

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

**DIFERENTES PADRÕES DE ATIVIDADE VOCAL DE ESPÉCIES DE ANUROS
AMAZÔNICOS FORMAM ASSEMBLEIAS ACÚSTICAS EM ESCALA DIÁRIA**

GABRIEL SALLES MASSELI

Manaus, Amazonas

Junho, 2021

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AMAZÔNICOS FORMAM ASSEMBLEIAS ACÚSTICAS EM ESCALA DIÁRIA**

ORIENTADOR: DR. IGOR LUIS KAEFER

COORIENTADOR: DR. ANDERSON SALDANHA BUENO

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia (INPA) como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 31 dias do mês de Maio do ano de 2021, às 14h00min, por videoconferência. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: **Dra. Cintia Cornelius Frische**, da Universidade Federal do Amazonas-UFAM, o **Dr. Miquéias Ferrão da Silva Junior**, da Harvard University e o **Dr. Anthony Santana Ferreira**, do Instituto Nacional de Pesquisas da Amazônia - INPA, tendo como suplentes o Dr. Jair Max Furtunato Maia, Universidade Estadual do Amazonas -UEA, e o Dr. Marconi Campos Cerqueira Junior, da Sieve Analytics, sob a presidência do orientador, a fim de proceder à arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** do **GABRIEL SALLES MASSELI**, intitulado: “**DIFERENTES PADRÕES DE ATIVIDADE VOCAL DE ESPÉCIES DE ANUROS AMAZÔNICOS FORMAM ASSEMBLEIAS ACÚSTICAS EM ESCALA DIÁRIA**”, orientado pelo Dr. Igor Luis Kaefer, do Instituto Nacional de Pesquisas da Amazônia – INPA, co-orientado pelo Dr. Anderson Saldanha Bueno, do Instituto Federal Farroupilha –IFFar.

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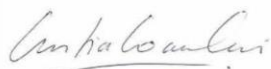
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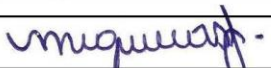
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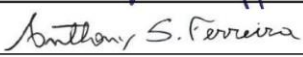
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SINOPSE

Investigou-se o efeito do fotoperíodo na distribuição diária da atividade vocal de 59 espécies de anuros em ilhas florestais e em floresta contínua na paisagem do arquipélago de Balbina, Amazônia central. A partir disso, determinou-se a formação de assembleias acústicas temporais ao longo do período nictemeral e o efeito do tamanho da ilha sobre a atividade vocal média das assembleias insulares de anuros.

Palavras-chave: Anuros, Assembleia Acústica, Detecção Automática de Espécies, Ecologia Acústica, Insularização, Monitoramento Acústico Passivo, Relação Espécie-Área.

DEDICATÓRIA

Dedico este estudo à ciência brasileira e a todos que de alguma forma estão ligados a ela, enfrentando os desafios, principalmente da atual desvalorização da ciência no Brasil, dedicando-se com muito amor e esmero em busca do conhecimento científico.

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“A vida sem ciência é uma espécie de morte” (Sócrates)

RESUMO

A atividade vocal dos anuros ao longo do dia é modulada principalmente pelo fotoperíodo e, em segundo lugar, pelo contexto social e ambiental. Portanto, as respostas de espécies divergentes a esses fatores podem resultar na formação de assembleias acústicas temporais - ou seja, conjuntos de espécies que são coativas vocalmente em momentos previsíveis ao longo do período nictemeral (ciclos de 24 horas). Os fotoperíodos são amplamente invariantes nas regiões tropicais ao longo dos ciclos anuais, garantindo assim que a amostragem da distribuição diurna das vocalizações não seja afetada pela época do ano. Aqui, nós (1) descrevemos a distribuição temporal da atividade vocal de várias espécies de anuros amazônicos em uma paisagem arquipelágica fragmentada pelo represamento de um rio e determinamos o momento mais eficaz para o levantamento de anuros; (2) investigar a formação e composição de assembleias acústicas temporais ao longo do dia; e (3) avaliar como o tamanho da ilha - como uma proxy dos contextos sociais intra e interespecíficos - afeta os tempos de atividade vocal dos anuros. Usamos sensores acústicos para amostrar 78 locais (74 ilhas e quatro locais de floresta continental) por cinco dias consecutivos entre julho e dezembro de 2015. Usamos um algoritmo de detecção automática para identificar espécies de anuros em um total de 216.217 registros de 1 minuto (> 3.600 horas) os registros para cada espécie foram classificados em quatro períodos de tempo: madrugada (05:00 - 06:55), dia (07:00 - 16:55), crepúsculo (17:00 - 18:55) e noite (19:00 - 04:55). A maioria das espécies de anuros foi registrada ao longo do período diário, embora também tenhamos observado atividade vocal concentrada durante os períodos crepuscular e noturno. Quatro períodos diários corresponderam a distribuições temporais marcadamente distintas, enquanto o período da Noite foi o mais distinto e coeso em termos de composição acústica. O tamanho da ilha, um *proxy* da riqueza de espécies e dos tamanhos populacionais, afetou positivamente o tempo de atividade vocal das assembleias de anuros, corroborando que existem fatores além do fotoperíodo que modulam a atividade vocal diária dessas espécies. Abrimos novos caminhos na classificação da atividade vocal de assembleias mega diversas de anuros na Amazônia, detectando a partição de assembleias estruturadas temporalmente ao longo do período diário.

ABSTRACT

Asynchronous circadian patterns of vocal activity in Amazonian anurans structure temporal acoustic assemblages

Anuran vocal activity throughout the day is primarily modulated by photoperiod, and secondly, social context and environmental setting. Therefore, divergent species responses to these factors can result in the formation of temporal acoustic assemblages — i.e. sets of species that are vocally co-active at predictable times throughout the nycthemeral period (24-h cycles). Photoperiods are largely invariant in tropical regions over annual cycles, thereby ensuring that sampling of the diurnal distribution of vocalizations is largely unaffected by time of year. Here, we (1) describe the temporal distribution of vocal activity of several species of Amazonian anurans in an archipelagic landscape fragmented by river damming and determine the most effective time to survey anurans; (2) investigate the formation and composition of temporal acoustic assemblages throughout the day; and (3) assess how island size — as a proxy of intra- and interspecific social contexts — affects anuran vocal activity times. We used acoustic sensors to sample 78 sites (74 islands and four mainland forest sites) for five consecutive days between July and December 2015. We used an automatic detection algorithm to identify anuran species in a total of 216,217 1-minute recordings (> 3,600 hours). Recordings for each species were classified into four time periods: dawn (05:00 - 06:55), day (07:00 - 16:55), dusk (17:00 - 18:55) and night (19:00 - 04:55). Most anuran species were recorded throughout the daily period, although we also observed concentrated vocal activity during the Dusk and Night periods. Four daily periods corresponded to markedly distinct temporal assemblages, whereas the Night period was the most distinct and cohesive in terms of acoustic composition. Island size, a proxy of population sizes and species richness, positively affected the vocal activity time of anuran assemblages, supporting that there are factors beyond photoperiod that modulate the daily vocal activity of these species. We have broken new ground in classifying the vocal activity of mega-diverse anuran assemblages in Amazonia by detecting the partition of temporally structured assemblages throughout the daily period.

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Material suplementar 2. Diagramas de rosas de atividades de vocalização nictemeral para 59 espécies de anuros ocorrentes no arquipélago de Balbina, Amazonas. O amarelo representa os períodos do amanhecer e do dia, enquanto a cor cinza representa os períodos de crepúsculo e noturno; as barras internas (pétalas do gráfico de rosa) representam a proporção dos registros da atividade vocal no período diário.

INTRODUÇÃO GERAL

O ciclo circadiano, que influencia o ritmo biológico de quase todos os organismos, modula o período de atividade de vários táxons, como insetos (Saunders 2021), sapos (Both *et al.* 2008; Cui *et al.* 2011), pássaros (Daan & Aschoff 1975; Bradshaw & Holzapfel 2007) e morcegos (Hope & Jones 2013). A atividade vocal frequentemente conspícua de anfíbios anuros ao longo do período nictemeral (Oishi *et al.* 2004; Cui *et al.* 2011; Toledo *et al.* 2015) é afetada principalmente pela variação da luz do dia entre o dia e a noite, que é chamada de fotoperíodo (Bradshaw & Holzapfel 2007). O fotoperíodo pode, portanto, ser considerado o principal modulador da atividade diária dos anuros, que pode ser observado pela atividade predominantemente diurna ou noturna da maioria das espécies de anuros (Lima *et al.* 2012). Em altas latitudes, há maior variação do fotoperíodo ao longo do ano, que modula sazonalmente a atividade vocal das espécies (Both *et al.* 2008; Canavero & Arim 2009). Em contraste, o fotoperíodo é altamente sazonal em latitudes baixas, proporcionando excelentes condições para estudos supranuais (muitos meses e anos) relacionados à atividade vocal em escala nictemeral. Embora existam outras variáveis que potencialmente atuam como fatores extrínsecos secundários, como pressão atmosférica, temperatura, umidade do ar, ciclo lunar e ruído antropogênico (Oseen & Wassersug 2002; Amorim *et al.* 2009; Grant *et al.* 2009; Steelman & Dorcas 2010; Alvarez-Berríos *et al.* 2016; Underhill & Höbel 2018), o fotoperíodo é o principal modulador da atividade diária dos anuros (por exemplo, Both *et al.* 2008; Cui *et al.* 2011).

A estrutura do habitat e o contexto social são determinantes secundários importantes da atividade das espécies e envolvem a área do habitat e as interações intra e interespecíficas (Cui *et al.* 2011; Palmeirim *et al.* 2017; Souza *et al.* 2017). As relações espécie-área irão, então, influenciar o contexto social, pois áreas maiores abrigarão populações maiores e maior riqueza de espécies (MacArthur & Wilson 1963, 1967), determinando assim a saturação do espaço acústico da comunidade sonora (Aide *et al.* 2017). A saturação do espaço acústico de uma determinada área em um determinado período nictemeral corresponde aos sons de frequência sobrepostos distintos ou semelhantes emitidos por diferentes espécies vocalizantes (Campos-Cerqueira & Aide 2016; Fouquet *et al.* 2020). Isso pode determinar, em conjunto com o fotoperíodo, o nicho acústico temporal (intervalo espaço / tempo da atividade vocal de uma determinada espécie) e o período em que a espécie irá vocalizar, o que resulta na formação e

composição de assembleias acústicas temporais (Horseman *et al.* 1978; Villanueva-Rivera 2014; Toledo *et al.* 2015; Alvarez-Berríos *et al.* 2016). Assim, a riqueza de espécies pode afetar a atividade vocal de toda a assembleia tanto negativamente, por meio da supressão da atividade vocal devido à sobreposição de nichos acústicos (Cui *et al.* 2011; Villanueva-Rivera 2014), quanto positivamente por sinalizar que o ambiente é propício à reprodução (Fouquet *et al.* 2020).

