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

Atividade de morcegos insetívoros aéreos em resposta a luminosidade lunar, distúrbio do habitat, condições climáticas e interação presa-predador em florestas preservadas e alteradas da Amazônia Central

GIULLIANA APPEL

Manaus, Amazonas

Setembro, 2021

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ATIVIDADE DE MORCEGOS INSETÍVOROS AÉREOS EM RESPOSTA A LUMINOSIDADE LUNAR, DISTÚRBIO DO HABITAT, CONDIÇÕES CLIMÁTICAS E INTERAÇÃO PRESA-PREDADOR EM FLORESTAS PRESERVADAS E ALTERADAS DA AMAZÔNIA CENTRAL

Orientador: Paulo Estefano Dineli Bobrowiec

Co-orientador: Christoph Meyer

Tese apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Doutor em Biologia (Ecologia).

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ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA.

Aos 20 dias do mês de Agosto do ano de 2021, às 13h30min, por videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Enrico Bernard,** da Universidade Federal de Pernambuco, a Dra. **Ludmilla Moura de Souza Aguiar,** da Universidade de Brasília - UNB, o Dr. **Igor Luis Kaefer**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o **Dr. Fábio Zanella Farneda**, da Universidade Federal de Santa Maria – UFSM e a Dra. **Carolina Blefari Batista**, do Centro Universitário de Goiatuba/GO - UNICERRADO. Tendo como suplentes o Dr. Fábio de Carvalho Falcão, no momento atua em Empresa de consultoria e o Dr. José Luís Campana Camargo, do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do orientador, a fim de proceder a argüição pública do trabalho de **TESE DE DOUTORADO** da **GIULLIANA APPEL**, intitulada: "**ATIVIDADE DE MORCEGOS INSETÍVOROS AÉREOS EM RESPOSTA A LUMINOSIDADE LUNAR, DISTÚRBIO DO HABITAT, CONDIÇÕES CLIMÁTICAS E INTERAÇÃO PRESA PREDADOR EM FLORESTAS PRESERVADAS E ALTERADAS NA AMAZÔNIA CENTRAL**", orientada pelo Dr. Paulo Estefano Dinelle Bobrowiec, do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

X	APROVADO (A)		REPROVADO (A)
X	POR UNANIMIDADE		POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

DR. ENRICO BERNARD

DRA. LUDMILLA MOURA DE SOUZA AGUIAR

DR. IGOR LUIS KAEFER

DR. FÁBIO ZANELLA FARNEDA

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Sinopse: Nessa tese, foram utilizados dados de monitoramento acústico realizados em floresta preservadas (Reserva Ducke) e florestas alteradas (PDBFF) na Amazônia Central. Foram feitas análises em nível de espécie, para entender como a luminosidade lunar, o distúrbio do habitat, a temperatura, a chuva e a interação presa-predador afetam a atividade dos morcegos insetívoros aéreos em diferentes escalas temporais (entre noites e dentro de uma mesma noite).

Palavras-chave: Ecologia animal; Floresta secundária; Fragmentos florestais; Insetos noturnos; Monitoramento acústico; Morcegos insetívoros aéreos.

Dedico aos meus pais e minha irmã
que me apoiaram em minhas escolhas e
estiveram ao meu lado,
pelo amor e confiança.

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“Essa humanidade que não reconhece que aquele rio
que está em coma é também o nosso avô,
que a montanha explorada em algum lugar da América do Sul
e transformada em mercadoria em algum outro lugar
é também o avô, a avó, a mãe, o irmão
de alguma constelação de seres que querem continuar
compartilhando a vida nesta casa em comum que chamamos
de Terra”

Ailton Krenak (2019)

Resumo

O crescente desmatamento e as mudanças antropogênicas no uso da terra têm devastado a floresta amazônica e tem criado paisagens fragmentadas com florestas em estágios diferentes de distúrbio. Morcegos podem ser indicadores de qualidade ambiental e estão cada vez mais sendo usados em monitoramentos. Os morcegos insetívoros aéreos são os menos estudados na Amazônia, pois a maioria dos estudos usam apenas redes-de-neblina, método ineficiente para registrar estes morcegos. Assim é incompreendido como a atividade destes morcegos responde a fatores bióticos e abióticos em florestas preservadas e alteradas. Diante disso, nesta tese avaliei como a luminosidade lunar, o distúrbio do habitat, as condições climáticas e a interação presa-predador influenciam a atividade dos morcegos insetívoros aéreos em florestas preservadas e alteradas da Amazônia Central. Usei dados de monitoramentos acústicos feitos por gravadores autônomos instalados na Reserva Ducke e no PDBFF entre 2013-2019. No **capítulo 1**, avaliei que o uso dos gravadores se demonstrou o método mais eficiente para obter dados de distribuição dos morcegos insetívoros aéreos na Amazônia quando comparado com outros métodos. No **capítulo 2**, os resultados indicaram que as espécies responderam mais a luminosidade lunar e a temperatura do que a chuva entre noites. Apenas duas espécies responderam positivamente a temperatura e a chuva não limitou a atividade das espécies tanto entre noites como ao longo da noite. No **capítulo 3**, analisei que o distúrbio do habitat influencia mais a atividade das espécies do que a luminosidade lunar, sendo que a floresta secundária teve menor atividade indicando que é pouco atrativa para este grupo. Nos fragmentos tiveram seis espécies com atividade reduzida em noites claras quando comparadas a noites escuras. No **capítulo 4**, avaliei que a atividade dos morcegos é influenciada negativamente pelo distúrbio do habitat provavelmente pela menor massa de insetos, sendo observei que tem insetos mais leves na floresta secundária do que na floresta preservada. O risco de predação e a luminosidade lunar influenciam pouco a atividade dos morcegos insetívoros aéreos. Por fim, sugere-se que na floresta preservada a luminosidade lunar pode ter efeito mais pronunciado do que outros fatores abióticos. Mas em florestas alteradas, a luminosidade lunar tem efeito fraco, e a menor massa de insetos parece explicar a menor atividade dos morcegos insetívoros aéreos nestas áreas.

Abstract

Increasing deforestation and anthropogenic land use changes have devastated the Amazon rainforest and created fragmented landscapes with forests in different stages of disturbance. Bats can be indicators of environmental quality and are increasingly being used in monitoring. Aerial insectivorous bats are the least studied in the Amazon, as most studies only use mist nets, an inefficient method to register these bats. Thus, it is not understood how the activity of these bats responds to biotic and abiotic factors in preserved and disturbed forests. Therefore, in this thesis I evaluated how moonlight intensity, habitat disturbance, climatic conditions and prey-predator interaction influence the activity of aerial insectivorous bats in preserved and disturbed forests of Central Amazonia. I used acoustic monitoring data from autonomous recorders installed at Reserva Ducke and BDFFP between 2013-2019. In **chapter 1**, I assessed that the use of recorders proved to be the most efficient method to obtain distribution data for aerial insectivorous bats in the Amazon compared to other methods. In **chapter 2**, the results indicated that species responded more to moonlight intensity and temperature than to rainfall between nights. Only two species responded positively to temperature and rainfall did not limited species activity between nights and throughout the night. In **chapter 3**, I analyzed that habitat disturbance influences species activity more than moonlight intensity and secondary forest showed lower activity, indicating that despite ca. 30 years of forest regeneration, it is still less attractive as foraging habitat. Fragments had six species with lower activity compared to preserved forest on bright nights compared to dark nights. In **chapter 4**, I assessed that bat activity is negatively influenced by habitat disturbance probably due to the lower mass of insects, as I evaluated that secondary forest showed lower insect mass than preserved forest. Predation risk and moonlight intensity have weak effects on aerial insectivorous bat activity. Finally, it is suggested that in the preserved forest, moonlight intensity may have a more pronounced effect than other abiotic factors. But in disturbed forests, moonlight has a weak effect, and the lower insect mass seems to explain the lower activity of aerial insectivorous bats in these areas.

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INTRODUÇÃO

O uso de gravadores para amostragem dos morcegos insetívoros aéreos

Morcegos estão cada vez mais sendo utilizados em monitoramentos para avaliar o distúrbio de ambiente causado por ações antrópicas, como mudança no uso da terra, doenças, desmatamento, construções hidrelétricas e mudança climática (Voigt and Kingston 2016; Zamora-Gutierrez et al., 2021). Para amostragem de morcegos é possível utilizar um ou vários métodos de detecção, como redes-de-neblina, procura por abrigos, armadilhas de harpa (harp traps), gravadores de ultrassom e amostragens de E-DNA ambiental (Flaquer et al., 2007; Hourigan et al., 2008; Willig et al., 2009; Sales et al., 2020). Nos Neotrópicos, a maioria dos estudos e monitoramentos usam tradicionalmente redes-de-neblina, devido ao baixo custo de aquisição, baixa incerteza na identificação das espécies e a possibilidade de coleta de material biológico. No entanto, esses métodos de captura são invasivos, e necessitam de trabalho de campo exaustivo exigindo a presença dos pesquisadores durante todo o período de amostragem. Além disso, rede-de-neblina é um método eficaz para capturar os morcegos da família Phyllostomidae, que possuem chamados de ecolocalização menos intensos do que os morcegos insetívoros aéreos de outras famílias (O'Farrell & Gannon 1999; Yoh et al., 2020). Este enviesamento de captura faz com que ocorram lacunas de conhecimento sobre os morcegos insetívoros aéreos, estes são apenas eventualmente capturados com redes (MacSwiney et al., 2008; Meyer et al., 2011).

Os morcegos insetívoros aéreos incluem as espécies que usam a ecolocalização para forrageio e orientação e são caracterizados por se alimentarem de insetos em pleno voo (Kalko & Handley, 2001; Denzinger et al., 2013). O método mais eficaz para registrar os morcegos insetívoros aéreos é com o uso de gravadores de ultrassom (O'Farrell & Gannon, 1999; Froidevaux et al., 2014). O monitoramento passivo de morcegos não requer a presença do pesquisador durante a amostragem, pode ser programado com diferentes configurações e ainda permite instalar em vários locais ao mesmo tempo (Hintze et al., 2016; Hill et al., 2018).

A Amazônia é o bioma mais rico em espécies de morcegos do Brasil, podendo ocorrer 117 espécies de morcegos em simpatria em algumas localidades (Delgado-Jaramillo et al., 2020). Os morcegos insetívoros aéreos podem corresponder cerca de 50%

da assembleia de morcegos de um local da Amazônia (Bernard et al., 2011; Garbino et al., 2020). Mesmo a Amazônia que é um bioma rico, a maioria dos estudos com morcegos nesse ecossistema usam apenas redes-de-neblina, resultando em perdas de quase metade das espécies potenciais que podem estar presentes no local (Cunto & Bernard 2012; Silva & Bernard 2017). Além disso, usar apenas dados de redes-de-neblina para estudar os morcegos insetívoros aéreos pode resultar em dados de distribuição e abundância subestimados. Visando isso, meu **primeiro capítulo** teve como objetivo descrever o quão importante é o uso dos gravadores de ultrassom para estimar a distribuição dos morcegos insetívoros aéreos na Amazônia. Além disso, quis avaliar como a complementaridade de métodos e o uso de gravadores aumentam a riqueza de espécies de morcegos em diferentes locais da Amazônia, especialmente dos insetívoros aéreos.

Morcegos insetívoros aéreos tropicais e as relações com o ambiente e a lua

Morcegos são conhecidos por serem ecologicamente importantes nos ambientes tropicais pelos serviços ecossistêmicos que podem realizar como polinização, dispersão de sementes e produção de guano (Kunz et al., 2011; Enriquéz-Azevedo et al., 2020; Sakoui et al., 2020). Adicionalmente, morcegos insetívoros funcionam como supressores de populações de insetos considerados pestes agrícolas e insetos vetores de doenças humanas (Russo et al., 2018; Puig-Montserrat et al., 2020). Estima-se que um indivíduo de *Molossus molossus* pode consumir em média 22 mg de insetos por minuto na Mata Atlântica (Freitas et al., 2020). Este consumo de insetos pelos morcegos pode evitar perdas agrícolas de $3.7 a 53 bilhões de dólares por ano só nos Estados Unidos (Boyles et al., 2011; Kemp et al., 2019). Mais recentemente, no Brasil há evidências de morcegos se alimentarem de mosquitos *Anopheles* e *Culex* que transmitem a malária e a encefalite, respectivamente (Jordão, 2019). Portanto, é evidente que a atenção tenha aumentado nas últimas décadas para estudos que visam avaliar como os morcegos se relacionam com o ambiente e os fatores abióticos (Meyer et al., 2016; Arias-Aguilar et al., 2020).

As relações dos morcegos insetívoros aéreos com os fatores abióticos vem sendo estudadas mais profundamente na região temperada (Barclay & Brigham 1994; O'Donnell, 2000; Ciechanowski et al., 2007; Petit & O'Keefe 2017; Blomberg et al., 2021), provavelmente pelo fato de usarem o monitoramento acústico a mais tempo. O monitoramento acústico autônomo permite obter chamados de ecolocalização dos morcegos ao longo do tempo e portanto, obter uma medida de atividade temporal (Kuenzi

& Morrison 2003; Millon et al., 2015). Assim, é possível avaliar se a atividade dos morcegos está relacionada a fatores abióticos como a temperatura, chuva, e luminosidade lunar, e assim avaliar se a atividade é ajustada por estas condições em curtos ou longos períodos de tempo. Mesmo que na Amazônia a temperatura varie pouco durante a noite, a temperatura pode estar associada diretamente com a densidade de insetos e a temperatura corporal dos morcegos (Erkert 2000; Barros et al., 2014). Já a chuva pode interferir na propagação atmosférica da ecolocalização e pode afetar a termoregulação dos morcegos, inibindo a atividade dos mesmos (Baskaran et al., 2015; Russo & Voigt 2016).

A luminosidade lunar pode afetar negativamente a atividade de forrageio dos morcegos tropicais devido a maior diversidade e densidade dos predadores nos trópicos (Saldaña-Vásquez & Munguía-Rosas 2013). Para os morcegos insetívoros aéreos que são predadores e presas ao mesmo tempo, pode haver diferentes respostas à luminosidade lunar pois necessitam balancear o sucesso de forrageio com pressão de predação (Lang et al., 2006; Kolkert et al., 2020). Na Amazônia, já é conhecido que estes morcegos possuem respostas espécies-específicas à luminosidade lunar, com espécies aumentando ou diminuindo a atividade em noites claras (associadas a lua cheia) e outras não sendo afetadas (Appel et al., 2017). No entanto, a maioria dos estudos nos trópicos avaliam apenas um fator abiótico ou removem noites chuvosas, por exemplo (Dias-Silva et al., 2018; Vásquez et al., 2020). Além disso, é necessário entender se as espécies de morcegos são sensíveis a luminosidade lunar, são também sensíveis à fatores abióticos não tão previsíveis como a temperatura e chuva. Diante disso, meu **segundo capítulo** examinou como a atividade dos morcegos insetívoros aéreos responde a temperatura, chuva e luminosidade lunar em escalas temporais diferentes (entre noites e dentro de uma mesma noite).

Os morcegos insetívoros aéreos e as respostas aos efeitos do distúrbio da floresta e da lua

A fragmentação florestal na Amazônia Brasileira vem crescendo em taxas alarmantes, e só em 2017 houve um aumento de 70% no número de fragmentos florestais (Montibeller et al., 2020). Essa tendência tende a piorar devido às perdas florestais no

período entre 2018-19 (Barlow et al., 2020). A fragmentação na Amazônia tem sido originada do desmatamento, exploração madeireira e conversão das florestas para outros usos da terra, criando paisagens dominadas por habitats alterados e florestas degradadas (Fearnside, 2017). Nestas paisagens alteradas é cada vez mais comum ver florestas secundárias, que atualmente cobrem uma área de 17 milhões de hectares na Amazônia Brasileira (Almeida et al., 2016). Entender como florestas de diferentes níveis de distúrbio influenciam nos morcegos pode fornecer informações valiosas a respeito da vulnerabilidade dos animais com a crescente mudança antropogênica no uso da terra (Falcão et al., 2021). Além disso, é possível estimar as possíveis perdas ecossistêmicas com o declínio da atividade e extinção destes morcegos (Frick et al., 2020).

Eu já observei que a luminosidade lunar é um fator que regula a atividade de forrageio de algumas espécies de morcegos insetívoros aéreos em uma floresta primária (Appel et al., 2017). Em florestas alteradas e secundárias, a luminosidade lunar pode penetrar o interior da floresta com mais facilidade comparada a floresta primária (Giglioti & Diefenbach 2017). Já nos fragmentos a cobertura do dossel da floresta não se diferencia muito das florestas primárias (Almeida et al., 2019), resultando em riscos de predação similares. Mas espécies de morcegos que forrageiam em florestas podem possuir área de forrageio maior que a área dos fragmentos e assim serem forçados a irem para as bordas dos fragmentos ficando mais expostos aos predadores nas noites claras. Portanto, a luminosidade lunar pode acentuar reduções de atividade em resposta ao aumento do risco de predação em florestas alteradas e fragmentos pequenos (Bowers & Dooley 1993; Rocha et al., 2020).

Apesar de muitos estudos avaliarem o efeito da luminosidade lunar na atividade dos morcegos insetívoros aéreos (Saldaña-Vásquez & Muinguía-Rosas et al., 2013), poucos usam a luminosidade lunar como variável contínua e poucos usam em diferentes escalas temporais como o efeito lunar na atividade horária (Fenton et al., 1977; Mello et al., 2013; Vásquez et al., 2020). Além disso, estes efeitos raramente são avaliados em paisagens e florestas tropicais alteradas, com exceção de alguns poucos estudos (Jung & Kalko 2011; Musila et al., 2019). Avaliar como ocorre o efeito lunar na atividade de espécies de morcegos em florestas alteradas também pode trazer informações a respeito da sensibilidade das espécies à luminosidade artificial, visto que a luz artificial está crescendo cada vez mais nas áreas rurais (Guetté et al., 2018). O **terceiro capítulo** consistiu em avaliar como a luminosidade lunar modula os efeitos do distúrbio do habitat na atividade dos morcegos insetívoros aéreos em diferentes escalas temporais (entre

noites e dentro de uma mesma noite). Assim usei dados de monitoramento acústico feitos em 2012 a 2013 no Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF), o maior e mais duradouro experimento de fragmentação do mundo, localizado na Amazônia Brasileira Central (Laurance et al., 2017).

Lua e a interação presa-predador dos morcegos insetívoros aéreos em ambientes preservados e alterados

A interação presa-predador cria um conflito nos animais entre minimizar a exposição ao predador e maximizar a eficiência de forrageio (Lima 1985). Para os morcegos insetívoros aéreos, este conflito de decisões é ainda mais complexo, pois são presas e predadores ao mesmo tempo (Roeleke et al., 2020). Assim a decisão dos morcegos ao usar um determinado ambiente pode ser dependente de vários fatores, mas entre eles há o risco de predação e a disponibilidade de alimento que tem no ambiente. Os morcegos insetívoros aéreos que usam mais o interior da floresta ou bordas de floresta para forragear, são ainda dependentes da cobertura e complexidade vegetal e possivelmente a usam para se esconder dos predadores (de Araújo & Bernard 2016; Heer et al., 2015; Torrez et al., 2018). Fragmentos florestais e florestas em regeneração são ambientes cada vez mais comuns pela Amazônia (Broadbent et al., 2008; Smith et al., 2020), e por possuírem menor complexidade de vegetação podem expor os morcegos insetívoros aos seus predadores e podem conter disponibilidade de insetos noturnos mais baixa (Sampaio et al., 2003; Treitler et al., 2016; Mendes et al., 2017; Rocha et al., 2018). Além disso, a luminosidade lunar pode intensificar a visibilidade dos predadores que usam a visão para caçar e ao mesmo tempo pode influenciar a atividade dos insetos, já que alguns insetos diminuem a atividade com a luminosidade lunar, enquanto outros aumentam (Lang et al., 2006; Ciechanowski et al., 2007; Kolkert et al., 2020).

O entendimento de como o risco de predação, a disponibilidade de insetos e a luminosidade lunar modulam a atividade de forrageio dos morcegos insetívoros aéreos tropicais ainda não foi avaliado. Este tipo de estudo pode trazer informações valiosas a respeito dos mecanismos que explicam a sensibilidade dos morcegos a perturbação da floresta e a fragmentação, especialmente aqueles que forrageiam em florestas (Jung & Kalko 2010; Ethier & Fahrig 2011; Shapiro et al., 2019). Existem alguns estudos que avaliam como a massa de insetos e o risco de predação influenciam a atividade dos morcegos insetívoros (Scanlon & Pettit 2008; Lima & O'Keefe 2013), mas são analisados

separadamente. Na região temperada e tropical, há muita informação de que florestas alteradas e em regeneração podem conter menor qualidade de habitat e menor massa de insetos, influenciando negativamente a atividade dos morcegos insetívoros aéreos (Arrizabalaga-Escudero et al., 2015; Phommexay et al., 2011; Wright et al., 2021).

Poucos estudos em ambas as regiões têm avaliado o efeito do risco de predação e eles apontam respostas diferentes (Lima & O'Keefe 2013). Por meio de experimentos feitos em uma floresta do Canadá, Baxter et al., (2006) compararam a abundância de morcegos em noites que continham diferentes tratamentos: playback de chamados de corujas, playback de chamados de pica-pau e noites controle (sem playback). Os morcegos evitaram noites com som comparadas as noites sem som, mas evitaram ainda mais noites com chamados de corujas do que de pica-pau (Baxter et al., 2006). Em outro experimento feito nos EUA, Janos et al., (2014) não detectaram diferenças na atividade dos morcegos insetívoros entre noites com chamados de corujas e noites sem som. Na região tropical, apenas o trabalho de Breviglieri et al., (2017), o efeito de playback de chamados de corujas na atividade dos morcegos frugívoros do gênero *Artibeus*, e também não detectaram diferença com noites controles, no entanto viram diminuição da atividade dos morcegos quando instalaram uma coruja empalhada junto a árvores de figueira que os morcegos visitavam para consumir os frutos. Portanto, na região tropical ainda não se sabe como os morcegos insetívoros reagem ao risco de predação de corujas, e se o distúrbio da floresta intensifica o risco de predação com a maior exposição dos morcegos. Diante disso, no meu **quarto capítulo**, meu objetivo foi avaliar como o risco de predação, a massa de insetos e a luminosidade lunar influenciam a atividade dos morcegos insetívoros aéreos em uma paisagem perturbada no PDBFF.

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OBJETIVOS

O principal objetivo desta tese foi avaliar como a luminosidade lunar, o distúrbio do habitat, as condições climáticas e a interação presa-predador influenciam a atividade dos morcegos insetívoros aéreos usando monitoramento acústico autônomo em florestas primárias e alteradas na Amazônia Central.

Capítulo 1: Como a complementaridade de métodos de amostragem de morcegos contribui para o aumento do número de espécies de morcegos registradas na Amazônia?

- Testar se o uso de gravadores de ultrassom junto com redes-de-neblina incrementam em maior número de espécies de morcegos totais, Phyllostomídeos e morcegos insetívoros aéreos;
- Com uma revisão de levantamentos conduzidos na Amazônia, investigar quais métodos ou combinação de métodos contribuem para o maior número de espécies de morcegos amostradas.

Capítulo 2: Como a atividade dos morcegos insetívoros aéreos varia com as condições climáticas e a luminosidade lunar em uma floresta amazônica contínua?

- Avaliar se a atividade dos morcegos responde a temperatura, chuva e luminosidade lunar;
- Investigar se a atividade dos morcegos responde a condições climáticas (temperatura, chuva) diferentemente entre noites escuras (associadas a lua nova) e claras (associadas a lua cheia) de luminosidade lunar;
- Avaliar se a duração do tempo e o pico de atividade dos morcegos durante a noite são alterados depois de um período de chuva.

Capítulo 3: Como o distúrbio do habitat e da luminosidade lunar modula a atividade dos morcegos insetívoros aéreos?

- Avaliar como a atividade dos morcegos responde ao distúrbio do habitat e o ciclo lunar;

- Investigar se atividade dos morcegos varia entre noites escuras (associadas a lua nova) e claras (associadas a lua cheia) em cada habitat (floresta contínua, fragmento e floresta secundária);
- Entender se os picos na atividade horária dos morcegos muda entre noites escuras (associadas a luva nova) e claras (associadas a lua cheia) em cada habitat.

Capítulo 4: Como a atividade dos morcegos insetívoros aéreos varia com o risco de predação, a massa de insetos e a luminosidade lunar em florestas preservadas e alteradas?

- Avaliar como a atividade dos morcegos e a massa de insetos muda com o distúrbio do habitat;
- Investigar se os morcegos insetívoros respondem mais a massa de insetos ou ao risco de predação em cada habitat (floresta contínua, fragmento e floresta secundária);
- Avaliar a interação da luminosidade lunar com o risco de predação e a massa de insetos em cada habitat;
- Testar se o risco de predação afeta a atividade horária em cada habitat, comparando com noites controle.

Capítulo 1

Appel, G., Capaverde Jr., U. D., Oliveira, de L. Q., Pereira, L. G. do A., Tavares, V. Da C., López-Baucells, A., Magnusson, W. E., Baccaro, F. B. and Bobrowiec, P. E. D.

Use of complementary methods to sample bats in the Amazon.

Acta Chiropterologica, artigo aceito.

Abstract

Mist nets set at ground level is the traditional method of surveying bats and in the Amazon almost half of the bat surveys used this methodology. The sole use of ground-level mist nets biases surveys because of the lack of records of aerial insectivorous bats, which forage above the canopy or in other open areas. Canopy mist nets, roost searches and acoustic surveys are methods to survey bat assemblages, but their efficiency compared to ground-level mist nets has not been fully evaluated in the Amazon, the world's largest tropical rainforest. Here, we test how the complementarity of sampling methods contributes to the number of species recorded in bat surveys in the Amazonian rainforest. We simultaneously sampled bats using ground mist nets and ultrasonic recorders at the Ducke Reserve (Central Amazon) in Brazil and did a literature review of bat surveys conducted in the Amazon to assess how these methods have been used in field research during the recent decades. Forty-three bat species were identified using ground mist nets, and seventeen species and five acoustic sonotypes were identified using ultrasonic recorders in Ducke Reserve. The combination of ground mist nets and acoustic recorders registered the largest number of bat species. However, for phyllostomid species the sole use of mist nets was efficient in recording the highest number of species, whereas for aerial insectivores acoustic surveys was the most effective. Of the 54 bat surveys made in the Amazon, 27 localities used complementary methods: roost search, canopy mist nets, harp traps and acoustic surveys. The combination of ground and canopy nets, and ground nets with roost search did not record more phyllostomid bat species than the use of ground nets alone. However, the sole use of acoustic surveys recorded more aerial insectivorous species than any other combination of sampling methods. Using mist nets and acoustic surveys simultaneously, as in our study, results in a dramatic increase in species diversity and different guilds than using only mist nets in the Amazon. Canopy nets and roost search did not increase the total number of species or the number of phyllostomid species in bat surveys. By combining different survey methodologies, we can optimize the recorded diversity of bats, especially using both mist nets and acoustic monitoring.

Introduction

A major challenge in planning field surveys is to choose the most effective methods or combination of methods for the objectives of the study. When the objective is to compare assemblage structure, methods that detect most or all of the target species are preferred (Moreno *et al.*, 2000). Survey and monitoring protocols are often ineffective because sampling techniques vary in their ability to detect different species, and also the same species under different environmental conditions (MacSwiney *et al.*, 2008; Lopéz-Baucells *et al.*, 2019). For bats, a number of different detection methods are commonly used, such as mist nets, roost search, harp traps and ultrasonic recorders (Kunz and Parsons, 2009). In order to answer ecological questions about bat assemblages, and especially to implement bat monitoring studies, it is essential to survey them in a cost-effective manner (Hourigan *et al.*, 2008).

In the Neotropics, bats constitute the most abundant, species-rich and ecologically diverse mammal assemblages (Voss and Emmons, 1996; Wilson and Mittermeier, 2019). Bats are most commonly sampled by ground-level mist netting (Kunz and Parsons, 2009; Marques *et al.*, 2013). One of the advantages of capture methods, such as mist netting and harp-trap, is the possibility of the researcher to handle individual bats and conduct character-based species-level identifications, as well as collect biometric data, tissue and/or fecal samples, body fluids, ectoparasites and to collect voucher specimens for deposit in scientific collections (Flaquer *et al.*, 2007). However, mist netting requires the presence of researchers during the entire sampling period (Murray *et al.*, 1999), which limits the number of potential sampling sites. Captures conducted simultaneously in multiple locations require more time and/or people in the field, which increases the costs of research projects (MacSwiney *et al.*, 2008).

Phyllostomid bats are comparatively easy to sample with ground mist nets as they use senses in addition to echolocation for primary orientation and hunting (Schnitzler *et al.*, 2003; Denzinger and Schnitzler, 2013). Ground mist nets are not effective for capturing aerial insectivorous bats due to their foraging behavior in open spaces or above the canopy, their ability to detect and avoid the nets, and their capture is often considered "accidental" (O'Farrell and Gannon, 1999). As Neotropical bat species vary in the use of vertical space (Marques *et al.*, 2016; Silva *et al.*, 2020), setting mist nets in higher forest strata can increase the probability of capturing additional phyllostomid species (Bernard,

2001) and also some aerial insectivorous bats (Kalko and Handley, 2001; Sampaio *et al.*, 2003).

Passive continuous recordings of echolocation calls have been recognized as the most effective methods for detecting aerial insectivorous bat species (Froidevaux *et al.*, 2014; López-Baucells *et al.*, 2021) worldwide, but not for frugivorous or gleaning insectivorous species. Acoustic surveys are non-invasive methods that allow the identification of aerial insectivorous bat species by their species-specific calls, or the identification of sonotypes (species with similar calls that cannot be confidently distinguished) (Zamora-Gutierrez *et al.*, 2016; Russo and Voigt, 2016). Passive acoustic recorders do not require the presence of the researcher during the whole sampling period and can be programmed to operate with sampling schedules, if the focus is based on specific species (Hintze *et al.*, 2016; Hill *et al.*, 2018). Although the advancement of acoustic methods has allowed researchers to address several ecological and taxonomic questions, acoustic studies provide little data for research on systematics, physiology and parasitology (Flaquer *et al.*, 2007). However, differences in echolocation call structure between cryptic species (Jones and Parijs 1993; López-Baucells *et al.*, 2018), still require the capture of individuals to obtain morphological data, tissue samples and specimen vouchers for comprehensive taxonomy and systematics inferences (De Thoisy *et al.*, 2014; Pavan *et al.*, 2018).

