) between temporary lake sizes (tested with a Kruskal-Wallis test). If * is at the right side of the box from “Large” category, it indicates significant interaction between small and large size categories.

4.4. Activity patterns along the night

4.4.1. Emballonuridae

All species had the highest number of bat passes during the first hours of the night (18:00 – 19:00) in both habitats with the exception of the *Pteropteryx* species, that kept a constant low activity in the temporary lakes, and *Centronycteris maximiliani* in the primary forest (Figure 19). Moreover, *Cormura brevirostris*, *Rhynchonycteris naso*, *Saccopteryx bilineata* and *Saccopteryx leptura* had a second peak of activity in both habitats the last three hours of the night (Figure 19).

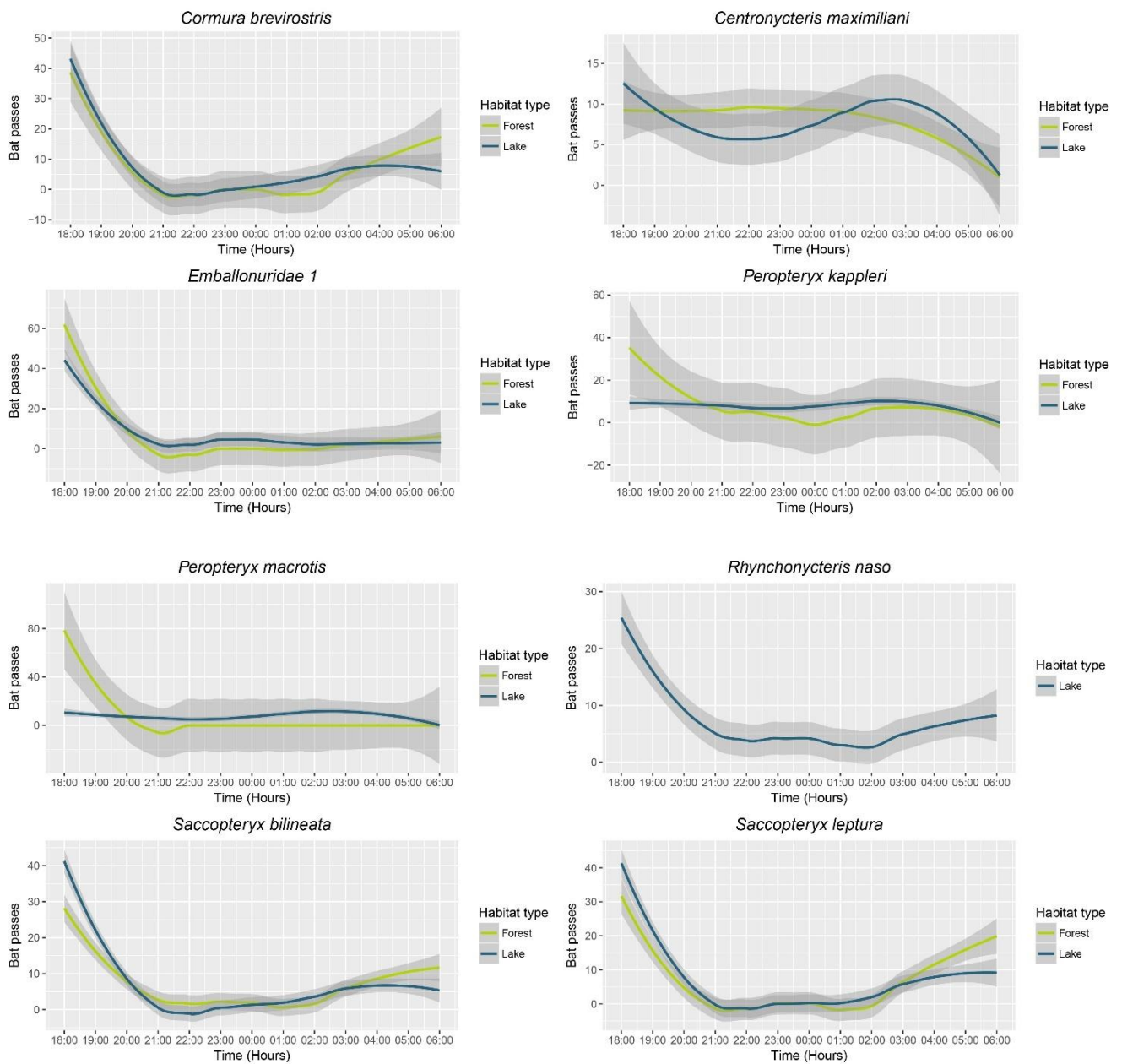


Figure 19. Activity patterns of each species of the Emballonuridae family along the night in each habitat type: primary forest and temporary lakes.

4.4.2. Molossidae

The sonotypes *Molossidae II* and *Molossidae III* were the only ones from the family Molossidae found in both habitats. All the sonotypes had the highest peak of activity the first hour of the night (18:00), then their activity decreased till 21:00 – 22:00 and kept more or less constant the rest of the night in both habitat types (Figure 20). Furthermore, for the sonotypes *Molossidae III* and *Promops 1* there was a second, although lower, peak of activity in the temporary ponds between 02:00 – 03:00 (Figure 20).

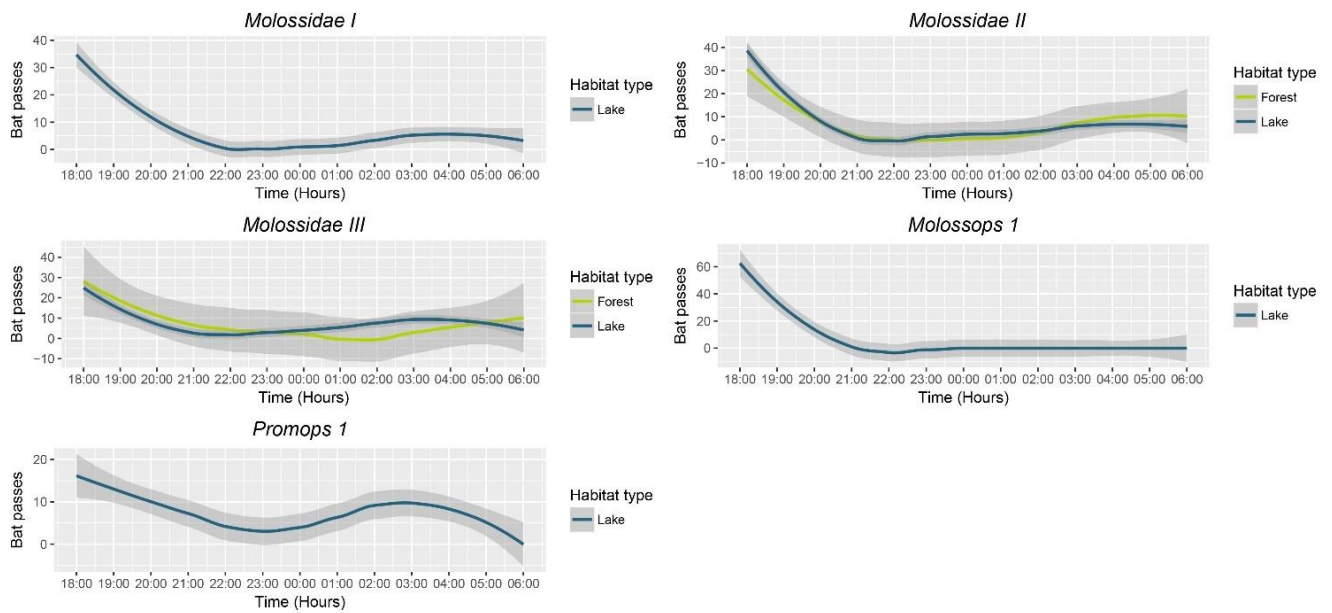


Figure 20. Activity patterns of each species of the Molossidae family, along the night in each habitat type: primary forest and temporary lakes.

4.4.3. Mormoopidae

All mormoopid species had similar activity patterns along the night. The activity reached its maximum between 22:00 – 00:00 in both habitats for all the species. *Pteronotus gymnonotus* and *Pteronotus personatus* were not detected in the primary forest and thus, their activity patterns have not been assessed in this habitat. Species-specific activity for all the species tended to decrease from midnight till sunset (Figure 21).