Aqui nós (1) descrevemos a distribuição temporal da atividade vocal de espécies de anuros durante o período nictemeral (ciclo de 24 horas) e determinamos o momento mais eficaz para pesquisar anuros; (2) investigamos a formação e composição das assembleias acústicas temporais durante o período nictemeral; e (3) avaliamos como o tamanho da ilha da floresta - uma proxy do contexto social intra e interespecífico - afeta a atividade vocal média das assembleias de anuros. Nossa hipótese para o segundo objetivo é que as assembleias acústicas irão divergir entre os quatro períodos diários amplamente conhecidos: madrugada (05:00 - 06:55), dia (07:00 - 16:55), crepúsculo (17:00 - 18:55) e à noite (19:00 - 04:55). Nossa hipótese para o terceiro objetivo é que ilhas maiores, e conseqüentemente maiores tamanhos populacionais e maior riqueza de espécies, levarão a uma diminuição no tempo médio de atividade vocal específica da espécie para minimizar a competição devido à sobreposição de nichos acústicos.

OBJETIVOS

Geral: Investigar como o tamanho da área e os diferentes padrões de atividade vocal em anuros do Arquipélago de Balbina formam assembleias acústicas temporais em período nictemeral.

Específico 1: Determinar a distribuição temporal da atividade vocal das espécies de anuros ao longo do período nictemeral;

Específico 2: Investigar a formação e composição das assembleias acústicas por janelas temporais distribuídas no período nictemeral;

Específico 3: Avaliar como o contexto social (intra e interespecífico), mediado pelo tamanho da área, afeta o tempo de atividade vocal das espécies de anuros.

Capítulo 1

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Authors: Gabriel S. Masseli^{1*}, Anderson S. Bueno², Carlos A. Peres^{3,4}, Igor L. Kaefer^{1,5}

¹Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, 69060-062, Brazil

²Instituto Federal de Educação, Ciência e Tecnologia Farroupilha, Júlio de Castilhos, RS, 98130-000, Brazil

³School of Environmental Sciences, University of East Anglia, Norwich, Norfolk, NR4 7TJ, United Kingdom

⁴Instituto Juruá, Rua das Papoulas, 97, Manaus, AM, 69083-300, Brazil

⁵Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Manaus, AM, 69067-005, Brazil

*Corresponding author: Gabriel S. Masseli. E-mail: masselisp@gmail.com

Abstract

Anuran vocal activity throughout the day is primarily modulated by photoperiod, and secondly, social context and environmental setting. Therefore, divergent species responses to these factors can result in the formation of temporal acoustic assemblages — i.e. sets of species that are vocally co-active at predictable times throughout the nycthemeral period (24-h cycles). Photoperiods are largely invariant in tropical regions over annual cycles, thereby ensuring that sampling of the diurnal distribution of vocalizations is largely unaffected by time of year. Here, we (1) describe the temporal distribution of vocal activity of several species of Amazonian anurans in an archipelagic landscape fragmented by river damming and determine the most effective time to survey anurans; (2) investigate the formation and composition of temporal acoustic assemblages throughout the day; and (3) assess how island size — as a proxy of intra- and interspecific social contexts — affects anuran vocal activity times. We used acoustic sensors to sample 78 sites (74 islands and four mainland forest sites) for five consecutive days between July and December 2015. We used an automatic detection algorithm to identify anuran species in a total of 216,217 1-minute recordings (> 3,600 hours). Recordings for each species were classified into four time periods: dawn (05:00 - 06:55), day (07:00 - 16:55), dusk (17:00 - 18:55) and night (19:00 – 04:55). Most anuran species were recorded throughout the daily period, although we also observed concentrated vocal activity during the Dusk and Night periods. Four daily periods corresponded to markedly distinct temporal assemblages, whereas the Night period was the most distinct and cohesive in terms of acoustic composition. Island size, a proxy of population sizes and species richness, positively affected the vocal activity time of anuran assemblages, supporting that there are factors beyond photoperiod that modulate the daily vocal activity of these species. We have broken new ground in classifying the vocal activity of mega-diverse anuran

assemblages in Amazonia by detecting the partition of temporally structured assemblages throughout the daily period.

Keywords: Acoustic assemblages; Acoustic ecology; Anurans; Automated species detection; Insularization; Passive acoustic monitoring; Species-area relationship; Tropical forest.

Introduction

The circadian cycle, which influences the biological rhythm of almost all organisms, modulates the period of activity of several taxa such as insects (Saunders 2021), frogs (Both *et al.* 2008; Cui *et al.* 2011), birds (Daan & Aschoff 1975; Bradshaw & Holzapfel 2007) and bats (Hope & Jones 2013). The often conspicuous vocal activity of anuran amphibians throughout the nycthemeral period (Oishi *et al.* 2004; Cui *et al.* 2011; Toledo *et al.* 2015) is mainly affected by variation in daylight between day and night, which is called the photoperiod (Bradshaw & Holzapfel 2007). The photoperiod can therefore be regarded as the principal modulator of the daily activity of anurans, which can be observed by the predominantly either daytime or nocturnal activity of most anuran species (Lima *et al.* 2012). At high latitudes, there is greater variation in the photoperiod throughout the year, which seasonally modulates the vocal activity of species (Both *et al.* 2008; Canavero & Arim 2009). In contrast, photoperiod is highly seasonal at low latitudes, thereby providing excellent conditions for supra-annual studies (many months and years) related to vocal activity on a nycthemeral scale. Although there are other variables that potentially act as secondary extrinsic factors, such as atmospheric pressure, temperature, air humidity, lunar cycle and anthropogenic noise (Oseen & Wassersug 2002; Amorim *et al.* 2009; Grant *et al.* 2009; Steelman & Dorcas 2010;

Alvarez-Berríos *et al.* 2016; Underhill & Höbel 2018), the photoperiod is the main modulator of the day-to-day activity of anurans (e. g. Both *et al.* 2008; Cui *et al.* 2011).

Habitat structure and social context are important secondary determinants of species activity, and involve habitat area and intraspecific and interspecific interactions (Cui *et al.* 2011; Palmeirim *et al.* 2017; Souza *et al.* 2017). Species-area relationships will then influence the social context as larger areas will harbor larger population sizes and higher species richness (MacArthur & Wilson 1963, 1967), thereby determining the saturation of the acoustic space of the soniferous community (Aide *et al.* 2017). The saturation of the acoustic space of a given area in a given nycthemeral period corresponds to the distinct or similar overlapping frequency sounds emitted by different vocalizing species (Campos-Cerqueira & Aide 2016; Fouquet *et al.* 2020). This can determine, together with photoperiod, the temporal acoustic niche (space/time range of a given species' vocal activity) and the period in which the species will vocalize, which results in the formation and composition of temporal acoustic assemblages (Horseman *et al.* 1978; Villanueva-Rivera 2014; Toledo *et al.* 2015; Alvarez-Berríos *et al.* 2016). Thus, species richness can affect the assemblage-wide vocal activity both negatively, through suppression of vocal activity due to overlapping acoustic niches (Cui *et al.* 2011; Villanueva-Rivera 2014), and positively by signalling that the environment is conducive to reproduction (Fouquet *et al.* 2020).

Here we (1) describe the temporal distribution of the vocal activity of anuran species during the nycthemeron (24-hour cycle) and determine the most effective time to survey anurans; (2) investigate the formation and composition of temporal acoustic assemblages during the nycthemeron; and (3) assess how forest island size — a proxy of intra- and interspecific social context — affects the mean vocal activity of anuran

assemblages. Our hypothesis for the second objective is that the acoustic assemblages will diverge across the four widely known daily periods: dawn (05:00 - 06:55), day (07:00 - 16:55), dusk (17:00 - 18:55), and night (19:00 - 04:55). Our hypothesis for the third objective is that larger islands, and consequently larger population sizes and higher species richness, will lead to a decrease in the average time of species-specific vocal activity to minimize competition due to overlapping acoustic niches.

Methods

Study area

The acoustic data collection was carried out on islands of varying sizes and in continuous forest sites at the Balbina Hydroelectric Reservoir landscape (0° 50 'to 1° 55' S; 58° 50 'to 60° 10' W), located 146 km north of Manaus, in the state of Amazonas, Brazil (Fig. 1). In 1987, the completion of the construction of the Balbina Hydroelectric Power Plant, on the Uatumã River, resulted in the creation of a reservoir that flooded a 2,996 km² area with a maximum length and width of 155 km and 75 km, respectively (IBAMA 1997). Thus, the lower elevation areas were submerged and the higher elevation areas formed more than 3,500 islands of sizes ranging from 0.2 to 4,878 hectares (ha) with varying configurations and degrees of isolation and the same isolation time (Benchimol & Peres 2015; Bicudo *et al.* 2016; Benchimol & Peres 2020). To offset the environmental impacts of the dam, it was created the 938,720-ha Uatumã Biological Reserve (Decree N°. 99.277/1990).

The study area is located in the transition between the Central Amazon and the Guianas Shield, with the predominant vegetation being Dense Submontane Tropical Forest, distributed over podzols and oxisols. The climate in the region is, according to the Köppen classification, humid and hot rainy tropical (Amw). The average temperature is

26.7 °C with little seasonal variation and monthly averages between 25.9 and 27.7 °C, and the average annual precipitation is 2,420 mm (IBAMA 1997; Alvares *et al.* 2014). This region has 13 recorded families of anurans, with 68 described species (Condrati 2009; Bueno *et al.* 2020).

Sampling design

Anuran surveys were carried out from July to December 2015 using 151 acoustic sensors developed by the Biodiversity Remote Monitoring Network research group (ARBIMON, <<https://www.sieve-analytics.com>>). The acoustic sensors consist of a smartphone inside a waterproof case connected to an omnidirectional microphone with a detection radius of approximately 50 m (Campos-Cerqueira & Aide 2016) attached to the outside. Each Acoustic Sensor (n = 151) was installed on the trunk of a tree positioned at a height of 1.5 m above the ground, with the omnidirectional microphone directed downwards acoustic sensors were installed on 74 islands and in 4 areas of continuous forest, totalling 78 sampling sites (Figure 1). The distance between the recorders was at least 500 m and at most 80 km, which were deployed on 74 islands varying from 0.45 to 1,699 hectares and in 4 continuous forest sites (Bueno *et al.* 2020).

Anuran acoustic surveys

Acoustic sensors were left unattended operating for 5 days from 00:00 to 23:55, making 1-minute recordings at 5-minute intervals, totalling approximately 1,440 1-minute segments for each acoustic sensor (n = 151) with a total of 216,217 recorded segments overall (> 3,600 hours). Subsequently, these recordings were downloaded to a computer and stored on the ARBIMON II web platform, which are freely available at <<https://arbimon.sieve-analytics.com/project/balbina>>.