Bats can also be detected by searching for roosts (Froidevaux *et al.*, 2020a). In the Neotropics, several species and guilds have been recorded by searching caves, tree hollows and foliage (Rodríguez-Herrera *et al.*, 2007; Lima *et al.*, 2017). For instance, some species of aerial insectivorous bats are also commonly found in man-made structures (buildings, bridges, culverts, mines, etc.). Therefore, roost searches can reveal species that are not usually captured in mist nets (Díaz and Linares García, 2012; Jung and Threlfall, 2018).

The Amazon harbours the world's largest tropical rainforest and is one of the biomes with the highest bat species richness; 117 species of bats can occur in sympatry in some Amazonian localities (Delgado-Jaramillo *et al.*, 2020). Even in this species-rich biome, few studies have used different sampling methods to estimate local and regional bat richness (e.g. Voss and Emmons, 1996; Barnett *et al.*, 2006; Moratelli *et al.*, 2010; Tavares *et al.*, 2017). The sole use of ground-level mist nets biases samples by the lack of records of aerial insectivores, resulting in the typical under-reporting of nearly half of the local diversity of potential species present. Although it is well known that acoustic

survey complements the sampling of bats with mist nets (MacSwiney *et al.*, 2008; Furey *et al.*, 2009; Meyer *et al.*, 2011; Trevelin *et al.*, 2017), there has been no assessment of how different methods, such as canopy nets, roost searching and ultrasonic recorders complement captures with ground mist nets.

We test the complementarity of sampling methods for bat species by analyzing data collected by ground mist nets and ultrasonic recorders at the same plots in a 25-km^2 area of continuous forest in Central Amazon. With a comprehensive literature review of bat surveys conducted in the Amazon, we investigate which methods (ground mist nets, canopy mist nets, roost search, and acoustic recorders) and combination of methods recover most of the assemblages of bats, especially phyllostomid species and aerial insectivorous species.

Material and Methods

Study area

The study was conducted in the Adolpho Ducke Forest Reserve (02° 55' – 03° 01' S; 59° 53' – 59° 59' W), administered by the National Amazon Research Institute (INPA), located between the city of Manaus and the AM-110 Highway, Amazonas State, Brazil (Fig. 1). The Ducke Reserve has an area of 10,000 ha of low-altitude rainforest and is part of the Brazilian Long-Term Ecological Research Program of the Brazilian National Research Council (Programa de Pesquisas Ecológicas de Longa Duração - PELD/CNPq). The climate is tropical humid with two seasons: a rainy season between November and May and a dry season between June and October (Oliveira *et al.*, 2008). The average annual temperature was 26.7º C, the annual humidity was above 80% and the average precipitation was 2,093 mm during the rainy period of 2013 (Ferreira *et al.*, 2012; Appel *et al.*, 2019). The reserve has a trail system that forms a 64 km^2 (8 × 8 km) grid (Fig. 1). The grid has 72 permanent plots distributed uniformly with a minimum separation of 1 km (Oliveira *et al.*, 2008). Each plot is 250 m long and follows an altitudinal contour of landscape to reduce variation in soil edaphic properties and consequently plant species composition (Magnusson *et al.*, 2014). Plot width can depend on the habitat sampled with riparian plots dictated by the edges of streams instead of following altitudinal contours.

Mist net sampling

We captured bats using mist nets in 10 non-riparian plots and in 10 riparian plots (Fig. 1) between October 2013 and February 2014 (Capaverde *et al.*, 2018; Pereira *et al.*, 2019) using eight ground-level mist nets (12 × 3 m, 19 mm mesh, Ecotone®, Poland) per plot. The mist nets remained open between 18:00 and 00:00 h and were inspected every 15 minutes (Serra-Gonçalves *et al.*, 2017). Each plot was visited for three non-consecutive nights, totalling 2,880 mist net hours (1 mist net hour = one mist net opened for one hour) (Straube and Bianconi 2002). The identification of bats was based on the dichotomous keys of Lim and Engstrom (2001), and descriptions of Simmons and Voss (1998) and Gardner (2007). The taxonomy followed Gardner (2007), Nogueira *et al.* (2014) and Garbino *et al.* (2020).

Ultrasonic-recorder sampling

We used automatic Song Meter SM2BAT® recording stations coupled to SMX-US® ultrasonic omnidirectional microphones (Wildlife Acoustics, Maynard, Massachusetts). We installed acoustic stations in the same 20 plots where the mist nets were opened (Fig. 1), during five months in the rainy season between January and May 2013 (De Oliveira *et al.*, 2015; Appel *et al.*, 2017). We placed the acoustic stations in the center of each plot and the microphones at a height of 1.5 m. In the riparian plots, the microphones were positioned over the streams. Recording started at 18:00 h and ended at 06:00 h, and each plot was sampled for four to six consecutive nights, totalling 101 sampling nights and 1,212 recording hours.

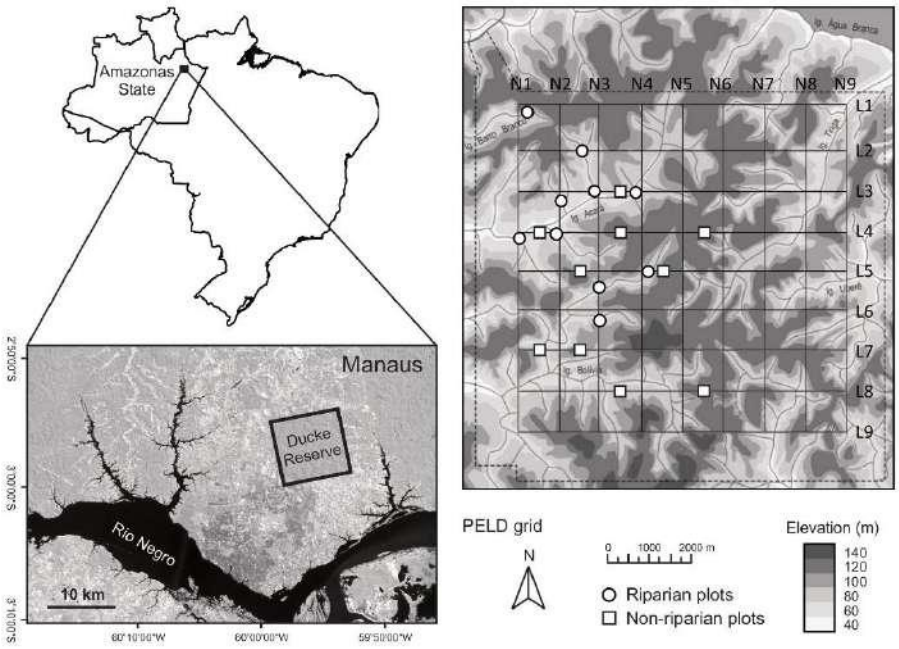

Figure 1. Map of the distribution of sampled plots for bats in the Ducke Reserve grid, Central Amazonia, Brazil.

We programmed the SM2BAT to real-time recording at a sample rate up to 384 kHz (covering pulse frequencies from 16 to 192 kHz), 16-bit full spectrum resolution with 1 s of pre-trigger and 0.1 s of post-trigger. We set them to record in files of 30-minute intervals for 12 hours per night. All recordings were segmented into smaller files up to 5 seconds long and a bat pass was a sequence of 5-s duration that had a minimum of two recognizable search-phase calls per species (Torrent *et al.*, 2018; Gomes *et al.*, 2020). We used the program Kaleidoscope 3.1.1. (Wildlife Acoustics, Maynard, Massachusetts) to convert, segment, view and classify all the recordings. We identified the species manually by comparing the structure and frequency parameters of the search-phase calls such as: call shape, frequency of maximum energy (FME), start, end, maximum and minimum frequency, and call duration. We compared the parameters using the acoustic-identification key for the bats from the Amazon, and studies of spectrograms of tropical bat species (Jung *et al.*, 2007, 2014; Barataud and Giosa, 2013; Arias-Aguilar *et al.*, 2018). For sonotypes (species difficult to distinguish from only the calls) we used the same sonotype groups described by López-Baucells *et al.* (2016). *Pteronotus rubiginosus* (identified as *P. parnellii* in Ducke Reserve by De Oliveira *et al.*, 2015) was identified by the taxonomic and acoustic description proposed by Pavan *et al.* (2018) (calls with frequency peak of 55 kHz, López-Baucells *et al.*, 2018). We recorded 223 bats

passes of Phyllostomidae, but due to the inability to differentiate species by call structures (Yoh *et al.*, 2020), we did not use this data in further analyses.

Literature review

We comprehensively searched the Web of Knowledge and Google Scholar for papers published between January 1979 and December 2019, but thesis and dissertations were not included. Published papers were selected based on the following search terms: "bats" OR "chiroptera" AND "Amazon", "Amazonian"; "inventory" AND "richness". We searched for papers using the same words in Portuguese and Spanish. A total of 102 papers included bat surveys in the Amazon, but only 43 studies at 54 localities met our criteria and were used in the analyses (Table S1). We only used bat-assemblage studies that identified the location of the capture, sampling method used, number of sampling nights, number of species, and names of the bat species recorded. For different papers conducted at the same location, we used the paper that reported the largest number of species. We selected articles that recorded at least 40% of the bat species presumed to be in the area to avoid studies with low sampling effort (Table S2). To check this, we compared the bat species richness observed in each study with the estimated richness obtained in the IUCN distribution maps for bat species of the family Phyllostomidae (IUCN, 2020). As some aerial insectivorous species are data deficient in IUCN distribution maps, we made the estimated richness only for Phyllostomidae species.

Data analysis

Complementarity of methods in Ducke Reserve: mist nets and ultrasonic recorders

To assess if the combination of sampling methods increases the number of species recorded compared to that registered from the exclusive use of ground mist nets at the Reserva Ducke, we used Gardner-Altman estimation plots and non-parametric permutation tests with 1000 bootstrap samples to estimate effect sizes and 95% confidence intervals for the difference of means. Statistical significance of differences among the methods was determined based on the lack of overlap in the frequency distributions of the data sets (Ho *et al.*, 2019). These analyses were done in R package "dabestr" (Ho *et al.*, 2019) and were made for assemblages of all bat species, phyllostomid species, and aerial insectivorous species.

Complementarity of methods in Amazonian bat studies

To assess whether the combination of sampling methods increases the number of bat species recorded compare to the exclusive use of ground mist nets, we used the Gardner-Altman estimation plots and non-parametric permutation tests with 1000 bootstrap samples (Ho *et al.*, 2019) with the literature survey data. Some combinations of methods were not included due to the low number of samples (e.g., acoustic survey with mist nets and harp traps).

Different sampling effort between studies (e.g., greater number of sampling nights) was balanced using Generalized Linear Models (GLM) with the number of bat species as the response variable, the methods employed as the predictor variable and the log-transformed number of sampling nights as offset in all models. For all bat species, phyllostomid species, and aerial insectivorous species, the results were the same for bootstrap analysis (Table S3); therefore, we used the Gardner-Altman analysis to graph the results. All analyses were undertaken in R studio version 1.2.5019 (RStudio Team 2020).

Results

Complementarity of methods in Ducke Reserve: mist nets and ultrasonic recorders

We registered 55 species and five sonotypes identified to genus using mist nets combined with ultrasonic recorders (Table 1). We captured 454 individuals with the mist nets representing 43 species from four guilds (nectarivores, frugivores, carnivores and gleaning insectivores). With the ultrasonic recorders, we registered 15,375 bat passes of 17 species and five generic sonotypes, all belonging to the aerial insectivorous guild. We recorded species of four families with both ground-level mist nets and ultrasonic recorders (Emballonuridae, Mormoopidae, Thyropteridae, and Vespertilionidae), one family exclusively in the ground-level mist nets (Phyllostomidae) and two families (Furipteridae and Molossidae) exclusively by ultrasonic recorders. Only *Carollia perspicillata* was recorded in all 20 plots by mist nets (n=156). Three species were present in all plots sampled with the ultrasonic recorders (*Cormura brevirostris*, *Saccopteryx bilineata* and *Pteronotus rubiginosus*).

Table 1. Bat species and guilds sampled using ground-level mist-nets and ultrasonic recorders at 20 plots in Ducke Reserve, Central Amazonia, Brazil. Number of records using mist-nets and the

number of bat passes using ultrasonic recorder with the number of plots each species/sonotype group was registered is given in parentheses. The bat guilds followed the classification proposed by Kalko *et al.*, (1998) and Schnitzler and Kalko (2001).

Family/Species	Guilds	Mist-nets	Ultrasonic recorder
Emballonuridae			
Centronycteris maximiliani (J. Fischer, 1982)	Aerial insectivore		604 (14)
Cormura brevirostris (J. A.Wagner, 1843)	Aerial insectivore	1 (1)	2685 (20)
Diclidurus ingens (Hernandez-Camacho, 1955)	Aerial insectivore		2 (1)
Peropteryx kappleri (Peters, 1867)	Aerial insectivore		14 (5)
Peropteryx leucoptera (W. Peters, 1967)	Aerial insectivore	2 (2)	
Peropteryx macrotis (J. A.Wagner, 1843)	Aerial insectivore		1 (1)
Peropteryx trinitatis (Miller, 1899)	Aerial insectivore		6 (4)
Saccopteryx bilineata (Temminck, 1838)	Aerial insectivore	1 (1)	3351 (20)
Saccopteryx gymnura/canescens	Aerial insectivore		14 (6)
Saccopteryx leptura (Schreber, 1774)	Aerial insectivore		1298 (18)
Phyllostomidae			
Anoura caudifera (É. Geoffroy St.-Hilaire, 1818)	Nectarivore	9 (6)	
Artibeus concolor (W. Peters, 1865)	Frugivore	2 (2)	
Artibeus gnomus (Handley, 1987)	Frugivore	3 (3)	
Artibeus lituratus (Olfers, 1818)	Frugivore	4 (4)	
Artibeus obscurus (Schinz, 1821)	Frugivore	11 (3)	
Artibeus planirostris (Spix, 1823)	Frugivore	14 (6)	
Carollia benkeithi (S. Solari and Baker, 2006)	Frugivore	16 (6)	
Carollia brevicauda (Schinz, 1821)	Frugivore	69 (16)	
Carollia perspicillata (Linnaeus, 1758)	Frugivore	156 (20)	
Choeroniscus sp.	Nectarivore	2 (2)	
Chrotopterus auritus (W. Peters, 1856)	Carnivore	1 (1)	
Glyphonycteris sylvestris (Thomas, 1896)	Gleaning insectivore	3 (2)	
Hsunycteris thomasi (J. A. Allen, 1904)	Nectarivore	35 (14)	
Lampronycteris brachyotis (Dobson, 1879)	Gleaning insectivore	1 (1)	
Lonchophylla sp.	Nectarivore	1 (1)	
Lophostoma carrikeri (J. A. Allen, 1910)	Gleaning insectivore	1 (1)	
Lophostoma schulzi (Genoways e Williams, 1980)	Gleaning insectivore	2 (2)	
Micronycteris hirsuta (Peters, 1869)	Gleaning insectivore	2 (2)	
Micronycteris megalotis (Gray, 1842)	Gleaning insectivore	3 (3)	
Micronycteris microtis (Miller, 1898)	Gleaning insectivore	5 (5)	
Micronycteris schmidtorum (Sanborn, 1935)	Gleaning insectivore	1 (1)	
Mimon crenulatum (É. Geoffroy, 1803)	Gleaning insectivore	15 (9)	
Phylloderma stenops (Peters, 1865)	Gleaning insectivore	1 (1)	

Phyllostomus elongatus (É. Geoffroy, 1810)	Gleaning insectivore	20 (9)	
Rhinophylla fischerae (Carter, 1966)	Frugivore	3 (3)	
Rhinophylla pumilio (Peters, 1865)	Frugivore	29 (11)	
Sturnira tildae (de la Torre, 1959)	Frugivore	1 (1)	
Tonatia saurophila (Koopman and Williams, 1951)	Gleaning insectivore	5 (5)	
Trachops cirrhosus (Spix, 1823)	Carnivore	4 (3)	
Trinycteris nicefori (Sanborn, 1949)	Gleaning insectivore	1 (1)	
Uroderma bilobatum (Peters, 1866)	Frugivore	1 (1)	
Vampyriscus bidens (Dobson, 1878)	Frugivore	9 (4)	
Vampyriscus brocki (Peterson, 1968)	Frugivore	1 (1)	
Mormoopidae			
Pteronotus gymnonotus (Wagner, 1843)	Aerial insectivore		1 (1)
Pteronotus rubiginosus (Wagner, 1843)	Aerial insectivore	8 (5)	3506 (20)
Furipteridae			
Furipterus horrens (F. Cuvier, 1828)	Aerial insectivore		63(12)
Thyropteridae			
Thyroptera lavali (Pine, 1993)	Aerial insectivore	2 (2)	
Thyroptera sp.	Aerial insectivore		25 (6)
Thyroptera tricolor (Spix, 1823)	Aerial insectivore	1 (1)	
Molossidae			
Cynomops abrasus/greenhalii	Aerial insectivore		12 (2)
Eumops sp.	Aerial insectivore		5 (1)
Molossus sinaloae/currentium/rufus	Aerial insectivore		333 (16)
Molossus molossus (Pallas, 1766)	Aerial insectivore		8 (1)
Vespertilionidae			
Eptesicus brasiliensis (Desmarest, 1819)	Aerial insectivore	1 (1)	6 (5)
Myotis albescens (É. Geoffroy, 1806)	Aerial insectivore	2 (2)	
Myotis nigricans (Schinz, 1821)	Aerial insectivore	1 (1)	
Myotis riparius (Handley, 1960)	Aerial insectivore	4 (4)	2156 (19)
Myotis sp.	Aerial insectivore		436 (6)
Lasiurus ega/egregius/castaneus/atratus	Aerial insectivore		587 (16)
Rhogeessa io/Lasiurus blossevillii	Aerial insectivore		262 (11)
Number of species		43	22
Number of records		454	15375

Most species were registered by only one of the sampling methods: 38 species solely with mist nets (60%), and 12 species and five sonotypes only with ultrasonic recorders (30.9%). Five species, all aerial insectivores, were recorded using both methods (9.1%) (Table 2) and in more than 90% of the sampled plots with acoustic records (with the exception of *Eptesicus brasiliensis*), but were recorded in only 25% of sampled plots with mist nets.

Table 2. Number of bat species (mean ± SD) recorded in 20 plots using different methods (ground mist nets and ultrasonic recorders) in Ducke Reserve, Central Amazon.

Sampling methods	N plots	All species	Phyllostomidae	Aerial Insectivores
Ground	20	43 (8.5 ± 2.6)	33 (7.6 ± 2.6)	10 (1.0 ± 0.9)
Acoustic	20	22 (10.4 ± 2.5)	0 (0 ± 0)	22 (10.4 ± 2.5)
Ground + Acoustic	20	60 (18.3 ± 4.0)	33 (7.6 ± 2.6)	17 (10.8 ± 2.4)

For all bats, the combination of ground mist nets and acoustic recorders documented the largest number of bat species in the Ducke Reserve (Fig. 2A). The combination of methods recorded 2.2 times more species/species groups per plot on average than ground mist nets alone. Ultrasonic recorders registered more species/species groups per plot than mist nets. Only ground mist nets recorded phyllostomid bats (Fig. 2B). For aerial insectivorous bats (Fig. 2C), acoustic recorders sampled on average 10.4 times more species than ground nets.

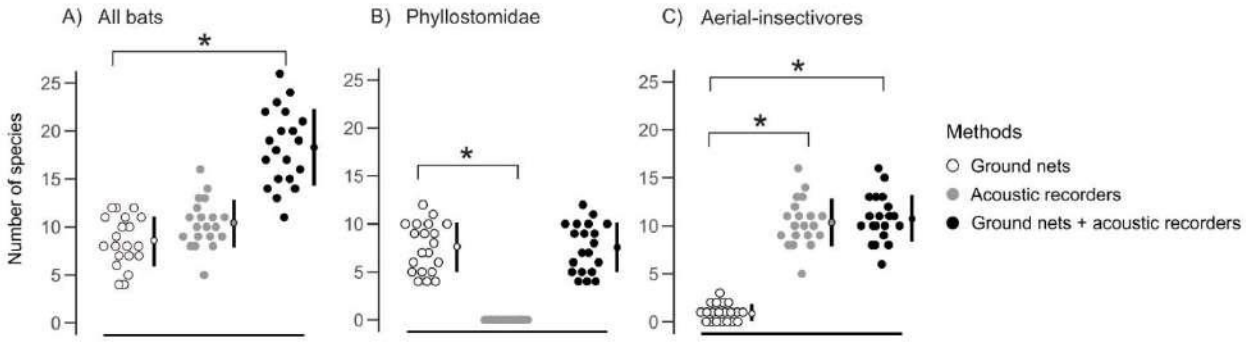

Figure 2. Bat species recorded by different sampling methods in Ducke Reserve, Central Amazonia, Brazil. Number of species sampled per plot for surveys based on ground mist nets (white circles), acoustic recorders (grey circles) and both methods combined (black circles) for all bats, phyllostomid bats, and aerial insectivorous bats. Mean (circles) ± standard deviation (vertical lines) are beside the plots of each sampling method. '*' means that the comparison between methods or combination of methods were significant.

Complementarity of methods in Amazonian bat studies

The different bat sampling methods found in our review included ground and canopy mist nets, roost searches, harp traps, and acoustic recordings (Table S1). Of the 54 localities, 51 (92.6%) used ground mist nets and 23 (42.3%) used exclusively this

method. Half of the localities used complementary methods and the most common combination was ground mist nets with roost searches (20.4%) followed by the combination of ground and canopy mist nets (18.5%). Only five localities (9.6%) used acoustic surveys, in which three localities used exclusively acoustics, and two used a combination of at least two methods. Harp traps were used to sample Amazonian bats in only 3.7% of the localities. The combination of ground mist nets with canopy mist nets and ground mist nets with roost search did not really affect the total number of all bat species or number of phyllostomid species than that recorded with ground nets alone (Fig. 3A and B). The use of acoustic survey alone recorded the highest number of aerial insectivorous species compared to other methods and combinations among them (Fig. 3C).

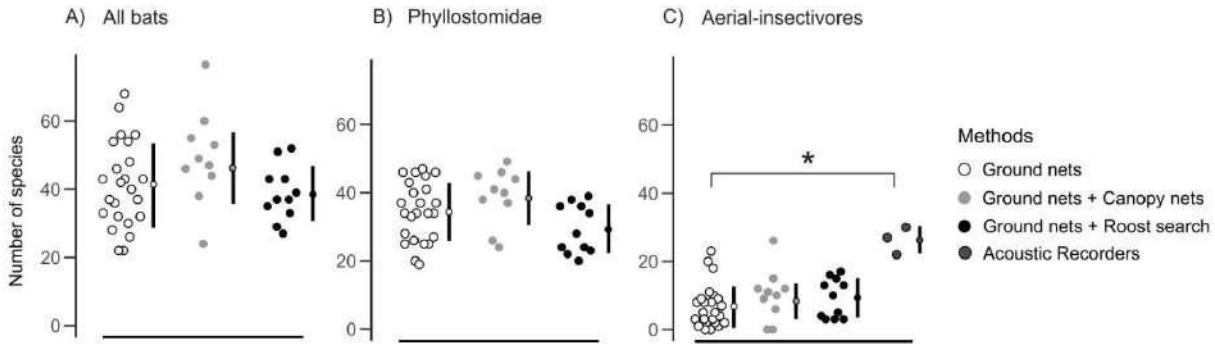

Figure 3. Bat species recorded by different sampling methods in Amazonian bat studies compiled from the literature. Number of species sampled per study for surveys based on ground mist nets (white circles), ground nets with canopy nets (light grey circles), ground nets with roost search (black circles) and acoustic recorders (dark grey circles) for all bats, phyllostomid bats, and aerial insectivorous bats. Mean (circles) ± standard deviation (vertical lines) are beside the plots of each sampling method. '*' means that the comparison between methods or combination of methods were significant.

Discussion

This study is the most complete list of bat species made in the Ducke Reserve using ground-level mist nets and ultrasonic recorders (Capaverde *et al.*, 2018; Appel *et al.*, 2019). The inclusion of ultrasonic recorders had a substantial impact on the number of bats recorded from Ducke Reserve, increasing by almost 45% the number of species we reported. Our analyses based on the literature review showed that the combination of two sampling methods other than acoustic recordings usually did not add more bat species, and exclusive use of ground-level mist nets resulted in the highest number of

phyllostomid species and total bat species. Nevertheless, if the focus of the study is on aerial insectivorous bat species, the exclusive use of recorders is the most effective method.

In Ducke Reserve, the use of ground mist nets resulted in a higher number of phyllostomid species (60% of total) than any other group, which comprises the second largest family of Chiroptera (Wilson and Mittermeier 2019). Phyllostomid species were not detected in our acoustic surveys because they emit similarly structured low intensity, multiharmonic and highly directional calls that make it almost impossible to identify differences among genera and species (Yoh *et al.*, 2020).

The exclusive use of ground-level mist nets in Ducke Reserve recorded only a few species of aerial insectivorous bats per plot compared to acoustic recorders. It has been demonstrated previously that the employment of ultrasonic recorders is the most efficient method for sampling aerial insectivorous bats in tropical forests (e.g. Meyer *et al.*, 2011; Britzke *et al.*, 2013; Silva and Bernard, 2017). Our acoustic survey in the Amazon corroborates this finding and added 14 species/sonotypes to the previous list of seven aerial insectivorous bat species known from the Ducke Reserve (Appel *et al.*, 2019). The increment of species by the use of acoustic surveys has been reported in other studies conducted in the Tropics, such as Venezuela (additional 11 species, Ochoa *et al.*, 2000), Vietnam (additional four species and five acoustic groups, Furey *et al.*, 2009), and in the Brazilian Caatinga (additional 22 species, Silva and Bernard, 2017). Only species from Noctilionidae and Natalidae were not detected in Ducke Reserve, probably because they are species associated with water bodies of open areas and caves that were not present in our study area (Voss *et al.*, 2016; Tavares *et al.*, 2017).

Pteronotus rubiginosus is the only aerial insectivore commonly included in community studies using ground mist nets in our study, and with its sister species *Pteronotus alitonus* in the forest of the Amazon (Peters *et al.*, 2006; Bobrowiec and Gribel, 2010; De Carvalho *et al.*, 2018; Silva *et al.*, 2020). Our study showed a discrepancy between sampling methods in relation to the number of plots in which this species was detected. Only 25% of plots sampled with ground mist nets registered *P. rubiginosus* in Ducke Reserve, against 100% of plots sampled with acoustic recorders. This indicates that acoustic survey is the most suitable method for recording this species. However, there was sampling bias in that mist nets were only open during the first half of the evening on three nights, whereas acoustic monitoring was done throughout the evening on 4-6 nights. Notwithstanding this discrepancy, we recommend caution in using

data on aerial insectivorous guilds for ecological studies when the records are based only on mist net surveys because distribution and abundance data can be underestimated by ground nets (Cunto and Bernard, 2012).

Our literature review confirmed that if the focus of the study is on phyllostomid species, ground mist netting is the most effective method and acoustic monitoring did not detect this family. By contrast, our study in Ducke Reserve indicates that ultrasonic recorders were an important sampling method for recording aerial insectivorous species that ground mist nets did not effectively capture. Therefore, if the focus of the study is overall bat diversity, the combination of the two methods is desirable to increase the number of species recorded. The combination of ground mist nets with canopy nets or searching for bats in their roosts did not increase the number of phyllostomid species or the total number of species in any substantive way. These methods probably are most effective in answering specific questions related to vertical stratification (Silva *et al.,* 2020) and the role of roosts in bat biology (Vargas-Mena *et al.*, 2020)

In terms of aerial insectivorous species, we found that the number of detected species was similar between the studies that used only ground nets and studies that used ground with canopy nets and roost searches. Canopy mist netting has been previously suggested as a potential method for capturing some species of aerial insectivores (Bernard, 2001; Marques *et al.*, 2016; Gregorin *et al.*, 2017; Silva *et al.*, 2020). Although this might apply to specific habitats, we did not find such an effect in the Amazonian rainforests. Furthermore, canopy sampling requires specialized (usually more expensive) equipment or types of mist nets and a higher effort for installation in the field (Kalko and Handley, 2001; Hourigan *et al.*, 2008), increasing project costs.

Regarding roost search, rocky outcrops found along the margins of streams, rivers and lakes (Voss *et al.*, 2016; Tavares *et al.*, 2017) and human-made constructions (Brosset *et al.*, 1996; Capaverde *et al.*, 2013) have been identified as important roosts for aerial insectivorous bats in the Amazon. However, these rocky outcrops are rare in the interior of Amazonian forest and are restricted to a few locations. Occupied roosts in foliage can be difficult to find because the lifetime of a tent can be short and the tent density can be lower in some forest areas (Timm 1987).

For aerial insectivorous species, we found that acoustic surveys recorded the highest number of species. This finding was expected based on other studies that compared bat sampling methods in tropical forests (Flaquer *et al.*, 2007; MacSwiney *et al.*, 2008; Wordley *et al.*, 2018). However, if the research objectives are beyond

monitoring and species diversity, then the use of mist nets and searches for roosts can be important for sampling aerial insectivorous bats because they provide an opportunity to sample biological material, collect species vouchers, and measure morphological attributes that cannot be obtained with bat recorders (Flaquer *et al.*, 2007). Gathering biological and morphological attributes is especially critical in the Amazon where such data is poorly known. In addition, the capture of aerial insectivorous bats allows recording of bat releases or zipline calls in order to expand and improve species-verified reference-call libraries (López-Baucells *et al.*, 2014, 2018; Arias-Aguilar *et al.*, 2018). Currently, this information for many species is lacking for the Amazon (López-Baucells *et al.*, 2019; Froidevaux *et al.*, 2020b).