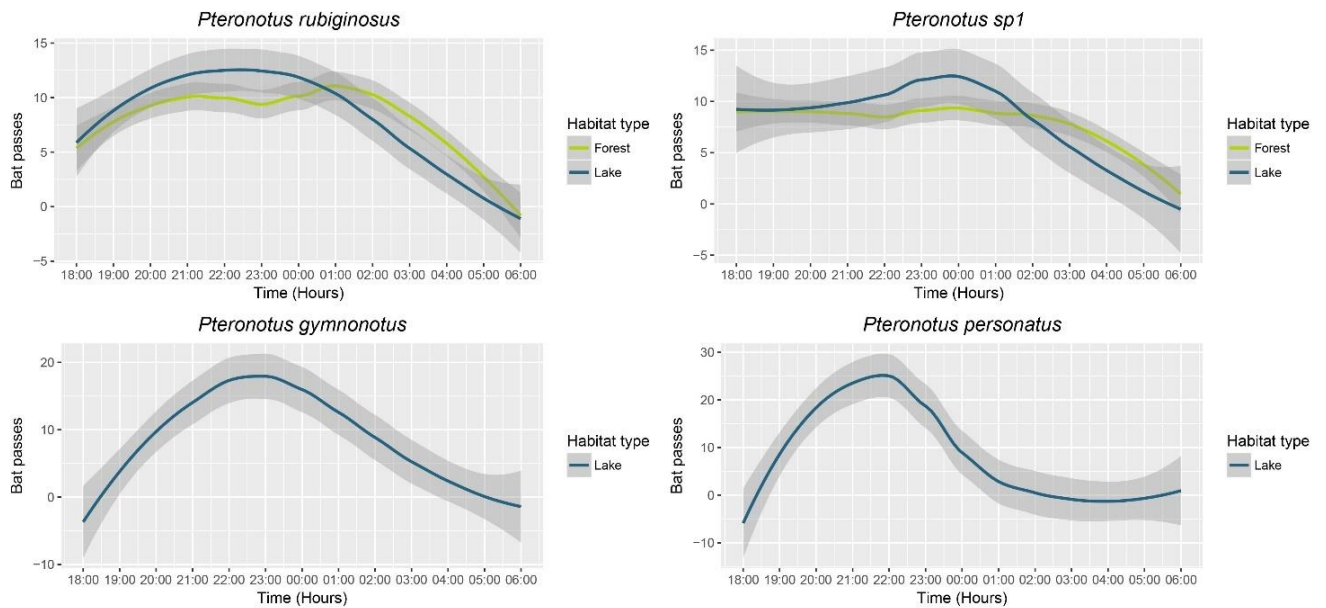


Figure 21. Activity patterns of each species of the Mormoopidae family, along the night in each habitat type: primary forest and temporary lakes.

4.4.4. Vespertilionidae and Furipteridae

The highest species-specific activity for the Vespertilionidae species was found the first two hours of the night (18:00 – 19:00) in both habitats with a second and lower activity peak at the end of the night (03:00 – 05:00). Both peaks were always a bit higher in the primary forest than in the temporary ponds, while the percentage of detections between 20:00 and 02:00 was almost always higher in the lakes than in the forest (Figure 22).

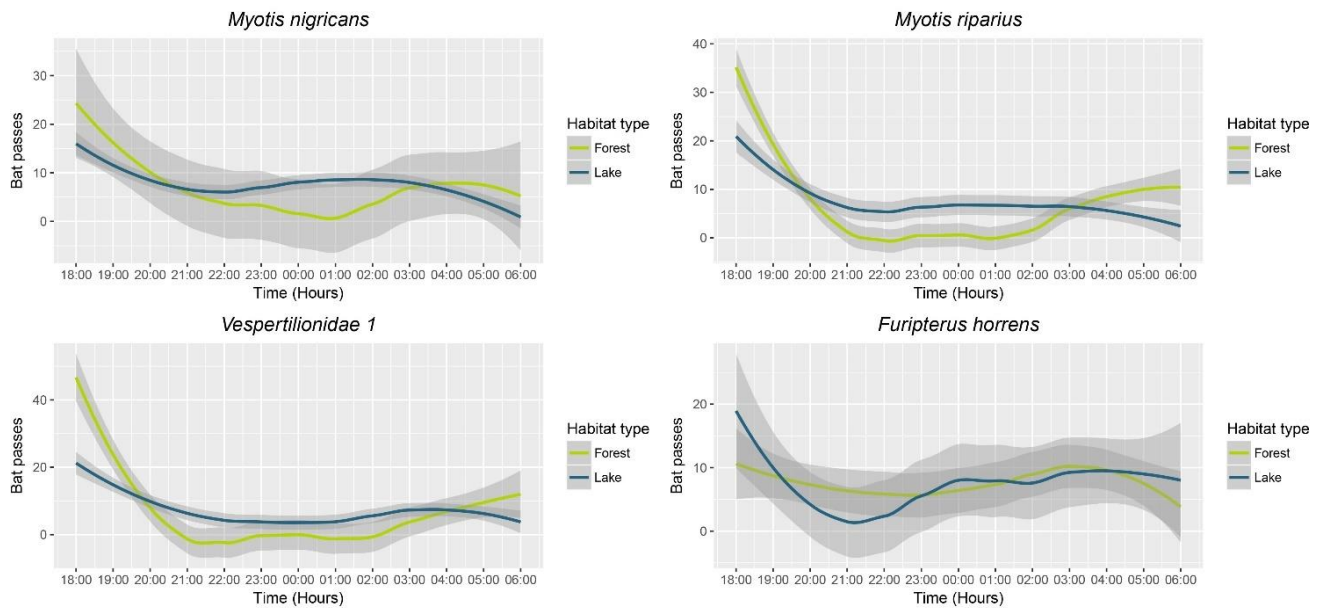


Figure 22. Activity patterns of each species of the Vespertilionidae and Furipteridae families, along the night in each habitat type: primary forest and temporary lakes.

5. Discussion

5.1. Effect of habitat, season and lake size on richness and total activity

Richness, total activity, number of buzz and social call sequences of the aerial insectivorous bats over the temporary ponds were more than twice the one of those recorded within the primary rainforest. Moreover, aerial insectivorous bats not only used the temporary ponds more than the primary forest to forage and drink, but also, contrary to what would be expected, bats used the temporary ponds more during the rainy season. Several factors can influence the significant differences I have found.

Riparian habitats and waterbodies, like temporary lakes, usually have higher abundance of insects than dense forests (Fukui *et al.*, 2006; Chan *et al.*, 2008; Hagen & Sabo, 2011) and especially during the rainy season (Dudgeon, 1989; 1996a, 1997; Chan *et al.*, 2008). Additionally, with the monthly increment of precipitation, lakes and pond have bigger water surfaces that provide more micro-habitats than during the dry season. Hence, greater diversity of aerial insectivorous bats can exploit the waterbodies. Additionally, most of the Neotropical temporary ponds are surrounded with dense vegetation that provides shade over its waters. This shade is beneficial for emerging aquatic insects, that seek for cover from the weather conditions such as wind and/or rain thus, it provides an excellent area for bats to forage. Moreover, the shade can also be used by the bat species which emerge early, few minutes before the dawn, allowing them to forage some more time.

Lakes and ponds have lower habitat complexity and the water surfaces are smoother than on flowing rivers and streams (Almenar *et al.*, 2006; Seibold *et al.*, 2013) which allows species with inferior maneuverability to forage and drink there. For example, the open, deep (1 – 1.5 m) and calm surfaces of water are ideal for all types of bats to drink as they have enough space to maneuver, independently of their wing morphology. Moreover, bat specialists on foraging in cluttered and open spaces must also reach the waterbodies to drink (Adams & Thibault, 2006; Russo *et al.*, 2012; Almeida *et al.*, 2014; Salvarina, 2016) and as some of the surveyed temporary ponds were partially connected to streams, bats can use these linear corridors as commuting routes (Palmeirim & Etheridge, 1985; Meyer *et al.*, 2005). In addition, the proximity to waterbodies seems to influence roost selection of some bat species (Campbell, 2009; Korine *et al.*, 2013).

Finally, studies have shown that emerging aquatic insect can suffer alterations of their assemblage structures and physiological changes due to climate change (Greig *et al.*, 2012; Jonsson *et al.*, 2015). Thus, modifications on the patterns of emergence of aquatic insects affect the terrestrial species that consume and mainly rely on this food source

e.g. birds (Strasevicius *et al.*, 2013). Therefore, climate-induced changes like rise in temperature and intensification of drought periods, can affect Neotropical aerial insectivorous bats too.

5.2. Effect of habitat type, season and lake size on species-specific activity

5.2.1. Emballonuridae

The family *Emballonuridae* is widely distributed in the tropical regions of America and in the study area, I recorded seven species and classified one sonotype, from the genera *Cormura*, *Centronycteris*, *Peropteryx*, *Rhynchonycteris* and *Saccopteryx*. Emballonurid bats have different habitat and foraging preferences: *Cormura brevirostris* is more associated with forest interior (Estrada-Villegas *et al.*, 2010), *Centronycteris maximiliani*, *Peropteryx kappleri*, *Peropteryx macrotis* and *Saccopteryx bilineata* mainly prefer the edge spaces (Jung *et al.*, 2007; Kalko *et al.*, 2008b; Barboza-Marquez *et al.*, 2014), and *Saccopteryx leptura* mostly forage in open spaces (Gardner, 2007; Jung *et al.*, 2007). My results on *Rhynchonycteris naso* foraging habitat coincide with the already existing literature, which proved that this species mainly forages over water (e.g. Nogueira & Pol, 1998; Fenton *et al.*, 1999a; Jung *et al.*, 2007; Pereira *et al.*, 2009). However, none of them specifically studied *R. naso* foraging activity over temporary ponds. Moreover, *R. naso* is the emballonurid bat most strongly associated with lakes, as it was never recorded in the primary forest during the whole study period. This is likely due to its foraging behavior, as it tends to forage over water bodies at a height of 3 m and mainly preys on mosquitos (Ceballos, 2014).

Some emballonurid bat species (*C. brevirostris*, *C. maximiliani* and *S. leptura*) were significantly more recorded in the rainy season than in the dry season because higher densities of aquatic insects in the riparian habitats are formed during the rainy season (Chan *et al.*, 2008). *C. maximiliani* and *S. leptura* are two species widespread across South America however, they are very elusive and difficult to sample with mist-nets. Hence, little is known about their ecology in the Neotropics and unfortunately, my results on them cannot be compared with many similar studies. My findings provide new natural history data for *C. maximiliani* was significantly more detected over small ponds. Small waterbodies are associated with dense surrounded vegetation (e.g. Lake G) that can provide edge specialist species, like *C. maximiliani* suitable foraging habitats. Moreover, my results on *S. leptura* foraging habitat are supported by Costa *et al.* (2012) which found similar findings in Rio de Janeiro lakes.