Passive acoustic monitoring enables the sampling of animal vocal activity on a nycthemeral scale, for many days throughout different periods of the year, with all recordings being permanently stored in an acoustic database, thus maximizing and optimizing the sampling effort (Acevedo *et al.* 2009; Tricas & Boyle 2009; Aide *et al.* 2013; Bueno *et al.* 2020). The result of this is large amounts of collected data, which causes problems not only with respect to storage, but mainly in data analysis. Such a problem can be solved with the recent development of algorithms that perform automated species identification from the vocalizations (Villanueva-Rivera & Pijanowski 2012; Aide *et al.* 2013; Campos-Cerqueira & Aide 2016; Shonfield & Bayne 2017; Burivalova *et al.* 2019).

Analysis of acoustic data

A list containing potential species occurring in the region was drawn up from studies of the composition of anuran species carried out in the study area (Condrati 2009; Bueno *et al.* 2020). Species nomenclature was validated and updated based on the Amphibian Species of the World database (Frost 2019). Afterwards, we selected a sonogram for 61 species listed (Tab. 1). These sonograms were inserted into the ARBIMON II platform as models for the automatic species detection algorithm.

We used a pattern matching technique, which trains an automatic species identification algorithm based on the digital image of the species' vocalization sound (sonogram) entered by the user. This process, called Pattern Matching, compares these sonograms (i.e., acoustic models) with the recording obtained in the field, thus streamlining and maximizing the acoustic analysis (Aloysius & Geetha 2017; Kao *et al.* 2018; Priyadarshani *et al.* 2018; LeBien *et al.* 2020).

To maximize the number of detections of the species present in the recordings via Pattern Matching, it was necessary first to test different values of the Threshold factor (i. e. similarity values between the sonograms inserted as acoustic models and the acoustic recordings analyzed). To determine the threshold to be used, we performed an exploratory analysis with thresholds of 0.1, 0.2, 0.3, 0.4 and 0.5 using the sonogram of *Rhinella marina* as the acoustic model. Since there were many false negatives for 0.4 and 0.5 and many false positives for 0.1 and 0.2, we determined that the most suitable Threshold factor for correlations between acoustic models (sonograms) and recordings was 0.3 (with 3,229 Matchings from 216,217 recordings / hit rate = 4.21%), a value that did not contain false negatives and had an acceptably low number of false positives. To further avoid false positives, all the automated species detections were visually validated by inspecting the sonograms and also aurally validated whenever there was any doubt about the similarity between the model sonogram and that of the acoustic recordings (Campos-Cerqueira & Aide 2016).

Statistical analysis

The daily vocalization cycle of each species was represented graphically by means of a circular “rose” histogram (Both *et al.* 2008; Kovach 2013). To visualize the structure of the 24-time assemblages of 1-hour, each 1-minute sample containing a record was distributed within each of the 4 periods defined *a priori* — dawn (05:00 - 06:55); day (07:00 - 16:55); dusk (17:00 - 18:55); night (19:00 - 04:55), as well as the dissimilarity in the species composition of the assemblage between the different time windows (hourly intervals). We summarized the composition of the anuran assemblages in two axes of multivariate ordering using the non-metric multidimensional scaling technique (NMDS) with the Bray-Curtis dissimilarity distance for species relative frequency data,

implemented in the “metaMDS” function. We also employed permutational multivariate analysis of variance (PERMANOVA) with 1,000 permutations (Anderson 2017), using the *adonis* function, to assess the similarity of composition between temporal acoustic assemblages among daily periods dawn, day, dusk and night. To visualize this assemblage structure in relation to the 24-h period and the spatial configuration of the landscape (islands and continuous forest), we produced graphs composed of direct ordering of the species in relation to the nycthemeral temporal gradient and the spatial gradient (size of the islands and continuous forest), using the “poncho” function (Dambros 2013).

We evaluated the effect of island size (predictor variable) on the average time of acoustic activity of anuran assemblages (response variable). The response variable represents the average time of vocal activity for each of the islands, calculated as the sum of summing the number of records of vocal activity of all species combined per island divided by the number of species therein. Subsequently, we used simple linear regression to analyse whether there was a relationship between the average time of vocal activity time of anuran assemblages and the log-transformed size of the island. All analyses were performed with the aid of the R Studio software (R Core Team 2019), using the ‘ggplot2’ (Wickham 2016) and ‘vegan’ packages (Oksanen *et al.* 2019).

Results

Species richness and records

We obtained 25,134 true positive records from 78 sampling sites (74 islands and 4 continuous forest sites) where we recorded a total of 59 species (97% of the species included as a model in the Arbimon) distributed among 13 families: Allophrynidae (n = 1); Aromobatidae (n = 2); Bufonidae (n = 7); Centrolenidae (n = 1); Ceratophryidae (n = 1); Craugastoridae (n = 4); Dendrobatidae (n = 2); Eleutherodactylidae (n = 1); Hylidae

(n = 21); Leptodactylidae (n = 9); Microhylidae (n = 5); Phyllomedusidae (n = 4); Pipidae (n = 1). The species *Allobates sumtuosus* and *Leptodactylus mystaceus* were not recorded by the automatic detection algorithm, possibly due to the period of sampling that did not include the peak period of activity of these species (January-May). The periods of vocal activity of four species were previously unknown according to the specialized literature: *Dendropsophus leucophyllatus* (05:00 to 18:00, with the peak of activity being between 11:00 and 12:00); *Dendropsophus marmoratus* (07:00 to 17:00, with peak vocal activity between 11:00 and 14:00); *Dendropsophus minusculus* (02:00 to 22:00, with peak activity being between 13:00 and 15:00); and *Pristimantis marmoratus* (00:00 to 23:00, with peak activity being between 16:00 and 19:00). The species richness on the 74 islands varied from 2 to 35 species ($\bar{X} = 13.68/\sigma = 7.29$), and the number of acoustic records ranged from 6 to 2248 ($\bar{X} = 290.29/\sigma = 377.68$). In the 4 continuous forest sites, species richness varied between 29 and 34 ($\bar{X} = 31.75/\sigma = 2.22$), and records between 550 and 1238 ($\bar{X} = 985.75/\sigma = 302.29$) (Supplementary material 1).

The species richness values per period were as follows: dawn (n = 51), day (n = 55), dusk (n = 56), and night (n = 52). Although the species richness was similar between the periods, the sampling time between the periods differed, with day and night being 10-hours and dawn and dusk only 2-hours. There was also a variation between the composition of species and the period that they are vocally active in the period (PERMANOVA: $r^2 = 0.783$, $p < 0.001$; Fig. 2). The number of records obtained for each period was as follows: dawn (n = 1,888), day (n = 6,136), dusk (n = 4,681), night (n = 12,429). Among the periods with a number of equivalent time windows (10-hours / 2-hours), night and dusk had a greater number of anuran records than day and dawn, respectively (Tab. 1).

We found the interval between 16:00 and 20:00 as the most effective time to survey anurans both because of the frequency of vocal activity and the number of species detected. Accordingly, 36% of the records of vocal activity (8,993 out of 25,134) and 97% of the anuran species (57 out of 59) were detected in this four-hour's time interval, with a peak at 17:00 (Fig. 3).

Temporal acoustic distribution of anuran species

The distribution of the species in relation to the nycthemeral temporal gradient showed that 45 of the 59 species were recorded in all of the four periods (dawn, day, dusk, night), regardless of the numbers of vocal activities recorded. However, 64.41% of the species showed preference for certain periods, since there were more than 50% of the records of these species for one of the four periods of the day. We observed that the dusk and night periods had a greater concentration of species activity records (Fig. 4a). However, 45 of the 59 species have records of vocal activity well distributed over the area size gradient (Fig. 4b).

Formation of temporal acoustic assemblages

With regards to the composition of the time windows, the previously defined periods of dawn, day, dusk and night are respectively grouped with the most distinct and cohesive periods being day and night. The groups representing the dawn and dusk periods formed temporal bridges between the day and night periods (Fig. 2).

Effect of island size on vocal activity

There was a positive relationship between the size of the islands ($n = 74$) and the average vocal activity time of the anuran assemblage ($r^2 = 0.342$; $p < 0.001$; Fig. 5). As

the size of the island is a proxy for the richness of species and the size of the population, this possibly modulates the vocal activity time of the anuran assemblages.

Discussion

We determined the period of vocal activity of 59 species of Amazonian anurans recorded within the Balbina archipelago and adjacent areas of continuous forest. In doing so, we provided a complete view of the diel cycle of calling activity for many species whose activity was elusive or even unknown. This was possible thanks to the use of passive acoustic monitoring, which allowed us to optimize the sampling of vocal activity, generating an expressive number of recordings (216,217 recordings of 1 minute). The automatic detection algorithm by Pattern Matching enabled us to perform the analysis on this large amount of data in a reasonable amount of time.

We quantitatively demonstrated a time period with relatively increased species vocal activity, beginning at the end of the day from 16:00 to 16:55, and extending between dusk and night from 17:00 to 20:00. This pattern corroborates studies that qualitatively suggested that the twilight period is the time when most species (both diurnal and nocturnal) engage in vocal activity in Amazonia (Menin *et al.* 2008; Dias-Terceiro *et al.* 2015). This shows that anuran surveys in Amazonia are more cost-effective if they are carried out over a period of time that encompasses the end of the day, dusk and at least part of the night, because these are the periods with the highest vocal activity and species richness.

It was possible to observe that the relationship between the circadian cycle of each species and the time of day models the heterogeneous distribution in vocal activities in anuran assemblages (Duellman & Trueb 1994; Wells 2007; Both *et al.* 2008; Llusia *et al.* 2013; Bueno *et al.* 2020). These factors define what we term here as *temporal acoustic*

assemblages, in a time scale of 1 hour from the acoustic record data. Thus, within the 24-time windows of 1-hour each, assemblages of species were active such that they could be distinguished from the dawn, day, dusk, and night periods, with remarkable heterogeneity among their compositions.

In accordance with MacArthur & Wilson's theory of island biogeography (1963 and 1967), we found a positive island effect of anuran species richness in a previous study (Bueno *et al.* 2020). In this study, we also revealed a positive island effect on the vocal activity of anuran assemblages. Some studies have shown that island size positively affects the communication and composition of acoustic bird assemblages (Bicudo *et al.* 2016). Furthermore, Rebouças *et al.* (2020) determined that insularization influenced the acoustic characteristics of anuran individuals on islands in relation to individuals on the continent, where social pressure on the islands caused overlapping of ecological and acoustic niche, thus adaptively causing changes in call parameters. As in the studies by Bicudo *et al.* (2016) and Rebouças *et al.* (2020), we observed that island size had a positive effect on species richness and vocal activity. In our case, such an effect was observed on the average vocal activity time of the anuran assemblages.