Although ultrasonic recorders are known to be the best method for sampling insectivorous bats, acoustic surveys can be costly, time-consuming to identify the bat calls and requires highly trained researchers to classify the recordings (Fischer *et al.*, 2009; Trevelin *et al.*, 2017). However, ultrasonic recorders, power requirements (battery supplies), memory cards and hard drives are becoming increasingly cheaper (Hill *et al.*, 2018). Automated identification software is not yet reliable for neotropical bats (Rydell *et al.*, 2017; Menon *et al.*, 2018) and the identifications need to be validated manually (Adams *et al.*, 2012; Hintze *et al.*, 2016; Lopéz-Baucells *et al.*, 2019). Indeed, there are some limitations such as the imperfect detection of certain species (Duchamp *et al.*, 2006; Torrez *et al.*, 2017), the inability to quantify individuals and obtain bat abundance (Adams *et al.*, 2015) and difficulties to separate sonotypes with similar echolocation call structure (Jung *et al.*, 2007; 2014; López-Baucells *et al.*, 2016). Despite this, passive ultrasonic recorders are quick to set up in the field, can be automated to run for the entire night and extended periods of time unsupervised, and can simultaneously sample a wide variety of habitats (Hourigan *et al.*, 2009), including different forest strata (Gomes *et al.*, 2020).

Different bat guilds have different detectability depending on the sampling techniques applied in the surveys (Meyer *et al.*, 2011) and conclusions about ecological relationships for one guild should not be extrapolated to another without empirical justification. Different conclusions about ecological relationships may be obtained for the same guild, if different sampling techniques are used (Cardoso *et al.*, 2011). Therefore, the ecological research question being examined will also determine the choice of technique to be used (Hourigan *et al.*, 2009). Using multiple techniques may reduce sampling efficiency and increase required effort, but our study suggests that a combination of ground-mist nets and acoustical monitoring is the best option, if

conclusions are to be made across most bat guilds and species. For the purpose of inventories and environmental impact studies, we encourage the combined use of ground mist nets and ultrasonic recorders. This provides a more complete database not only in terms of the number of bat species, but also of trophic guilds, habitat use, behavior and ecosystem services that bats perform. Our study provides to decision makers, consultants and environmental managers a reference source aimed at improving bat sampling in the Amazon and tropical forests elsewhere. The use of ultrasonic recorders is still uncommon for sampling bats in Brazil (Aguiar *et al.*, 2020, Mendes and Srbek-Araujo, 2021), but that has been changing rapidly and contributing to our knowledge of the distribution and ecology of aerial insectivorous bats (Hintze *et al.*, 2020; Appel *et al*., 2021).

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Supplementary Material

Table S1. List of 43 papers with 54 localities of bat assemblages in the Amazon from our literature review: locality, country, source, number of Phyllostomidae species, number of aerial insectivorous species, total number of species, number of sampling nights, methods used, and the number of methods. Sampling methods are ground mist nets, roost searches, canopy mist nets, harp traps, and acoustic recorders.

Local	Country	Source	Phyllostomidae species	Aerial insectivorous species	All species	Sampling nights	Methods	N of methods
Village of Balta	Peru	Voss and Emmons, 1996	28	15	43	96	ground + roost	2
Xingu River	Brazil	Voss and Emmons, 1996	36	16	52	80	ground + roost	2
Cocha Cashu Biological Station	Peru	Voss and Emmons, 1996	42	14	56	72	ground + canopy + roost	3
Lower Arataye	French Guiana	Voss and Emmons, 1996	44	0	44	59	ground + canopy	2
Cunucunuma River	Venezuela	Voss and Emmons, 1996	32	14	46	52	ground + roost + harptrap	3
Esracion Biologica Pakicza	Peru	Ascorra *et al.*, 1996	33	12	45	25	ground + canopy + roost	3
Paracou Station	French Guiana	Simmons and Voss, 1998	59	19	78	168	ground + canopy + acoustic + roost	4
Lower Urubamba Region	Peru	Solari *et al.*, 2001	45	23	68	154	ground	1

Guamá Research Ecological Area	Brazil	Kalko and Handley, 2001	38	11	49	98	ground + canopy	2
Iwokrama Forest Reserve	Guyana	Lim and Engstrom, 2001	48	25	73	79	ground + canopy	2
Amazonian National Park	Brazil	Bernard, 2001	26	12	38	64	ground + canopy	2
Alter do Chão	Brazil	Bernard and Fenton, 2002	46	18	64	135	ground	1
Llanos de Moxos	Bolivia	Aguirre, 2002	20	17	37	51	ground + roost	2
Biological Dynamics of Forest Fragments Project (BDFFP)	Brazil	Sampaio *et al.*, 2003	46	9	55	312	ground + canopy	2
Tinigua Park	Colombia	Rojas *et al.*, 2004	25	5	30	12	ground	1
Jaú National Park	Brazil	Barnett *et al.*, 2006	24	25	49	77	ground + roost + acoustic	3
Kayapo Indigenous Area	Brazil	Peters *et al.*, 2006	37	10	47	24	ground + canopy	2
Tumucumaque Mountains National Park (Place I)	Brazil	Martins *et al.*, 2006	24	5	29	16	ground + roost	2
Rio Iratapuru Sustainable Development Reserve	Brazil	Martins *et al.*, 2006	24	3	27	9	ground + roost	2
Flona Amapá	Brazil	Martins *et al.*, 2006	39	4	43	8	ground + roost	2
Tumucumaque Mountains National Park (Place II)	Brazil	Martins *et al.*, 2006	36	3	39	8	ground + roost	2
Cerrado do Amapá Mazagão	Brazil	Martins *et al.*, 2006	34	3	37	9	ground + roost	2
Tiputini Biodiversity Station	Ecuador	Rex *et al.*, 2008	41	12	53	87	ground + canopy	2
Carrasco National Park	Bolivia	Vargas Espinoza *et al.*, 2008	46	25	71	79	ground + canopy + harptrap	3
Los Amigos Conservation Concession	Peru	Bravo *et al.*, 2008	37	0	37	30	ground	1

Bragança Viseu highway	Brazil	Andrade *et al.*, 2008	28	4	32	24	ground	1
Amanã Sustainable Development Reserve	Brazil	Pereira *et al.*, 2009	45	15	60	80	ground + canopy	2
Tapajós National Forest	Brazil	Castro-Arellano *et al.*, 2009	38	13	51	51	ground + roost	2
Iquitos	Ecuador	Klingbeil and Willig, 2010	43	0	43	168	ground	1
Zoobotanic Park	Brazil	Calouro *et al.*, 2010	26	2	28	36	ground	1
Pozuzo	Peru	Mena, 2010	34	8	42	30	ground	1
Barcelos	Brazil	Moratelli *et al.*, 2010	22	13	35	20	ground + roost	2
Madeira River	Brazil	Bobrowiec, 2012	19	3	22	11	ground	1
Aripuanã River	Brazil	Bobrowiec *et al.*, 2012	20	2	22	11	ground	1
Uauaçu lake	Brazil	Bobrowiec *et al.*, 2014	34	3	37	40	ground	1
Medium Teles Pires River	Brazil	Miranda *et al.*, 2015	25	8	33	36	ground	1
Lower Juruena River	Brazil	Dalponte *et al.*, 2016	23	10	33	38	ground + roost	2
Amanã Sustainable Development Reserve	Brazil	Marques *et al.*, 2016	0	30	30	20	acoustic	1
Lower Madeira River	Brazil	Bobrowiec and Tavares, 2017	46	10	56	197	ground	1
Alta Floresta	Brazil	Martins *et al.*, 2017	40	3	43	72	ground	1
Chiribiquete National Park	Colombia	Mantilla-Meluk *et al.*, 2017	46	8	54	70	ground	1
Loreto Region	Peru	Ramos-Rodríguez *et al.*, 2017	40	6	46	50	ground + canopy	2
Seringal Cachoeira Lodging	Brazil	Dos Santos *et al.*, 2017	25	1	26	20	ground	1

Rupununi Savannah	Guyana	Lim and Lee, 2018	34	20	54	43	ground	1
Sipaliwini Savannah	Suriname	Lim and Lee, 2018	37	9	46	18	ground	1
BDFFP	Brazil	López-Baucells *et al.*, 2019	0	27	27	250	acoustic	1
Jaci Paraná	Brazil	Durán and Oviedo Morales, 2019	47	9	56	62	ground	1
Caynarachi District	Peru	Carrasco-Rueda and Loiselle, 2019	41	2	43	48	ground	1
Jutaí Solimões Ecological Station	Brazil	Sabino-Santos *et al*., 2019	33	7	40	19	ground	1
Auati Paraná Extractive Reserve	Brazil	Sabino-Santos *et al.*, 2019	37	11	48	17	ground	1
Pampa Hermosa National Sanctuary	Peru	Arias and Pacheco, 2019	27	5	32	14	ground	1
Catuaba Experimental Farm	Brazil	Silva *et al.*, 2020	24	0	24	8	ground + canopy	2
Saut Pararé Nourages Research Station	French Guiana	Gomes *et al.*, 2020	0	20	20	9	acoustic	1
Ducke Reserve	Brazil	Present study	33	27	60	166	ground + acoustic	2

Table S2. The estimated richness obtained in the IUCN distribution maps (IUCN, 2020) and the observed richness in the 40 papers on bat assemblages in the Amazon. We considered only species of Phyllostomidae due to the lack of information for aerial insectivorous bat species, thus we have not considered studies that used only acoustic methods. This list contains (in descending order) only the selected papers that recorded at least 40% of the bat species presumed to be in the area in order to avoid studies with low sampling effort.

Local	Source	Estimated richness (IUCN)	Observed richness	Percentage
Alta Floresta	Martins *et al.*, 2017	31	40	129
Carrasco National Park	Vargas Espinoza *et al.*, 2008	37	46	124
Kayapo Indigenous Area	Peters *et al.*, 2006	33	37	112
Jaci Paraná	Durán and Oviedo Morales, 2019	42	47	112
Lower Madeira River	Bobrowiec and Tavares, 2017	44	46	105
Paracou Station	Simmons and Voss, 1998	59	59	100
Amanã Sustainable Development Reserve	Pereira *et al.*, 2009	49	45	92
Alter do Chão	Bernard and Fenton, 2002	51	46	90
Biological Dynamics of Forest Fragments Project	Sampaio *et al.*, 2003	51	46	90
Medium Teles Pires River	Miranda *et al.*, 2015	29	25	86
Lower Urubamba Region	Solari *et al.*, 2001	55	45	82
Iquitos	Klingbeil and Willig, 2010	53	43	81
Chiribiquete National Park	Mantilla-Meluk *et al.*, 2017	57	46	81
Xingu River	Voss and Emmons, 1996	48	36	80

Lower Arataye	Voss and Emmons, 1996	56	44	79
Guamá Research Ecological area	Kalko and Handley, 2001	48	38	79
Iwokrama Forest Reserve	Lim and Engstrom, 2001	61	48	79
Tapajós National Forest	Castro-Arellano *et al.*, 2009	48	38	79
Caynarachi District	Carrasco-Rueda and Loiselle, 2019	53	41	77
Flona Amapá	Martins *et al.*, 2006	51	39	76
Tiputini Biodiversity Station	Rex *et al.*, 2008	55	41	75
Loreto Region	Ramos-Rodríguez *et al.*, 2017	54	40	74
Auati Paraná Extractive Reserve	Sabino-Santos *et al.*, 2019	50	37	74
Pozuzo	Mena, 2010	47	34	72
Uauaçu lake	Bobrowiec *et al.*, 2014	47	34	72
Sipaliwini Savannah	Lim and Lee, 2018	53	37	70
Cocha Cashu Biological Station	Voss and Emmons, 1996	61	42	69
Cerrado do Amapá Mazagão	Martins *et al.*, 2006	50	34	68
Tumucumaque Mountains National Park (Place II)	Martins *et al.*, 2006	53	36	67
Jutaí Solimões Ecological Station	Sabino-Santos *et al*., 2019	49	33	67
Los Amigos Conservation Concession	Bravo *et al.*, 2008	57	37	65
Ducke Reserve	Present study	33	51	64
Lower Juruena River	Dalponte *et al.*, 2016	37	23	63
Bragança Viseu highway	Andrade *et al.*, 2008	46	28	61
Rupununi Savannah	Lim and Lee, 2018	57	34	60

Pampa Hermosa National Sanctuary	Arias and Pacheco, 2019	45	27	60
Amazonian National Park	Bernard, 2001	44	26	59
Zoobotanic Park	Calouro *et al.*, 2010	44	26	59
Esracion Biologica Pakicza	Ascorra *et al.*, 1996	61	33	54
Village of Balta	Voss and Emmons, 1996	53	28	53
Cunucunuma River	Voss and Emmons, 1996	61	32	52
Seringal Cachoeira Lodging	Dos Santos *et al.*, 2017	48	25	52
Catuaba Experimental Farm	Silva *et al.*, 2020	47	24	51
Jaú National Park	Barnett *et al.*, 2006	51	24	47
Rio Iratapuru Sustainable Development Reserve	Martins *et al.*, 2006	51	24	47
Llanos de Moxos	Aguirre, 2002	44	20	45
Tumucumaque Mountains National Park (Place I)	Martins *et al.*, 2006	53	24	45
Aripuanã River	Bobrowiec *et al.*, 2012	45	20	44
Tinigua Park	Rojas *et al.*, 2004	60	25	42
Barcelos	Moratelli *et al.*, 2010	52	22	42
Madeira River	Bobrowiec, 2012	45	19	42

Table S3. Summary of GLM results comparing the total number of species, Phyllostomidae species and aerial insectivorous species recorded comparing ground nets to combined methods in bat surveys in the Amazon. Sampling effort of the studies was controlled by using the argument offset in the models. Bold values indicate $p < 0.05$.

		Ground nets *vs.* Ground + Canopy nets	Ground nets *vs.* Ground + Roost search	Ground nets *vs.* Acoustic recorders
All species	Estimate	0.09	-0.09	
	Std. Error	0.06	0.05	
	z value	1.57	-1.69	
	Pr(>|z|)	0.11	0.08	
Phyllostomidae species	Estimate	0.07	-0.19	
	Std. Error	0.06	0.06	
	z value	1.08	-2.95	
	Pr(>|z|)	0.27	**0.003**	
Aerial insectivorous species	Estimate	0.2	0.28	1.5
	Std. Error	0.14	0.12	0.13
	z value	1.43	2.03	10.99
	Pr(>|z|)	0.15	0.051	**0.0001**

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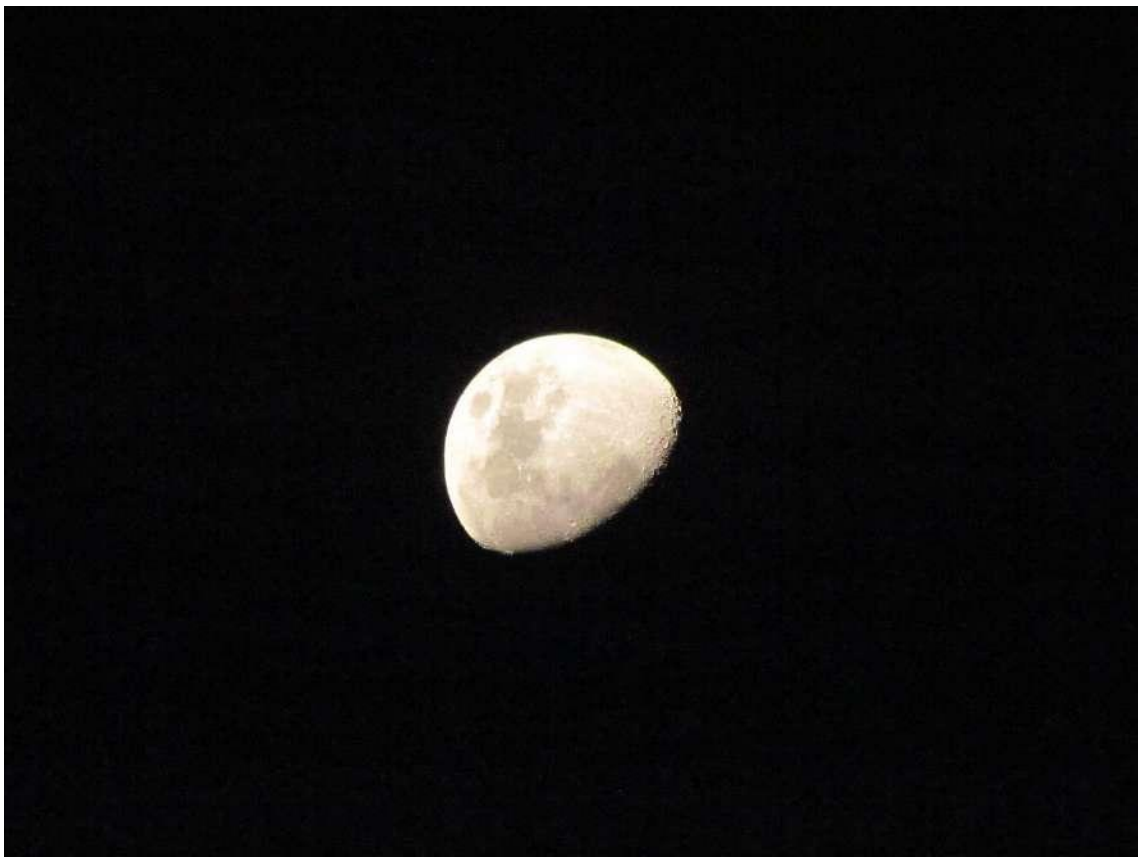

Capítulo 2

Appel, G., López-Baucells, A., Magnusson, W. E. and Bobrowiec, P. E. D. **Temperature, rainfall, and moonlight intensity effects on tropical insectivorous bat activity**

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Abstract

The extrinsic factors that most influence animal activity are weather and light conditions, which can be assessed at hourly, monthly, and even lunar-cycle timescales. We evaluated the responses of tropical aerial-insectivorous bats to temperature, rainfall, and moonlight intensity within and among nights. Temperature positively affected the activity of two species (*Cormura brevirostris* and *Saccopteryx bilineata*). Moonlight reduced *Myotis riparius* activity and increased the activity of *Pteronotus rubiginosus* and *S. leptura*. Rainfall can promote an irregular activity peak during the night compared to nights without rainfall, but the bats in our study were not active for a longer time after a rainfall event. Our findings indicate that moonlight and temperature are the variables with the highest impact on the activity of tropical insectivorous bat species and that some species are sensitive to small variations in rainfall among and within nights.

Key words: acoustic monitoring, activity pattern, Amazon, Chiroptera, moon cycle, temperature, rainfall

Resumo

Os fatores extrínsicos que mais afetam a atividade dos animais são o clima e a lua, e as respostas podem ser determinadas em escalas horárias, mensais e em ciclos lunares. O estudo avaliou as respostas dos morcegos insetívoros aéreos tropicais aos efeitos da temperatura, chuva e luminosidade lunar entre noites e dentro de uma mesma noite. A temperatura afetou positivamente a atividade de duas espécies (*Cormura brevirostris* e *Saccopteryx bilineata*). A luminosidade lunar reduz a atividade de *Myotis riparius* e aumenta as atividades de *Pteronotus rubiginosus* e *S. leptura*. A chuva pode promover picos irregulares ao longo da noite comparado com noites sem chuva, mas os morcegos não são ativos por mais tempo após uma chuva. Os resultados indicam que a luminosidade lunar e a temperatura são as variáveis que mais afetam a atividade das espécies de morcegos insetívoros aéreos e algumas espécies são sensíveis a pequenas variações de chuva entre noites e dentro de uma mesma noite.

Introduction

Animals commonly adjust their activity to extrinsic factors such as weather and light conditions (Davies et al. 2012). By studying the effects of such factors over a period of time, we can evaluate temporal variation in animal activity, thereby improving our understanding of their ecology and behavioral patterns (Aschoff et al. 1982). The effects of weather and light conditions can be assessed at different timescales (e.g., hourly, monthly, according to the lunar cycle, or seasonally), resulting in different responses of animal activity (Erkert 1982; Mccann et al. 2017). The weather conditions that most commonly affect diurnal animal activity are temperature, humidity, and rainfall (Vickery and Bider 1981; Asmus et al. 2018). However, moonlight also strongly affects foraging behavior in some nocturnal animals (Prugh and Golden 2014; English et al. 2017; Underhill and Höbel 2018).

Moonlight increases the activity of nocturnal animals that use vision to forage. Bright nights increase prey visibility and, consequently, increase foraging success of predators. Animals that are simultaneously prey and predators face the crucial trade-off between increasing foraging success and the risk of predation (Lang et al. 2006; Clarke 2014; Blubaugh et al. 2017; Musila et al. 2019). For instance, tropical rodents use ambient light to detect insects, being more active during periods of full moon; however, since they are common prey of owls, they have to use their higher visual acuity during those nights to detect the owls (Maestri and Marinho 2014; Rubolini et al. 2014). In contrast, the foraging activity of some bat species that primarily use other senses (e.g., olfaction or echolocation) decreases on bright nights to avoid visually oriented predators (Pech-Canche et al. 2010; Saldaña-Vázquez and Munguía-Rosas 2013).

Temperature, humidity, and rainfall are less predictable than lunar cycles and usually vary within the same day and between days, substantially affecting the activity of numerous animal species (Hayes 1997; Adams and Hayes 2008). Ambient temperature has a profound effect on energy expenditure to maintain body heat in warm-blooded animals. Therefore, low temperature usually results in decreased activity of many species in both tropical and temperate latitudes (Giné et al. 2015; Klüg-Baerwald et al. 2017). The effects of humidity vary among species; some animals, such as bats, are less active at relatively low humidity levels to avoid the atmospheric attenuation to their echolocation calls, but nocturnal birds increase foraging activity because prey availability is generally higher (Digby et al. 2014; Chaverri and Quirós 2017). Rainfall negatively

affects thermoregulation, especially of small mammals such as bats, rodents, and marsupials, by wetting their fur and also because flight is impeded during strong rainfall events (Brandt and Lambin 2005; Snell-Rood 2012).

The effects of moonlight, temperature, relative humidity, and rainfall have been studied mostly using relatively long time intervals (e.g., seasonally; Pearce-Higgins et al. 2015; Pettit and O'Keefe 2017). However, daily or nocturnal variations can also have marked effects on animal foraging activity (Milne et al. 2005). Some species can adjust their activity to rapid changes in these factors to take advantage of the most favorable conditions (e.g., torpor; Smit et al. 2011). For example, heavy rain at the beginning of the night can cease the activity of some bat species (Kunz 1973; Weinbeer and Meyer 2006). The effects of weather conditions and moonlight over hourly intervals has rarely been studied due to difficulties in registering the activity of most species during short intervals of time (Sánchez-Ferrer et al. 2016; Davimes et al. 2017). However, due to the rapid technological advances in non-invasive and remote-sensing sampling methods, it is now possible to monitor the activity of some species by registering acoustic calls, photographs, or even skin temperature at short time intervals (Froidevaux et al. 2014; Attias et al. 2018).

For bats, the upsurge of ultrasound recorders and acoustic-analysis software allows the passive and autonomous continuous monitoring of many species throughout the night (Britzke et al. 2013). The total number of search-phase calls is directly associated with foraging activity (Fenton 2013; Adams et al. 2015) and is therefore a direct measure of bat activity levels or relative abundance (Oliveira et al. 2015; Torrent et al. 2018). Bats are small endothermic mammals, and their activity behavior is strongly associated with weather conditions and moonlight intensity (Burles et al. 2009; Ciechanowski et al. 2007; Appel et al. 2017). For aerial insectivorous bats, environmental temperature is crucial because they need to maintain a stable body temperature and because it largely influences insect activity (Agosta et al. 2005; Barros et al. 2017). Humidity and rainfall also interfere with atmospheric propagation of echolocation, and heavy rain can influence the thermoregulation of bats, thereby hindering foraging activity and directly affecting flight ability (Voigt et al. 2011; Russo and Voigt 2016). Effects of moonlight intensity are species-specific and can be related to the species´ flight speed and prey availability (Lang et al. 2006; Appel et al. 2017; Roeleke et al. 2018). In general, lunar phobia is more evident in tropical bat species than in temperate species and more

commonly found in species that forage over the water and forest canopy and are therefore more exposed to predators (Saldaña-Vázquez and Munguía-Rosas 2013).

The influences of environmental cues on bat activity have been documented for numerous temperate aerial-insectivorous bat species (Geluso and Geluso 2012; Farneda et al. 2015; Pettit and O'Keefe 2017), but rarely for tropical insectivorous species (Meyer et al. 2004; Appel et al. 2017; Barros et al. 2017; Dias-Silva et al. 2018). Furthermore, most studies in the tropics have evaluated only one environmental factor or entirely removed periods with unfavorable conditions, such as rainy nights (Appel et al. 2017; Dias-Silva et al. 2018). In this study, we examined how activity of aerial-insectivorous bats responds to air temperature (factor negatively correlated with humidity), rainfall, and moonlight intensity among nights and how hourly activity of bats responds to rainfall within a night. We only examined the influence of rainfall on hourly activity. Other factors such as temperature have low variation (a few degrees) during the same night. Therefore, our main research questions and predictions were as follows:

1) Does bat activity respond to temperature, rainfall, or moonlight intensity between nights? We predicted that bat activity would be positively associated with air temperature and negatively with rainfall among nights. We also predicted that responses to moonlight intensity would be species-specific.
2) Does bat activity respond to weather conditions (temperature, rainfall) differently between dark and bright nights? We expected that the bat species with higher activity on dark nights would be less affected by temperature and rainfall on dark than on bright nights. We also predicted that bat species with higher activity on bright nights would be less influenced by weather conditions on bright nights than on dark nights.
3) Do the duration time and hour of the activity peak within a night change after rainfall? Bats show peaks of activity throughout the night, and most species are active shortly after sunset because more insects are available soon after sunset. Rainfall during the peak period could require the bats to increase their activity at other times. We therefore predicted that the hour of the activity peak would be later after a rainfall event and that bats would be active longer after rainfall to compensate for the loss in foraging activity. For nights without rainfall, we predicted that bats would forage for a shorter time, with activity concentrated immediately after sunset.

Material and Methods

Study area

The study was conducted at the Reserva Florestal Adolpho Ducke (2°58' S, 59°55' W; hereafter Ducke Reserve), a protected area of 10,000 ha in central Amazonia, Brazil. The site supports mainly terra firme rainforest with different vegetation structures, based on the relief and soil composition (Hopkins 1999). The climate in this region is characterized by a dry season that usually occurs between June and November and a rainy season between December and May (Oliveira et al. 2008). The average temperature was 26.7°C, and the average annual precipitation was 2,400 mm, with a maximum of 299 mm in February and a minimum of 93 mm in June, in the period from 1965 to 1994 (Ferreira et al. 2012). During the rainy period of 2013, the average temperature of the Ducke Reserve was 24.7 ºC and the average precipitation was 2,093 mm.

The reserve has a trail system that forms a 64-km² grid (5×5 km), with nine trails oriented north-south and nine trails east-west. We used a subsection of the trail system with six trails oriented north-south and six trails east-west, covering an area of 25 km^2. The trail system was established according to the RAPELD method (RAP component: rapid biodiversity survey; PELD component: studies of long-term ecological research; Magnusson et al. 2005). Ducke Reserve is part of the Brazilian Long-Term Ecological Research Program of the Brazilian National Research Council (PELD–CNPq) and a site of the National Program for Biodiversity Research (PPBio; Magnusson et al. 2005, 2014). Each plot is 250 m long, with an irregular shape that minimizes within-plot topographic variation and consequently minimizes variations in soil properties, drainage, and plant-species composition (Magnusson et al. 2005). We sampled 10 plots in riparian and 10 in non-riparian areas within the grid (Fig. 1), with a distance of 0.56 to 8.1 km between plots.

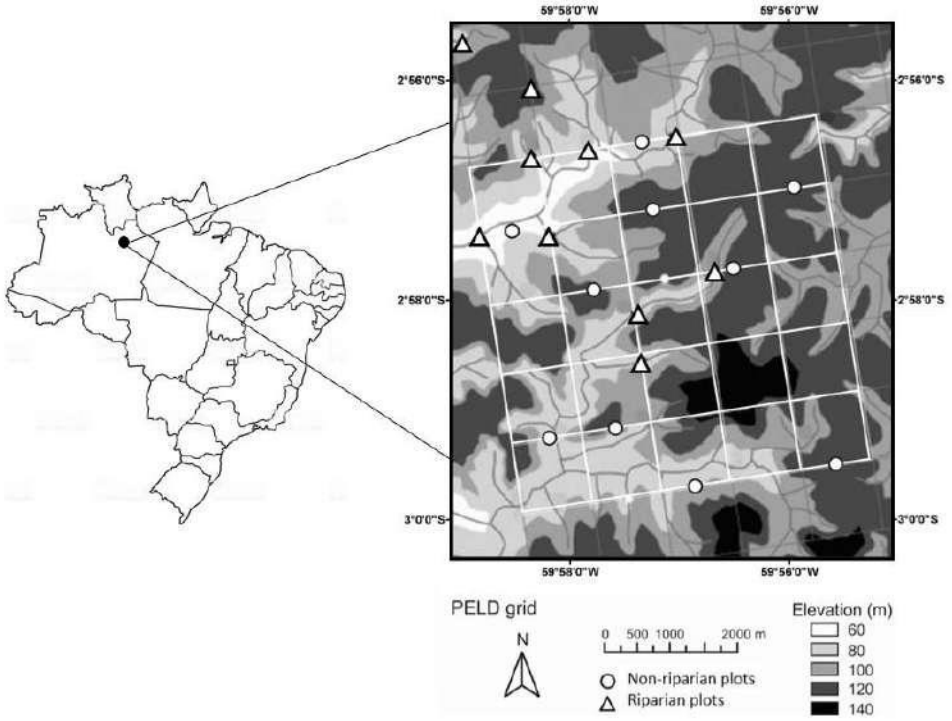

Fig. 1.—Ducke Reserve, north of Manaus, Amazonas, Brazil. Distribution of sampled plots in the PELD grid, including topography and streams. The circles represent the non-riparian plots and the triangles correspond to the riparian plots.