Ceballos (2014) described how *S. bilineata* prefers to forage over waterbodies at a height of 1 – 2 m protected by the shade of trees which could justify why I detected it more often in large and medium ponds. Additionally, *S. bilineata* must commute to the waterbodies to drink (Costa *et al.*, 2012; Russo *et al.*, 2012).

Marques *et al.* (2015) found greater total number of bat passes for *P. kappleri* and *P. macrotis* in riparian sites at ground and subcanopy levels which could be related to the type of roost they mainly use. Voss *et al.* (2016) found they prefer to roost under or inside fallen trees. Moreover, medium and large temporary lakes can provide *P. kappleri* and *P. macrotis* with edge spaces around the pond to hunt insects and water surfaces to drink (Costa *et al.*, 2012).

5.2.2. Molossidae

The family *Molossidae* is highly diverse in tropical and subtropical regions (Simmons, 2005) and is characterized for having narrow and long wings, which involves high speed flights and quite little maneuverability (Norberg & Rayner, 1987). Molossids from the New World, with *Molossops temmickii* as the exception (Guillén-Servent & Ibáñez, 2007), are open space specialists thus, habitats such as open landscapes and above the forest canopy are perfect for them to forage (Mora *et al.*, 2004; Kalko *et al.*, 2008). It is a group difficult to sample within the rainforest with mist-nets, even with canopy nets. The best way to obtain information of their presence is by using acoustic methods on potential foraging habitats like waterbodies and open areas or by surveying known roosts. Molossid species like *Cynomops abrasus*, *Molossus molossus* and *Molossus rufus* were highly detected over lakes in an area of Rio de Janeiro, specially *M. molossus* (Costa *et al.*, 2012). Hence, my results confirmed that this family can be significantly found over waterbodies as the mentioned species were included in the Molossidae sonotypes (*Molossidae I*, *Molossidae II* and *Molossidae III*).

Although *Promops centralis* is extensively distributed across Central and South America, few is known of this species ecology (González-Terrazas *et al.*, 2016) and I provide new information about its presence in temporary Neotropical lakes. In my data, *P. centralis* was in the sonotype group *Promops 1*. Furthermore, *Molossops temminckii* mainly forage near clutter and *Molossops neglectus* on edge spaces (Guillén-Servent & Ibáñez, 2007; Loureiro & Gregorin, 2015). Both species are grouped in the sonotype *Molossops 1* which had significantly greater activity over temporary ponds during the dry season. Therefore, I suggest the species grouped as sonotypes *Molossops 1* and *Promops 1* especially needed to visit the temporary lakes to drink in the driest month of the year as they were significantly more recorded during the driest months.

The principal reason why molossid bats were mainly recorded in the waterbodies might be because it represents the main accessible drinking area in a landscape characterized by small streams and dense vegetation (Myers & Wetzel, 1983; Grindal *et al.*, 1999; González-Terrazas *et al.*, 2016). Larger lakes and ponds allow molossid bats to easily maneuver over the water surface to forage and drink, thus, higher number of species are recorded there (Adams & Simmons, 2002; Costa *et al.*, 2012). Furthermore, Malagasy molossids have been found to eat many beetles (Andrianaivoarivelo *et al.*, 2006; Andriafidison *et al.*, 2007), which have a high content in water (Gray, 1944). Thus, Malagasy molossid bats do not need to visit waterbodies that often. However, as Amazonian molossids diet is not clear yet, perhaps their prey contains less water which compels them to supply the deficit drinking from the temporary lakes.

5.2.3. Mormoopidae

The family Mormoopidae is only found in the New World humid tropical to semiarid tropical habitats and I recorded four species of the genus *Pteronotus*. My results on the habitat selection by mormoopid bats can be described by their intrinsic behavior. Amongst them, *Pteronotus sp1* was the species most closely associated with continuous rainforest, while the others (*P. rubiginosus*, *P. gymnonotus* and *P. personatus*) were equally frequently detected in lakes and forests. *Pteronotus gymnonotus* and *P. personatus* are insectivorous bats that mainly hunt insects in background-cluttered habitats like in the edges and the gaps of a forest. However, the species *P. parnellii* typically forages in highly cluttered environments (Schnitzler & Kalko, 2001; Sampaio *et al.*, 2003; Emrich *et al.*, 2014; de Oliveira *et al.*, 2015). Several authors have recently described that the species complex *P. parnellii* include two sympatric sister species in the region of Amazonia based on molecular, morphological and acoustic analysis (e.g. Clare *et al.*, 2013; Thoisy *et al.*, 2014). Therefore, I provide the first comparative quantification of activity patterns, species-specific activity and occurrence of both species (*P. rubiginosus* and *P. sp1*) in a Neotropical area.

I confirmed that both *P. rubiginosus* and *P. sp1* were similarly more related to highly cluttered habitats than the rest of the species from the genus. In some tropical regions, greater insect abundances are associated with higher density of plants at different strata (Basset *et al.*, 2003; Brehm, 2007). However, this source of prey can mainly be exploited by the bat species specialized in foraging within highly cluttered spaces (Kalko *et al.*, 1996). *P. rubiginosus* and *P. sp1* are evolutionarily specialized on detecting and hunting insects within dense foliage environments.

Little is known about *Pteronotus personatus* behavior and ecology (Smotherman & Guillén-Servent, 2008). De la Torre and Medellín (2010) described that it is associated with lowlands of semideciduous forest flying over watercourses and arroyos with dense vegetation and Voss *et al.* (2016) described they mainly roost in caves and rocks. *Pteronotus gymnonotus* is a species that in general has been very little recorded and there is scarce information about its behavior and ecology. Kalko *et al.* (2008b) and Estrada-Villegas *et al.* (2010) associated *P. gymnonotus* with forest habitats rather than open spaces and Voss *et al.* (2016) indicated it prefer to roost inside caves and rocks. For that reason, in this study I provide new information about both species foraging strategy and ecology. My results indicate *P. gymnonotus* and *P. personatus* have significantly higher activity over temporary ponds (Figure 6, Figure 11 and Table 6 in Appendix 2). On the other hand, I did not find a statistically significant preference for any lake size probably because I had fewer recording of them than for the other *Pteronotus* species (Figure 18 and Table 7 in Appendix 2). Additionally, as *P. gymnonotus* and *P. personatus* are edge space specialists, have small body size and an efficient echolocation system I suggest they prefer smaller ponds surrounded by dense vegetation, e.g. Lake G (Kalko *et al.*, 1996; Costa *et al.*, 2012).

5.2.4. Vespertilionidae and Furipteridae

The family *Furipteridae* comprises two species of different genera, *Amorphochilus* and *Furipterus*, and only the latter has been found in the Amazon rainforest and thus, in my recordings. *Furipterus horrens* is a very elusive species, difficult to catch with nets and even to record with acoustic methods probably because it emits short and low intensity calls to hunt moths (Falcão *et al.*, 2015). Its habits are not completely known and new records of its presence are published every few years. Hence, its habitat preferences are poorly known (Novaes *et al.*, 2012). On the other hand, it has been described that *F. horrens* prefers to roost inside cavities of fallen trees (Voss *et al.*, 2016). Hence, it make sense to suggest *F. horrens* prefers to forage within the primary forest. My results also indicate *F. horrens* was significantly more active over large temporary waterbodies probably to drink during the night because it mainly feed on moths (Fenton *et al.*, 1999b), which have less water content than other invertebrate families (Gray, 1944).

The family *Vespertilionidae* is the largest bat family globally, comprising more than 300 species and is found on all continents except Antarctica. Four genera are known in the Amazon rainforest: *Eptesicus*, *Lasiurus*, *Myotis*, and *Rhogeessa*. I identified two species and I classified one sonotype. My findings indicate that *M. nigricans* and *M. riparius* were both significantly more active over temporary ponds which matches with Costa *et al.* (2012) results on these species. However, whereas *M. nigricans* was frequently detected

on large lakes, *M. riparius* was more often recorded over small ones (Figure 12 and Table 6 in Appendix 2 **Error! Reference source not found.**; Figure 18 and Table 7 in Appendix 2). Several authors suggested that *M. riparius* small size and echolocation characteristics (short duration and high repetition rate of the pulses) provided this species the capacity to forage very close to the understory foliage (Norberg & Rayner, 1987; Fenton *et al.*, 1999a; Kalko & Handley, 2001; Woodman, 2003). Hence, that could explain why *M. riparius* was more often detected over the small ponds. Furthermore, for *M. nigricans* I recorded significantly greater species-specific activity during the rainy season, which could indicate this species preferentially forages on the aquatic insects that increase its densities in this period of the year (Chan *et al.*, 2008).

5.3. Species-specific activity patterns

My results indicate all recorded emballonurid bats roost inside the primary rainforest but spend most of the night foraging over temporary lakes and ponds. The peaks of activity of most species were right after sunset and between 04:00 – 06:00 in both habitats. Specifically for *Cormura brevirostris* and *Saccopteryx bilineata* in the same study area, Appel *et al.* (2016) described similar nocturnal activity patterns (Figure 19). Moreover, *Pteronotus kappleri* and *Pteronotus macrotis* prefer to roost under or inside fallen trees within the rainforest (Voss *et al.*, 2016). The activity pattern of *Saccopteryx leptura* is new information I provide with my results. I suggest the species emerges from their diurnal roosts on standing tree trunks which are available in both habitats because its nocturnal activity pattern showed two peaks, at the beginning and end of the night (Voss *et al.*, 2016) (Figure 17, Figure 19 and Table 7 in Appendix 2). Rocha *et al.* (2015) found one individual of *Centronycteris maximiliani* roosting inside a tree cavity and my results on its activity pattern, indicate a constant activity along the night inside the rainforest. Finally, my results on *Rhynchonycteris naso* activity pattern coincide with the already existing literature on this species which mainly use of waterbodies (e.g. Pereira *et al.*, 2009).