Contrary to our *a priori* hypothesis, we did not find that by increasing the size of the island, and consequently increasing the number of species, it would decrease the average time of vocal activity, as individuals would avoid overlapping of acoustic niche, as suggested by the ecological niche theory (Oseen-Wassersug 2002; Villanueva-Rivera 2014). Thus our alternative *a posteriori* hypotheses for the result are: 1) The positive relationship between the average time of the vocal activity of anuran assemblages and island size is a result of the stimulus of competition within and among species by the acoustic space, mainly by explosive breeding species (Hödl 1990; Madden & Jehle 2017;

Chang *et al.* 2018); and 2) the acoustic cues created by anuran vocalizations are stimuli to individuals of both the same species and other species to initiate vocal activity. This stimulus is possibly because species sense that if other individuals are actively vocal and mating, then the spatial and temporal environments are also favourable for them (Gerhardt & Huber 2002; Magrath *et al.* 2015; Radford *et al.* 2015; Ulloa *et al.* 2019; Fouquet *et al.* 2020; Sugai *et al.* 2020).

Our result corroborates what was found by Fouquet *et al.* (2020), in which the vocal activity of anurans attracts other anurans to areas close to vocalizing individuals, and they vocalize jointly, because the environment is favorable for both vocal and reproductive activity. As the size of the island increases, the environmental heterogeneity of the landscape consequently accompanies this increase, reflecting in the species richness and thus providing a strong social relationship between species, where they signal through acoustic cues the ecological conditions favourable to their environment (Sugai *et al.* 2020). Hence, the species can influence others in intraspecific and/or interspecific ways, their reproductive behaviour and consequently their vocal activity, due to cues emitted by individuals who are vocally active in a certain time and space, which in this way signal an environment with ecological characteristics conducive to reproduction.

Conclusions

We revealed that certain species have a wide temporal distribution in vocal activity, whereas other species are vocally active at certain periods throughout the diel cycle. Such a heterogeneous temporal distribution of vocal activity in anurans leads to the formation of temporal acoustic assemblages with the most distinct and cohesive being the assemblage of the night period. With that we determined that the most efficient timeframe

for anurans sampling is the one that includes times between the end of day, dusk and early night, as they have high vocal activity and species richness. Finally, island size positively affects the average time of vocal activity, possibly due to the knock-on effect of acoustic signalling by other species provoking others into vocal activity.

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Table 1. Records of vocal activities of anuran species in the Balbina archipelago distributed over the following periods: dawn (05:00 - 06:55); day (07:00 - 16:55); dusk (17:00 - 18:55); night (7:00 pm - 4:55 am). Values in bold show the time period of preference of each species.

Species	Records per period			
	Dawn (05:00-06:55)	Day (07:00-16:55)	Dusk (17:00-18:55)	Night (19:00-04:55)
<i>Adenomera hylaedactyla</i>	16	111	14	6
<i>Allobates femoralis</i>	85	322	66	27
<i>Allophryne ruthveni</i>	7	7	231	2240
<i>Amazophrynella minuta</i>	307	127	1287	7277
<i>Ameerega trivittata</i>	113	174	56	4
<i>Anomaloglossus stepheni</i>	17	169	41	104
<i>Atelopus hoogmoedi</i>	24	172	103	76
<i>Boana boans</i>	1	1	26	136
<i>Boana calcarata</i>	67	259	148	209
<i>Boana cinerascens</i>	5	26	53	160
<i>Boana fasciata</i>	2	30	18	1
<i>Boana multifasciata</i>	18	24	11	13
<i>Boana punctata</i>	24	90	30	71
<i>Ceratophrys cornuta</i>	46	127	36	2
<i>Chiasmocleis hudsoni</i>	18	301	178	4
<i>Chiasmocleis shudikarensis</i>	4	183	172	100
<i>Dendropsophus brevifrons</i>	8	109	41	3
<i>Dendropsophus leucophyllatus</i>	24	154	19	4
<i>Dendropsophus minusculus</i>	2	57	7	5
<i>Dendropsophus minutus</i>	79	850	63	2
<i>Dendropsophus parviceps</i>	44	56	68	46
<i>Elachistocleis bicolor</i>	310	247	735	481
<i>Leptodactylus knudseni</i>	7	30	7	38
<i>Leptodactylus longirostris</i>	159	1078	43	47
<i>Leptodactylus pentadactylus</i>	63	328	70	266
<i>Leptodactylus petersii</i>	4	12	7	3
<i>Leptodactylus rhodomystax</i>	13	117	31	19
<i>Leptodactylus stenodema</i>	19	87	32	179
<i>Lithodytes lineatus</i>	6	21	7	1
<i>Osteocephalus buckleyi</i>	5	7	5	8
<i>Osteocephalus taurinus</i>	3	10	7	23
<i>Phyllomedusa vaillantii</i>	7	24	26	49
<i>Phyzelaphryne miriamae</i>	2	4	23	311
<i>Pipa pipa</i>	2	27	6	1
<i>Pristimantis fenestratus</i>	27	22	87	20
<i>Pristimantis marmoratus</i>	20	64	73	27
<i>Pristimantis ockendeni</i>	22	70	53	108
<i>Pristimantis zimmermanae</i>	57	246	177	127
<i>Rhinella margaritifera</i>	20	34	27	7
<i>Rhinella marina</i>	24	23	20	69
<i>Rhinella proboscidea</i>	3	8	4	9
<i>Synapturanus mirandaribeiroi</i>	5	9	12	3
<i>Synapturanus salseri</i>	17	45	101	63
<i>Trachycephalus coriaceus</i>	23	46	64	11
<i>Vitreorana ritae</i>	54	59	84	3
<i>Adenomera andreae</i>	8	4	17	
<i>Boana lanciformis</i>		18	13	1
<i>Callimedusa tomopterna</i>		4	31	52
<i>Phyllomedusa tarsius</i>	1		3	1
<i>Rhaebo guttatus</i>	7	19	10	
<i>Rhinella merianae</i>	74	31	200	
<i>Scinax garbei</i>	2	1	1	
<i>Scinax ruber</i>		43	17	1
<i>Ameerega hahneli</i>		2		8
<i>Boana geographica</i>	13		4	
<i>Osteocephalus oophagus</i>		2	8	
<i>Trachycephalus resinifictrix</i>			8	2
<i>Dendropsophus marmoratus</i>		45		
<i>Phyllomedusa bicolor</i>				1
<i>Allobates sumtuosus</i>	NA	NA	NA	NA
<i>Leptodactylus mystaceus</i>	NA	NA	NA	NA
Total	1888	6136	4681	12429

Figure 1. Study area located at the Balbina Hydroelectric Reservoir landscape, State of Amazonas, Brazil. Locations in red represent the sampled islands and points in black represent the areas sampled in continuous forest. The orange line marks the buffer area of the Uatumã Biological Reserve (dashed lines in black).

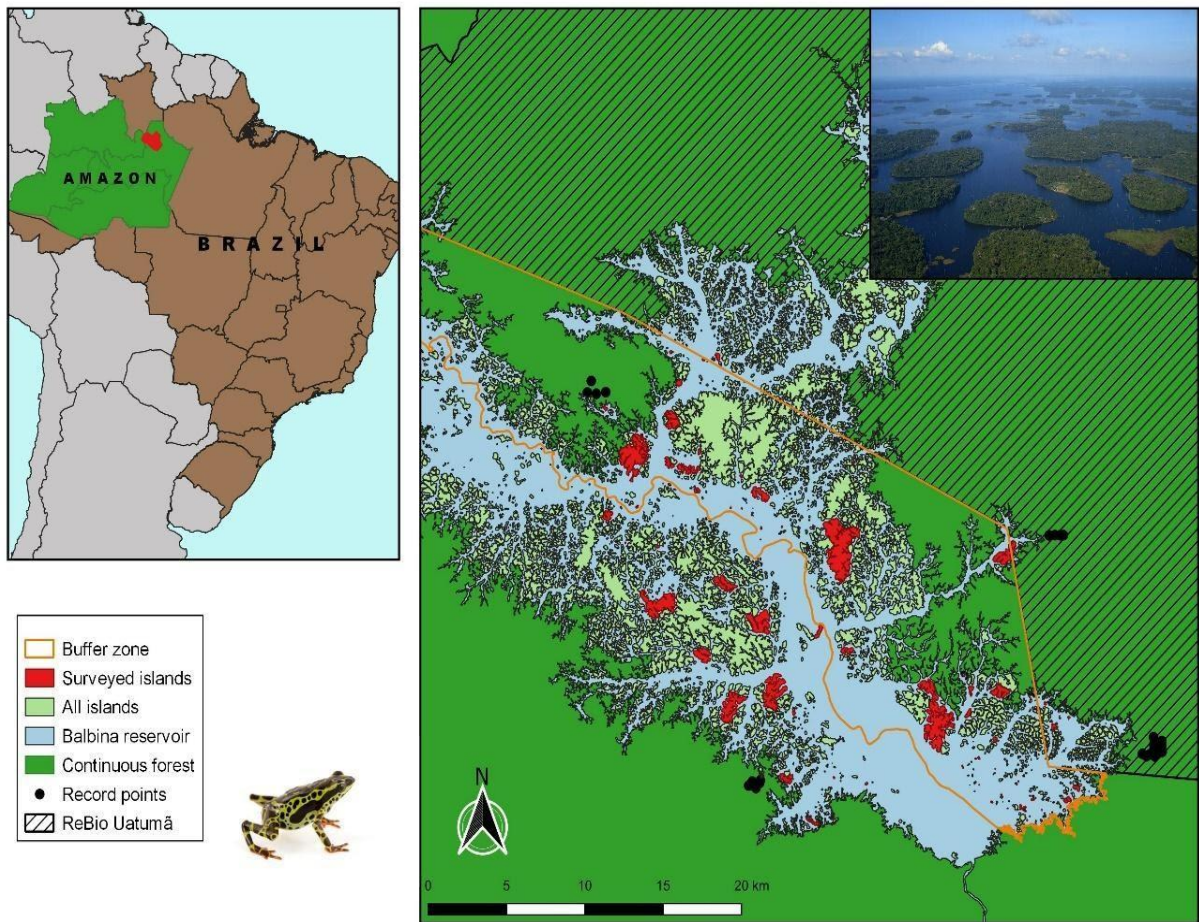


Figure 2. Non-metric multidimensional scaling (NMDS) showing the relationship between the composition of anuran species from the 24-time windows of 1-hour each, within the 4 periods in the Balbina archipelago.