Bat acoustic survey

We used automatic recording detectors (Song Meter SM2Bat+), coupled to omnidirectional ultrasonic SMX-US microphones (Wildlife Acoustics, Maynard, Massachusetts), to register aerial-insectivorous bat activity. The SM2Bat+ units were configured to passively register bat activity in real time, with a 16-bit full spectrum resolution, 1-s pre-trigger, 0.1-s post-trigger, High Pass Filter set at fs/32 (12 kHz), and trigger level of 18 SNR. The recorders were programmed to monitor bat activity between 18:00 and 06:00 h. The recorders were placed at the center of each plot and the microphones at a height of 1.5 m. In riparian plots, we installed 3-m cables to position the microphones over the center of the stream. Each plot was monitored from four to six consecutive nights during the 2013 rainy season (January to May), and the detectors were not necessarily set to record in both plots at the same time. The recording effort resulted in 104 nights and 1,248 effective recording hours.

Bat activity was considered as the number of bat passes per hour and night. A bat pass was defined as a 5-second recording that contained at last two search-phase calls

characteristic of a bat species (Oliveira et al. 2015; Appel et al. 2017). Thus, all bat recordings were segmented into files of 5 seconds and visualized in the Kaleidoscope program 3.1.1 (Wildlife Acoustics). All bat passes were manually identified to species level or sonotypes when it was not possible to confidently identify a particular species (Torrent et al. 2018). The classification was based on the library of Amazonian bat ultrasounds (López-Baucells et al. 2018) and on call characteristics available in the literature (Jung et al. 2007, 2014; Barataud et al. 2013; Briones-Salas et al. 2013; Aguilar-Arias et al. 2018). We did not include feeding buzzes and social calls in the analysis because of small sample sizes and difficulties in their classification; we only considered search-phase calls easily distinguishable from background noise.

Bat-species identification

We identified 15,321 bat passes from 17 aerial insectivorous bat species and five acoustic complexes. The limited range of species detection by recorders (< 50 m around recorder) can introduce bias into estimates of species activity. We minimized any potential detection-related biases by focusing on species that are well sampled with SM2 recordings. We determined a minimum of 12 plots (60% of sampled plots) and a minimum of 20 nights as the cutoff, sufficient sampling to run the analysis (see Supplementary Data SD1). The results include the following species: mustached bat, *Pteronotus rubiginosus* (named as *P. parnellii* in Oliveira et al. 2015 and Appel et al. 2017, but revised by López-Baucells et al. 2017) and Pavan et al. 2018); thumbless bat, *Furipterus horrens*; shaggy bat, *Centronycteris maximiliani*; chestnut sac-winged bat, *Cormura brevirostris*; greater sac-winged bat, *Saccopteryx bilineata*; lesser sac-winged bat, *Saccopteryx leptura*; and riparian myotis, *Myotis riparius*.

Moonlight intensity and weather conditions

We used the Moontool 2.0 software to estimate moonlight intensity (Walker 2016, adapted by Meeus 1991). The software calculates luminance based on the portion of the lunar disc that reflects sunlight and considers the position of the Earth in relation to the sun, showing the time of moonrise and moonset. To test the effect of dark and bright nights, we classify the type of night (dark or bright) using the threshold of 0 to 30% of moonlight intensity as dark nights and 70 to 100% as bright nights as proposed by Appel et al. (2017).

Canopy openness and presence of clouds can influence negatively in the penetration of moonlight intensity inside a forest, with consequent effects upon bat activity. We obtained data on canopy openness for three riparian and four non-riparian plots sampled in this study (Research Program on Biodiversity 2012). The information indicated low variation in the percentage of canopy openness between sampled plots (mean ± SD min-max; 7.63% ± 1.07, 6.13%–9.17%). Because of the low variation among plots, we assume that moonlight penetrates into the forest similarly among the plots sampled, therefore the influence of canopy openness on bat activity was similar. Presence of clouds was assessed by the accumulated rainfall data from the Climatological Station. Rainfall data for this case was used for detection of cloudy nights, since it was not possible to monitor cloud cover across the study period. Nights were considered 'cloudy' when rainfall ranged from 0.1 to 10 mm per hour, generally classified as weak to moderate rain. To test if the occurrence of clouds affected bat activity, an ANCOVA was used with cloudy nights as a covariate (categorical variable) and the moonlight intensity percentage as a predictor (continuous variable). For all studied bat species, cloud cover did not affect bat activity and therefore was not used in subsequent models (see Supplementary Data SD2).

To evaluate weather conditions, we used data on accumulated rainfall, relative humidity, and air temperature from the Ducke Reserve Meteorological Station. These data were collected every 30 minutes between January and May 2013 by the technical team of the Coordination of Climate and Water Resources Research (CPCR) of the National Institute of Amazonian Research (INPA). We used the means of air temperature, relative humidity, and accumulated rainfall for each hour. Air temperature (ºC) and relative humidity (%) were measured by a HMP45C instrument (Campbell Scientific, São Paulo, Brazil). Data on accumulated rainfall in millimeters were obtained from a rain gauge that recorded this information automatically.

Data analysis

To test how the activity of each bat species responded to moonlight intensity and weather conditions, we used Generalized Linear Mixed Models (GLMM) with the 'lme4' R package (Bolker et al. 2009; Bates et al. 2016). To control overdispersion of the data, we used a quasi-Poisson distribution for six species; because of zero-inflated data, we fitted our models for one species (*F. horrens*) with the negative-binomial distribution.

Temperature was correlated with relative humidity (Pearson correlation = -0.77), and we opted to use only temperature and rainfall as predictor variables in all analyses. The response variable (total number of bat passes per night – *P*) was transformed to log (*P*+1) to enhance linearity. Predictor variables were standardized to a mean of 0 and a standard deviation of 1 to facilitate comparison of their relative effects. To account for the temporal autocorrelation in the data and to account the differences of the non-riparian and riparian plots, we included type of plot (non-riparian or riparian plot) as random variable in the GLMMs. We also calculated the independent contribution of each variable in the model, using hierarchical partitioning (HP) with the 'hier.part' R package (Nally and Walsh 2004). We used a total of 104 sampling nights in this analysis.

We tested the influence of weather conditions on bat activity between the types of night (dark and bright) through an analysis of covariance (ANCOVA), using GLMMs. The response variable was bat activity (log-transformed), the predictor variables were rainfall or temperature, the covariate variable was the type of night, and we included type of plot (non-riparian or riparian plot) as a random variable. We used ANCOVA for each species, with rainfall, temperature, and the interaction between rainfall, temperature, and the covariate (type of night). If the interaction between rainfall or temperature and the covariate (type of night) was significant, this indicated that bat activity was affected by the weather conditions differently between dark and bright nights. We used 29 dark and 38 bright nights in this analysis.

To test the effect of rainfall on the activity peak (Question 3), we used analysis of variance (ANOVA) with post hoc Tukey´s tests to compare bat activity among 12 hours of records for nights without rainfall and for nights with rainfall during the interval of peak activity. We defined the activity peak as the highest activity in the whole night and visualized the peak using percentiles of activity in the "quantile" R package (Adams et al. 2015). For most species, the activity peak was between 18:00 and 22:00 h, and therefore, we considered the occurrence of rainfall as a minimum of 2 hours between 18:00 and 22:00 h (n = 25 nights). In particular for *Pteronotus rubiginosus,* hourly activity peaked in the middle of the night, and for this species, we considered the occurrence of rainfall when there was a minimum of 2 hours between 21:00 and 02:00 h (n = 10 nights). We considered accumulated rainfall between 0.3 and 10 mm per hour as weak to moderate (MetOffice 2007), which can inhibit bat activity (Erkert 1982; Ciechanowski et al. 2007). Heavier rainfalls occurred on only three nights in our study period; because of low numbers of heavy rainfalls, we not included for this analysis. To test if the duration of bat

activity was higher after a rainfall event, we used Student's *t*-test to compare the durations of bat activity (in minutes after sunset) after rainfall to the same time interval (x-y hours) on nights without rainfall (control). For example, if the rain occurred between 18:00 and 22:00 h (5 hours of rain), we summed the minutes with bat activity during 5 hours after the rainfall (23:00 to 05:00) and compared this with the duration of bat activity of the same interval (23:00 to 05:00) on nights without rainfall.

Results

Effects of weather conditions and moonlight intensity on bat activity among nights

Of the seven species studied, the activity of five species was affected by temperature, rainfall, or moonlight intensity, but the variable that most contributed to hierarchical partitioning values was moonlight intensity (Table 1). *Pteronotus rubiginosus* and *S. leptura* were positively associated with moonlight intensity, and *M. riparius* responded negatively to moonlight. Temperature positively affected *Cormura brevirostris* and *S. bilineata*. *Centronycteris maximiliani* and *F. horrens* were not influenced by any of the tested factors (Table 1).

Table 1. Summary of Generalized Linear Mixed Models (GLMMs) examining bat activity of each species in terms of moonlight intensity, rainfall, and air temperature, considering random variable as type of plot (riparian or non-riparian plot) and all 103 sampling nights in the Ducke Reserve, Brazil. The R^2 values represent the variance explained by the model. Hierarchical partitioning (HP) indicated independent effects of each predictor variable on bat activity. * indicates $P \leq 0.05$.

Species	R^2	Moonlight intensity		Rainfall		Temperature	
		Z	HP (%)	*Z*	HP (%)	*Z*	HP (%)
P. rubiginosus	0.21	3.11*	70.92	0.12	0.31	1.31	28.76
F. horrens	0.03	0.81	48.56	-0.69	46.82	0.1	4.6
C. maximiliani	0.08	-2.12	86.69	1.12	1.68	1.74	11.64
C. brevirostris	0.04	1.63	73.94	-0.7	3.25	2.19*	22.79
S. bilineata	0.09	1.02	71.24	-1.2	8.25	2.48*	20.5
S. leptura	0.1	2.61*	76.43	-0.95	3.93	1.2	19.62
M. riparius	0.1	-3.03*	94.42	0.35	2.42	1.1	3.14

Effects of weather conditions on bat activity during dark and bright nights

The activity of *M. riparius* was higher on dark nights, while *S. leptura* and *P. rubiginosus* had higher activity on bright nights (Table 2). The interaction between rainfall and type of night for *P. rubiginosus* showed that this species increased its activity during rainfall on bright nights and decreased activity during rainfall on dark nights (Table 2). The interaction between temperature and type of night was not significant for any bat species activity (Table 2).

Table 2. Results of ANCOVAs with temperature or rainfall as predictor variables, type of night and interaction between the predictor variables and covariate, and bat activity as the response variable. The type of night was determined by the quantity of moonlight intensity: dark nights are between 0 to 30% and bright nights are between 70 to 100% of moonlight intensity. * indicates $P \leq 0.05$.

Species	Rainfall		Temperature		Type of night (dark or bright)		Rainfall* Type of night		Temperature*Type of night	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
P. rubiginosus	1.05	0.29	1.26	0.2	-2.58	0.01*	-2.35	0.02*	0.34	0.72
F. horrens	1.76	0.08	-0.18	0.85	-0.57	0.56	-1.27	0.2	-0.49	0.62
C. maximiliani	0.64	0.51	0.87	0.38	1.43	0.15	-0.31	0.75	-0.97	0.33
C. brevirostris	1.5	0.13	0.25	0.79	-1.37	0.17	-0.69	0.49	-0.3	0.76
S. bilineata	0.31	0.75	0.83	0.4	-1.76	0.08	-0.83	0.4	-0.05	0.95
S. leptura	0.3	0.75	0.19	0.84	-2.66	0.01*	-0.73	0.46	-0.07	0.94
M. riparius	0.31	0.08	1.89	0.06	3.2	0.002*	-1.57	0.12	-1.95	0.055

Effects of rainfall on hourly activity of bats

The activity of *C. brevirostris* and *S. leptura* was more irregular on nights with rainfall, especially during the hours in which rainfall occurred (Table 3). On nights without rainfall, *C. brevirostris* and *S. leptura* had activity peaks during the first 60 minutes after sunset, but rainfall during this period caused them to be more active during the whole night (Fig. 2). *Pteronotus rubiginosus* did not show activity peaks on nights with rainfall different from those on nights without rainfall (Table 3; Fig. 2).

Furipterus horrens, *Saccopteryx bilineata*, and *Myotis riparius* did not alter their period of peak activity regardless of rain (Table 3).

Table 3. Hourly bat activity in nights without rainfall and in nights with rainfall for peak species activities. Values represent the total number of bat passes (mean standard ± deviation). Gray boxes represent the occurrence of rainfall in the night (0.3-10 mm). Means of minutes after sunset that share the same letter are not significantly different from each other (Tukey's HSD, $P \leq 0.05$).

Species activities	Mins after sunset	*Pteronotus rubiginosus*	*Furipterus horrens*	*Centronycteris maximiliani*	*Cormura brevirostris*	*Saccopteryx bilineata*	*Saccopteryx leptura*	*Myotis riparius*
Nights without rainfall	0	0 (0 ± 0) ab	3 (0.12 ± 0.43) a	5 (0.2 ± 0.65) a	397 (15.88 ± 35.83) a	475 (19 ± 23.70) a	297 (11.88 ± 21.64) a	69 (2.76 ± 12.56) a
	60	14 (0.56 ± 1.08) a	0 (0 ± 0) a	50 (2 ± 7.01) a	16 (0.64 ± 1.43) b	83 (3.32 ± 6.92) b	1 (0.2 ± 0.04) b	79 (3.16 ± 15.38) a
	120	146 (5.84 ± 9.36) a	0 (0 ± 0) a	9 (0.36 ± 1.07) a	2 (0.08 ± 0.4) b	16 (0.64 ± 2.11) b	2 (0.08 ± 0.27) b	2 (0.08 ± 0.4) a
	180	99 (3.96 ± 5.20) a	1 (0.04 ± 0.2) a	9 (0.36 ± 0.95) a	3 (0.12 ± 0.6) b	5 (0.2 ± 0.81) b	0 (0 ± 0) b	2 (0.08 ± 0.27) a
	240	93 (3.72 ± 5.74) a	0 (0 ± 0) a	16 (0.64 ± 1.93) a	7 (0.28 ± 0.97) b	1 (0.04 ± 0.2) b	0 (0 ± 0) b	3 (0.12 ± 0.43) a
	300	89 (3.56 ± 5.06) a	1 (0.04 ± 0.2) a	12 (0.48 ± 1.68) a	4 (0.16 ± 0.62) b	0 (0 ± 0) b	0 (0 ± 0) b	7 (0.28 ± 1.02) a
	360	110 (4.4 ± 6.51) a	0 (0 ± 0) a	5 (0.2 ± 0.64) a	0 (0 ± 0) b	2 (0.08 ± 0.4) b	0 (0 ± 0) b	7 (0.28 ± 0.84) a
	420	92 (3.68 ± 5.45) a	0 (0 ± 0) a	16 (0.64 ± 1.82) a	0 (0 ± 0) b	0 (0 ± 0) b	0 (0 ± 0) b	7 (0.28 ± 0.79) a
	480	82 (3.28 ± 7.30) a	0 (0 ± 0) a	20 (0.8 ± 1.93) a	0 (0 ± 0) b	4 (0.16 ± 0.8) b	0 (0 ± 0) b	13 (0.52 ± 2.00) a
	540	43 (1.72 ± 4.65) a	0 (0 ± 0) a	5 (0.2 ± 0.81) a	17 (0.68 ± 2.46) b	27 (1.08 ± 4.27) b	0 (0 ± 0) b	29 (1.16 ± 4.11) a
	600	12 (0.48 ± 0.87) ab	0 (0 ± 0) a	4 (0.16 ± 0.8) a	5 (0.2 ± 0.57) b	5 (0.2 ± 1) b	0 (0 ± 0) b	12 (0.48 ± 2.4) a
	660	8 (0.32 ± 0.85) ab	1 (0.04 ± 0.2) a	18 (0.72 ± 3.03) a	102 (4.08 ± 9.67) b	112 (4.48 ± 6.83) b	6 (0.24 ± 1.01) b	21 (0.84 ± 1.99) a
Nights with rainfall on peak	0	0 (0 ± 0) a	4 (0.16 ± 0.37) a	40 (1.6 ± 5.45) a	444 (17.76 ± 37.57) a	624 (24.96 ± 30.80) a	397 (15.88 ± 53.38) a	107 (4.28 ± 17.71) a
	60	10 (1 ± 2) a	3 (0.12 ± 0.43) a	21 (0.84 ± 1.88) a	91 (3.64 ± 10.11) b	187 (7.48 ± 14.12) b	30 (1.2 ± 2.32) ab	273 (10.92 ± 51.35) a
	120	25 (2.5 ± 4.88) a	13 (0.52 ± 2.21) a	15 (0.6 ± 1.65) a	91 (3.64 ± 8.57) b	18 (0.72 ± 1.36) b	4 (0.16 ± 0.62) b	37 (1.48 ± 4.69) a
	180	27 (2.7 ± 5.14) a	1 (0.04 ± 0.2) a	21 (0.84 ± 2.15) a	134 (5.36 ± 18.88) ab	102 (4.08 ± 17.29) b	78 (3.12 ± 15.18) ab	13 (0.52 ± 1.47) a

species activities	240	55 (5.5 ± 8.48) a	0 (0 ± 0) a	19 (0.76 ± 2.87) a	24 (0.96 ± 3.51) b	1 (0.04 ± 0.2) b	0 (0 ± 0) b	1 (0.04 ± 0.2) a
	300	57 (5.7 ± 13.20) a	2 (0.08 ± 0.4) a	11 (0.44 ± 1.41) a	3 (0.12 ± 0.43) b	13 (0.52 ± 2.4) b	0 (0 ± 0) b	16 (0.64 ± 1.38) a
	360	13 (1.3 ± 2.35) a	2 (0.08 ± 0.27) a	5 (0.2 ± 0.5) a	116 (4.64 ± 21.14) ab	14 (0.56 ± 2.12) b	3 (0.12 ± 0.6) b	10 (0.4 ± 1.22) a
	420	12 (1.2 ± 1.68) a	0 (0 ± 0) a	0 (0 ± 0) a	9 (0.36 ± 1.25) b	0 (0 ± 0) b	0 (0 ± 0) b	8 (0.32 ± 1.06) a
	480	9 (0.9 ± 1.37) a	4 (0.16 ± 0.47) a	1 (0.04 ± 0.2) a	36 (1.44 ± 7.2) b	2 (0.08 ± 0.4) b	0 (0 ± 0) b	12 (0.48 ± 2.02) a
	540	4 (0.4 ± 0.84) a	0 (0 ± 0) a	1 (0.04 ± 0.2) a	3 (0.12 ± 0.43) b	2 (0.08 ± 0.4) b	0 (0 ± 0) b	5 (0.2 ± 0.57) a
	600	1 (0.1 ± 1.31) a	0 (0 ± 0) a	1 (0.04 ± 0.2) a	3 (0.12 ± 0.43) b	4 (0.16 ± 0.37) b	0 (0 ± 0) b	13 (0.52 ± 1.44) a
	660	0 (0 ± 0) a	0 (0 ± 0) a	42 (1.68 ± 7.87) a	178 (7.12 ± 15.80) ab	98 (3.92 ± 5.05) b	13 (0.52 ± 1.04) b	81 (3.24 ± 12.55) a

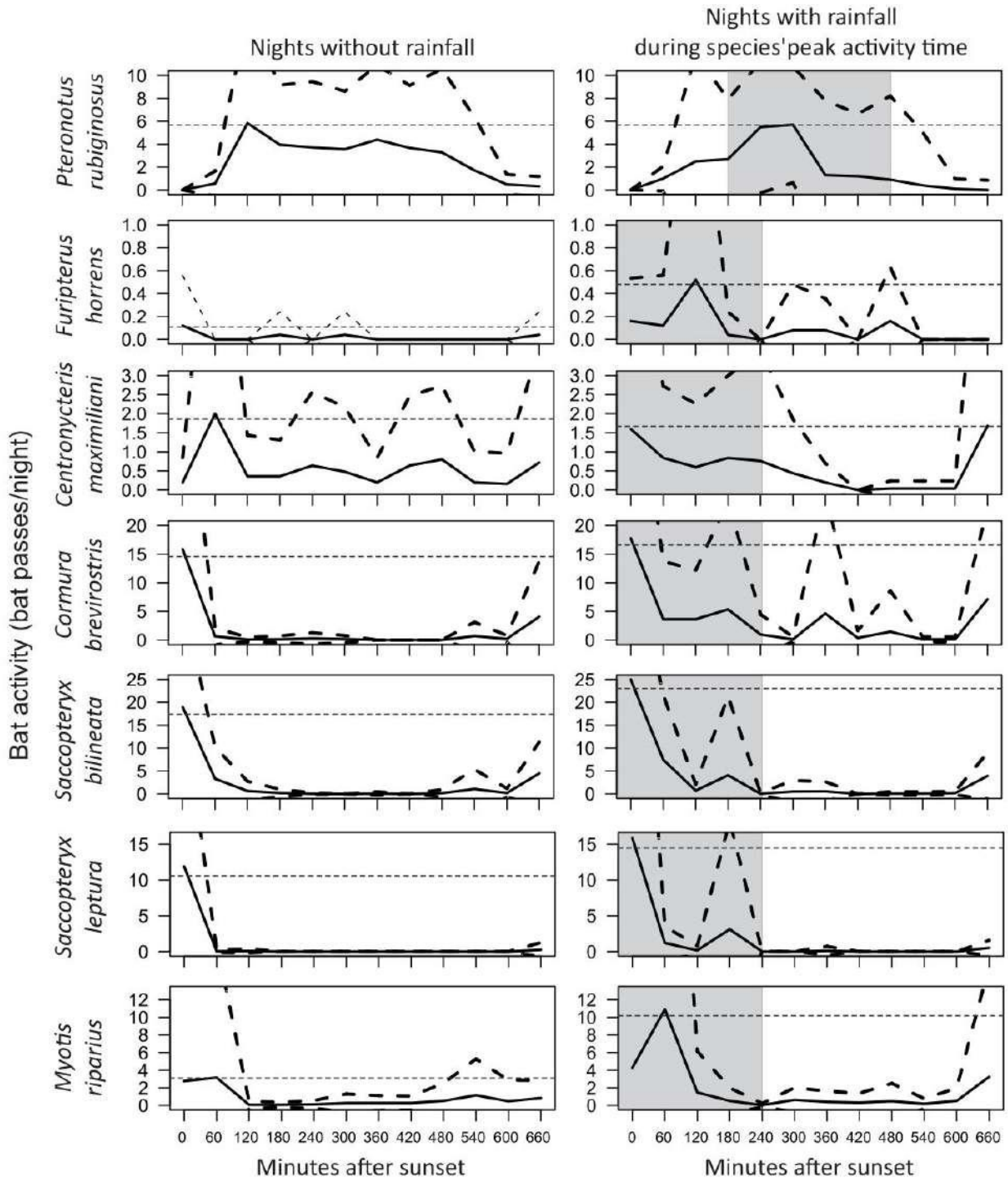

Fig. 2.—Hourly activity of seven species of insectivorous bat on nights without rainfall (n = 25) and nights with rainfall during species' peak activity time (n = 18; for *Pteronotus rubiginosus* n = 9). The gray boxes represent the interval of light rainfall during the night (0.3–10 mm). The solid line is the average activity and the dotted line represents the standard deviation of activity. Dotted horizontal lines indicate the 99th percentile, which represents the peak activity of each bat species.

The duration of activity after a rainfall event changed for *P. rubiginosus* and *S. leptura* (Table 4). *Saccopteryx leptura* (after rain = 21.6 min ± 34.11; same interval without rain = 4.8 min ± 16.61) was active for longer after a rainfall event compared to nights without rainfall. On the other hand, *P. rubiginosus* decreased activity time after the rain (after rain = 18 min ± 28.9; same interval without rain = 50.84 min ± 68.58). The other five species showed no changes in activity duration between the interval after a rainfall event compared to a night without rain.

Table 4. Results of Student's t test comparing duration of activity (minutes after sunset) between nights that occurs rainfall at the beginning of the night to nights without rainfall (control). The duration of activity was between 23:00 to 6:00 PM, and for *P. rubiginosus* we used the interval 03:00 to 06:00 PM. The nights with rainfall were consisted to nights with rainfall event between 18:00 to 23:00 PM. Values represent the minutes of bat activity (mean standard ± deviation). * indicates $P \leq 0.05$.

Species	*t*	Duration of activity (minutes) after a rainfall	Duration of activity (minutes) on nights without rainfall
Pteronotus rubiginosus	1.96*	18 ± 28.9	50.84 ± 68.58
Furipterus horrens	1.03	14.4 ± 39.79	4.8 ± 24
Centronycteris maximiliani	-0.8	28.8 ± 57.75	45.6 ± 87.08
Cormura brevirostris	1.89	72 ± 72.5	40.8 ± 48.12
Saccopteryx bilineata	1.2	67.2 ± 63.21	48 ± 48.98
Saccopteryx leptura	2.21*	21.6 ± 34.11	4.8 ± 16.61
Myotis riparius	0.85	74.4 ± 87.08	55.2 ± 71.24

Discussion

Our results indicate that some tropical bat species respond to weather conditions and moonlight intensity in a predictable way. Moonlight intensity, followed by temperature, influenced the activity of the aerial insectivorous bats more than rainfall. We found a general trend of increasing bat activity on warmer nights. Some species tended to increase their activity on bright nights, whereas other species tended to increase activity on dark nights. The effect of rainfall was mostly evident on the activity peak; bats tended to have peaks at other times on nights with rain. Bats generally did not compensate the duration of activity after a rainfall event (e.g., *P. rubiginosus* increased activity and *S. leptura* reduced activity after rainfall compared to nights without rainfall).

The addition of temperature and rainfall to our models did not change the results in relation to moonlight intensity, as reported in our previous study (Appel et al. 2017). Species whose activity increased with moonlight intensity might have adopted strategies to take advantage of bright nights to avoid predators or find food (Arndt et al. 2018; Roeleke et al. 2018). *Pteronotus rubiginosus* and *S. leptura* are forest species that increased their activity on bright nights, but use more cluttered vegetation areas to forage, probably to avoid being detected by predators (Jung and Kalko 2011). Predator avoidance is stronger in slow-flying species, and *Myotis riparius* is a slow-flying species that increases its activity on dark nights, as reported for other *Myotis* species (Azam et al. 2015). However, species such as *S. bilineata* and *C. brevirostris*, which did not change their activity in response to moonlight intensity, have been reported to forage closer to vegetation during full moon than during new moon (Jung and Kalko 2011). Canopy cover reduces the amount of light inside the forest and may prevent the bats from being detected by predators (Breviglieri 2011; Halat et al. 2018; Roeleke et al. 2018).

Air temperature is an important variable that positively influences bat activity (Russ et al. 2003). This relationship is particularly evident for temperate species, who use hibernation as a strategy to minimize energy expenditure, often associated with lack of insect availability (Stawski et al. 2014; Klüg-Baerwald et al. 2016). In our study, only a few species responded to air temperature, possibly because the temperature varied little among the nights, and they can maintain a stable body temperature when air temperature does not drop to extremely low values (Erkert 2000). The higher activity of some species during warmer nights may be a response to prey availability (O'Donnell 2000; Fukui et al. 2006). High temperature increases the flight activity of many tropical insects, especially species of Lepidoptera, Diptera, and Hymenoptera (Taylor 1963; Stangler et al. 2014). A positive effect of temperature on bat activity has also been suggested for other tropical aerial-insectivorous bat families, such as Molossidae, Vespertilionidae, and Emballonuridae (Meyer et al. 2004; Barros et al. 2017; Dias-silva et al. 2018). However, the relationships between insect prey and bat predators in the tropics are poorly understood and need further investigation (Lima and O'Keefe 2013).

Reproductive status can also influence the response of female bats to air temperature (Crichton and Krutzsch 2000). Pregnant and lactating females are more sensitive to heat loss and decrease their activity in low temperatures to reduce energy expenditure and water loss (Kunz et al. 1995; Chruszcz and Barclay 2002). Female *C. brevirostris*, *S. leptura*, and *S. bilineata* are usually pregnant during the rainy season

(Bradbury and Vehrencamp 1976; Yancey et al. 1998a, 1998b), which is also the case in the Ducke Reserve. Although it is not possible to differentiate males from females or to assess female reproductive status from ultrasound recordings, the higher activity on warmer nights may be linked to the reproductive status of females.

Rain events decrease bat activity (Ciechanowski et al. 2007; Pettit and O'Keefe 2017), but in our study, the amount of rainfall was not sufficient to lead to different levels of bat activity among nights. The rainfall volume analyzed in our study is considered low to moderate (< 10 mm/hour) and was not enough to inhibit bat activity. Rainfall also did not sufficiently reduce air temperature to influence bat activity (nights with rain: 23.4ºC ± 0.66; nights without rain: 23.3ºC ± 1.23). Since weak rain does not reduce insect availability in the forest, foraging in light rainfall may not be disadvantageous for bats (Erkert 1982; Belwood and Morus 1984). Some studies reported that only strong rainfall suppresses bat activity by affecting the echolocation accuracy and increasing the inherent flight energy costs (Fenton et al. 1977; Voigt et al. 2011; Geluso and Geluso 2012).

Only *P. rubiginosus* activity differed between dark and bright nights in relation to rainfall. Light rainfall did not influence the activity of *P. rubiginosus* on bright nights, but activity decreased on dark rainy nights. Insect availability on dark and rainy nights is lower in some orders of insects that *P. rubiginosus* eats (e.g., Diptera), and therefore, the negative effect of rainfall on their availability may compromise bat foraging success under dark, rainy conditions (Fenton et al. 1977; Voigt et al. 2011; Rolfe and Kurta 2012; Gonsalves et al. 2013).

Some bat species changed their peak activity time on nights with light rainfall. On nights without rain, peak activity was concentrated in the early evening (Appel et al. 2017), but rain caused the activity peak to be extended during or after rain. This change in foraging behavior probably meets the energetic requirement of bats. Our results indicate that foraging activity was not interrupted by light rain, suggesting that potential insect prey of bats are also active during weak rains (Fenton et al. 1977; DeCoursey and DeCoursey 2014). Because bats begin the night with low energy levels, the costs of maintaining body temperature during rain is likely compensated by rapid energy gain through feeding (Thies et al. 2006; Weinbeer and Meyer 2006).