Brown (1968) and Esbérard and Bergallo (2010) conducted mist-net surveys over water bodies and found similar activity patterns for the species *Molossus ater* and *Molossus molossus*, which correspond to the sonotypes *Molossidae II* and *Molossidae I* respectively. The first peak of activity can be connected with the peak associated with crepuscular and nocturnal insects on which molossid bats prey (Brown, 1968; Meyer *et al.*, 2004). Furthermore, several authors (e.g. Isaac & Marimuthu, 1993; Weinbeer *et al.*, 2006; Russo *et al.*, 2009) suggested some bat species restrict their activity till it is dark

to reduce attacks by diurnal predators. In addition, some species included in the sonotypes *Molossidae I, II* and *III* are described to prefer to roost in the foliage and inside cavities of standing trees situated within the rainforest (Voss *et al.*, 2016). Hence, I suggest some molossid bats were probably recorded in the rainforest when heading back to their roosts inside the forest at the end of the night. This activity pattern can be appreciated in the form of a tiny peak the last hour of the night in the primary forest (Figure 20).

The results obtained for the nocturnal activity pattern of *Pteronotus gymnonotus* and *Pteronotus personatus* provide new information on this species' ecology. Moreover, it supports my hypothesis that they are highly dependent on temporary ponds as their peak of activity was only found in the aquatic habitat between 22:00 – 00:00 (Figure 21). Furthermore, the mormoopid bats were the only family which did not have a peak of activity at the beginning and/or end of the night. Perhaps mormoopid species compete for the aerial space over the temporary ponds with species from other families like the Emballonuridae (e.g. *Rhynchonycteris naso* and *Peropteryx kappleri*) or the Molossidae. Hence, when the presence of the others decrease along the night, the activity of mormopid bats increases concurrently.

Voss *et al.* (2016) described that *Furipterus horrens* prefers to roost inside cavities of fallen trees. Hence, the decrease of *F. horrens* activity over the temporary ponds during part of the night perhaps could be explained as the species returns to its roost inside the rainforest to rest (Figure 12, Figure 18 and Figure 22). Moreover, *F. horrens* increment of detectability the last hours of the night could be explained because it needs to drink water, as it has a preference for moths which have lower water content than other insects (Gray, 1944; Fenton *et al.*, 1999b).

Vespertilionid bats started and ended the night with higher number of bat passes in the primary forest however, during most of the night their flight and foraging activity was constantly higher over the temporary ponds (Figure 22). Appel *et al.* (2016) found similar results for *M. riparius* which indicated that these species had the greatest activity within the first three hours of the night inside the rainforest. In addition, Voss *et al.* (2016) suggested that *M. nigricans* roosts preferentially in cavities of vertical trees. Therefore, my results indicate that *M. nigricans* and *M. riparius* roost inside the primary forest and commute to forage over temporary ponds.

5.4. Conservation implications

There is a close relationship between aerial insectivorous bats and the characteristics of the habitat in which they inhabit. Their species-specific activity is a factor highly influenced by habitat complexity (Sleep & Brigham, 2003) because when bats forage in very cluttered spaces, they not only receive information on the presence of potential prey but also from their immediate surroundings (Schnitzler & Kalko, 2001). Therefore, the flight costs to navigate, detect and catch prey are higher in the middle of a primary forest than over a temporary pond or open areas. Furthermore, for some nonflying mammals' waterbodies can influence directly their movement as it acts like a barrier. On the other hand, for bats, which have free movement, waterbodies indirectly affect the understory vegetation and thus, can provide bats with new suitable foraging habitats. I could not find any studies describing the characteristics of waterbodies, e.g. streams and ponds on non-terrestrial species movement, from the Amazon rainforest. However, research is being done on improving remote sensing techniques to detect masses of water in the dense rainforests of the Tropics (Da Silva *et al.*, 2010). Moreover, these tools will be very useful to better describe and analyze the rise in temperatures and drought periods due to climate change and how it affects the terrestrial fauna like bats (Anderson *et al.*, 2010; Wagner *et al.*, 2011).

Despite the fact, I applied a similar sampling effort in both habitat types, sampling bat activity with detectors within the primary rainforest recorded by far less species than over temporary lakes, a mean of five in the primary forest compared to a mean of thirteen species per night (Figure 7). It is widely acknowledged that surveying only within the primary forest means we might be partially studying some species habitat, which could provide incomplete or biased results (Berry *et al.*, 2004; Kalko *et al.*, 2008; Meyer *et al.*, 2011). Another aspect could be that within the dense rainforest, bat calls can be missed due to the foliage and that the echolocation calls are emitted at a minor intensity (Monadjem *et al.*, 2010b). Thus, I must have under consideration that these aspects could have caused an underestimation of my recordings from the primary forest for e.g. species from the family *Vespertilionidae* and for *Furipterus horrens*.

With this study, I describe the high concentration of bat activity found in the tropical waterbodies and underline the importance of maintaining these temporary ponds for the conservation of Neotropical aerial insectivorous bats. Other studies also stress the importance of preserving waterbodies for insectivorous bats (e.g. MacSwiney *et al.*, 2009; Costa *et al.*, 2012). Moreover, Pereira *et al.* (2009) did a similar study in Amazonian flooded areas and concluded insectivorous bats were more abundant in the

inundated forest than in the dry ones because waterbodies provided bats suitable foraging habitats. Furthermore, as all the species must fly towards waterbodies to drink each night, surveying these habitats with acoustic methods provides greater information than within the forest (MacSwiney *et al.*, 2009; Meyer *et al.*, 2011; Almeida *et al.*, 2014).

Recent studies indicate that climate change can affect the emergence of aquatic insect and cause physiological changes on the insects in tropical regions (Greig *et al.*, 2012; Jonsson *et al.*, 2015). Hence, the consequences of longer drought periods associated with climate change might put at risk some of the bat species most dependent on the temporal aquatic habitats to obtain their prey (e.g. *Rhynchonycteris naso*, molossid bats and *Myotis nigricans*). Additionally, aerial insectivorous bats that mainly forage over water surfaces, in the absence of the waterbodies might be forced to fly farther distances to find suitable habitats. Even open and edge specialists would be forced to forage farther away from their roosts because they would need to reach the water sources to drink, which could also imply the necessity of switching their diurnal roosts. I recommend to gather more data on the mentioned aspects to better understand the consequences climate change will have for aerial insectivorous bats in the Tropics.

Conservation measures in the Tropics should be implemented having under consideration the climate change influence on the driest months and the ecological needs of the target species to protect. As most of the species were recorded in the medium-sized and large lakes, I suggest that the creation of waterbodies with a maximum size of 3000 m² would be enough to provide a foraging and drinking habitat for most of the Neotropical aerial insectivorous bats. Furthermore, small temporary lakes, with a maximum water surface of 200 m² should also be created to favor the most clutter-adapted bat species. To conclude, it is especially crucial to preserve all temporary lakes during the dry season as it is the period with the least water availability.

6. Conclusions

The results from this study indicate that temporary lakes and ponds are important foraging and drinking habitats for most Neotropical aerial insectivorous bats and that both, lakes and bats, should be more studied and protected. The results for overall richness and the species-specific activity of 18 of 21 species recorded and identified were significantly more active over the temporary lakes and ponds than in the primary forest. Furthermore, while overall richness and the species-specific activity of 5 species were significantly higher during the rainy season, species-specific activity for 2 species was greatest in the dry season. Hence, the rainy season seems to have greater activity of aerial insectivorous bats probably because it matches with aquatic insect blooms. However, the results are not as conclusive as the ones regarding habitat type preferences.

The size of the waterbody influenced species richness and total activity of bats as well as species-specific activity. Temporary lake size had a significant but differential effect on species-specific activity: while 6 species were more active over the largest lakes, other 4 species showed greater species-specific activity over small waterbodies. Species preferences in relation to pond size seemed to be related with their foraging strategy and the need to intake water.

In terms of activity patterns most of the recorded bat families had the highest activity peak the first two hours of the night, with the exception of all mormoopid bats, which had it around midnight. My findings suggest that all the aerial insectivorous bats, even the open space and cluttered specialists, use the temporary lakes to forage and drink. The recorded molossid bats were all significantly more active over the waterbodies and vespertilionid bats spent most of the night foraging over the water surfaces. More studies should be focused on these temporary ecosystems to obtain additional information about the more elusive aerial insectivorous bat species (e.g. *S. leptura*, *C. maximiliani*, *P. gymnonotus*, *P. personatus* and *F. horrens*) given they make considerable use of them.

To conclude, I suggest it is possible to improve and protect the habitat of many aerial insectivorous bats which are facing difficulties due to climate change rise in temperatures and drought intensification. By creating temporary ponds with a surface area between 200 m² and 3000 m² and preserving the existent ones we can provide suitable foraging and drinking habitats for all aerial insectivorous bats. The finding, that a great proportion of aerial insectivorous bats forages over temporary ponds in the BDFFP possibly can be extrapolated to other rainforest regions of the world which also have waterbodies, similar diversities of species and are facing climate change influences.