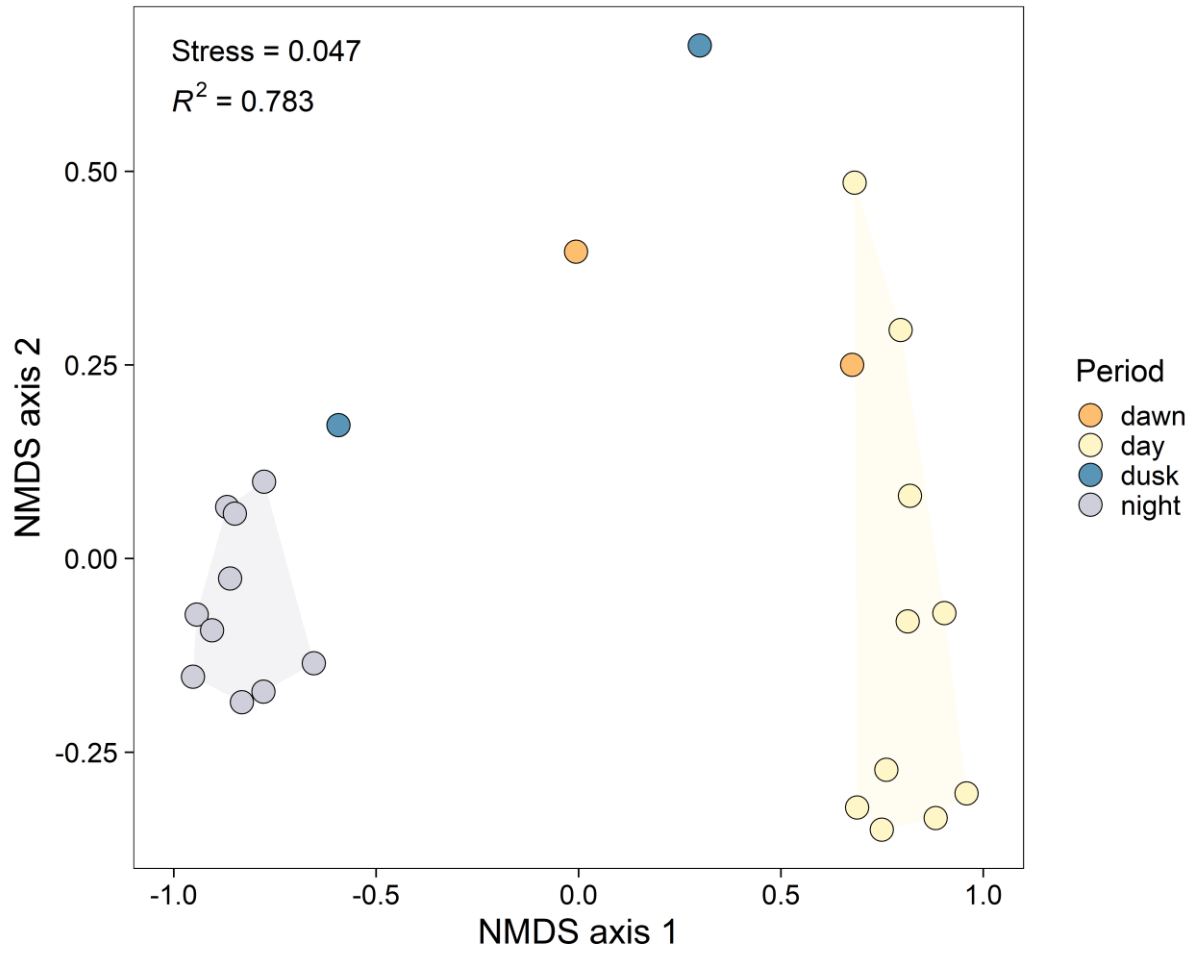


Figure 3. Diagram representing the distribution of vocal activity on a daily scale (24-h cycle) and in the dawn (orange background), day (yellow background), dusk (blue background) and night (gray background) periods of the anuran metacommunity in the Balbina archipelago. The variation in species richness is represented by hot colors (greater richness) and cold colors (lower richness). The size of the ranges and the numbers in whiteboards represent the frequency of vocal activity.

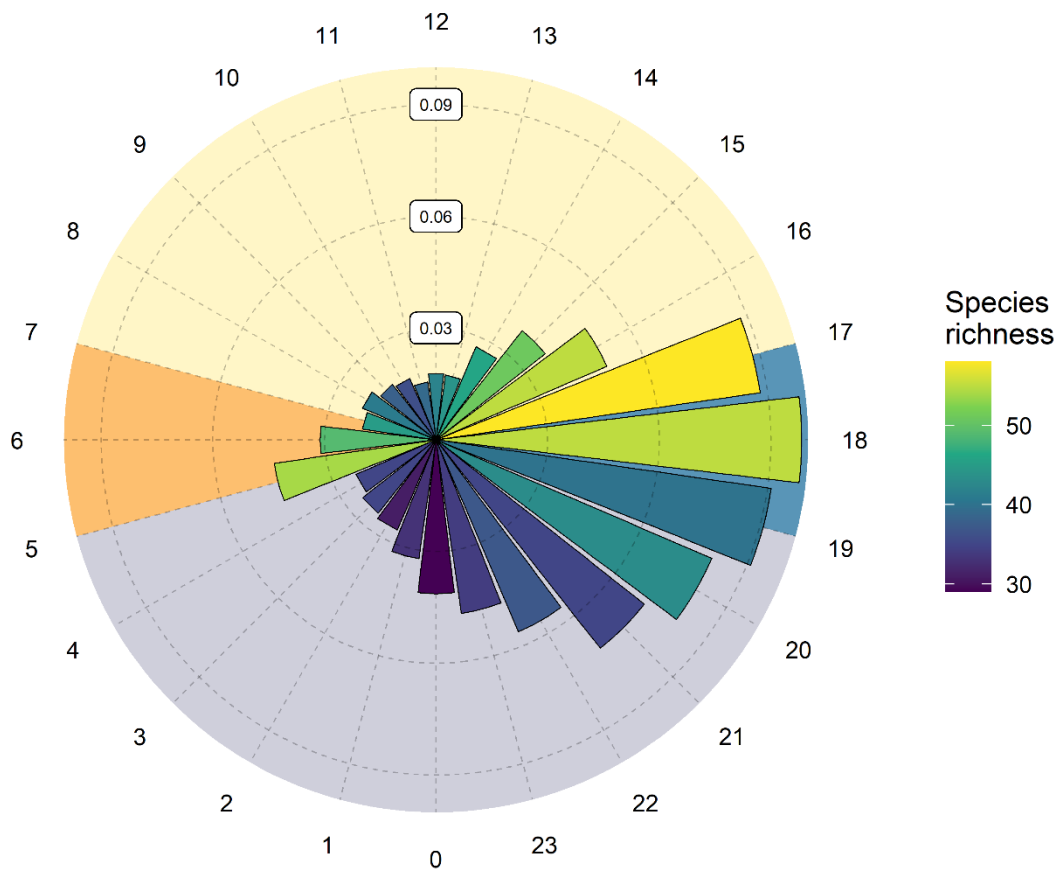


Figure 4. A) Anuran species occurrences in order of nycthemeral time gradient (24-hours); B) Anuran species occurrences ordered by island size in the Balbina archipelago reservoir, Central Amazonia.

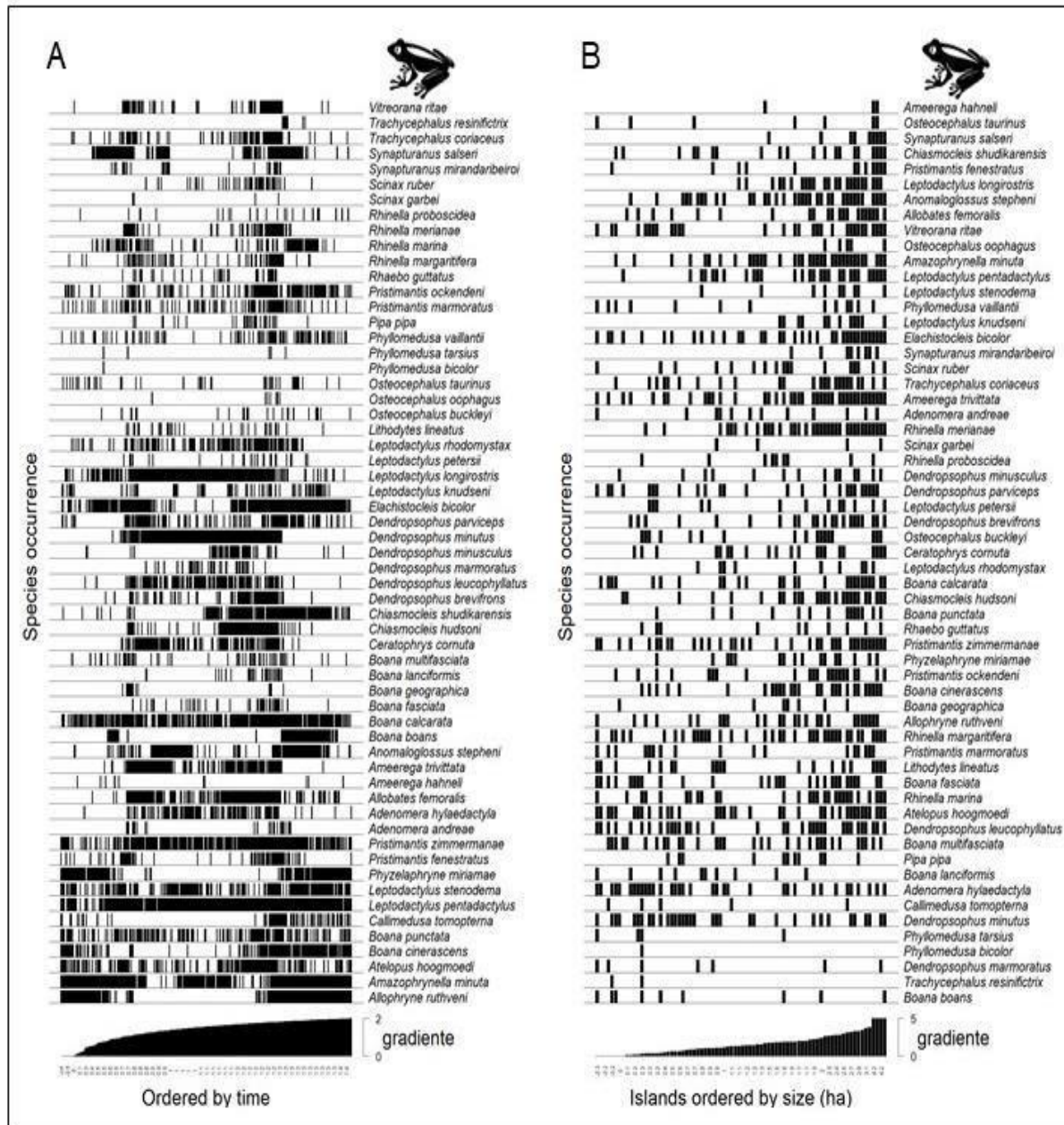
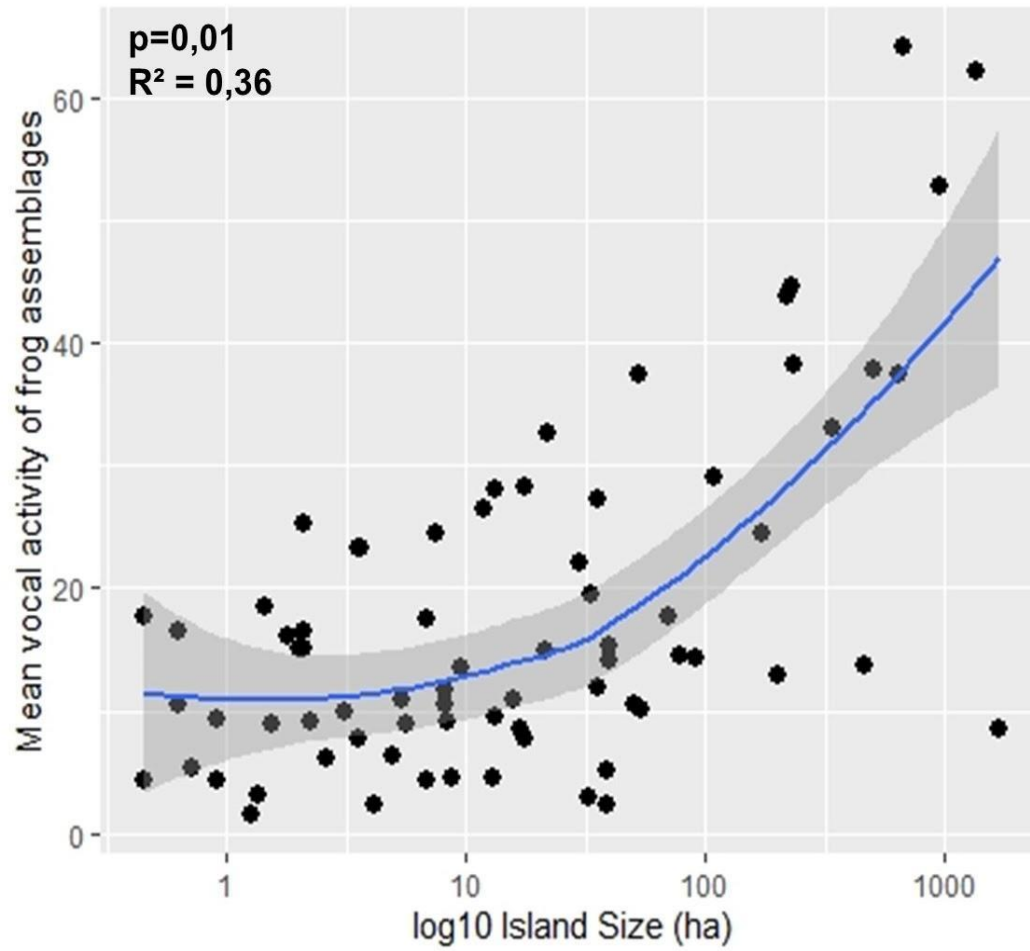