Contrary to our expectations, the duration of foraging did not increase after the rain stopped and possibly even decreased in *P. rubiginosus*. These results are in accordance with other studies that found that insectivorous bats continue to fly in light rain (Weinbeer and Meyer 2006; DeCoursey and DeCoursey 2014). In contrast,

frugivorous bats decrease their activity if it starts raining during the night (Thies et al. 2006). This difference in foraging behavior in relation to rain is probably related to the type of food ingested — insects have more energy by weight unit compared to fruits. Thus, insectivorous bats acquire energy more quickly, compensating for foraging during light rains (Fenton et al. 1977). Frugivorous bats avoid flying in rainy nights to not cool the body and lose energy. *Pteronotus rubiginosus* also decreased activity on rainy nights. This bat feeds mainly on Lepidoptera (Rolfe and Kurta 2012), which should avoid flying during rains, even light ones, because their wings are damaged when wet. Only *S. leptura* was more active after rainfall; this species may spend more time active after rain to compensate for the energetically costly flights during rainfall (O'Donnell 2000; Salvarina et al. 2018).

Rainy seasons in the Amazonian forests are likely to experience rain almost every day, thus aerial insectivorous bats species are expected to show adaptability to forage in rainy conditions. We showed that hourly activity varied after rainfall events, which may depend on insect availability during these hours and could be associated with an individual's experience from the previous night. We used data on rainfall collected by the Climatological Station of the Reserve for our analysis, but it is important to evaluate rainfall at a more local scale because rainfall events are not necessarily equal for all studied plots. In addition, canopy cover could affect rainfall intensity inside the forest.

Our findings demonstrate that responses to temperature, rainfall, and moonlight intensity vary among tropical forest aerial-insectivorous bat species. Small changes in air temperature (20.6 to 25.4°C) were sufficient to influence the forage activity of some aerial-insectivorous bats, while light rain (0.3 to 10 mm) affected the hourly activity more than the duration of activity of bat species. However, the explanatory power of our models was low ($R^2 < 0.21$), indicating that other variables probably also influence bat activity patterns and foraging behavior. Ecological interactions, such as insect availability and predator presence, can shape the nocturnal and hourly activity of bats, but they are considerably harder to quantify than weather and moonlight variables. Other weather variables as barometric pressure and wind are environmental cues that directly and indirectly may affect bat activity and insect availability. Climatic conditions are unpredictable variables that fluctuate widely between nights and within the same night. The behavioral response of bats to unpredictable climatic conditions is not instantaneous and should be more perceptible and predictable over long (seasonal) time scales.

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Supplementary Material

Table S1. Summary of acoustic activity (number of bat passes) of the seven aerial insectivorous bats species. The values represent total number of bat-passes (mean ± standard deviation).

Species	N of calls	N of calls on dark nights	N of calls on bright nights	N of calls on nights without rainfall	N of calls on nights with rainfall on bat peak activity species
Pteronotus rubiginosus	3508 (34.03 ± 59.43)	391 (13.03 ± 14.37)	1541 (40.55 ± 48.76)	788 (31.52 ± 37.54)	213 (21.30 ± 32.29)
Furipterus horrens	63 (0.61 ± 1.85)	13 (0.43 ± 1.19)	21 (0.55 ± 1.34)	6 (0.24 ± 0.83)	29 (1.16 ± 3.26)
Centronycteris maximiliani	605 (5.87 ± 13.10)	249 (8.30 ± 17.82)	131 (3.44 ± 6.52)	169 (6.76 ± 15.09)	177 (7.08 ± 10.74)
Cormura brevirostris	2653 (25.75 ± 58.39)	545 (18.16 ± 29.49)	1790 (47.10 ± 87.60)	533 (22.12 ± 41.92)	1132 (45.28 ± 94.85)
Saccopteryx bilineata	3351 (34.03 ± 59.43)	391 (13.03 ± 14.37)	1541 (40.55 ± 48.75)	730 (29.2 ± 39.05)	1065 (42.60 ± 45.52)
Saccopteryx leptura	1298 (12.60 ± 38.54)	262 (8.73 ± 20.78)	892 (23.47 ± 58.75)	306 (12.24 ± 21.88)	526 (21 ± 70.22)
Myotis riparius	1889 (18.33 ± 58.72)	809 (26.96 ± 68.33)	161 (4.23 ± 9.32)	251 (10.04 ± 30.32)	576 (23.04 ± 83.66)

Table S2. Results of ANCOVA, with the predictor variable moonlight intensity, the covariate cloud, and the interaction between moonlight intensity and cloud. * indicates $P \leq 0.05$.

Species	Moonlight intensity		Cloud		Moonlight intensity*Cloud	
	F	*P*	*F*	*P*	*F*	*P*
Pteronotus rubiginosus	2.66	0.009*	0.94	0.34	-1.38	0.16
Furipterus horrens	0.83	0.4	-0.99	0.92	-0.17	0.86
Centronycteris maximiliani	-0.43	0.66	0.77	0.44	-1.22	0.22
Cormura brevirostris	1.53	0.12	-1.24	0.21	0.38	0.69
Saccopteryx bilineata	0.54	0.58	-1.58	0.11	0.97	0.32
Saccopteryx leptura	1.93	0.04*	-0.01	0.98	0.11	0.91
Myotis riparius	1.95	-0.04*	-0.84	0.39	-1.38	0.16

Capítulo 3

Appel, G., López-Baucells, A., Rocha, R., Meyer, C. F. J. and Bobrowiec, P. E. D. **Habitat disturbance trumps moonlight effects on the activity of tropical insectivorous bats**

Animal Conservation, https://doi.org/10.1111/acv.12706

Abstract

Changes in moonlight intensity can affect predation risk and induce changes in habitat use and activity of nocturnal species. However, the effect of moonlight on animal activity is rarely evaluated in human-modified landscapes and can be of vital importance to understand possible changes in ecosystem services provided by light-sensitive taxa, such as insectivorous bats. Fragmentation changes forest structure and affects light penetration across the landscape. In this case, the effects of fragmentation on bat activity can be modulated by cyclical variations of moonlight intensity. We acoustically quantified the activity of nine aerial insectivorous bat species in relation to moonlight at the Biological Dynamics of Forest Fragments Project, Central Amazonia. We aimed to understand species-level variation in activity across habitats (continuous forest, fragments and secondary forest) at different temporal scales: lunar cycle, dark *vs* bright nights, and within nights. Amazonian aerial insectivorous bats responded more to habitat type than to moonlight, with two and six species showing reduced activity in fragments and secondary forest, respectively, compared to continuous forest. The lower activity in secondary forest suggests that despite ca. 30 years of secondary forest regeneration, it is still less attractive as foraging habitat. An interactive effect of habitat type and moonlight on bat activity was most evident when contrasting dark and bright nights. Our results indicate that fragments have reduced bat activity on extremely bright nights, probably due to higher predation risk in small fragments. Species that emit constant-frequency calls (*Pteronotus* spp.) were the ones that most modulated their responses to habitat disturbance and moonlight. Otherwise, moonlight had little effect on hourly activity levels, irrespective of habitat type. Moonlight is capable of modulating the responses of some bat species in disturbed habitats, particularly in fragments.

Key-words: Acoustic monitoring; Anthropogenic impact; Conservation; Habitat fragmentation; Light pollution; Tropical forest.

Introduction

Anthropogenic habitat loss and fragmentation are key drivers of biodiversity change and erosion of ecological processes (Barlow *et al.*, 2016; Pfeifer *et al.*, 2017), especially in species-rich tropical regions such as the Amazon rainforest (Betts *et al.*, 2019). Worryingly, forest fragmentation in the Brazilian Amazon is progressing faster than ever; in 2017, there was an increase of nearly 70% in the number of fragments (Montibeller *et al.*, 2020) and this trend can be assumed to have worsened due to the high levels of forest loss in 2018-19 (Barlow *et al.*, 2020). Forest fragmentation results in the formation of isolated patches, surrounded by an anthropogenically modified matrix (Haddad *et al.*, 2015). The type of human-made matrix can act as selective filter for the movements of species (Watling *et al.*, 2011), altering the abundance, composition, phylogenetic, and functional diversity of animal assemblages (Mendenhall *et al.*, 2014; Aninta *et al.*, 2019; Rutt *et al.*, 2020).

Risk of predation is a major determinant of habitat use by animals (Atkins *et al.*, 2019; Pringle *et al.*, 2019). For nocturnal species, moonlight is an important source of information that affects foraging habitat selection (Waap *et al.*, 2017). Prey species commonly curtail their activity under bright moonlight so as to reduce the probability of predation by visually oriented predators (Navarro-castilla & Barja, 2014; Miranda et al., 2020). On the other hand, predator species can more easily locate prey under brighter conditions and thus increase their activity to maximize hunting success (Pratas-Santiago *et al.*, 2016; Bhatt, Sarma & Lyngdoh, 2018). However, species that are both prey and predators need to strike a balance between guaranteeing high foraging success and predator avoidance (Penteriani *et al.*, 2011; Linley *et al.*, 2020).

An increase in the perceived risk of predation during moonlit nights can force prey species to forage in cluttered habitats such as primary forest, in which dense canopies limit the amount of moonlight reaching the understory (Gigliotti & Diefenbach, 2017). However, moonlight exposure in disturbed landscapes may differ from that in continuous primary forest. Canopy openness in forest fragments and continuous forest may be similar (Almeida *et al.*, 2019; Rocha *et al.*, 2020), resulting in comparable levels of moonlight reaching the undergrowth and consequently predation risk. However, the foraging area of a species may often be larger than the fragment area, forcing the animals to forage at fragment edges and in regrowth vegetation where exposure to bright light levels during moonlit nights is greater (Bernard & Fenton, 2003). Therefore, relative to continuous

forest, predation risk can be expected to be higher in smaller fragments and in the surrounding matrix (Bowers & Dooley, 1993; Rocha *et al.*, 2020).

Bats are a group of essentially nocturnal animals which provide vital functions in the maintenance of tropical ecosystems through pollination, seed dispersal and insect population suppression (Kunz *et al.*, 2011). Studies involving the effect of moonlight on bats go back a considerable time, in fact the term "lunar phobia" was coined by Morrison (1978) for Neotropical frugivorous bats. Lunar phobia is a behavioural response to increased moonlight intensity and is probably an adaptation for reducing exposure to visually orientated nocturnal predators (Morrison 1978; Haeussler & Erkert, 1978). For aerial insectivorous bats, the relationship with moonlight is more complex because they simultaneously face the trade-off of being both prey and predator (Holland *et al.*, 2011; Roeleke *et al.*, 2018; Vásquez, Grez & Pedro, 2020). In Amazonian bats, moonlight seems to have species-specific effects, with some species either increasing or decreasing their activity in brighter nights, while others are unaffected (Appel *et al.*, 2017).

Although there are many studies that evaluated the effect of moonlight on aerial insectivorous bat activity, these studies are concentrated in temperate regions (Saldaña-Vázquez & Munguía-Rosas, 2013; Perks & Goodenough, 2020). While previous research has shown that some aerial insectivorous bat species respond to moonlight in undisturbed tropical rainforest (Appel *et al.*, 2017, 2019), such effects have rarely been evaluated in the context of human-modified landscapes (Jung & Kalko, 2011; Lima & O'Keefe, 2013; Kolkert *et al.*, 2020 but see Musila *et al.*, 2019). Assessing the effect of moonlight on the activity patterns of aerial insectivorous bats in human-modified landscapes is important to understand possible changes in ecosystem services provided by this bat ensemble (Pianka, 1973; Presley *et al.*, 2009). In agricultural landscapes, this issue is relevant for the management of fragments because of the potential role of insectivorous bats in the suppression of agricultural pests (Kemp *et al.*, 2019).

Here, we used the experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon to evaluate the hypothesis that moonlight modulates the effects of habitat disturbance on aerial insectivorous bat activity at different temporal scales. We acoustically quantified bat activity in continuous forest and in disturbed habitats (forest fragments and within the intervening secondary forest matrix) to understand variation in species-level activity across these habitat types in relation to moonlight. We conducted our analyses at different temporal resolutions, focussing on variation in moonlight intensity: i) associated with the

lunar cycle, ii) between dark and bright nights, and iii) within nights. Accordingly, we predicted that:

i. Species sensitive to habitat disturbance and moonlight will respond negatively to moonlight intensity in fragments and secondary forest, as previous research indicates that some Amazonian aerial insectivorous bats respond to habitat disturbance (Núñez *et al.*, 2019) and moonlight (Appel *et al.*, 2017).
ii. Species sensitive to habitat disturbance and moonlight will show increased activity in fragments and secondary forests on dark nights (associated with new moon) compared to bright nights (associated with full moon), whereas in continuous forest responses to moonlight will be species-specific.
iii. In fragments and secondary forest, bat species will reduce activity in the early evening to avoid the time of greatest predation risk. In continuous forest, within-night activity will be concentrated in the early evening, both on bright and dark nights, to maximize foraging opportunities during the peak in prey abundance.

Material and Methods

Study site

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) (2°25'S; 59°50'W), located ~80 km north of Manaus, Brazil (Fig. 1), a long-term fragmentation experiment that has been running for ~40 years to study the effects of forest fragmentation on Amazonian biota (Laurance *et al.*, 2018). The climate is characterized by a dry season from July to November when precipitation drops below 100 mm/month and a rainy season from November to June, when precipitation can exceed 300 mm/month (Ferreira *et al.*, 2017). The study landscape consists of 11 forest fragments (five of 1 ha, four of 10 ha and two of 100 ha), surrounded at the time of the study by a matrix of tall secondary forest, and extensive areas of continuous primary forest that act as experimental controls (Laurance *et al.*, 2018). In the early 1980s, forest fragments were experimentally isolated and the vegetation around them has since been periodically cleared to maintain isolation, last in 2014 (Rocha *et al.*, 2017a), after data collection for this study. The site supports lowland evergreen *terra firme* rainforest at 50 to 100 m of elevation, and the temperature ranges from 19 to 39 °C (Laurance & Williamson, 2001). The secondary forest is dominated by *Vismia* spp. in areas that were cleared and burned and dominated by *Cecropia* spp. in areas that were only cleared (Mesquita *et al.*, 2001).

Percent canopy cover varies little between habitat types (continuous forest interiors: 85.4 ± 5.2 [mean ± *SD*], fragment interiors: 87.4 ± 1, secondary forest: 75.1 ± 6.7; Rocha *et al.*, 2017a). Canopy height in the largest fragments and continuous forest averages 28 m (Almeida *et al.*, 2019), while in the well-developed secondary forest the average canopy height is 15 m (Jakovac *et al.*, 2014; Mokross *et al.*, 2018).

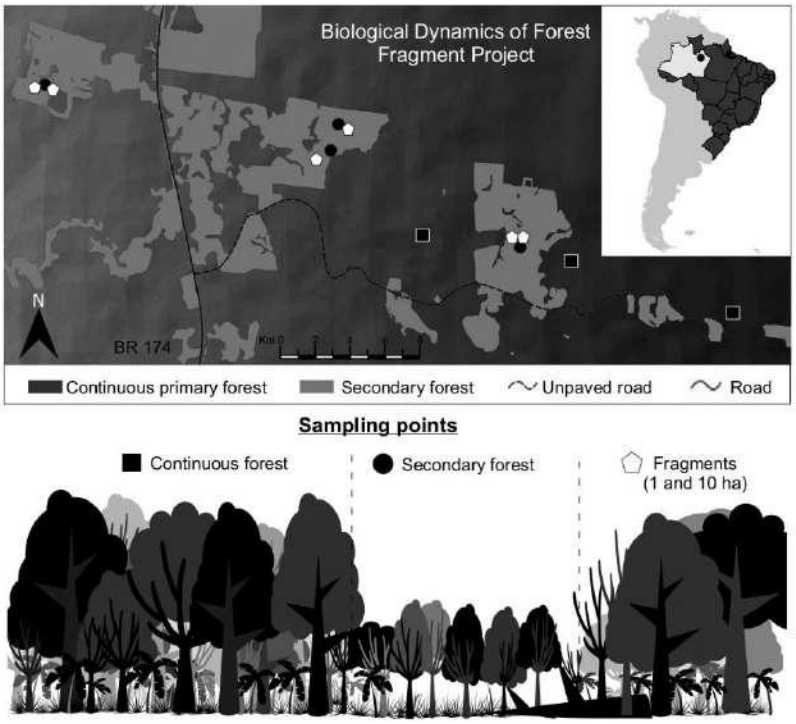

Figure 1. Location of the Biological Dynamics of Forest Fragments Project (BDFFP) and the distribution of sampling points in continuous forest, fragments of 1 and 10 ha, and secondary forest. Continuous forest is represented in dark gray and secondary forest (matrix) in light gray. The map in the upper right corner shows the location of the study area in the Central Amazon. The schematic figure illustrates the vegetation structure in the three habitat types.

Bat acoustic sampling

We sampled 13 sites across the BDFFP landscape between 2011 and 2013: three in continuous forest (Cabo Frio, Florestal and Km 41 camps), six forest fragments (3 fragments of 1 and 10 ha in Colosso, Dimona and Porto Alegre camps) and four in the secondary forest matrix (Cabo Frio, Colosso, Dimona, Florestal and Porto Alegre camps) (Fig. 1). Each site was visited twice during both dry and rainy seasons. At each sampling site, we installed an automatic ultrasound recorder (Song Meter SM2Bat+) with an

omnidirectional ultrasonic SMX-US microphone (Wildlife Acoustics, Inc., USA) placed at a height of 1.5 m above the ground (López-Baucells *et al.*, 2019). Ultrasound recorders were positioned in the center of the fragments, in the secondary forest 100 m away from the edge of each fragment, and in the interior of continuous forest 1000 m away from the edge. The recorders were configured to passively register bat activity in real time, with a full spectrum resolution of 16 bit, a high-pass filter set at fs/32 (12 kHz), and an adaptive trigger level relative to noise floor of 18 SNR. The SM2Bat units were programmed to record bat activity between 18:00 and 06:00 for four to five consecutive nights per sampling site (Table S1). Total sampling effort was 727 nights, with 8,278 recording hours. The number of sampling nights in each season was similar in fragments and secondary forest (Table S1). Although for continuous forest sampling effort was higher in the dry season (Table S1), we contend that the number of nights sampled in the rainy season (77 nights) was sufficient to avoid seasonal biases, and differences in sampling effort were also accommodated in the analysis.

All recordings were split into five-second segments and a bat pass was defined as a sequence with a minimum of two recognizable search phase calls per species in each five-second segment (Torrent *et al.*, 2018; Appel *et al.*, 2019). All bat passes were manually identified to species or sonotype level following López-Baucells *et al.* (2016). We used Kaleidoscope Pro Software (version 4.0.4.) (Wildlife Acoustics, Inc. Maynard, Massachusetts, USA) for manual verification. Activity was calculated as the sum of five-second segments with bat passes per night (nightly activity) and per hour (hourly activity).

In the total of ~190,000 bat passes we identified 18 aerial insectivorous bat species and four sonotypes. We minimized potential detection biases by focusing on species that were detected in at least 10% (73 nights) of the total nights and in all three sampling years. This resulted in the selection of nine species for analysis: *Pteronotus alitonus*, *P. rubiginosus* (revised by López-Baucells *et al.*, 2018; Pavan, Bobrowiec & Percequillo, 2018), *Furipterus horrens*, *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *S. leptura*, *Myotis riparius* and *Eptesicus brasiliensis* (Table S2).

Moonlight intensity

Moonlight intensity for each night was estimated using the “sunmoon” software (Conrad, 2017), a robust method for quantifying the amount of sunlight reflected by the moon. This software employs the illuminance model of Janiczek & DeYoung (1987).

To test whether bat activity varied between dark and bright nights, we classified those nights with 0–30% moon illuminated as dark and those with 70–100% as bright, following Appel *et al.* (2017, 2019). We used this broad categorization instead of the moon phase because moonlight intensity can vary greatly within the same moon phase (e.g. moonlight intensity in the waning phase can vary from 3% to 55%, Appel *et al.*, 2017). Indeed, we used this categorization because these nights are characterized by little variation in moon presence (during bright nights) and absence (during dark nights) in order to avoid the influence of moonrise and moonset times on bat activity (Appel *et al.*, 2017).

Cloud presence can influence the amount of moonlight that penetrates the forest, and thus potentially distort bat activity responses to moonlight. In order to test for an effect of cloud presence, we used data on cumulative rainfall per hour collected at the metereological tower of the Large-scale Biosphere–Atmosphere Experiment in Amazonia (LBA) ZF-3 installed at KM 34 within the BDFFP. Nights were considered "cloudy" when rainfall ranged from 0.1 to 10 mm/h, generally classified as weak to moderate rain (Appel *et al.*, 2019; Vásquez *et al.*, 2020). Nights with more than 10 mm rain per hour were nights with heavy rain, therefore were removed from the analyses (Carvalho *et al.*, 2011).

Data analysis

To model the effects of habitat type (continuous forest, fragments and secondary forest) and moonlight on species-specific bat activity levels, we performed generalized linear mixed models (GLMMs) using the function glmmTMB from the package "glmmTMB" (Bolker *et al.*, 2020). The response variable in the GLMM models was the number of bat passes recorded in a single night per species. Models were fitted using a negative binomial distribution and, whenever the respective activity distribution showed a signal of zero inflation, were implemented as zero-inflated models (Zuur *et al.*, 2008). For each model, habitat type was specified as categorical fixed effect and moonlight as a continuous fixed effect (percentage of moonlight intensity) and sampling night nested within research camp as a random effect. We chose to model moonlight intensity only jointly with habitat type because we were interested in evaluating the effect of moonlight for each habitat and not its independent effect. The aforementioned random effects structure was chosen to account for not only the spatial but also the temporal

autocorrelation of the data - moonlight intensity of one night depends on the moonlight intensity of the previous night. To compensate for differences in sampling effort between habitat types (Table S2), we used the log-transformed sampling effort per habitat type as offset in all models. Parameter estimates were visualized using R package "ggstatsplot" (Patil, 2020). We used the full data set of the 727 sampling nights in the GLMMs. To test if cloud presence affects bat activity, we performed GLMMs analyzing bat activity in relation to moonlight, cloud presence and their interaction effect. There was no effect of cloud presence on the activity of any of the focal bat species (Table S3).

For each habitat type, differences in bat activity levels between dark and bright nights were visualized using Gardner-Altman estimation plots and statistically evaluated using non-parametric permutation tests with 1000 bootstrap samples to estimate effect sizes and 95% confidence intervals for the difference of means using R package "dabestr". Statistical significance of the difference between dark and bright nights was determined based on the lack of overlap in the frequency distributions of the data sets (Ho *et al.*, 2019).

Hourly activity levels between dark and bright nights for each habitat type were compared using Kolmogorov-Smirnov 2-sample tests. Bat activity was pooled into 12 sampling intervals (hourly intervals) - e.g. bat passes recorded between 18:00 and 18:59 were assigned to the same time interval (18:00). For comparisons between dark and bright nights, we used data from 206 nights in continuous forest (118 dark, 88 bright), 124 nights in fragments (65 dark, 59 bright) and 195 nights in secondary forest (97 dark, 98 bright). All analyses were conducted in softwares R 4.0.2 and R Studio 4.0.2 (R Core Team, 2020; RStudio Team, 2020).

Results

Bat activity responses to habitat type

Based on the GLMM results, habitat type had by far the greatest effect on bat activity. Most significant responses were observed for secondary forest, followed by fragments (Fig. 2). Six species (*S. bilineata, S. leptura*, *C. maximiliani*, *C. brevirostris*, *E. brasiliensis* and *F. horrens*) exhibited reduced activity in secondary forest, whereas *P. alitonus* and *P. rubiginosus* showed elevated activity levels in this habitat (Fig. 2). On the other hand, two species (*P. alitonus* and *F. horrens*) had significantly lower activity in fragments than in continuous forest (Fig. 2).

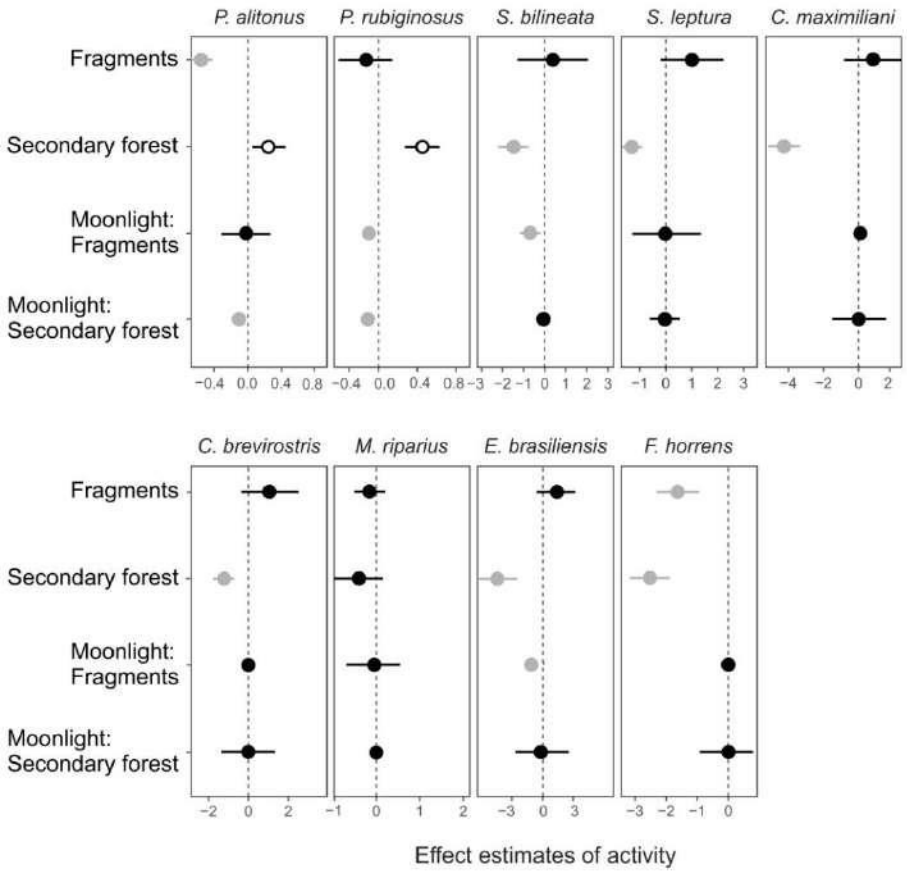

Figure 2. Effects of moonlight, habitat type, and their interaction on activity of the nine focal species in the BDFFP evaluated using generalized linear mixed models. Effect estimates are based on the fixed effect posterior distribution, characterized by its mean (dot) and credible intervals (95% CI, lines). Gray circle estimates indicate significant negative effects, white circle estimates significant positive effects and black estimates non-significant effects.

Bat activity responses to habitat type and moonlight intensity

The activity of three species (*P. rubiginosus*, *S. bilineata* and *E. brasiliensis*) in fragments was negatively affected by moonlight as suggested by the significant interaction effect (Fig. 2). Similarly, moonlight significantly curtailed activity levels of *P. alitonus* and *P. rubiginosus* in secondary forest, albeit the effect was small (Fig. 2).

In relation to habitat-specific comparisons of activity between dark and bright nights, all species, except *S. leptura,* showed changes in activity between dark and bright nights in some habitat type (Fig. 3). In continuous forest, *P. rubiginosus* and *P. alitonus* were more active on bright nights, whereas *F. horrens* had greater activity during dark nights (Fig. 3). *Pteronotus rubiginosus, S. bilineata, C. maximiliani, C. brevirostris, M. riparius* and *E. brasiliensis* exhibited greater activity during dark than bright nights in

fragments (Fig. 3). In secondary forest, only *P. alitonus* and *P. rubiginosus* showed greater activity on dark nights, opposite to the pattern in continuous forest (Fig. 3).

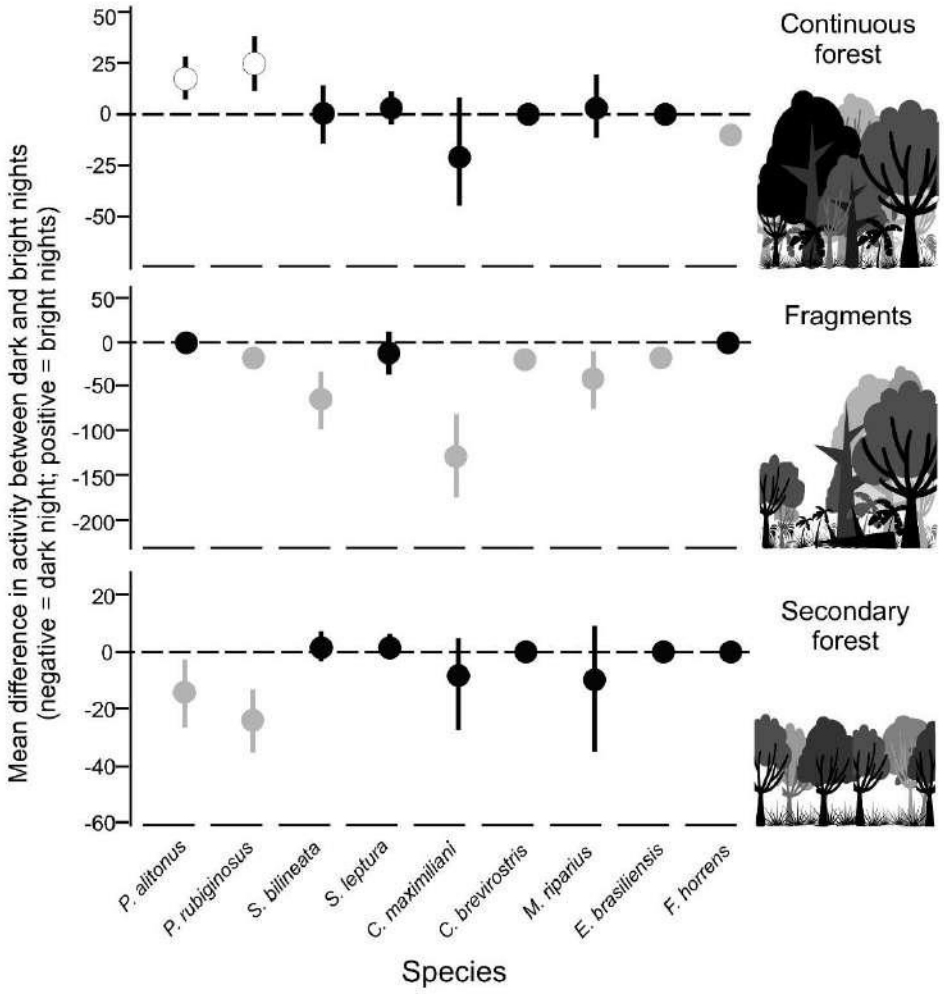

Figure 3. Gardner-Altman estimation plots showing the effect size (mean difference) of bat activity between dark and bright nights in each type of forest - continuous, fragments and secondary forest at the BDFFP. Dark nights were considered those with between 0 and 30% moonlight intensity and bright nights those above 70%. The mean is indicated by a dot, error bars represent the 95% confidence interval. Gray circle estimates indicate significant negative effects (higher activity on dark nights), white circle estimates significant positive effects (higher activity on bright nights) and black estimates non-significant effects.