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8. Appendix

8.1. Appendix 1

In this section I explain the basic concepts to broadly understand how the sound analysis was carried out.

8.1.1. Graphical representations of the sound

The **oscillogram** visually represents the time versus the amplitude of a sound; the **power spectrum** represents the amplitude of a sound versus the frequency and the **spectrogram** or **sonogram** represents the time versus the frequency and the amplitude is symbolized by the intensity of a color (**Figure 23**).

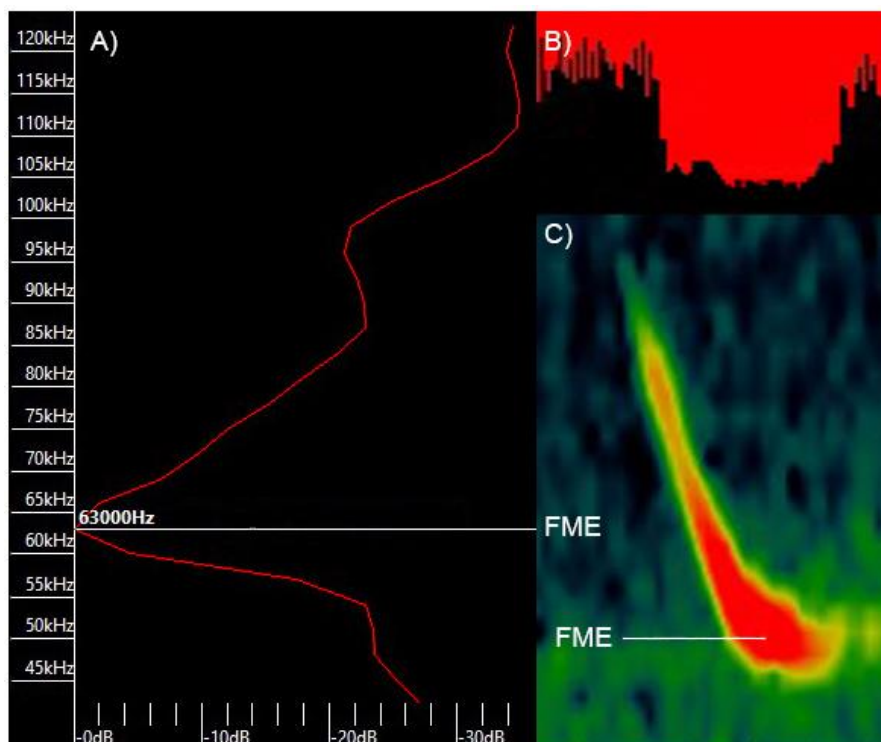


Figure 23. A) Power spectrum; B) Oscillogram and C) Spectrogram. FME – frequency of maximum energy.

8.1.2. Key information and general concepts about echolocation call analysis

Bats have several types of echolocation calls which vary depending on several factors such as type of habitat (open versus cluttered); presence of other individuals and/or prey; mating or breeding seasons and dangerous situations. Each kind of sequences of pulses, called phase, gives us specific information which implies a specific behavior.

The **search phase** indicates when a bat is in transit, a traveling movement between two points separated by a defined distance (Figure 24). Depending on the rhythm it is possible to identify three types of sequences: active and passive transit phases and active search phase. Whereas the active transit phase is used by bats when there is the possibility to run into obstacles and/or preys, the passive transit phase is used to reduce energy expended throughout the flight within a habitat that does not need the constant gathering of precise information, either because there are few chances to run into obstacles and/or preys; or due to the animal's well knowledge of the used pathway. Finally, the active search phase is used to actively look for obstacles and/or preys (Barataud, 2015).

The **approach phase** indicates when a bat is getting close to a target of interest, which could be a possible prey or an object of the immediate environment. Moreover, the interpulse interval is reduced, compared with the search phase, to gather more information (Figure 24).

The **buzz sequence** or **terminal phase** indicates when a bat is about to begin and try to successfully execute, an attempt of capturing a prey. It is distinguished from the search and approach phases because the pulses emitted are of shorter bandwidth and interpulse interval; and of lower frequency than the previous phases (Figure 24).

The **social calls** are vocal communications that bats use for a broad range of situations, for instance, to defend a territory, attract females or alert. Moreover, social calls are of greater complexity, louder and mainly emitted at lower frequency than echolocations (Middleton *et al.*, 2014) (Figure 24).

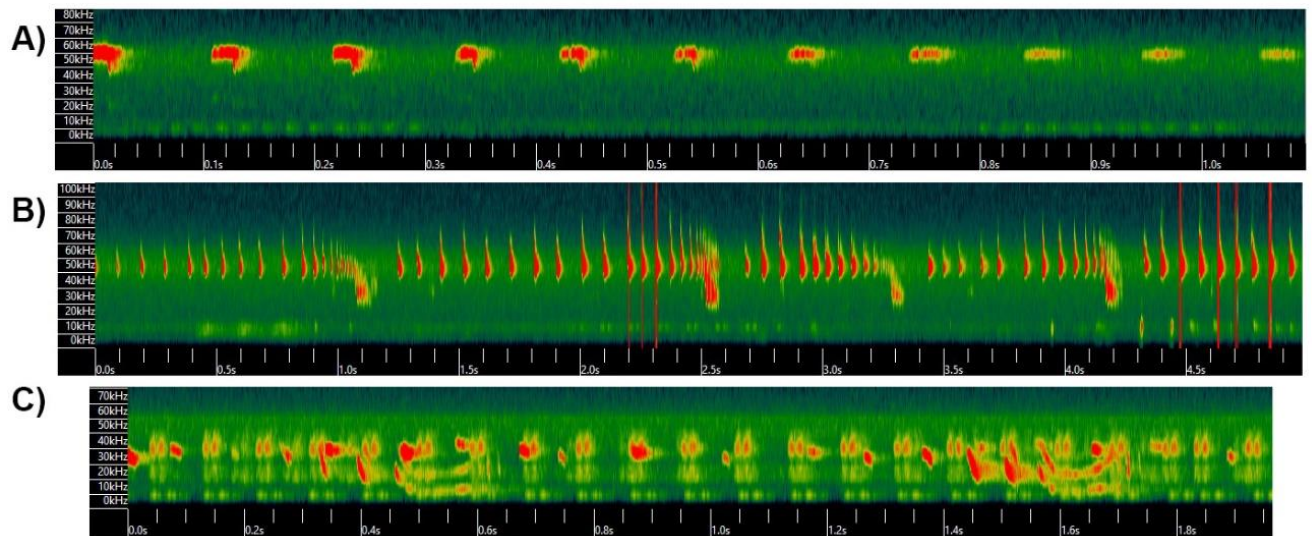


Figure 24. A) Search phase; B) Approach phase followed by Buzz sequences and C) Social calls.

8.1.3. Acoustic measurements

By measuring some acoustic features of bat echolocation pulses, it is possible to identify many sequences to species level. The following parameters are the most commonly used for this task.

The **frequency of maximum energy (FME)**, **frequency at maximum amplitude** or **peak frequency** is the frequency that has the greatest intensity of an emitted pulse and can be measured with the power spectrum (Figure 25).

The **start (SF)** and **end (EF) frequencies** are measured where the oscillogram amplitude starts to constantly increase or decrease beyond the background noise (López-Baucells *et al.*, 2016) (Figure 25).

The **pulse interval** or **interpulse interval** is the time between the start of an echolocation pulse and the start of the following pulse.

The **maximum (MaxFreq)** and **minimum (MinFreq) frequencies** are measured where the pulse differs the most from the background noise and can be obtained from the power spectrum and/or the spectrogram (López-Baucells *et al.*, 2016) (Figure 25).

The **bandwidth (BW)** indicates the intensity and is the difference between the maximum and the minimum frequencies. Its measurement is taken from the power spectrum and the units are decibels (dB) (Figure 25).

When there is an increment of the pressure in the air that is used to generate sounds the **harmonics** are formed (Figure 26). The harmonics are always related to the fundamental or base call frequencies (e.g. if a fundamental frequency is emitted at 20 kHz, its harmonics will appear at the frequencies of 40 kHz, 60 kHz and so on). Bats produce harmonics mainly to increment the bandwidth of a call and thus, increment the resolution to detect objects (Russ, 2012).

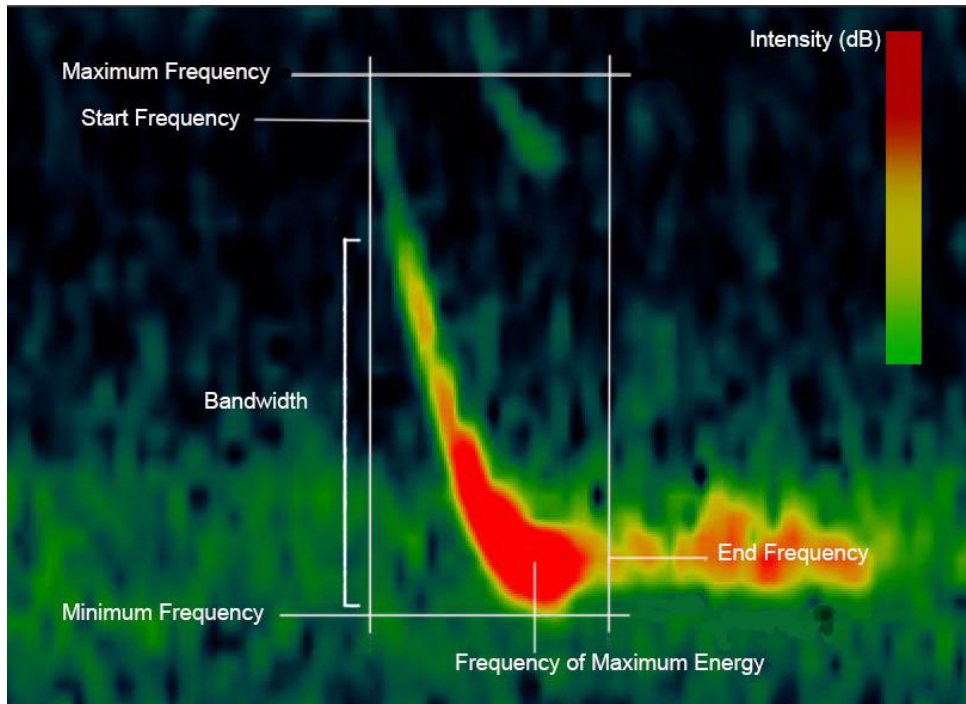


Figure 25. Pulse measurements and its terminologies. The more reddish is the pulse the greater is the intensity of it.