Figure 5. Simple linear regression between the average time of vocal activity of the anuran assemblage and the size of the island. Each point represents an island.



Supplementary material 1. Table of vocal activity records detected by the Pattern Matching (automatic detection algorithm). The species inserted in the Arbimon but never detected are represented by “NA”.

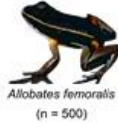
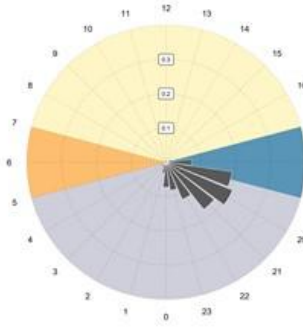
Taxon	Matchings	False positives	True positives	Hit rate (%)
Allophrynidae				
<i>Allophryne ruthveni</i>	47326	44841	2485	5.25
Aromobatidae				
<i>Allobates femoralis</i>	10491	9991	500	4.77
<i>Allobates sumtuosus</i>	0	0	0	NA
<i>Anomaloglossus stepheni</i>	3834	3503	331	8.63
Bufonidae				
<i>Atelopus hoogmoedi</i>	4507	4132	375	8.32
<i>Amazophrynella minuta</i>	65215	56217	8998	13.8
<i>Rhaebo guttatus</i>	6768	6732	36	0.53
<i>Rhinella margaritifera</i>	6095	6007	88	1.44
<i>Rhinella marina</i>	3229	3093	136	4.21
<i>Rhinella merianae</i>	7210	6905	305	4.23
<i>Rhinella proboscidea</i>	2412	2388	24	1
Centrolenidae				
<i>Vitreorana ritae</i>	5339	5139	200	3.75
Ceratophryidae				
<i>Ceratophrys cornuta</i>	17201	16990	211	1.23
Craugastoridae				
<i>Pristimantis fenestratus</i>	30953	30797	156	0.5
<i>Pristimantis marmoratus</i>	42907	42723	184	0.43
<i>Pristimantis ockendeni</i>	16210	15957	253	1.56
<i>Pristimantis zimmermanae</i>	42241	41634	607	1.44
Dendrobatidae				
<i>Ameerega hahneli</i>	177	167	10	5.65
<i>Ameerega trivittata</i>	6573	6226	347	5.28
Eleutherodactylidae				
<i>Phyzelaphryne miriamae</i>	29874	29534	340	1.14
Hylidae				
<i>Boana boans</i>	3291	3127	164	4.98
<i>Boana calcarata</i>	63712	63029	683	1.07
<i>Boana cinerascens</i>	7875	7631	244	3.1
<i>Boana aff. fasciata</i>	4377	4326	51	1.17
<i>Boana geographica</i>	4300	4283	17	0.4
<i>Boana lanciformis</i>	3136	3104	32	1.02
<i>Boana multifasciata</i>	4429	4363	66	1.49
<i>Boana punctata</i>	37237	37022	215	0.58
<i>Dendropsophus brevifrons</i>	18341	18180	161	0.88
<i>Dendropsophus leucophyllatus</i>	22645	22444	201	0.89
<i>Dendropsophus marmoratus</i>	8995	8950	45	0.5
<i>Dendropsophus minusculus</i>	2666	2595	71	2.66

<i>Dendropsophus minutus</i>	8810	7816	994	11.28
<i>Dendropsophus parviceps</i>	11819	11605	214	1.81
<i>Osteocephalus buckleyi</i>	4111	4086	25	0.61
<i>Osteocephalus oophagus</i>	1895	1885	10	0.53
<i>Osteocephalus taurinus</i>	1015	972	43	4.24
<i>Scinax garbei</i>	1134	1130	4	0.35
<i>Scinax ruber</i>	8746	8685	61	0.7
<i>Trachycephalus coriaceus</i>	2367	2223	144	6.08
<i>Trachycephalus resinifictrix</i>	89	79	10	11.24
Leptodactylidae				
<i>Adenomera andreae</i>	5659	5630	29	0.51
<i>Adenomera hylaedactyla</i>	793	646	147	18.54
<i>Leptodactylus fuscus</i>	11811	11811	0	0
<i>Leptodactylus knudseni</i>	11830	11748	82	0.69
<i>Leptodactylus longirostris</i>	48680	47353	1327	2.73
<i>Leptodactylus mystaceus</i>	157	157	0	0
<i>Leptodactylus pentadactylus</i>	8118	7391	727	8.96
<i>Leptodactylus petersii</i>	6575	6549	26	0.4
<i>Leptodactylus rhodomystax</i>	58918	58738	180	0.31
<i>Leptodactylus stenodema</i>	12729	12412	317	2.49
<i>Lithodytes lineatus</i>	749	714	35	4.67
Microhylidae				
<i>Chiasmocleis hudsoni</i>	4959	4458	501	10.1
<i>Chiasmocleis shudikarensis</i>	8229	7770	459	5.58
<i>Elachistocleis bicolor</i>	8354	6581	1773	21.22
<i>Synapturanus mirandaribeiroi</i>	10035	10006	29	0.29
<i>Synapturanus salseri</i>	9203	8977	226	2.46
Phyllomedusidae				
<i>Callimedusa tomopterna</i>	44270	44183	87	0.2
<i>Phyllomedusa bicolor</i>	775	774	1	0.13
<i>Phyllomedusa tarsius</i>	9577	9572	5	0.05
<i>Phyllomedusa vaillantii</i>	16527	16421	106	0.64
Pipidae				
<i>Pipa pipa</i>	1404	1368	36	2.56

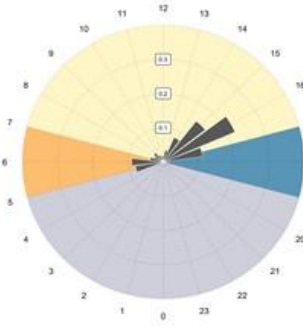
Supplementary material 2. Rose diagrams of nyctemeral vocalization activities for 59 anuran species occurring in the Balbina archipelago, Amazonas. Yellow represents the dawn and day periods, while the gray color represents the dusk and night periods; the inner bars (petals of the rose graph) represent the proportion of records of vocal activity in the daily period.