Hourly activity varied little between dark and bright nights and only five species exhibited some change in activity pattern between dark and bright nights in the same habitat (Table 2; Fig. S1). In continuous forest, *P. rubiginosus* and *S. leptura* were more active on bright nights. On the other hand, hourly activity of *C. maximiliani* and *F. horrens* steadily decreased on bright nights in continuous forest. In these two species, activity on dark nights increased at the end of the night. In fragments, *M. riparius*, *P.*

rubiginosus and *C. maximiliani* increased their activity on dark nights, with greater activity in the middle of the night in the latter two species. In secondary forest, only *P. rubiginosus* showed significant differences, with an elevated activity during dark nights.

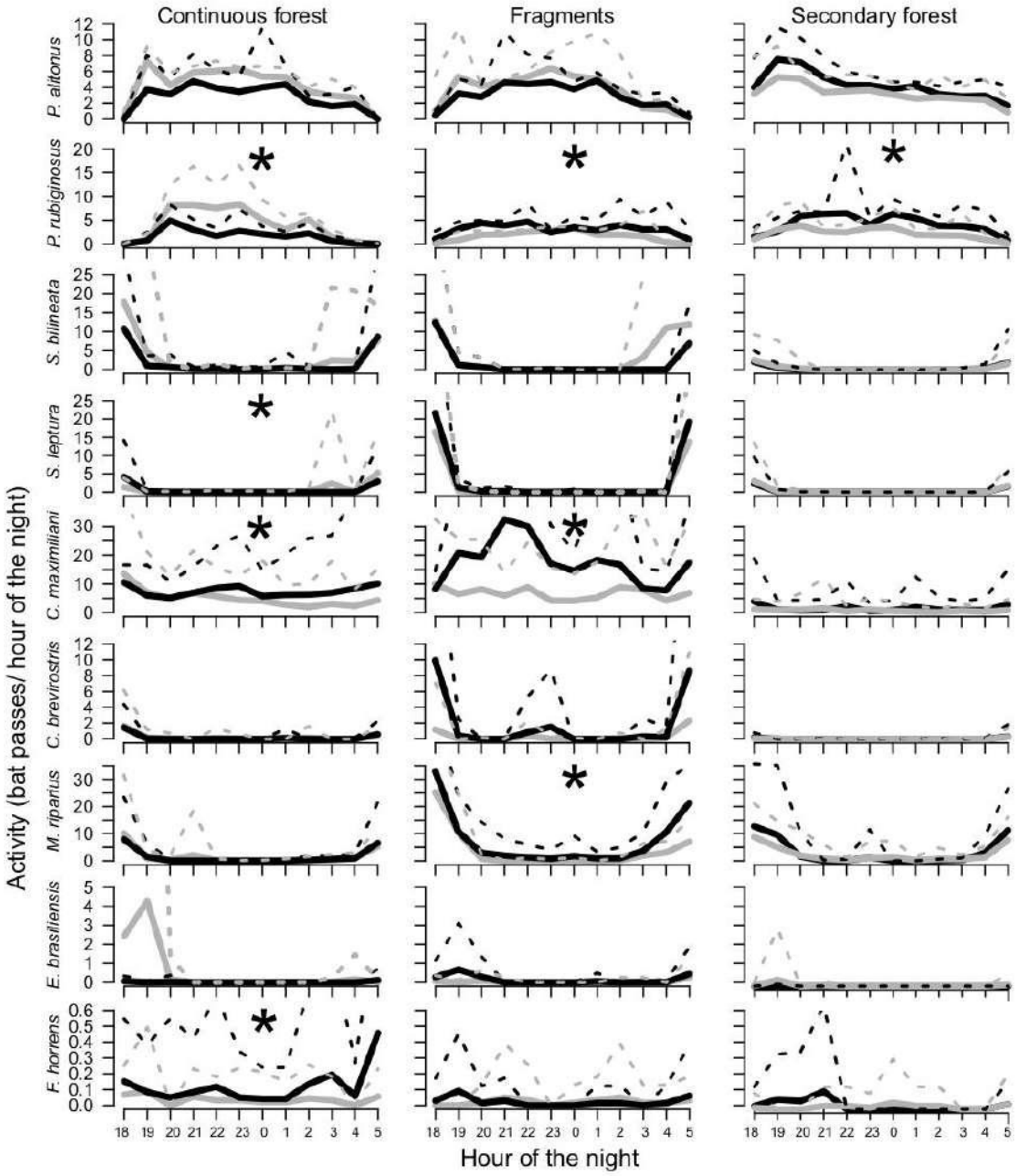

Figure 4. Hourly activity of nine species of aerial insectivorous bat in each habitat type (continuous forest, fragments and secondary forest) on dark nights (0-30% of moonlight intensity) and bright nights (70-100% of moonlight intensity). Black lines denote dark nights, gray lines bright nights. The solid line is the average activity and the dotted line represents the standard deviation of activity. * indicates a significant difference between dark and bright nights based on Kolmogorov-Smirnov 2-sample tests.

Discussion

Numerous studies have targeted the effects of forest fragmentation on tropical bats (Meyer, Struebig & Willig, 2016; Mendes & Srbek-Araujo, 2020). Yet, in the Neotropics, most research has been limited to the impacts of fragmentation on phyllostomid bats (e.g. Klingbeil & Willig, 2009; Rocha *et al.*, 2017b, 2018), and fragmentation effects on aerial insectivores remain poorly explored (but see Estrada-Villegas, Meyer & Kalko, 2010; Núñez *et al.*, 2019). Over the past two decades, intensive research at the BDFFP has provided valuable information about taxonomic, functional, phylogenetic and behavioural responses of bats to the dynamic nature of fragmented landscapes (e.g. Bobrowiec & Gribel, 2010; Farneda *et al.*, 2015; Rocha *et al.*, 2018, 2020; Aninta *et al.*, 2019). Although less researched than their phyllostomid counterparts, aerial insectivorous bats at the BDFFP were found to exhibit trait-related responses to fragmentation, with understory and constant-frequency and frequency-modulated echolocating bats being particularly vulnerable to forest disturbance (Núñez *et al.*, 2019). Here, we further advance current understanding about the responses of aerial insectivorous bats to fragmentation, by analyzing how temporal activity patterns of this bat ensemble are molded by variation in moonlight intensity. As hypothesized, we found that moonlight can modulate responses to habitat disturbance but only in extremely bright nights. Importantly, a joint effect of moonlight and habitat disturbance was most evident only in species that emit constant-frequency calls (*Pteronotus* spp.).

Our results show that Amazonian aerial insectivorous bats respond more to habitat type than to the interaction between habitat and moonlight. Most species had lower activity in secondary forest and two showed lower activity in fragments compared to continuous forest. This suggests that despite ca. 30 years of secondary forest regeneration, secondary forest is still less attractive as foraging habitat for most aerial insectivorous bat species. These results are consistent with those commonly reported for gleaning animalivorous bats, whose capture rates typically decrease in disturbed habitats (Rocha *et al.*, 2017b; Webala *et al.*, 2019; Willig *et al.*, 2019), probably due to being poorer foraging and roosting areas (Meyer & Kalko, 2008; Carballo-Morales, Saldaña-Vásquez & Villalobos, 2021). Yet, they contrast with results from nectarivorous and frugivorous bats, which normally increase in abundance in fragments and in secondary forest due the higher density of food resources (Bobrowiec & Gribel, 2010; Farneda *et al.*, 2015).

The effect of moonlight intensity on activity differed between habitat types for *P. alitonus*, *P. rubiginosus*, *S. bilineata* and *E. brasiliensis.* These four species exhibit a

flexible behaviour, changing their activity in disturbed environments when light conditions are not favourable. The interaction between fragmentation and moonlight shows that for some species the effects of fragmentation can be more acute than expected, since at least during part of the lunar cycle their activity in fragments may be suppressed.

Bat activity over the lunar cycle is shaped by predator-prey interactions, as aerial insectivorous bats are simultaneously predators and prey (Lang *et al.*, 2006; Vásquez, Grez & Pedro, 2020). *Pteronotus rubiginosus* and *P. alitonus* increase their activity with moonlight in continuous forest probably due to higher foraging success, as some insect orders increase their activity in nights of high moon illumination (Kolkert *et al.*, 2020). The observed lunar philia of *P. rubiginosus* agrees with the pattern found in other areas of Amazonian continuous forest (Appel *et al.*, 2017; Durán & Oviedo Morales, 2019). On the other hand, the observed decrease in the activity of *Pteronotus* spp. with increasing moonlight indicates that in disturbed areas the perceived risk of predation is probably greater. These bats may avoid leaving fragments as some visually oriented avian predators forage preferentially along fragment edges and open areas (Chalfoun, Thompson & Ratnaswamy, 2002; Spanhove *et al.*, 2009).

Although the interactive effect of moonlight and habitat type on bat activity was weak, our analyses showed that the effects of habitat type were most evident when evaluated at the extremes of the lunar cycle (dark *vs.* bright nights). In fragments, the activity of six species decreased on very bright nights, whereas, with the exception of *P. alitonus* and *P. rubiginosus* (which showed greater activity on bright nights in continuous forest), it was unaltered in continuous forest. The home ranges of aerial insectivorous bats (e.g. *P. parnelli* and *S. bilineata*) are generally much greater than the size of fragments studied (≤10 ha; Bradbury & Vehrencamp, 1976; Estrada, Coates-Estrada, & Meritt, 1993; Hoffmann *et al.*, 2007). As such, bats inhabiting forest fragments might need to forage/commute in the surrounding matrix, which on brighter nights, may increase exposure to predators. This increase in predation risk may therefore reduce bat activity in small fragments during nights with more intense moonlight (Bowers & Dooley, 1993). Thus, on bright nights probably bats reduced their home range avoiding the edges of the fragments, specially *Pteronotus* spp., since they are less active in secondary forest on bright nights.

The two extremes of the lunar cycle, bright *vs.* dark nights, had little effect on hourly activity levels indicating that bats do not respond to changes in moonlight during short periods of time. Yet, two species had higher hourly activity on bright nights in

continuous forest and two species were more active at the end of dark nights. However, in fragments, hourly activity only changed for three species, all exhibiting lower activity at dusk on bright nights, which might be a strategy to reduce predation risks (Appel *et al.*, 2017). A similar result was found for phyllostomids in early successional forest, small agricultural fields and forest subjected to reduced-impact logging in the Amazon (Castro-Arellano *et al.*, 2009; Presley *et al.*, 2009). *Cormura brevirostris* and *S. bilineata* did not change the hourly activity between the extremes of brightness. This may relate with their foraging strategies (Gomes, Appel & Barber, 2020), as both species have been suggested to feed closer to vegetation in brighter nights (Jung & Kalko, 2010). The apparent absence of a moon effect on hourly activity of insectivorous bats was also found by Appel *et al.*, (2017) in a continuous forest location in Central Amazonia and by Thomas & Jacobs (2013) in South Africa.

Our results show that moonlight is an abiotic variable that can modulate bat activity levels in tropical human-altered landscapes, but for most aerial insectivorous species the effect is either weak or absent, and responses are more evident only in extremely bright nights in fragments. Species that emit constant frequency calls such as *P. rubiginosus* and *P. alitonus* showed the strongest response in activity levels as manifested by a change from a positive relationship with moonlight in continuous forest to a negative one in fragments and secondary forest. Therefore, moonlight can augment the effects of fragmentation on the activity of bats that echolocate using constant frequency calls. This is concerning because habitat disturbance might reduce the temporal window in which foraging conditions are favorable and thus limit the ability of species to meet their daily dietary requirements (Vásquez, 1994; Castro-Arellano *et al.*, 2009; Rocha *et al.*, 2020). This physiological stress may increase exposition to pathogens (Turmelle & Olival, 2009), and there are several examples of how anthropogenic land-use change can have a major impact on the infection and circulation of zoonoses (Gibb *et al.*, 2020; White & Razgour, 2020). Future research investigating how behavioral responses translate into fitness consequences (e.g. mortality and reproductive success) in fragmented landscapes is needed to better understand long-term population persistence.

Conservation implications

Fragmentation and forest disturbance have been identified as the major causes of biodiversity loss in the tropics. Some of the insectivorous bat species studied here are

fragmentation sensitive (Núñez *et al.* 2019). In our study, habitat disturbance was the main factor underlying decreases in the activity of aerial insectivorous bats, but moonlight accentuated reductions in activity for some species in fragments and might impact their capacity to provide their crucial ecosystem services as insect predators. Insectivorous bats are key suppressors of herbivorous insects in both humanized and natural habitats and they can prevent rice loss at an estimated cost of $1,2 million/year and more than $3,7 billion/year in general agricultural losses (Boyles *et al.*, 2011; Wanger *et al.*, 2014; Kemp *et al.*, 2019). However, it is important to mention that the BDFFP fragments are surrounded by secondary forest at an advanced stage of succession, which can buffer the impacts of fragmentation and create better foraging conditions for aerial insectivorous bats than in other human-modified landscapes (Rodríguez-San Pedro & Simonetti, 2015). Fragments in landscapes dominated by large-scale agriculture commonly exhibit abrupt margins, are embedded within a homogeneous matrix and suffer additional anthropogenic disturbances (e.g., effects of roads and artificial illumination) which may considerably reduce the ecological services provided by light-sensitive bat species (Put, Fahrig & Mitchell, 2019).

Artificial light at night has been increasing over time in biodiversity hotspots (Guetté *et al.*, 2018) and this is concerning because the increasing human pressure in the periphery of forested areas can leave forest fragments in a state of constant illumination during the night. Although artificial light attracts insects consumed by insectivorous bats, some bat species studied here are sensitive to urbanization (Jung & Kalko, 2010; Alpízar, Rodríguez-Herrera, & Jung, 2019). It is known that lit areas can influence the quality of roosts and fragment commuting routes for some bat species with negative consequences for the reproduction and behaviour of bats (Downs *et al.*, 2003; Laforge *et al.*, 2019; Straka *et al.*, 2019). In view of the recent increase of fragmentation and artificial light at night in the Brazilian Amazon due the development of cities, agricultural areas and expanding road networks (Haddad *et al.*, 2015; Lovejoy & Nobre, 2018; Vilela *et al.*, 2020), the protection of undisturbed forests is crucial for the conservation of light-sensitive aerial insectivorous bats. Moreover, bats actively prey on mosquitoes responsible for disease transmission (Puig-Montserrat *et al.*, 2020) and as tropical urban areas have a proliferation of these insects, the promotion of large forest fragments in urban areas can be an alternative to attract more activity of insectivorous bats.

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Supplementary Material

Table S1. Number of nights recorded per habitat type and per season across the Biological Dynamics of Forest Fragments Project camps. Each ultrasound recorder was programmed to register bat passes from 18:00 PM to 06:00 AM for four to five consecutive nights during the dry and rainy seasons of 2011-13.

	Continuous forest		Fragments		Secondary Forest		Total
Camps	wet	dry	wet	dry	wet	dry	
Km 41	16	52	-	-	-	-	68
Cabo Frio	35	75	-	-	14	20	144
Florestal	26	79	-	-	12	21	138
Dimona	-	-	19	31	38	47	135
Porto Alegre	-	-	36	29	38	37	140
Colosso	-	-	24	30	31	17	102
Total	77	206	79	90	133	142	727

Table S2. Number of bat passes (mean ± SD), in total and broken down by habitat type, for the nine aerial-insectivorous bat species studied.

Species	Total	Continuous forest	Fragments	Secondary forest
Pteronotus alitonus	31864 (43.82 ± 47.71)	11351 (40.10 ± 40.78)	7004 (41.44 ± 49.79)	13509 (49.12 ± 52.31)
Pteronotus rubiginosus	27658 (38.04 ± 52)	8922 (31.52 ± 45.12)	5638 (33.36 ± 36.41)	13098 (47.62 ± 63.94)
Saccopteryx bilineata	22198 (30.53 ± 98.59)	8657 (30.59 ± 97.79)	12435 (73.57 ± 149.79)	1106 (4.92 ± 15.09)
Saccopteryx leptura	10253 (14.10 ± 39.74)	2020 (7.13 ± 22.81)	6457 (38.20 ± 65.15)	1776 (6.45 ± 23.76)
Centronycteris maximiliani	54909 (75.52 ± 192.41)	21153 (74.74 ± 172.25)	29521 (174.68 ± 285.84)	4235 (15.40 ± 86.43)
Cormura brevirostris	5185 (7.13 ± 36.98)	576 (2.03 ± 6.95)	4443 (26.28 ± 72.89)	166 (0.60 ± 2.36)
Myotis riparius	27681 (38.07 ± 85.90)	6551 (23.14 ± 59.89)	11900 (70.41 ± 118.50)	9230 (33.56 ± 79.34)
Eptesicus brasiliensis	1019 (1.40 ± 15.03)	705 (2.49 ± 23.66)	244 (1.44 ± 4.59)	70 (0.25 ± 2.47)
Furipterus horrens	511 (0.70 ± 2.49)	406 (1.43 ± 3.66)	48 (0.28 ± 0.99)	57 (0.20 ± 1.06)

Table S3. Summary of Generalized Linear Mixed Models examining bat activity of each species in terms of moonlight, cloud presence and their interaction. Sampling night nested within research camp was specified as random effect, and data from 534 nights were used for this analysis. Bold values indicate $P < 0.05$.

Species	Moonlight			Cloud.presence			Moonlight:Cloud.presence		
	Estimate	z	P	Estimate	z	P	Estimate	z	P
Pteronotus alitonus	0.0002	0.17	0.86	-0.01	-0.13	0.89	-0.002	-0.99	0.31
Pteronotus rubiginosus	-0.001	-0.73	0.46	-0.25	-1.44	0.14	0.002	0.71	0.47
Saccopteryx bilineata	-0.003	-1.08	0.28	-0.58	-1.58	0.11	0.005	0.76	0.44
Saccopteryx leptura	0.001	0.31	0.75	-0.34	-0.7	0.48	0.001	0.11	0.9
Centronycteris maximiliani	0.001	0.35	0.72	-0.24	-0.48	0.62	-0.001	-0.12	0.9
Cormura brevirostris	-0.01	-1.94	0.051	0.01	-0.03	0.97	0.004	0.41	0.67
Myotis riparius	-0.004	-1.49	0.13	-0.32	-1.03	0.3	-0.001	-0.19	0.84
Eptesicus brasiliensis	-0.006	-0.61	0.54	-1.75	-1.55	0.12	0.03	1.4	0.16
Furipterus horrens	-0.004	-1.31	0.18	-0.07	-0.22	0.82	0.003	0.55	0.58

Table S4. Number of bat passes (mean ± SD) of the nine aerial-insectivorous bat species whose activity levels were compared during dark and bright nights.

Species	Dark nights			Bright nights		
	Continuous forest	Fragments	Secondary forest	Continuous forest	Fragments	Secondary forest
P. alitonus	3903 (33.07 ± 40.21)	2301 (35.4 ± 36.62)	4955 (51.08 ± 43.54)	4379 (49.76 ± 42.98)	2570 (43.55 ± 50.72)	3758 (38.34 ± 42.36)
P. rubiginosus	2329 (19.73 ± 24.57)	2419 (37.21 ± 34.88)	4869 (50.19 ± 46.25)	4232 (48.09 ± 64.05)	1155 (19.56 ± 20.61)	2597 (26.50 ± 29.24)
S. bilineata	2656 (22.50 ± 51.13)	5990 (92.15 ± 120.70)	438 (4.51 ± 13.57)	3125 (35.51 ± 128.71)	2410 (40.84 ± 156)	529 (5.39 ± 20.67)
S. leptura	866 (7.33 ± 23.42)	2777 (42.72 ± 70.87)	386 (3.97 ± 11.18)	832 (9.45 ± 28.92)	1806 (30.61 ± 62.56)	512 (5.22 ± 16.94)
C. maximiliani	10646 (90.22 ± 204.47)	13706 (210.86 ± 280.6)	1763 (18.17 ± 70.65)	5407 (61.44 ± 151.96)	6032 (102.23 ± 279.33)	951 (9.70 ± 34.56)
C. brevirostris	266 (2.25 ± 6.29)	1425 (21.92 ± 58.76)	54 (0.55 ± 2.02)	241 (2.73 ± 9.65)	1264 (21.43 ± 76.97)	38 (0.38 ± 1.50)
M. riparius	2150 (18.22 ± 42.13)	5860 (90.15 ± 144.74)	3879 (39.98 ± 97.74)	1844 (20.95 ± 55.78)	2910 (49.32 ± 79.82)	2945 (30.05 ± 52.62)
E. brasiliensis	21 (0.17 ± 6.29)	116 (1.78 ± 1.78)	1 (0.01 ± 0.10)	41 (0.46 ± 1.14)	31 (0.52 ± 1.96)	6 (0.06 ± 0.60)
F. horrens	174 (1.47 ± 3.23)	18 (0.27 ± 0.79)	27 (0.27 ± 1.39)	17 (0.19 ± 1.59)	16 (0.27 ± 1.20)	17 (0.17 ± 0.58)

Table S5. Summary of Generalized Linear Mixed Models examining bat activity of each species in terms of habitat type and interactions between moonlight and habitat type. Sampling night nested within research camp was specified as random effect, and data from 727 nights were used for this analysis. Bold values indicate $P < 0.05$.

Species	Fragments			Secondary forest			Moonlight:Fragments			Moonlight:Secondary forest		
	Estimate	z	P	Estimate	z	P	Estimate	z	P	Estimate	z	P
Pteronotus alitonus	-0.66	18.16	**0.001**	0.33	2.04	**0.04**	-0.0003	-1.36	0.17	-0.01	-4.78	**<0.0001**
Pteronotus rubiginosus	-0.19	-0.88	0.37	0.41	2.3	**0.02**	-0.01	-4.63	**<0.0001**	-0.02	-6.19	**<0.0001**
Saccopteryx bilineata	0.13	0.46	0.64	-1.39	-5.89	**<0.0001**	-0.01	-3.55	**<0.0001**	-0.005	-1.81	0.18
Saccopteryx leptura	1.05	1.72	0.08	-1.02	-1.96	**0.049**	-0.01	-1.83	0.06	-0.006	-0.85	0.39
Centronycteris maximiliani	0.09	0.17	0.86	-4.29	-8.18	**<0.0001**	-0.001	-1.4	0.16	0.01	1.85	0.06
Cormura brevirostris	0.7	1.2	0.23	-1.56	-3.13	**0.001**	0.001	1.58	0.11	0.004	-0.55	0.11
Myotis riparius	-0.1	-0.21	0.83	-0.52	-1.33	0.18	-0.003	-0.56	0.57	-0.001	-0.35	0.73
Eptesicus brasiliensis	1.83	1.52	0.12	-3.32	-2.78	**0.005**	-0.04	-2.31	**0.02**	0.002	0.14	0.88
Furipterus horrens	-1.95	-3.81	**0.0001**	-2.59	-4.97	**<0.0001**	0.0004	0.06	0.95	0.01	1.42	0.15

Table S6. Results of Kolmogorov-Smirnov 2-sample tests comparing the distribution of hourly activity between dark and bright nights for each forest type (continuous forest, fragments and secondary forest). Dark nights are those with 0-30% of moonlight intensity and bright nights those with 70-100%. Bold values indicate $P \leq 0.05$.

Species	Continuous forest		Fragments		Secondary forest	
	D	P-value	D	P-value	D	P-value
Pteronotus alitonus	0.50	0.09	0.41	0.24	0.50	0.09
Pteronotus rubiginosus	0.60	**0.03**	0.66	**0.009**	0.58	**0.03**
Saccopteryx bilineata	0.25	0.86	0.16	0.99	0.41	0.24
Saccopteryx leptura	0.58	**0.03**	0.25	0.84	0.41	0.24
Centronycteris maximiliani	0.66	**0.007**	0.75	**0.001**	0.41	0.25
Cormura brevirostris	0.33	0.51	0.33	0.51	0.16	0.99
Myotis riparius	0.33	0.51	0.58	**0.03**	0.41	0.24
Eptesicus brasiliensis	0.33	0.51	0.33	0.51	0.33	0.51
Furipterus horrens	0.58	**0.03**	0.41	0.24	0.25	0.84

Capítulo 4

Appel, G., Haugaasen, T.; Meyer, C. F. J.; Bobrowiec, P. E. D.

Fear or food? Prey availability is more important than predation risk in determining insectivorous bat responses across a disturbed tropical forest landscape

Artigo em preparação para *Basic and Applied Ecology*

Abstract

Habitat disturbance affect directly and indirectly the predation risk and the availability of food to animals. For aerial insectivorous bats, habitat disturbance is one of the big threats to conservation of this group of bats. However, we still not understand which mechanisms explain the negative effect of habitat disturbance on forest aerial insectivorous bats, and evaluate the changes in prey-predator interaction in disturbed habits can provide useful informations to management of protected reserves. We evaluated how predation risk, insect biomass and moonlight intensity affect the bat activity levels in preserved and disturbed forests (fragments and secondary forest). Our results suggested that preserved forest holds higher bat activity than fragments and secondary forest, and probably is associated to higher insect mass in preserved compared to secondary forest. Insect mass seems the best predictor to activity change in disturbed habitats compared to predation risk and moonlight. Predation risk does not modulate the bat activity in any habitat type. The effect of moonlight intensity appeared only in three species in different habitats, and it seems that these responses was related to the abundance of specific insect orders and not predation risk. Overall, our findings emphasizes the importance of evaluating the prey-predactor interaction on the behaviour of bats, specially the foraging eficiency, as the effects of habitat disturbance can affect lower trophic levels and consequently influence not only the bats but others animals that were insect consumers.

Key-words Acoustic sampling; Amazon forest; Fragmentation; Prey-predator interactions; Secondary forest

Introduction

Prey-predator interactions involve a trade-off between minimizing exposure to predators and maximizing feeding efficiency (Lima, 1985; Pyke, 2010). Predators are categorized as either ambush predators (i.e. sit-and-wait strategy) or cursorial predators (i.e. active hunting strategy) (Gable, Howkes, & Johnson-bice, 2021; Schmitz 2008;). Antipredator decisions by prey can hinge on the hunting mode used by their predator, and prey species can use different forms of escape behaviour such as fleeing (ie. evasion), and hiding (using cover, crypsis or freezing) (Sih, Englund, & Wooster, 1998; Wirsing, Cameron, & Heithaus, 2010). For prey species that use cover to reduce exposure to a predator, environmental variables such as canopy cover and habitat quality can be key factors determining habitat use (Lima & Dill 1990; Massé & Côté 2006).

Variables that strongly affect prey-predator interactions at the local scale are habitat quality and vegetation cover (Calkoen et al., 2018; Komers, 1997). From a predator perspective, habitat quality can influence prey availability and for predators that use vision to forage, high vegetation cover can limit prey visibility (Lima & Dill, 1990; Riginos & Grace 2008). Indeed, cluttered habitats can be accessible only to predator species capable of maneuvering around obstacles (Wywialowski, 1987). On the other hand, from a prey perspective, the quality of the habitat is crucial to find partners, food and shelter (Abrams, 2000), and vegetation cover can reduce the risk of predation, especially for species with low mobility (Verdolin, 2006). Thus, heterogeneous landscapes can create different situations of fear and forage (Kotler & Brown, 1999), but it is intuitive that lower-quality habitats tend to affect negatively both predators and prey. Several studies have addressed foraging and antipredatory behaviour under risk in heterogeneous habitats (Verdolin, 2006), but have largely focused on open landscapes, such as deserts, grasslands and savannas (Brown, 1988; Manu & Creshwell, 2013; Pitt, 1999; Steinhoff *et al*., 2020). Tropical ecosystems have received little attention (Drakeley, Lapiedra, & Kolbe, 2015), especially anthropogenic landscapes where environmental changes may strongly alter the foraging decisions of prey and predators (Chejanovski et al., 2017; Schneider 2001).

Forest loss and fragmentation are the main drivers of anthropogenic changes that are modifying tropical landscapes (Barlow et al., 2016). Forest fragmentation results in landscapes of primary forest fragments surrounded by an anthropogenically disturbed matrix (Broadbent et al., 2008). One of these human-disturbed habitats is secondary

regenerating forest, which is increasing faster than ever in extent in the Brazilian Amazon, amounting to an area of 180, 215 km² (Smith et al., 2021). These disturbed habitats differ from preserved habitats in local variables, such as biotic, structural and the intensity of abiotic conditions which can alter predator-prey interactions in complex ways by affecting prey availability and facilitating foraging opportunities for predators (Haddad et al., 2015; Michalko et al., 2021). Forest fragments surrounded by a low-contrast matrix, for example, can suffer from edge effects including reduced forest cover, which exposes prey species to greater predation risk relative to those experienced in larger fragments and continuous primary forest (Morrison et al., 2010; Tufto, Linnell, & Andersen, 1996). Indeed, secondary regenerating forest have lower plant species richness and differ in species composition compared to primary forest, and consequently affect the availability of different prey species for predators. Overall, the habitat quality of fragments and secondary forest can directly affect the prey-predator interaction, but some abiotic conditions can indirectly influence both prey and predator in human-modified lanscapes.