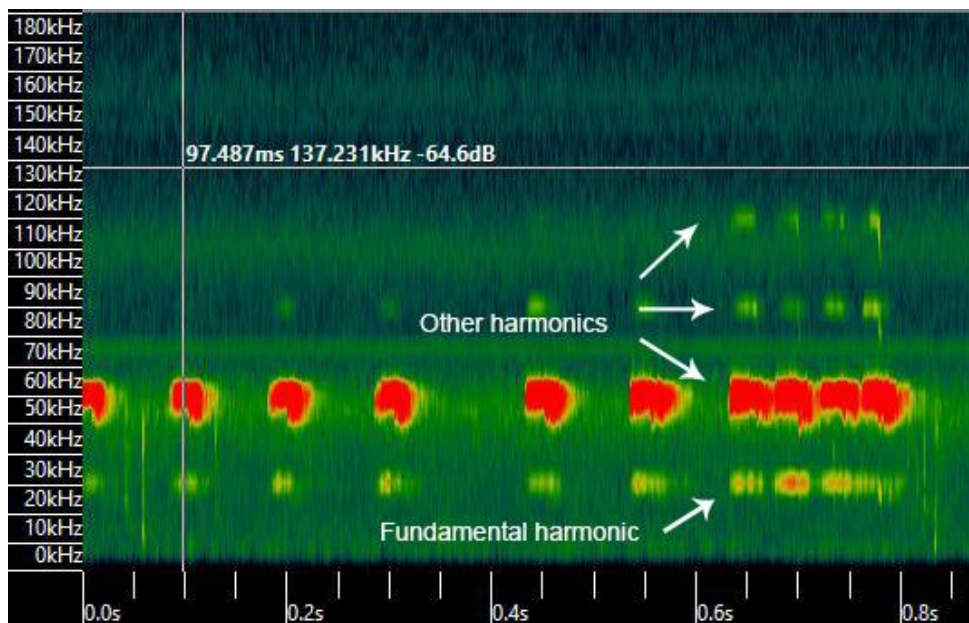


Figure 26. Representation of harmonics in an echolocation sequence of *Pteronotus rubiginosus*.

8.2. Appendix 2

Table 5. Correlation R^2 between each species total number of bat passes and buzz sequences.

Species scientific name	R^2
<i>Cormura brevirostris</i>	0.76
<i>Centronycteris maximiliani</i>	0.96
<i>Emballonuridae 1</i>	0.96
<i>Vespertilionidae 1</i>	0.61
<i>Furipterus horrens</i>	NA
<i>Molossidae I</i>	0.75
<i>Molossidae II</i>	0.75
<i>Molossidae III</i>	0.61
<i>Molossops 1</i>	0.45
<i>Myotis nigricans</i>	0.89
<i>Myotis riparius</i>	0.91
<i>Pteronotus rubiginosus</i>	0.34
<i>Pteronotus sp1</i>	0.41
<i>Promops 1</i>	0.37
<i>Pteronotus gymnonotus</i>	0.62
<i>Peropteryx kappleri</i>	0.74
<i>Peropteryx macrotis</i>	0.97
<i>Pteronotus personatus</i>	0.88
<i>Rhynchonycteris naso</i>	0.76
<i>Saccopteryx bilineata</i>	0.69
<i>Saccopteryx leptura</i>	0.71

Table 6. Summary of MCMC - GLMM to predict species-specific activity in each habitat type, season and the interaction of both. Significant p-values (<0.05) are marked in bold.

Model: Y ~ Season * Type + (1 Locality)					
<i>Cormura brevirostris</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	2.59	0.60	4.62	188.81	p<0.05
Habitat type	4.40	1.31	6.85	76.25	p<0.05
Intercept	0.11	-2.59	2.74	251.49	0.92
<i>Centronycteris maximiliani</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	4.20	2.74	5.52	505.5	p<0.05
Habitat type	1.98	0.20	3.75	844.7	p<0.05
Intercept	-2.77	-4.64	-0.62	946.7	p<0.05
<i>Emballonuridae 1</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	2.41	-1.99	6.18	173.73	0.246
Habitat type	5.01	1.18	8.93	176.85	p<0.05
Intercept	-1.65	-6.15	2.86	199.29	0.49
<i>Vespertilionidae 1</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	1.52	0.45	2.60	274.0	p<0.05
Habitat type	6.67	5.54	7.70	285.3	p<0.05
Intercept	-3.43	-4.87	-2.13	311.7	p<0.05
<i>Furipterus horrens</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-0.09	-0.98	0.88	779.8	0.82
Habitat type	-3.04	-4.45	-1.61	365.9	p<0.05
Intercept	-0.40	-2.11	1.12	612.2	0.61
<i>Molossidae I</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	11.66	0.06	23.72	4.42	0.08
Habitat type	32.20	20.93	44.80	4.31	p<0.05
Intercept	-13.54	-26.71	-2.73	4.71	0.06
<i>Molossidae II</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.49	-1.02	1.86	30.40	0.48
Habitat type	6.87	5.67	8.06	36.50	p<0.05
Intercept	-0.80	-2.44	0.80	33.56	0.30
<i>Molossidae III</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-6.74	-11.45	-1.83	4.59	p<0.05
Habitat type	5.64	4.05	7.52	29.66	p<0.05
Intercept	6.44	1.71	11.46	5.03	p<0.05
<i>Myotis nigricans</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-2.24	-3.97	-0.51	13.05	p<0.05
Habitat type	8.53	7.49	9.58	52.44	p<0.05
Intercept	2.33	0.46	4.41	21.89	p<0.05
<i>Molossops 1</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-10.57	-41.06	19.99	4.22	p<0.05
Habitat type	15.20	4.82	28.62	14.45	p<0.05
Intercept	12.35	-18.73	43.11	4.48	p<0.05
<i>Myotis riparius</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-0.66	-1.77	0.41	556.6	0.21
Habitat type	1.99	0.82	2.99	458.4	p<0.05
Intercept	0.67	-0.85	2.06	807.8	0.34
<i>Pteronotus rubiginosus</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-0.29	-0.75	0.12	1000	0.16
Habitat type	-0.38	-0.88	0.13	1000	0.12
Intercept	-0.74	-1.39	-0.09	1000	p<0.05

<i>Pteronotus sp1</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.02	-0.28	0.35	1000	0.90
Habitat type	-1.54	-2.02	-1.20	1236	p<0.05
Intercept	-0.47	-0.98	0.10	1000	0.08
<i>Promops 1</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-0.07	-9.23	9.89	9.80	p<0.05
Habitat type	13.03	6.57	20.05	11.62	p<0.05
Intercept	-0.86	-10.99	8.04	7.84	p<0.05
<i>Pteronotus gymnotus</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-5.71	-17.72	1.89	5.66	0.32
Habitat type	9.23	4.54	14.42	17.79	p<0.05
Intercept	3.95	-3.94	15.68	6.14	0.60
<i>Peropteryx kappleri</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	2.21	-1.10	4.90	5.79	0.19
Habitat type	10.21	8.02	12.39	12.07	p<0.05
Intercept	-1.28	-4.54	1.79	7.10	p<0.05
<i>Peropteryx macrotis</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	1.439	-3.381	6.774	17.63	0.552
Habitat type	11.565	7.292	15.837	16.48	p<0.05
Intercept	-1.432	-7.370	3.710	19.30	0.614
<i>Pteronotus personatus</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-12.71	-36.43	9.67	3.06	0.42
Habitat type	18.08	4.33	29.62	6.23	<0.001
Intercept	10.76	-12.00	34.83	3.18	0.56
<i>Rhynchonycteris naso</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	-14.55	-33.59	6.41	1.12	0.31
Habitat type	19.45	12.25	26.89	10.43	p<0.05
Intercept	13.01	-8.80	32.06	1.23	0.37
<i>Saccopteryx bilineata</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.24	-0.61	1.17	350.6	0.60
Habitat type	1.85	0.83	3.04	545.7	p<0.05
Intercept	0.31	-1.06	1.65	365.0	0.66
<i>Saccopteryx leptura</i>					
Coefficients:	Post.mean	l-95% CI	u-95% CI	Eff. samp	pMCMC
Season	0.95	0.02	1.97	346.9	p<0.05
Habitat type	1.49	0.41	2.53	505.9	p<0.05
Intercept	0.05	-1.22	1.43	441.7	0.94

Figure 27. Emballonurid bats interaction effect between species-specific activity and habitat type and season. The * indicates significance ($p < 0.05$).