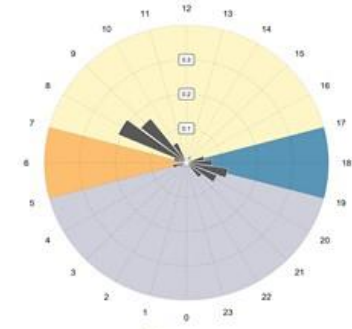
Allophryne ruthveni
(n = 2485)



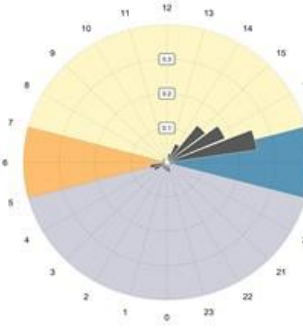
Allobates femoralis
(n = 500)



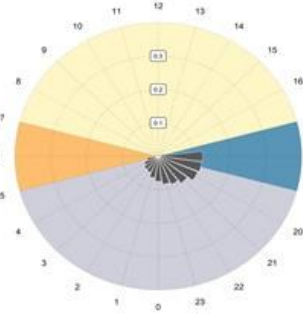
Anomaloglossus stephensi
(n = 331)



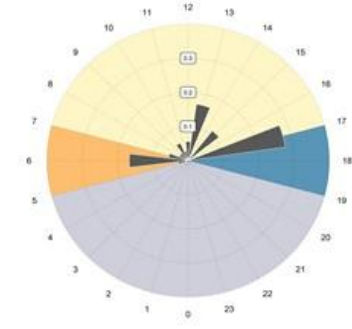
Atelopus hoogmoedi
(n = 375)



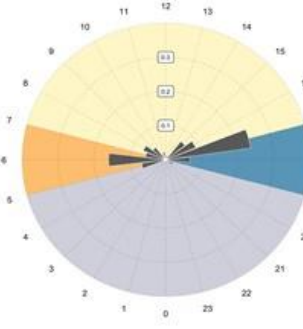
Amazophrynella minuta
(n = 8998)



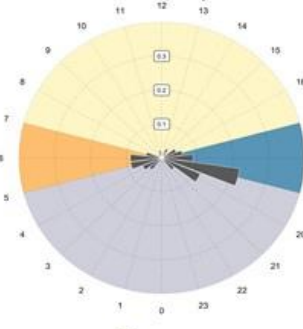
Rhaebo guttatus
(n = 36)



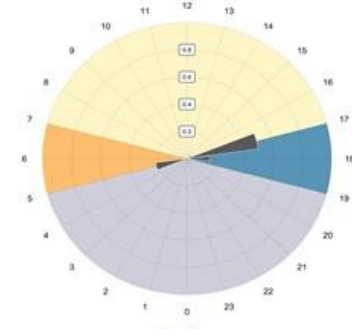
Rhinella margaritifera
(n = 88)



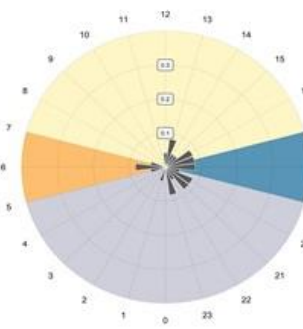
Rhinella marina
(n = 136)



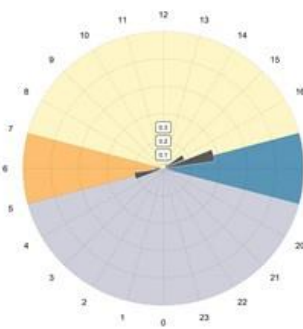
Rhinella morioanae
(n = 305)



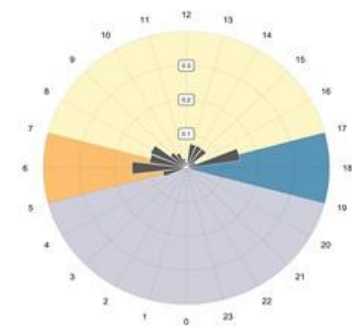
Rhinella proboscidea
(n = 24)



Vitreorana nitae
(n = 200)

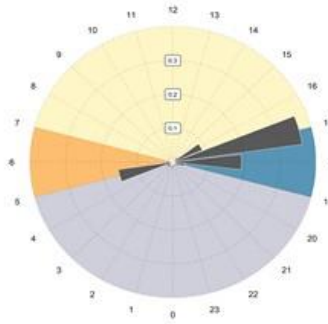


Ceratophrys cornuta
(n = 211)

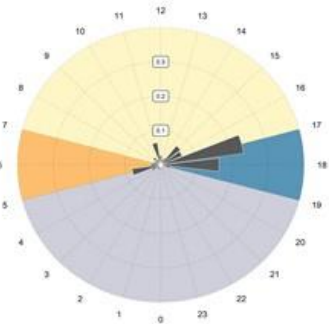




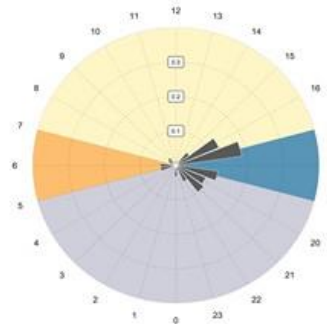
Pristimantis fenestratus
(n = 156)



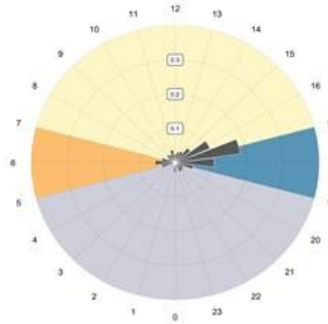
Pristimantis marmoratus
(n = 184)



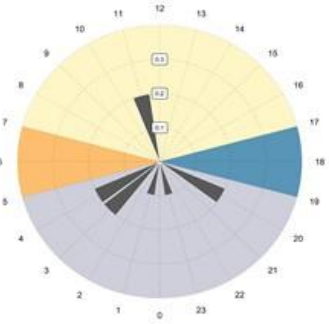
Pristimantis ockendeni
(n = 253)



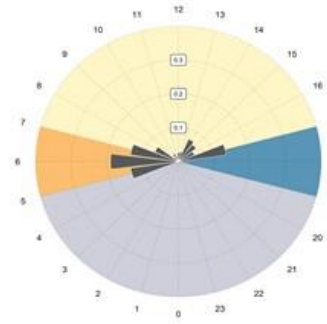
Pristimantis zimmermanae
(n = 607)



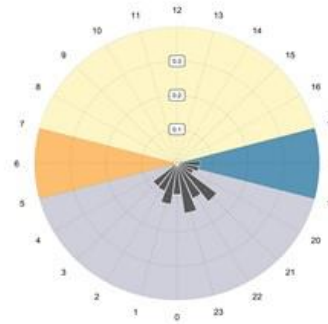
Ameerega hahnelti
(n = 10)



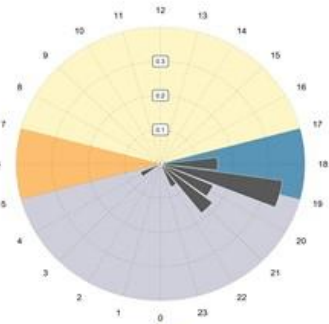
Ameerega trivittata
(n = 347)



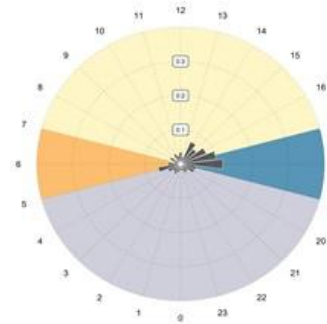
Phyzelaphryne miriamae
(n = 340)



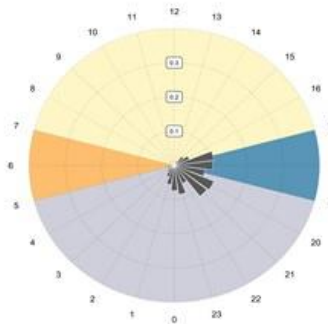
Boana boans
(n = 164)



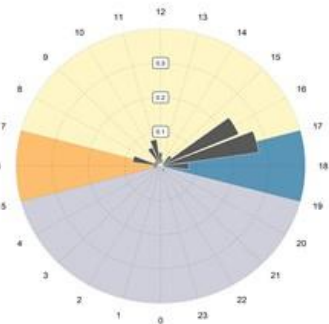
Boana calcarata
(n = 683)



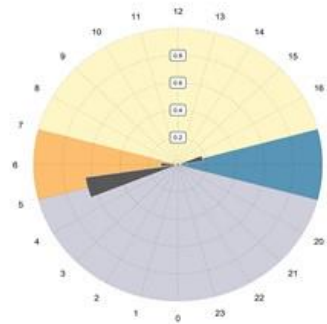
Boana cinerascens
(n = 244)



Boana aff. fasciata
(n = 51)

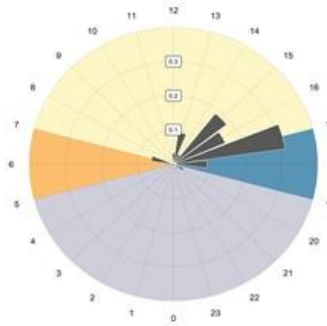


Boana geographica
(n = 17)

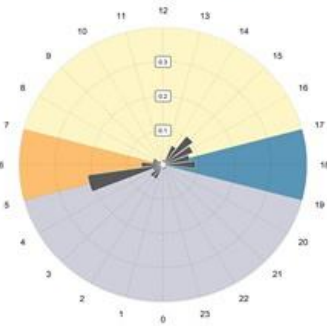




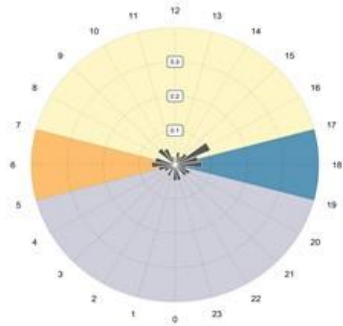
Boana lanciformis
(n = 32)



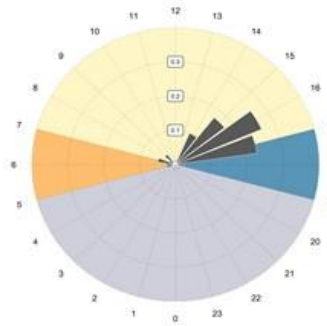
Boana multifasciata
(n = 66)



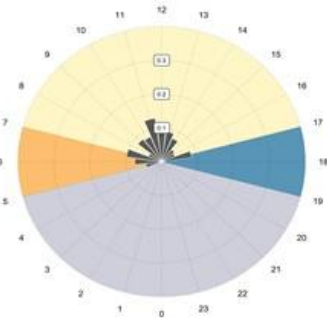
Boana punctata
(n = 215)



Dendropsophus brevifrons
(n = 161)



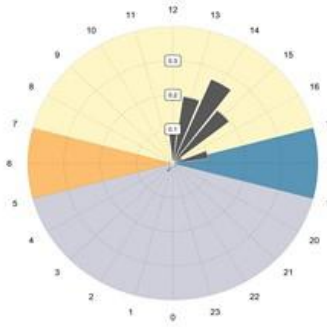
Dendropsophus leucophyllatus
(n = 201)



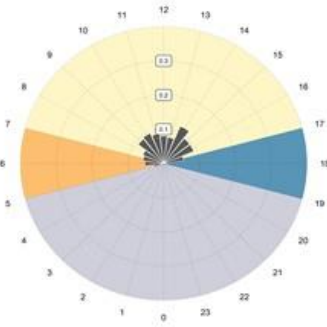
Dendropsophus marmoratus
(n = 45)