Moonlight intensity can influence foraging activity and can have opposite effects depending on the foraging mode of species (Bhatt, Sarma, & Lyngdoh, 2018; Rabaiotti & Woodroffe, 2019). Prey species that primarily use vision to forage can detect predators visually on bright nights and may increase their activity, whereas those that use other senses (e.g. olfaction, echolocation) usually decrease the activity (Prugh & Golden, 2014). Moreover, some prey species can shift their activity from open to cluttered habitats on full moon nights, in order to avoid the periods of greater visibility to predators (Brown et al., 1988; Hemami et al., 2011). In a fragmented landscape, bright nights can increase the predation risk in smaller fragments and in the surrounding matrix, especially for animals that have foraging areas which are larger than the fragment area (Bowers & Dooley, 1993). In contrast, moonlight tends to increase the activity of visually oriented nocturnal predators (Prugh & Golden, 2014), but when prey availability is reduced on bright nights, some species may increase their activity on dark nights to achieve better foraging success (Penteriani et al., 2013). Moonlight effects can be complex for animals that are both predators and prey at the same time, and insectivorous bats are known to constantly modulate their activity with the moonlight (Saldaña-Vázquez & Munguía-Rosas, 2013).

Aerial insectivorous bats provide crucial ecosystem services such as supressors of agricultural pests (Boyles et al., 2013; Montauban et al., 2021) and mosquitos that transmit diseases (Puig-Montserrat et al., 2020), and they can be sensitive to

anthropogenic habitat disturbance (Russo, Salinas-Ramos, & Ancilloto, 2021; Voigt & Kingston 2015). Indeed, forest-dwelling species are the group of aerial insectivores that respond most negatively to habitat disturbance, showing curtailed activity in disturbed habitats (Estrada-Villegas, Meyer, & Kalko, 2010; Falcão, Donov, & Caselli, 2021; Jung & Kalko, 2010; de Araújo & Bernard, 2016). Even though aerial insectivorous species play key roles in ecosystems and are threatened by habitat loss, responses of this bat ensemble to land-use change in the tropics remain understudied (Mendes & Srbek-Araujo, 2020; Meyer et al., 2016). In the Amazon, activity of some aerial insectivorous species can decrease in fragments (Núnez et al., 2019), as well in secondary regenerating forest, with six forest species reducing their activity (Appel et al., 2021). The mechanisms that explain this reduction in bat activity in disturbed habitats may be related to changes in prey-predator interactions and abiotic conditions (Arrizabalaga-Escudero et al., 2015). These bats were less active on extremely bright nights, probably due to higher vulnerability to predators when bats need to fly over the matrix (Appel et al., 2021). Indeed, abundance and biomass of moths, one of the main dietary components of aerial insectivores, are strongly determined by local plant diversity and vegetation complexity (Alonso-Rodríguez, Finegan, & Fiedler, 2017; Hawes et al., 2009). Thus, habitats with different vegetation cover and degree of disturbance may affect the trophic interaction between bats and their prey (Treitler et al., 2016), and can provide useful information about the management of fragments and secondary forest in bat conservation.

In this study, we evaluated how habitats with different degree of disturbance influence the activity of seven aerial insectivorous bat species in relation to food availability, predation risk and moonlight intensity. We acoustically quantified bat activity in the disturbed landscape of the Biological Dynamics of Forest Fragments Project (BDFFP), specifically in continuous forest (control) and in disturbed habitats (forest fragments and secondary forest) to examine variation in species-level activity. Playback experiments in each habitat type were conducted to determine the effect of perceived predation risk on bat activity. To assess food availability, we collected aerial insects around the acoustic recorders in each habitat type and determined their biomass. We also considered the percentage of moonlight intensity due to possible differences in foraging behaviour in each habitat type (Appel et al., 2021). Our general hypothesis was that the activity of aerial insectivorous bats would be highest in continuous forest due to greater available insect biomass and would be lower in disturbed habitats due to the higher

predation risk as a result of reduced forest cover. Thus, across the disturbed landscape, we tested the following predictions:

(1) We expected that secondary forest will exhibit reduced bat activity compared to continuous forest. Fragments will exhibit reduced activity compared to continuous and secondary forest particularly for *Pteronotus* species, which have been shown to be sensitive to habitat disturbance (Appel et al., 2021).

(2) For food availability, insect biomass will be greater in continuous forest than fragments and secondary forest, but will not differ between fragments and secondary forest .

(3) We anticipated that most of aerial insectivorous bat species would respond to insect biomass rather than predation risk in continuous forest. By contrast, in disturbed habitats (fragments and secondary forest), most aerial insectivorous bat species would respond to predation risk than insect biomass. These responses would reflect the diversity of food available across the primary forest and the greater exposure to predators in disturbed habitats due to the reduced vegetation cover.

(4) We expected that interaction of moonlight intensity with insect biomass and predation risk will not affect bat activity in continuous forest, where vegetation cover and insect biomass are higher than in the disturbed habitats. In the disturbed habitats, we predicted that most bat species will be negatively affected by moonlight intensity and predation risk (Appel et al., 2021).

(5) Predation risk will only affect the hourly activity of bat species in fragments and secondary forest, with higher activity at the beginning of the nights without owl calls.

Material and Methods

Study site

The study was done at the Biological Dynamics of Forest Fragments Project (BDFFP) (2°25'S; 59°50'W), located ~80 km north of Manaus, Brazil (Fig. S1), one of the world's largest and longest-running experimental investigations of habitat fragmentation (Laurance et al., 2018). Located in Central Amazonia, the area contains lowland evergreen *terra firme* rainforest at 50 to 100 m of elevation (Laurance & Williamson, 2001). The study area includes 11 forest fragments (five of 1 ha, four of 10

ha and two of 100 ha) surrounded mainly by a matrix of secondary forest in advanced stage of regeneration and large extensions of primary forest that act as experimental controls (Laurance et al., 2018). Periodically, the fragments are re-isolated by clearing the forest up to 100 meters around the fragments; the last re-isolation took place in 2014 (Rocha et al., 2017). The secondary forest is dominated by *Cecropia* spp. in areas that were only cleared and by *Vismia* spp. in areas that were cleared and burned (Mesquita et al., 2001). The dry season typically is from July to November when precipitation is less than 100 mm/month and the rainy season occurs from November to June, when precipitation can be 300 mm/month (Ferreira et al., 2017). We estimated the canopy using the average of four shperical densiometer readings in each habitat type, and we observed that canopy varies little between habitat types (continuous forest interior: 91.5 ± 1.32 [mean ± *SD*]; fragments of 10 ha interior: 89.7 ± 0.55; secondary forest: 86.7 ± 2.82). Canopy height in the largest fragments and continuous forest averages 28 m (Almeida et al., 2019), while in the well-developed secondary forest the average canopy height is 15 m (Jakovac et al., 2014; Mokross et al., 2018). We assumed that moonlight intensity penetrates into the forest similarly among the habitats, because of the low variation in canopy cover.

Bat acoustic sampling and bat identification

We sampled at nine sites across the BDFFP landscape: three sites in continuous forest (Cabo Frio, Florestal and 41), three 10 ha fragments (Porto Alegre, Colosso and Dimona) and three sites in secondary forest (Porto Alegre, Cabo Frio and Dimona) (Fig. S1). Each site was visited twice in each season (dry season of 2018 and rainy season of 2019) and the number of sampling nights in each season was similar between habitats (Tab. S1). We positioned the passive ultrasound recorders in the center of the fragments, in the secondary forest at least 1000 m away from the edge of a fragment or continuous forest, and in the interior of continuous forest 1000 m away from the edge. At each site, we installed an automatic ultrasound recorder (Song Meter SM2Bat+) with an omnidirectional ultrasonic SMX-US microphone (Wildlife Acoustics, Inc., USA) placed at a height of 1.5 m above the ground. The recorders were programmed to passively register bat activity in real time, with a full spectrum resolution of 16 bit, a high-pass filter set at fs/32 (12 kHz), and an adaptive trigger level relative to noise floor of 18 SNR. We configured to record bat activity between 17:30 and 06:30 for two to four consecutive

nights per visit, totalling at least 40 nights per sampling site (Tab. S2). We recorded during 138 nights, totalling 1,794 recording hours.

Each recording night was divided into five-second segments using Kaleidoscope software (Wildlife Acoustics, Inc.,USA) and we defined a bat pass as a five-second segment with at least two recognizable search-phase calls per species (Appel et al., 2019; Gomes, Appel & Barber, 2020). We manually identified the bat passes to species level or sonotype level when it was impossible to identify the call to a particular species. Identification followed the acoustic key in (López-Baucells et al., 2016). For manual identification of each recording, we used Kaleidoscope Software (version 4.0.4). We calculated the activity as the sum of five-second segments with bat passes per night (nightly activity) and per hour (hourly activity).

We identified ~39,800 bat passes of 13 aerial insectivorous bat species and 10 sonotypes. We minimized potential detection biases by focusing on species that were detected in at least 45% (63 nights) of the total nights. Thus we selected seven species for analysis: *Pteronotus alitonus*, *P. rubiginosus* (revised by López-Baucells et al., 2018; Pavan, Bobrowiec & Percequillo, 2018), *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *S. leptura* and *Peropteryx kappleri* (Table S3).

Predator call experiment

To test if predation risk influences the activity of aerial insectivorous bats, we performed playback experiments with three treatments at all sites: a) playback of owl species calls; b) noise treatment; c) without owl calls or noise (control treatment). Each night of acoustic sampling, we ran one of the treatments, maintaining an order that did not repeat the treatment of the previous night. Owl calls and noise sound were played using a JBL (Clip 2) speaker connected to a portable battery and a cell phone that contained one playlist. The speaker was installed five meters away from the ultrasound recorder at a height of 1.5 m above ground level. Predator and noise treatments lasted for the same duration of the deployment of the ultrasound recorder (17:30 to 06:30) and were broadcasted every 15 minutes for a duration of one minute. This temporal vocal activity pattern of owls is in agreement with that observed for owl species at the BDFFP (Bonamoni *et al.*, *field observation*). Indeed, we used a different playlist order of owl species calls to avoid repetition of the same playlist from a previous night. We used the noise treatment to validate the treatment of owl calls, if bats respond to noise this means

240 that a possible response to the owl calls is not validated. For each treatment, we had at
241 least 11 nights in each habitat type (Tab. S2).
242 For the treatment of owl calls, we selected the following species that were reported
243 to prey on bats and that were previously registered at the BDFFP (Bonamoni, 2013):
244 *Lophostrix cristata*, *Megascops watsonii*, *Strix huhula*, *Strix virgata* and *Pulsatrix*
245 *perspecillata* (Almeida et al., 2021; Cadena-Ortiz, Freile, & Bahamonde-Vinueza, 2013;
246 Carvalho et l., 2011; Rocha & López-Baucells, 2014; Serra-Gonçalves, López-baucells,
247 & Rocha, 2017). Owl calls were obtained from the Xeno-canto website (available:
248 https://www.xeno-canto.org/), which is an open repository of bird songs . We measured
249 the owl vocalizations during playbacks and were in a frequency range between 8-20 kHz,
250 which is a range that our focal bat species can hear: *Pteronotus* (10-112 kHz, Kössl &
251 Vater, 1996) and Emballonuridae species such as *S. bilineata* and *S. leptura* (5-100 kHz,
252 Lattemkamp et al., 2021). The noise treatments had a frequency range between 0 and
253 8268.8 kHz and was obtained from the SimplyNoise website (available from:
254 https://simplynoise.com/). This noise sound was used by other studies which tested the
255 influence of noise on animal activity (Medeiros et al., 2017).
256

257 *Nocturnal insect sampling*

258 Nocturnal flying insects (hereafter insects) were sampled at each site in parallel to
259 acoustic sampling of bats and predator experiments. To avoid possible biases associated
260 with the use of light traps while recording bats (Froidevaux, Fialas, & Jones, 2018), we
261 used Malaise traps to capture insects (1.60 m height x 1.50 m length). These traps are
262 known to collect a great variety and abundance of insects eaten by bats such as Diptera,
263 Coleoptera, Lepidoptera, Hymenoptera, Hemiptera and Orthoptera (Table S4). We
264 installed four malaise traps around the ultrasound recorder whereby each malaise trap was
265 placed 20 meters from the recorder in the four cardinal directions (Fig. S2). In order to
266 collect only nocturnal insects, we installed the traps before sunset (17:30) and took them
267 down at sunrise (06:00).
268 Insects were preserved in bottles containing 90% alcohol, which were properly
269 labeled and taken to the Animal Biology Laboratory of the Federal University of
270 Amazonas (UFAM) for sorting and identification. The identifications were made by
271 entomologists of UFAM and National Institute for Amazonian Research (INPA) and
272 identified to order level based in identification keys by Rafael et al., (2012). For each

insect order, we counted the individuals and weighed them to estimate the total biomass of insects per night. To remove excess alcohol of the insects, we dried them with filter paper and weighed each order of insect on a precision balance (precision limit 0.0001 g; Ohaus Discovery, Pine Brook, New Jersey). We estimated the average insect biomass per night by dividing the mass by the number of insects collected (Oliveira et al., 2015).

Moonlight intensity

Moonlight intensity for each night was calculated using the "sunmoon" software (Kyba, Conrad, & Shatwell, 2020), a robust method for quantifying the amount of sunlight reflected by the moon. This software employs the illuminance model of Janiczek & DeYoung (1987). We used the percentage of moonlight intensity instead of the moon phase because moonlight luminosity varies greatly within the same moon phase (Appel et al., 2017; 2021). At each site and for each treatment, we sampled nights with different percentage of moonlight intensity in order to cover the whole gradient in variation of moonlight intensity (0 to 100%).

Data analysis

We performed generalized linear mixed models (GLMMs) in the R package "glmmTMB" (Bolker et al., 2020) to test each prediction. First, we tested the effect of habitat type (continuous, fragment and secondary forest) on total and species-specific bat activity levels. The response variable was the number of bat passes recorded in a single night, total and per species. Models were fitted using a negative binomial distribution and we used zero-inflated models when the species distribution showed a signal of zero inflation (Zuur et al., 2009). For each model, habitat type was the categorical fixed effect and to account for the temporal autocorrelation in the data, we used sampling night nested within research camp as a random effect. In order to compare activity levels between fragments and secondary forest, we evaluated these differents using least-squares means (predicted marginal means) analysis with lsmeans package (Lenth, 2016).

To test the effects of insect biomass and owl calls on bat activity in each habitat, we also performed GLMMs for each species and for total bat activity. First, we made a model testing the additive effects of insect biomass and playback treatment (control, noise and owl calls) on bat activity level. Second, we tested the additive effects of insect

biomass and moonlight intensity and also interactive effect on bat activity level, and the predictors of this model were standardized to a mean of 0 and a SD of 1 to facilitate comparison of their relative effects. Third, we made a model with the additive effects of playback treatment and moonlight intensity, also the interactive effect on bat activity level, in this model we not standardized the predictors due the categorical predictor of playback threatment. For all models, to account for the temporal autocorrelation in the data, we used sampling night nested within research camp as a random effect and the distribution of response variables were negative-binomial.

As we analysed the effects of predictors per bat species, we used only the insect orders that each bat species consumes according to the literature (Tab. S5). We further tested the influence of habitat type on insect biomass using Gardner-Altman estimation plots and evaluated statistical differences using non-parametric permutation tests with 1000 bootstrap samples to estimate effect sizes and 95% confidence intervals for the difference of means with the package "dabestr" (Ho et al., 2019). Statistically significant differences in insect biomass between habitat types were determined based on the lack of overlap in the frequency distributions of the data.

Differences in hourly activity levels between owl call playback treatment and control treatment for each habitat type were assessed using Kolmogorov-Smirnov 2-sample tests. Bat activity of each species was divided into 12 intervals (hourly intervals). For comparisons between these two treatments, we used data from 36 nights in continuous forest (17 nights of owl calls, 19 of control), 30 nights in fragments (13 nights of owl calls, 17 of control) and 30 nights in secondary forest (15 nights of owl calls, 15 of control). All analyses were performed in the software R 4.02. and R Studio 4.0.2 (R Core Team, 2021; Rstudio Team, 2021).

Results

Effects of habitat type on bat activity and nocturnal insect mass

Total bat activity was higher in continuous forest compared to disturbed habitats (Tab. 1), where activity levels were 2.06 and 1.84 times higher in continuous forest, respectively, compared to fragments and secondary forest (Tab. S3). Fragments had the most negative effect on species-specific responses. Activity of two species (*C.*

maximiliani and *C. brevirostris*) were significantly lower in fragments than continuous forest (Tab. 1). *Pteronotus rubiginosus* activity was significantly lower in secondary forest than continuous forest, in contrast to *P. alitonus* and *P. kappleri* that showed higher activity in secondary forest than continuous forest (Tab. 1). When comparing fragments with secondary forest, four species (*P. alitonus*, *C. maximiliani*, *C. brevirostris* and *P. kappleri*) had higher activity in secondary forest while only *P. rubiginosus* had higher activity in fragments (Tab. 1).

Tab.1 Summary of Generalized Linear Mixed Models examining bat activity of each species in response to habitat type. Habitat types are: continuous forest (Continuous), forest fragment (Fragment) and secondary forest (Secondary). Bold values indicate $P < 0.05$.

	Continuous vs. Fragment			Continuous vs. Secondary			Fragment vs. Secondary		
	Estimate	z-value	P	Estimate	z-value	P	Estimate	z-value	P
Pteronotus alitonus	-0.25	-0.46	0.65	1.37	2.51	**0.01**	-1.62	-2.80	**0.01**
Pteronotus rubiginosus	0.09	0.67	0.50	-0.37	-3.85	**0.0001**	0.45	4.61	**<0.0001**
Saccopteryx bilineata	0.61	0.99	0.32	0.94	1.48	0.14	-0.01	-0.02	1.00
Saccopteryx leptura	-0.23	-0.46	0.65	-0.81	-1.70	0.09	0.57	1.20	0.45
Centronycteris maximiliani	-1.53	-2.11	**0.03**	-1.17	-1.65	0.09	-0.74	-2.34	**0.05**
Cormura brevirostris	-2.77	-2.23	**0.02**	-1.40	-1.24	0.22	-1.36	-2.86	**0.01**
Peropteryx kappleri	0.28	0.36	0.72	1.65	2.16	**0.03**	-1.37	-3.13	**0.006**
Total activity	-1.00	-2.70	**0.006**	-0.72	-1.95	**0.05**	-0.28	-0.71	0.76

We sampled a total of 46.401 nocturnal insects and Diptera represented 61.7% of all sampled individuals, followed by Hymenoptera with 17.13%, Collembola with 9.2% and Lepidoptera with 3.7% (Tab. S4). The remaining orders (e.g., Hemiptera, Coleoptera, Orthoptera, Isoptera, Blattodea, Trichoptera) accounted for 9% of total insects. Nocturnal insect biomass (based on insect orders relevant to the diet of most bat species; *P. alitonus, P. rubiginosus*, *S. bilineata*, *C. maximiliani*, *C. brevirostris* and *P. kappleri*) in secondary forest was significantly and on average 3.1 times lower than in continuous forest (Tab. 2). No significant differences in insect biomass were found between continuous forest and fragments (Tab. 2). On the other hand, the biomass of insects featuring in the diets of *S. bilineata*, *C. maximiliani* and *P. kappleri* was on average two times lower in secondary forest compared to fragments (Tab. 2).

Tab.2 Comparison of the effect size (mean difference) estimates of insect mass between habitat types for the focal bat species. Habitat types are: continuous forest (Continuous), forest fragment (Fragment) and secondary forest (Secondary). Bold values indicate a significant and positive effect.

	Continuous vs. Fragment			Continuous vs. Secondary			Fragment vs. Secondary		
Species diet	Effect size	Lower CI	Upper CI	Effect Size	Lower CI	Upper CI	Effect Size	Lower CI	Upper CI
P. alitonus and *P. rubiginosus*	-0.0002	0.025	-0.039	**0.020**	0.047	0.003	0.02	0.063	0.001
S. bilineata	0.007	0.031	-0.012	**0.017**	0.043	0.004	**0.010**	0.032	0.001
S. leptura	-0.01	0.029	-0.078	0.015	0.051	-0.012	0.026	0.097	-0.009
C. maximiliani	0.007	0.031	-0.012	**0.017**	0.042	0.004	**0.010**	0.033	0.001
C. brevirostris	-0.001	0.001	-0.003	0.001	0.002	-0.0005	0.006	0.029	0.001
P. kappleri	0.007	0.030	-0.013	**0.017**	0.043	0.004	**0.011**	0.034	0.002
All species	0.012	0.032	-0.006	0.011	0.031	-0.009	0.023	0.097	-0.011

Effects of insect mass and owl calls on bat activity in each habitat type

We found a positive relationship between activity of four species (*P. alitonus*, *P. rubiginosus*, *S. bilineata* and *C. brevirostris*) and insect biomass in continuous forest (Fig. 1). Conversely, in secondary forest, total bat activity and activity of *P. alitonus* were negatively related to insect biomass. We did not find any influence of owl call playback on bat activity in any habitat, except for *P. kappleri* which responded negatively to the owl calls, but also to noise, indicating that this species is affected by any type of sound, not necessarily the predator call. We also did not find any relationship between insect biomass and owl call with bat activity in the fragments.

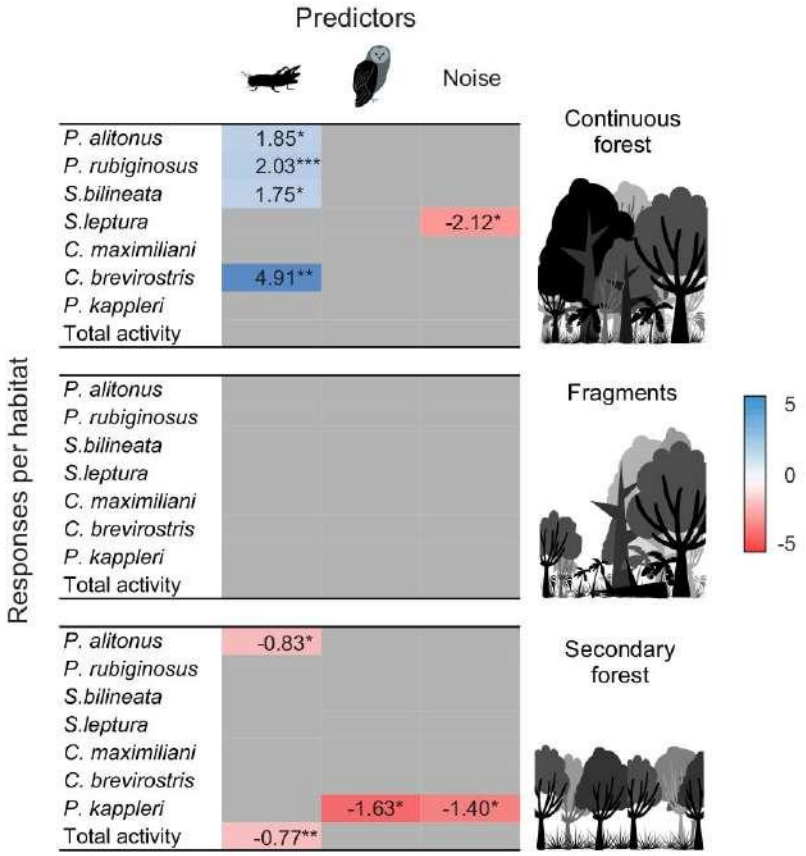


Fig. 1. Heatmap of the significant results of GLMM based on the effects of insect biomass, owl calls and noise sound for each bat species and habitat type. The colour gradient indicates the magnitude of a predictor's estimate for individual response variables. Grey boxes indicate lack of statistical significance. Coloured boxes indicate significant effects, '*' $P < 0.05$, '**' $P < 0.01$ and '***' $P < 0.001$.

Effects of moonlight intensity, insect mass and owl calls on bat activity

Only three bat species responded to moonlight intensity, when we compare with insect biomass in each habitat type (Fig. 2). In continuous forest, only *C. maximiliani* was less active during brighter nights with greater insect biomass (Fig. 2). In fragments, *P. alitonus* reduced activity with increasing moonlight intensity and *P. kappleri* was more active during brighter nights with greater insect biomass (Fig. 2). In secondary forest, only *P. rubiginosus* was less active on brighter nights with lower insect biomass (Fig. 2).

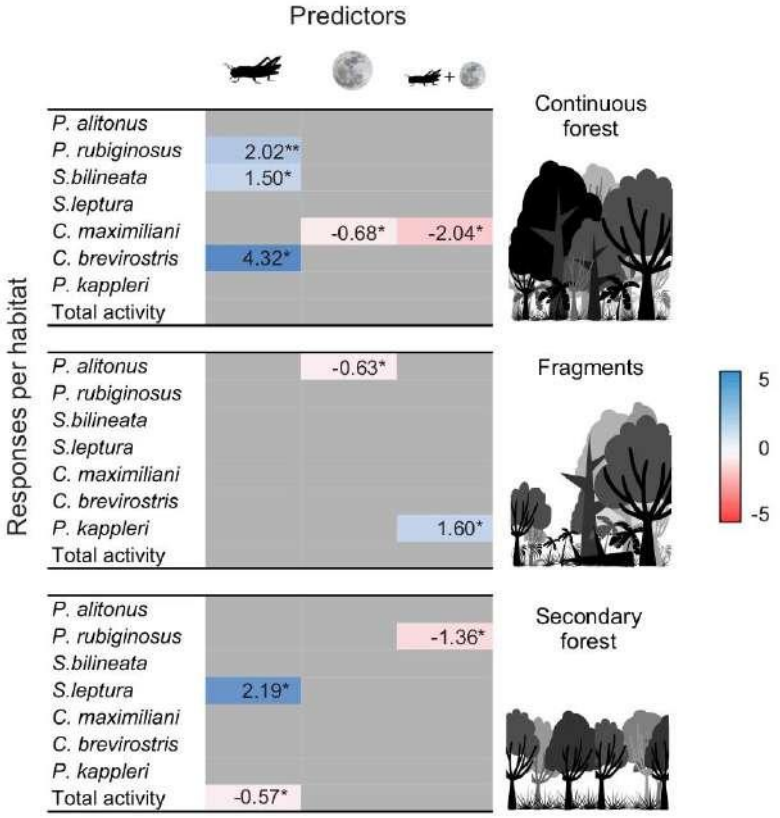
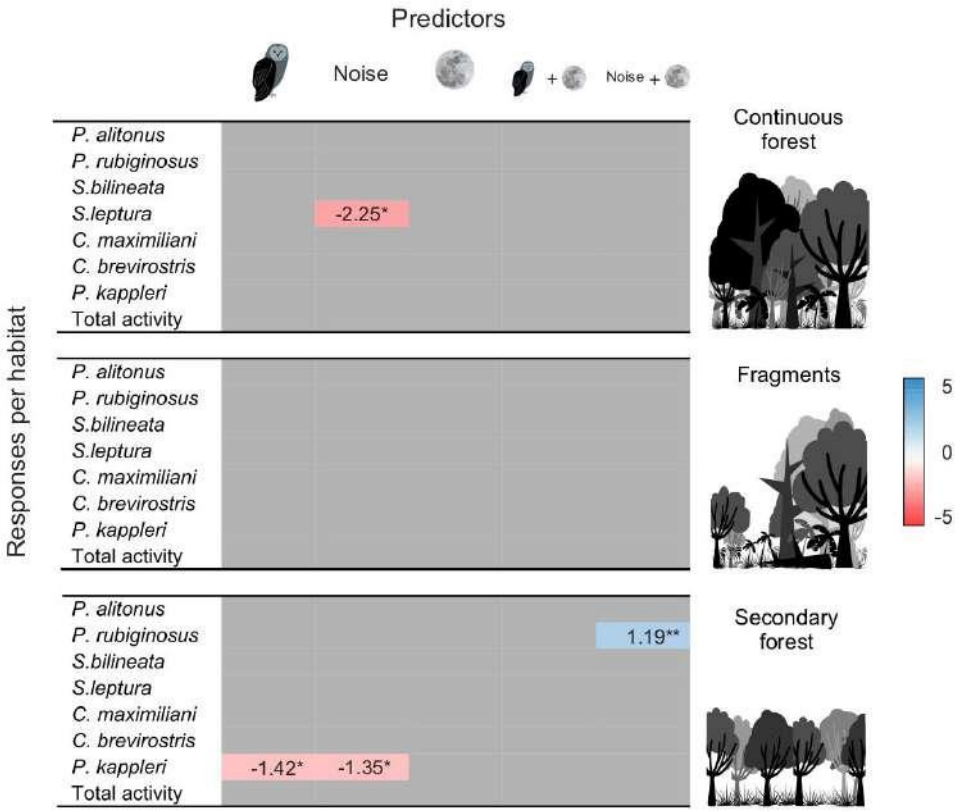


Fig. 2. Heatmap of the significant results of GLMM based on the effects of insect biomass, moonlight and interaction for each bat species and habitat type. The colour gradient indicates the magnitude of a predictor's estimate for individual response variables. Grey boxes indicate lack of statistical significance. Coloured boxes indicate significant effects, '*' $P \leq 0.05$, '**' $P < 0.01$ and '***' $P < 0.001$.

There were no significant effects of moonlight and owl call playback on bat activity in any habitat (Fig. 3). The only significant result (*P. rubiginosus* in secondary forest) was associated with noise and therefore were not considered (Fig. 3).