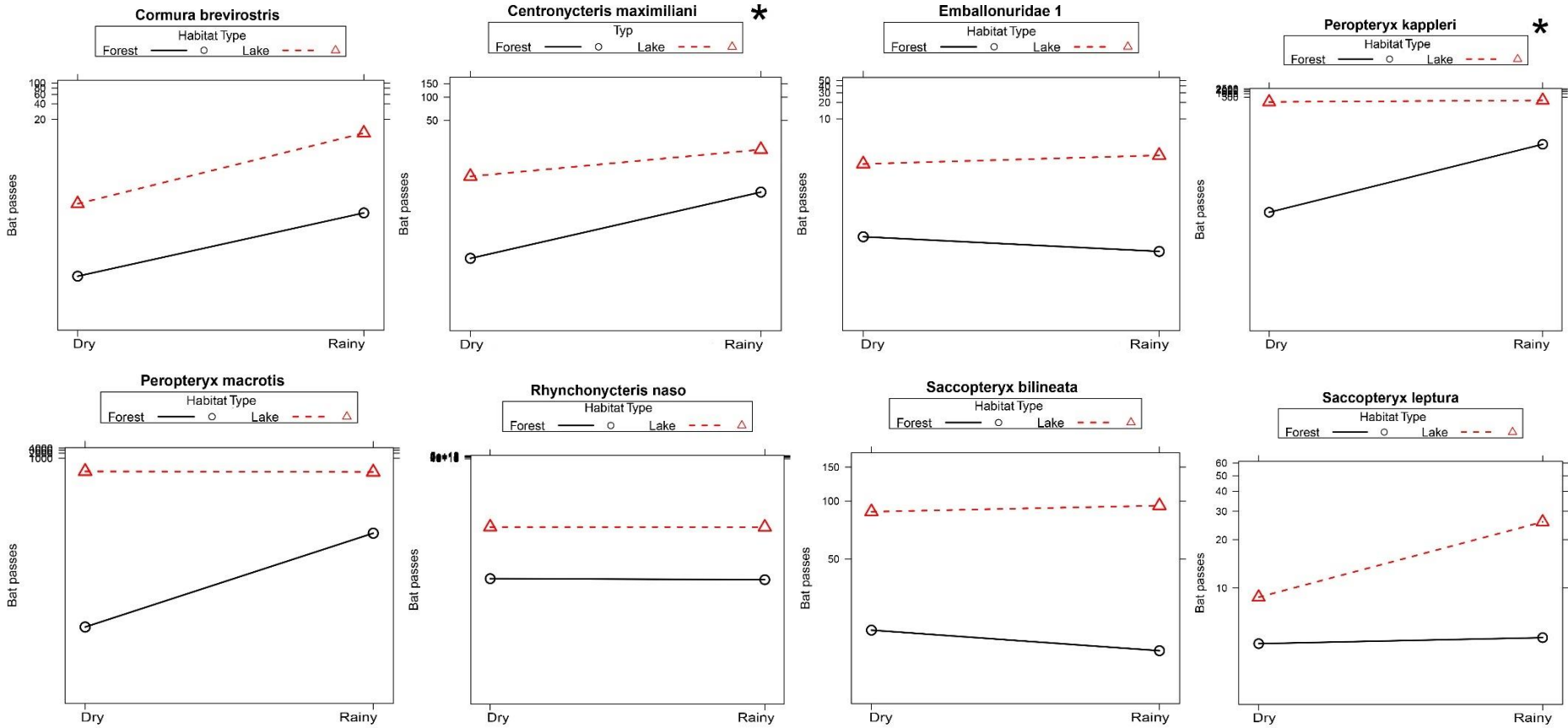


Figure 28. Molossid bats interaction effect between species-specific activity and habitat type and season. The * indicates significance ($p < 0.05$).

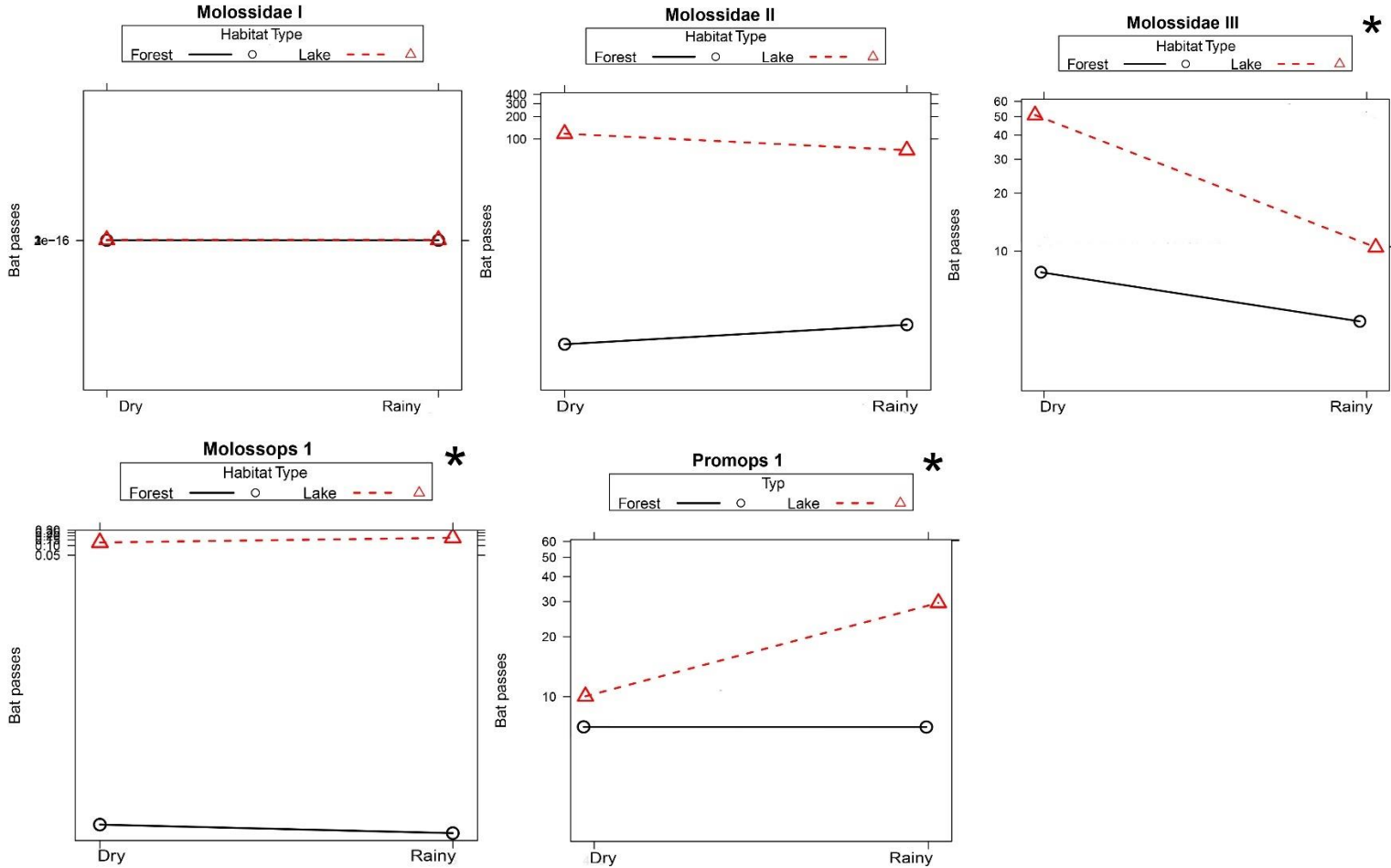


Figure 29. Mormoopid bats interaction effect between species-specific activity and habitat type and season. The * indicates significance ($p < 0.05$).