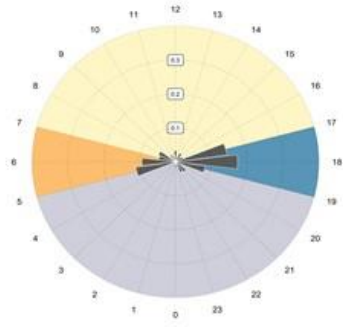
Dendropsophus minusculus
(n = 71)



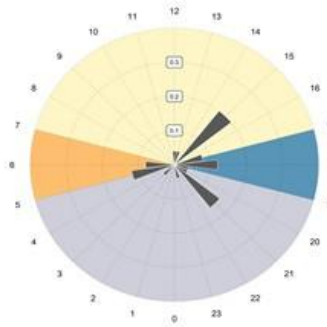
Dendropsophus minutus
(n = 994)



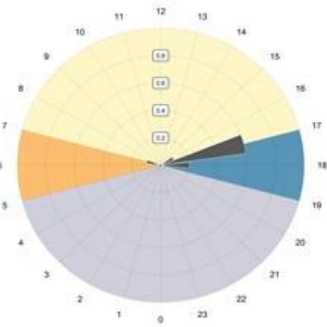
Dendropsophus parviceps
(n = 214)



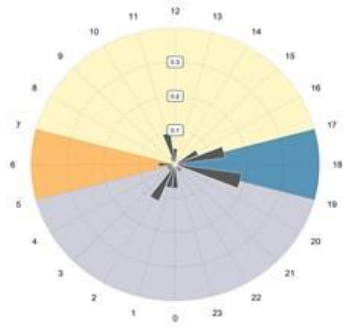
Osteocephalus buckleyi
(n = 25)



Osteocephalus oophagus
(n = 10)

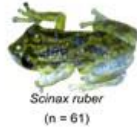
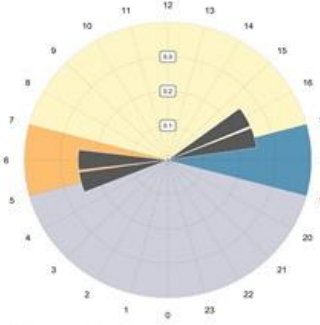


Osteocephalus taurinus
(n = 43)

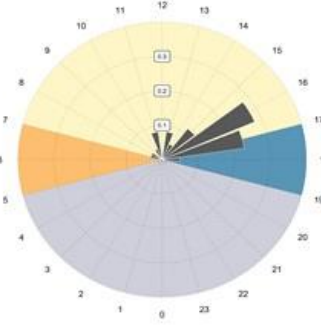




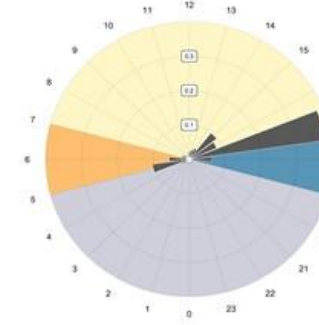
Scinax garbei
(n = 4)



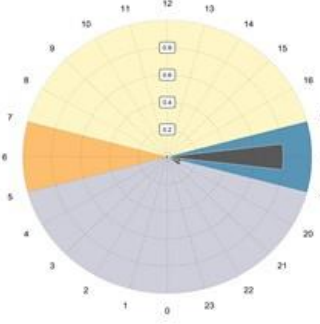
Scinax ruber
(n = 61)



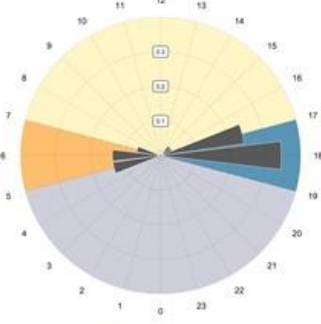
Trachycephalus coriaceus
(n = 144)



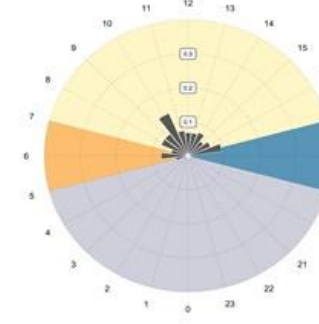
Trachycephalus resiniflatrix
(n = 10)



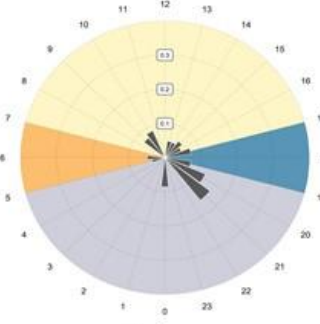
Adenomera andreae
(n = 29)



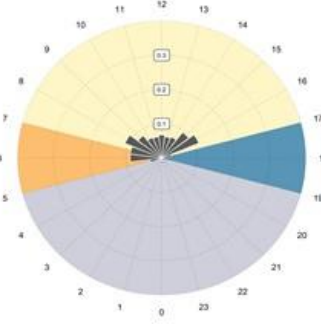
Adenomera hylaedactyla
(n = 147)



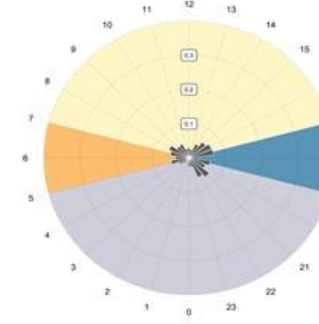
Leptodactylus knudseni
(n = 82)



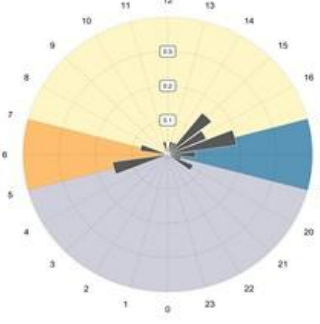
Leptodactylus longirostris
(n = 1327)



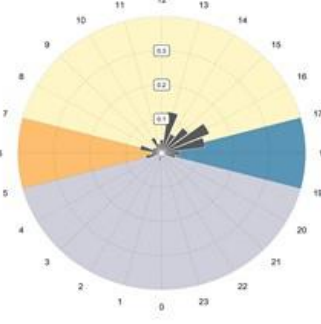
Leptodactylus pentadactylus
(n = 727)



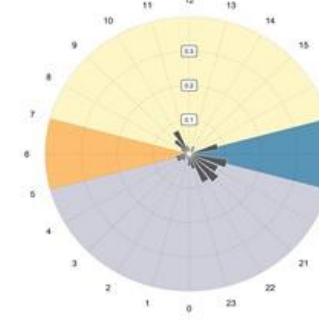
Leptodactylus petersii
(n = 26)



Leptodactylus rhodomystax
(n = 180)

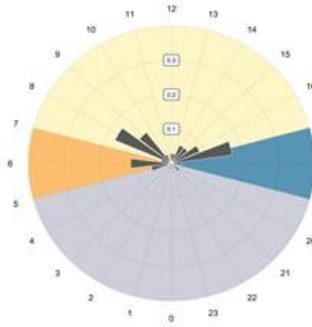


Leptodactylus stenodema
(n = 317)

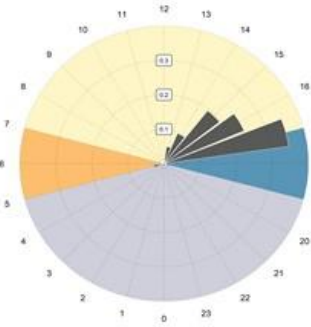




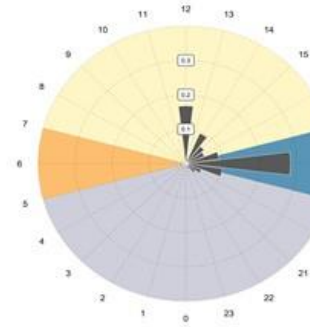
Lithodytes lineatus
(n = 35)



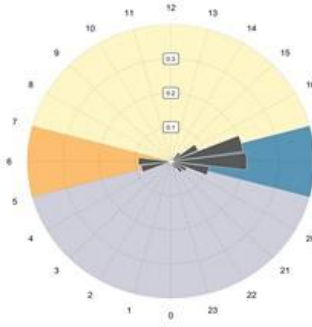
Chiasmocleis hudsoni
(n = 501)



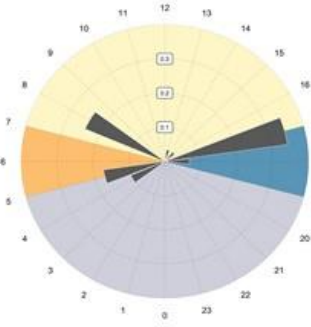
Chiasmocleis shudikarensis
(n = 459)



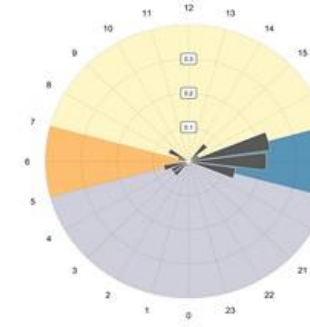
Elachistocleis bicolor
(n = 1773)



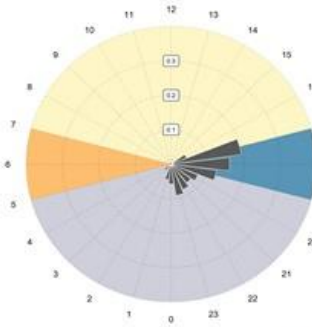
Synapturanus mirandaribeiroi
(n = 29)



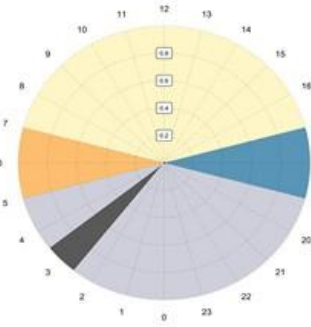
Synapturanus salseri
(n = 226)



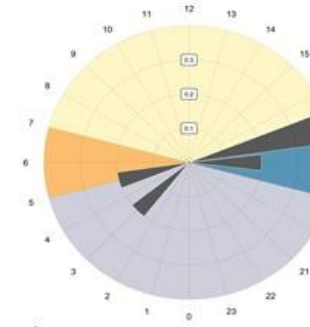
Callimedusa toropterna
(n = 87)



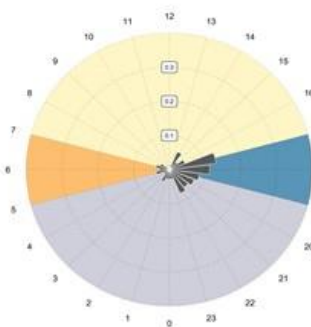
Phyllomedusa bicolor
(n = 1)



Phyllomedusa tarsius
(n = 5)



Phyllomedusa vaillantii
(n = 106)



Pipa pipa
(n = 36)