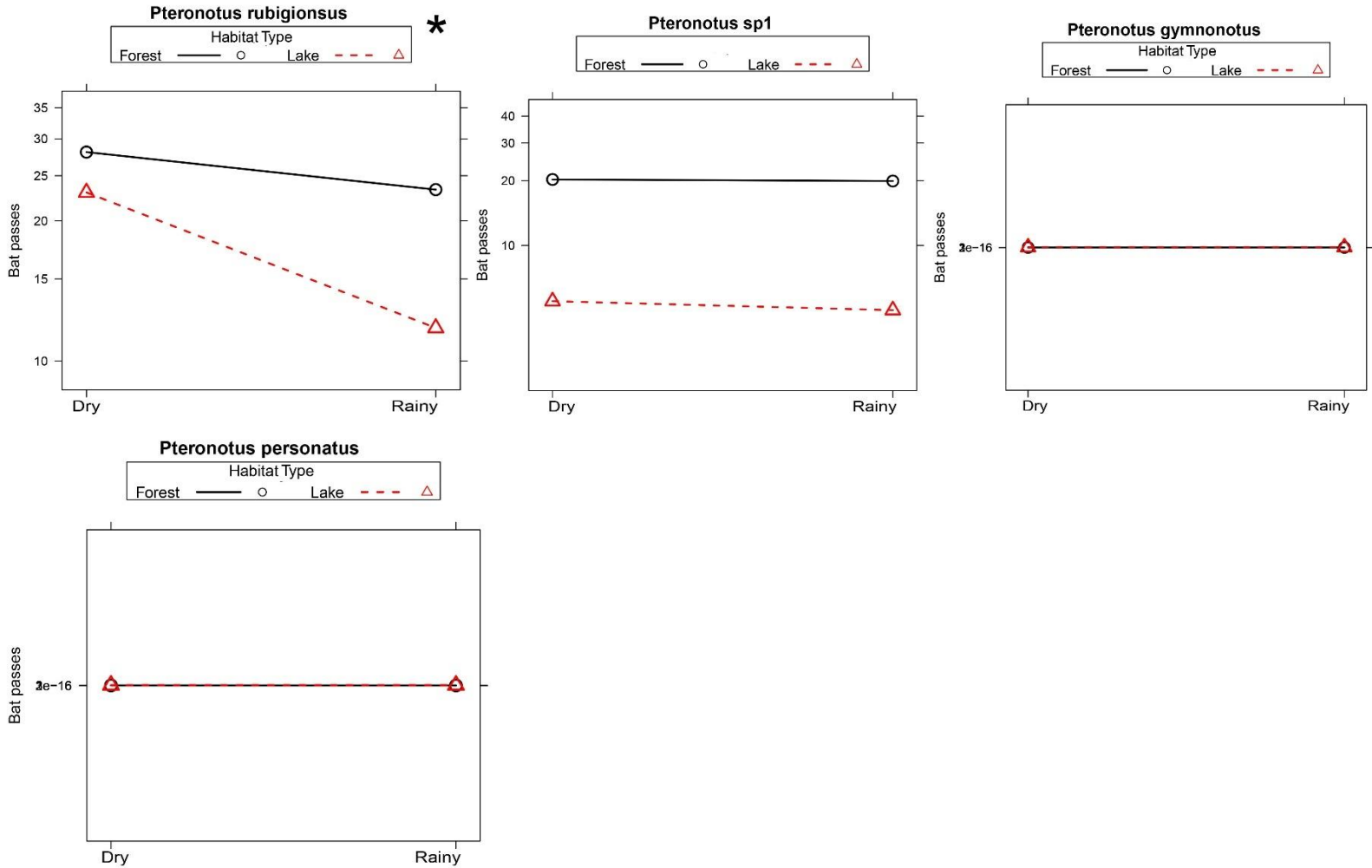


Figure 30. Vespertilionid and furiferid bats interaction effect between species-specific activity and habitat type and season. The * indicates significance ($p < 0.05$).

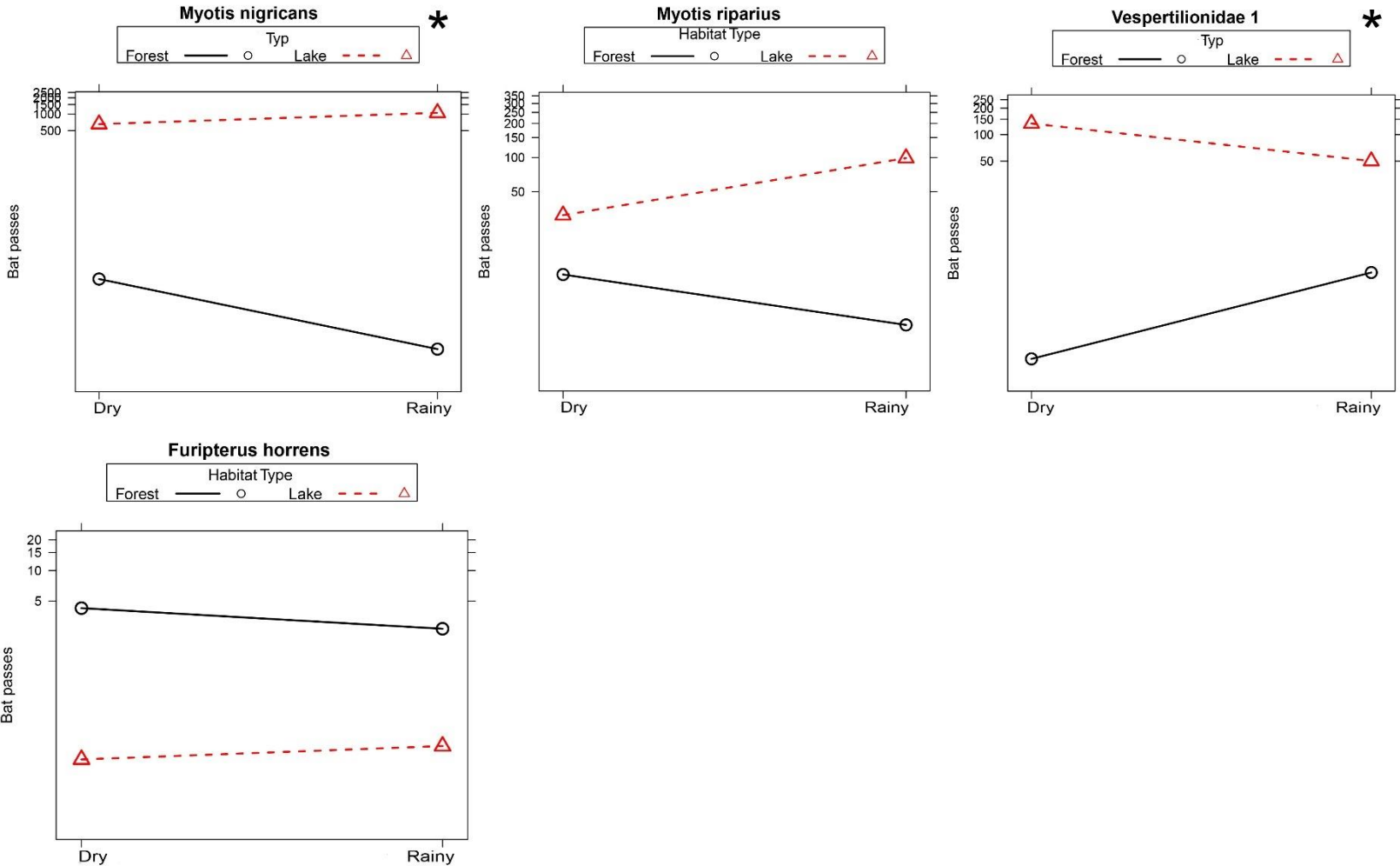


Table 7. Summary of multiple comparison, with Kruskal-Wallis test, between species-specific activity and each lake size category (small, medium and large). Significant p-values (<0.05) are marked in bold.

<i>Cormura brevirostris</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	-9.93	0.34	-25.12	5.26
Small-Large	-12.40	0.21	-28.89	4.09
Small-Medium	-2.47	1.00	-16.08	11.15
<i>Centronycteris maximiliani</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	-2.48	1.00	-18.01	13.05
Small-Large	-18.36	p<0.05	-35.22	-1.51
Small-Medium	-15.88	p<0.05	-29.80	-1.97
<i>Emballonuridae 1</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	13.51	0.39	0.52	26.50
Small-Large	36.60	p<0.05	22.49	50.71
Small-Medium	23.09	p<0.05	11.44	34.74
<i>Vespertilionidae 1</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	13.19	0.20	-4.22	30.60
Small-Large	9.58	0.66	-9.32	28.49
Small-Medium	-3.61	1.00	-19.22	12.00
<i>Furipterus horrens</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	20.92	p<0.05	10.86	30.97
Small-Large	26.60	p<0.05	15.68	37.52
Small-Medium	5.68	0.38	-3.33	14.70
<i>Myotis nigricans</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	35.02	p<0.05	19.83	50.20
Small-Large	29.75	p<0.05	13.26	46.23
Small-Medium	-5.27	1.00	-18.88	8.34
<i>Myotis riparius</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	1.60	1.00	-11.78	14.97
Small-Large	-36.76	p<0.05	-51.29	-22.24
Small-Medium	-38.36	p<0.05	-50.35	-26.37
<i>Pteronotus rubiginosus</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	2.67	1.00	-12.44	17.77
Small-Large	-28.18	p<0.05	-44.57	-11.78
Small-Medium	-30.84	p<0.05	-44.38	-17.30
<i>Pteronotus sp1</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	-5.54	0.77	-17.35	6.28
Small-Large	-44.36	p<0.05	-57.19	-31.54
Small-Medium	-38.83	p<0.05	-49.42	-28.24
<i>Pteronotus gymnonotus</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	-0.61	1.00	16.53	-15.31
Small-Large	8.85	0.64	-8.43	26.13
Small-Medium	9.46	0.33	-4.81	23.73
<i>Peropteryx kappleri</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	7.68	0.25	-3.07	18.43
Small-Large	50.20	p<0.05	38.53	61.87
Small-Medium	42.52	p<0.05	32.89	52.16
<i>Peropteryx macrotis</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	15.57	p<0.05	3.69	27.45
Small-Large	50.29	p<0.05	37.39	63.18
Small-Medium	34.72	p<0.05	24.07	45.37

<i>Pteronotus personatus</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	-6.83	0.63	-20.00	6.33
Small-Large	-4.62	1.00	-18.92	9.67
Small-Medium	2.21	1.00	-9.59	14.02
<i>Rhynchonycteris naso</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	26.91	p<0.05	15.14	38.69
Small-Large	46.59	p<0.05	33.80	59.37
Small-Medium	19.67	p<0.05	9.11	30.23
<i>Saccopteryx bilineata</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	9.08	0.51	-6.90	25.06
Small-Large	30.16	p<0.05	12.82	47.51
Small-Medium	21.09	p<0.05	6.76	35.41
<i>Saccopteryx leptura</i>				
Coefficients:	Difference	pvalue sig.	LCL	UCL
Medium-Large	-0.56	1.00	-18.16	17.04
Small-Large	-4.21	1.00	-23.32	14.89
Small-Medium	-3.64	1.00	-19.43	12.13