390

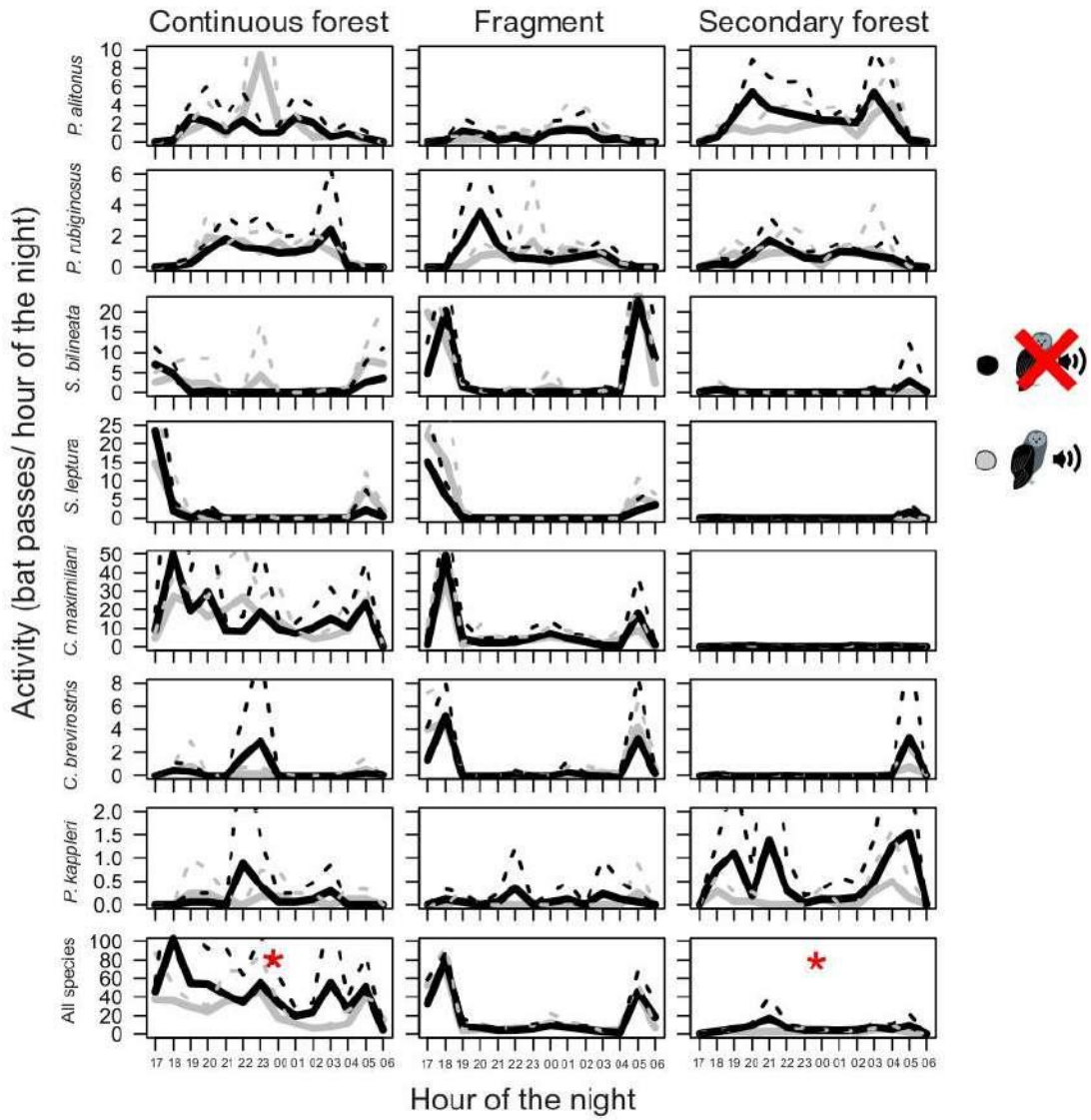
391 **Fig. 3.** Heatmap of the significant results of GLMM based on the effects of owl calls, moonlight
392 and interaction for each bat species and habitat type. The colour gradient indicates the magnitude
393 of a predictor's estimate for individual response variables. Grey boxes indicate lack of statistical
394 significance. Coloured boxes indicate significant effects, '*' $P \leq 0.05$, '**' $P < 0.01$ and '***' P
395 < 0.001.

396

397 *Effects of owl calls on hourly bat activity in each habitat type*

398 In continuous and secondary forest, total hourly bat activity was significantly
399 greater during nights without owl calls than those with playback, particularly in the early
400 evening (Fig. 4). However, at the species level, hourly activity did not differ between
401 nights with owl calls and control nights, irrespective of habitat type (Fig. 4).

402



403

404 **Fig. 4.** Hourly activity of aerial insectivorous bat species in each habitat type (continuous,
405 fragments and secondary forest) on control nights (without sound) and nights with owl calls.
406 Black lines denote control nights, grey lines depict nights with owl calls. The solid line is the
407 average activity and dotted line is the standard deviation of activity. '*' indicates a significant
408 difference between the treatments based on Kolgomorov-Sminorv 2-sample tests ($P \leq 0.05$).

409

410 **Discussion**

411 At the BDFFP, there is growing research into understanding ecological aspects of
412 how forest disturbance affects the functional, taxonomic, and behavioural responses of
413 aerial insectivorous bats (López-Baucells et al., 2019, 2021; Meyer et al., 2016; Núñez
414 et al., 2019; Torrent et al., 2018). Several studies have shown that Amazonian aerial
415 insectivorous bats are particularly vulnerable to habitat disturbance and fragmentation,

especially the understory bats and species that emit constant-frequency calls (Appel et al., 2021; Núnez et al., 2019; López-Baucells et al., 2021). Our results indicate that predation risk does not modulate the activity of understory insectivorous bats in disturbed habitats and the higher activity in continuous forest is related to higher insect biomass. We also found that moonlight does not intensify the predation risk effect and does not interfere with insect consumption in preserved and disturbed habitats.

Overall, the total activity of aerial insectivorous bat species was negatively affected by habitat disturbance. Our results suggest that total activity in disturbed habitats (fragments and secondary forest) is half that observed in continuous forest. The reduced activity in human-disturbed habitats especially for forest-dependent aerial insectivorous species has commonly been reported (Estrada-Villegas et al., 2010; Falcão Donov, & Caselli, 2021; Meyer et al., 2016), and this might be caused by a decrease of resources, such as roosts, food and safe environments for foraging (Bernard & Fenton, 2002; Evelyn, Stiles, & Young, 2004; Pereira, Fonseca, & Aguiar, 2018). As expected, insect mass is higher in continuous forest than secondary forest, but is similar in fragments to continuous forest. Thus, heavier insects in continuous forest probably create better foraging opportunities for aerial insectivorous bats. This positive relationship between activity of forest aerial insectivorous species and insect biomass has previously been identified in some studies (Oliveira et al., 2015; Ketzler, Comer, & Twedt, 2018; Put, Mitchell, & Fahrig, 2018; Scanlon & Petit, 2008). This difference in insect biomass between continuous forest and secondary forest might be related to the plant-assemblage composition of these areas (Alonso-Rodríguez et al., 2017; Hawes et al., 2009). Herbivorous insects often consume specific plant genera or species (Haddad et al., 2009), so well-preserved habitats commonly have higher diversity and biomass of vegetation-associated insects (Ebeling et al., 2019; Welti & Kaspari, 2020). Secondary forests dominated by *Vismia* have lower plant diversity (Jokovac et al., 2014) and consequently, insects are probably less diverse and may have lower body dry mass in disturbed habitats (Salomão et al., 2018).

Fragments had more species with negative responses of activity compared to secondary forest, and five species had lower activity in fragments than secondary forest. This result is different from what we expected, because based on intensive acoustic sampling conducted at the BDFFP between 2011 and 2013 we showed that most aerial insectivorous species were less active in secondary forest (Appel et al., 2021). This was probably due to the reisolation of the fragments in 2014 (Rocha et al., 2017). The acoustic

sampling of the present study (2018-2019) was done in fragments surrounded by a secondary forest at an early stage of regeneration compared to 30 years of matrix regeneration in the previous study (Appel et al., 2021). Fragment isolation had substantial negative effects on total activity of aerial insectivorous, even after four years of forest regeneration. *Pteronotus alitonus* and *Peropteryx kappleri* were clearly more active in secondary forest than in continuous and forest fragments. In the temperate region, Wright et al., (2021) found higher bat activity in young regenerating forests and this could be associated with the prey and the foraging strategy of the species which prefer to fly in uncluttered spaces. In fact, *P. kappleri* may forage in open-space areas, as some studies demonstrate that this species has higher activity in pastures (Falcão et al., 2021) and in the canopy than understory (Gomes, Appel & Barber, 2020). *Pteronotus alitonus* was previously suggested to be associated with highly cluttered habitats, but can be found at lakes at the BDFFP (Torrent et al., 2018).

As expected, most aerial insectivorous bat species responded to insect biomass rather than predation risk in continuous forest. Bat species can maximize the energy gain with higher insect biomass and minimize exposure with the protective cover of continuous forest, therefore the benefits outweighed the risk of predation (Jung & Kalko, 2010; Rydell, Entwistle, & Racey, 1996). However, contrary to our expectations, predation risk did not affect bat activity responses in disturbed habitats. In fact, our results indicate that owl calls do not alter aerial insectivorous bat activity in any habitat type. A lack of response of bats to owl calls was also found for temperate species (Janos & Root, 2014) and for neotropical frugivorous species (Breviglieri et al., 2013). There are some possible reasons to this absence of response on bat activity: (1) Owls use their vision to hunt, and they cannot hear ultrasound calls emitted by bats as the upper limit of hearing frequency of owls is between 7-18 kHz (Beason, 2004; Konishi, 1973). Thus, for owls easy access to prey is commonly more important than prey abundance as some species have been shown to prefer sites with low vegetation cover where prey accessibility is presumably high (Apolloni et al., 2017). Thus, the response of bats to owls presumably might be higher in open areas such as pastures and agricultural lands. (2) Bats probably perceived the owl calls as nonthreatening nocturnal noise in forested sites (Janos & Root, 2014) as the vocal activity of owls is not associated with hunting, but with territorial advertising and mate attraction (Penteriani & Delgado, 2009); (3) The acoustic stimulus is not strong enough to trigger anti-predator responses in bats compared to other stimuli such as visual cues, odor, movement and vocalization of an attacked bat (Breviglieri et

al., 2013; Fenton et al., 1994). We only used owl calls as predation risk stimulus and we evaluated only the changes in activity as antipredator response of bats, thus further investigation is needed to test other stimuli, predators and different response measures of bats (Baxter et al., 2006; Knörnschild & Tschapka, 2012).

Our results also show that variation in moonlight intensity has a weak effect on bat activity, and does not suppress the activity of most bat species in disturbed habitats. Our previous study showed that moonlight variation between nights affects little the aerial insectivorous bat activity in disturbed habitats (Appel et al., 2021). Some bat species responded to moonlight in conjunction with insect biomass, and no species responded to moonlight associated with predation risk. Even so, the effect of the moon-insect interaction was only evident in three species in different habitats. We suggest that some aerial insectivorous species can modulate their activity with the moonlight probably via an indirect effect of insect availability and not associated with predation risk (Lang et al., 2007). Insects orders eaten by *P. alitonus* and *P. rubiginosus* decrease with moonlight in fragments and secondary forest (analysis of variance: Estimate: -0.002; t: -5.24; p: <0.0001 for fragments, and Estimate: -0.002; t: -6.47; p<0.0001 for secondary forest). By contrast, Lepidoptera is more abundant with the moonlight in fragments, so could explain the higher activity of *P. kappleri* on bright nights in fragments (Estimate: 0.006; t: 4.18; p<0.001). For *C. maximiliani*, we found no statistical effect of moonlight for the insects orders that this species eats which are Lepidoptera and Coleoptera (Estimate: 0.001; t: 1.17; p<0.65), and maybe this related to the lack of knowledge of other insects that *C. maximiliani* eats, since we only found two studies.

We found a reduction of hourly total activity in nights with owl calls in continuous and secondary forests. In continuous forest, total bat activity was lower at the beginning of the night and at 2 and 3 pm in nights with owl calls compared to control nights. In secondary forest, total bat activity in nights with owl calls was also slightly reduced the whole night compared to control nights. This provides some evidence that tropical aerial insectivorous bats may change activity in response to predation risk for short periods of time throughout the night. Some bats species tend to emerge later when the predator is present (Russo et al., 2011; Welbergen, 2006). Bats need to feed at the beginning of the night, but when predation risk is high, they can optimize and distribute their activity over the course of the night, especially gleaning insectivorous species whose food is evenly distributed over the night (Kalko et al., 1999; Weinbeer & Kalko 2004).

Despite species-specific differences, in general total bat activity was higher in continuous forest compared to disturbed habitats, likely a consequence of the higher insect biomass of continuous forest. Thus, the effects of habitat disturbance on aerial insectivorous bat activity appeared to be more related to insect biomass than predation risk and moonlight. Even though we found that activity levels were influenced by insect biomass, foraging opportunities for insectivorous bats can be ephemeral (Wright et al., 2021), and the regeneration of the matrix at the BDFFP will likely alter bat activity levels over time. Nonetheless, we strongly prioritize areas that have hotspots of nocturnal insect biomass as protected reserves for bat conservation, since changes in insect biomass may have cascading effects on bat activity (Froidevaux et al., 2021). Many birds and other vertebrates are linked to prey of insectivorous bats, so the conservation of these foraging habitats ensures the nocturnal trophic structure to be preserved (Arrizabalaga-Escudero et al., 2015). Otherwise, other characteristics such as vegetation structure, forest composition, weather conditions and roost quality can shape bat activity (Barros, Pessoa, & Rui, 2014; Meyer, Schwarz, & Fahr, 2004; Russo et al., 2016) in disturbed habitats, and they need to be considered in further investigations to better understand the local needs of bats.

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Supporting Information

Fear or food? Prey availability is more important than predation risk in determining insectivorous bat responses across a disturbed tropical forest landscape

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This supporting information contains:

Table S6. GLMM results examining bat activity in response to insect mass and predator treatments for each habitat.

Table S7. GLMM results examining bat activity in response to insect mass, moonlight and their interaction for each habitat.

Table S8. GLMM results examining bat activity in response to predator treatments, moonlight and their interaction for each habitat.

Table S9. Results of Kolmogorov-Smirnov 2-sample tests comparing the hourly activity between control nights and nights with predator sounds played back, broken down by forest type.

Figure S1. Location of the Biological Dynamics of Forest Fragments Project (BDFFP) and the distribution of sampling points in continuous forest, 10 ha fragments, and secondary forest. Continuous forest is represented in dark green and secondary forest (matrix) in light green. The map in the upper right corner shows the location of the study area (red point) in the Central Amazon.

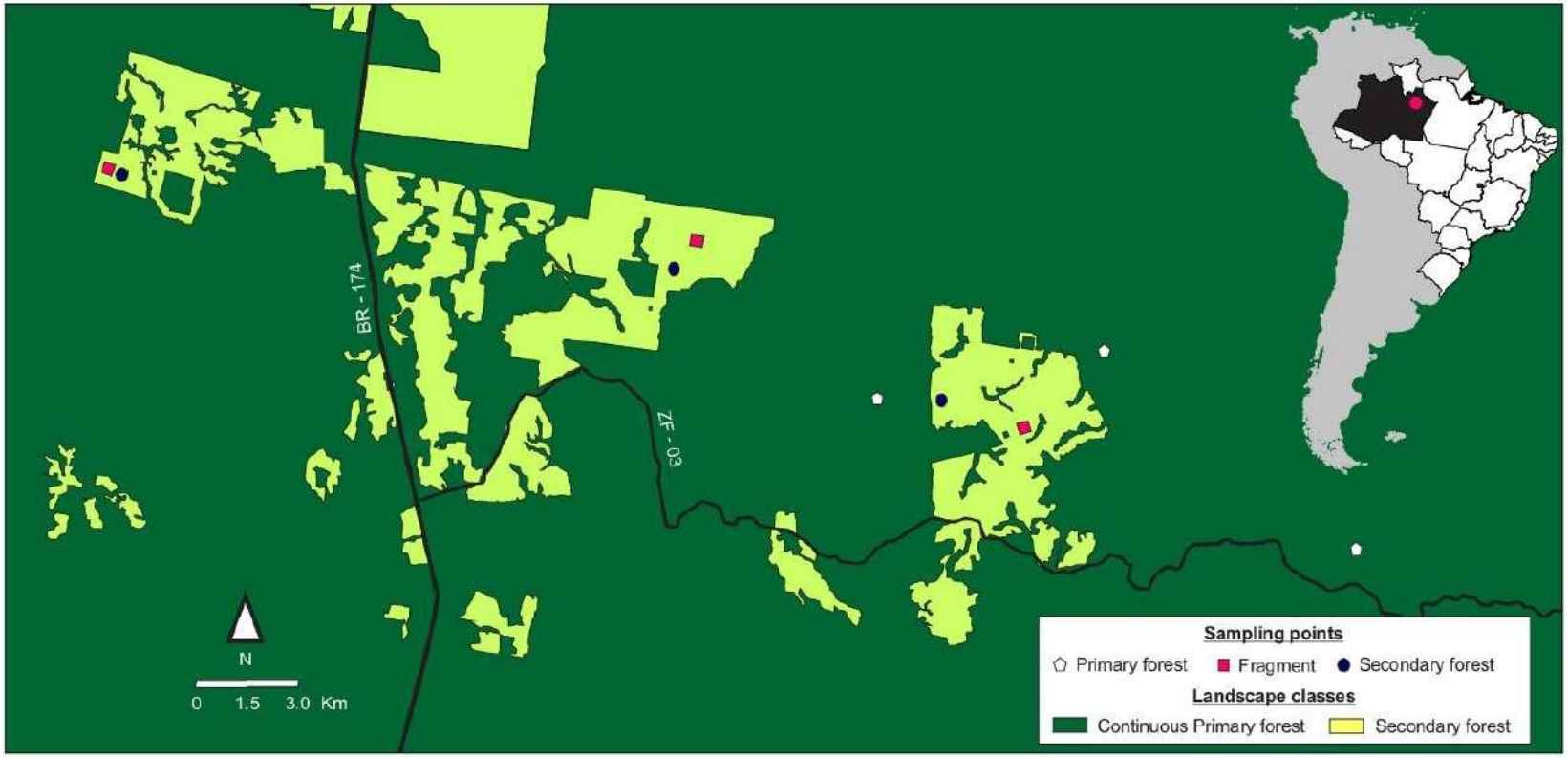

Figure S2. Schematic figure of the distribution of malaise traps in relation to the ultrasound recorder (Song Meter S2M+Bat). Each malaise trap was placed 20 meters away from the recorder and was installed in all focal habitat types (continuous forest, fragments and secondary forest).

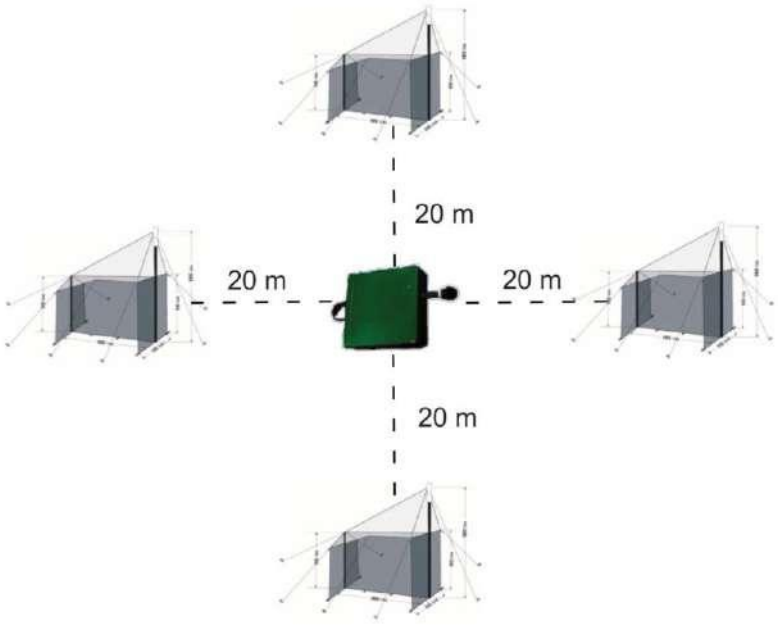

Figure S3. Comparison of the activity of each bat species between continuous forest (green boxes), fragments (yellow) and secondary forest (orange) at the BDFFP. Significant comparisons ($P \leq 0.05$) are indicated with '*'

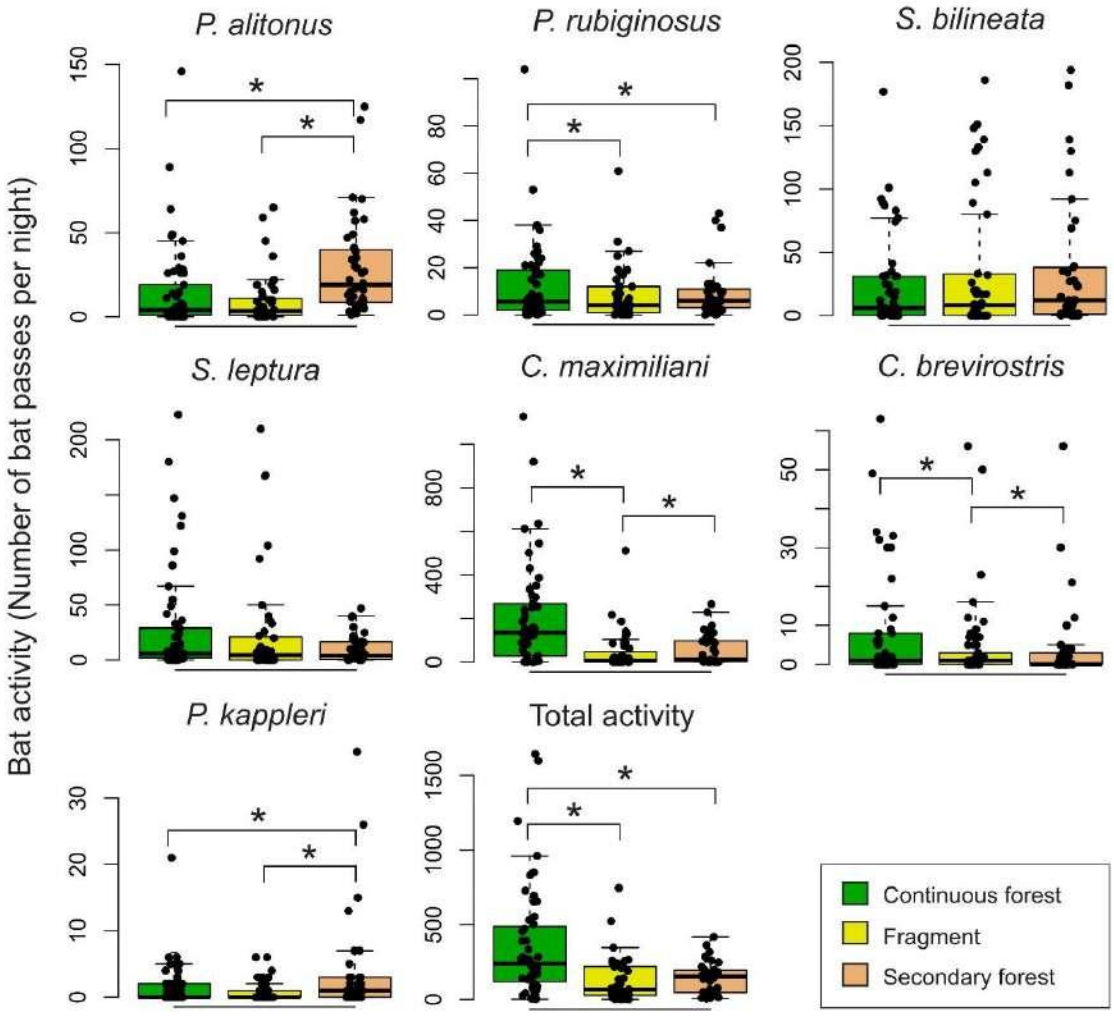

Table S1. Number of nights recorded per habitat type and per season across the Biological Dynamics of Forest Fragments Project camps. Each ultrasound recorder was programmed to register bat passes from 18:00-06:00 AM for two to four consecutive nights during the dry and rainy season of 2018-19.

	Continuous forest		Fragments		Secondary Forest		Total
Camps	wet	dry	wet	dry	wet	dry	
Km 41	16	8	-	-	-	-	24
Cabo Frio	6	7	-	-	6	7	26
Florestal	8	8	-	-	-	-	16
Dimona	-	-	9	5	9	8	31
Porto Alegre	-	-	6	8	3	8	25
Colosso	-	-	8	8	-	-	16
Total	30	23	23	21	18	23	138

Table S2. Number of nights recorded per habitat type and per treatment across the Biological Dynamics of Forest Fragments Project camps. Each ultrasound recorder was programmed to register bat passes from 18:00 - 06:00 for two to four consecutive nights during the dry and rainy season of 2018-19.

	Continuous forest	Fragments	Secondary Forest	Total
Control	19	17	15	51
Noise treatment	17	14	11	42
Predator treatment	17	13	15	45
Total	53	44	41	138

Table S3. Number of bat passes (mean ± SD), in total and broken down by habitat type, for the six aerial-insectivorous bat species studied. The total activity is the sum of activity of the six bat species studied.

Species	Total	Continuous forest	Fragments	Secondary forest
Pteronotus alitonus	2391 (17.45 ± 25.24)	793 (14.96 ± 26.1)	430 (9.77 ± 15.09)	1168 (29.2 ± 29.09)
Pteronotus rubiginosus	1386 (10.11 ± 13.96)	645 (12.4 ± 17.4)	365 (8.29 ± 11.39)	376 (9.17 ± 10.01)
Saccopteryx bilineata	4606 (33.62 ± 57.29)	1290 (24.33 ± 37.35)	1920 (44.65 ± 78.58)	1396 (34.04 ± 51.15)
Saccopteryx leptura	3387 (25.54 ± 48.68)	1531 (28.88 ± 49.44)	1061 (24.11 ± 48.52)	795 (19.39 ± 48.19)
Centronycteris maximiliani	14338 (106.2 ± 173.74)	10099 (201.98 ± 237.79)	1934 (43.95 ± 90.04)	2305 (56.21 ± 69.66)
Cormura brevirostris	1120 (8.17 ± 25.08)	647 (12.20 ± 36.93)	310 (7.2 ± 14.46)	163 (3.97 ± 10.3)
Peropteryx kappleri	260 (1.89 ± 4.65)	80 (1.5 ± 3.25)	41 (0.95 ± 1.57)	139 (3.39 ± 7.34)
Total activity	27127 (196.57 ± 203.93)	15085 (284.62 ± 263.47)	6061 (137.75 ± 167.8)	6342 (154.68 ± 120.62)

Table S4. Abundance and weight (mg) per insect order collected (Sum; mean ± SD) in total and broken down by habitat type. All orders is the sum of the insect orders studied.

	Insect order	Continuous forest	Fragments	Secondary Forest
Abundance	Diptera	8930 (168.4 ± 162.9)	5618 (127.6 ± 77.3)	5321 (129.7 ± 79.5)
	Coleoptera	270 (5.09 ± 3.68)	196 (4.45 ± 2.68)	275 (6.7 ± 5.33)
	Lepidoptera	529 (9.98 ± 7.73)	455 (10.34 ± 6.19)	419 (10.21 ± 6.97)
	Hymenoptera	1419 (26.77 ± 33.48)	1418 (32.22 ± 28.25)	1266 (30.87 ± 40.48)
	Orthoptera	115 (2.16 ± 1.98)	66 (1.5 ± 1.71)	66 (1.6 ± 2.5)
	Hemiptera	304 (5.73 ± 3.38)	232 (5.27 ± 3.16)	385 (9.39 ± 6.99)
	Blattaria	31 (0.58 ± 0.79)	23 (0.52 ± 0.66)	30 (0.73 ± 1.11)
	Isoptera	19 (0.35 ± 0.76)	7 (0.15 ± 0.42)	11 (0.26 ± 0.67)
	Trichoptera	67 (1.26 ± 3.09)	67 (1.52 ± 2.56)	81 (1.97 ± 2.86)
	All orders	11684 (220.4 ± 168.1)	8082 (183.6 ± 86.4)	7399 (180.4 ± 96.3)
Weight per individual	Diptera	0.03 (0.0006 ± 0.0008)	0.016 (0.0003 ± 0.0005)	0.02 (0.0004 ± 0.0006)
	Coleoptera	0.42 (0.007 ± 0.03)	0.34 (0.007 ± 0.03)	0.06 (0.001 ± 0.002)
	Lepidoptera	0.91 (0.01 ± 0.05)	0.45 (0.01 ± 0.02)	0.28 (0.007 ± 0.01)
	Hymenoptera	0.07 (0.001 ± 0.002)	0.09 (0.002 ± 0.003)	0.03 (0.0009 ± 0.001)
	Orthoptera	0.46 (0.008 ± 0.02)	0.63 (0.01 ± 0.07)	0.278 (0.006 ± 0.02)
	Hemiptera	0.06 (0.001 ± 0.003)	0.09 (0.002 ± 0.005)	0.02 (0.0006 ± 0.001)
	Blattaria	0.7 (0.01 ± 0.03)	1.05 (0.02 ± 0.12)	0.71 (0.01 ± 0.05)
	Isoptera	0.01 (0.0003 ± 0.001)	0.02 (0.0005 ± 0.003)	0.12 (0.0003 ± 0.001)
	Trichoptera	0.0003 (0.0000001 ± 0.00001	0.00004 (0.00001 ± 0.00002)	0.008 (0.0002 ± 0.001)
	All orders	1.78 (0.03 ± 0.05)	2.25 (0.05 ± 0.15)	1.16 (0.02 ± 0.06)

Table S5. Insect orders eaten by the focal bat species based on relevant literature sources. As *P. rubiginosus* and *P. alitonus* were only recently described (Pavan et al., 2018), the diet of these bats comes from *P. parnelli*.

	Diptera	Coleoptera	Hemiptera	Hymenoptera	Lepidoptera	Orthoptera	Blattodea	Isoptera	Tricoptera
Pteronotus rubiginosus and *P. alitonus*	5, 9, 11, 12, 13, 14, 16	2, 5, 7, 9, 11, 12, 13, 14, 16, 17	5, 12	5, 12, 14	5, 7, 9, 12, 13, 14, 16, 17	5, 8, 12, 14, 16	2, 17		
Centronycteris maximiliani		18			15				
Cormura brevirostris		2							
Saccopteryx bilineata	3, 17, 19	3, 17, 19			17, 19				
Saccopteryx leptura	1	1, 4, 11	1, 4	1, 4, 10	1, 4, 17		1, 4		
Peropteryx kappleri	6	3		6	6				6

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Table S6. Summary of Generalized Linear Mixed Models examining bat activity in response to insect mass and predator treatments (owl, noise and control) for each habitat. * P ≤ 0.05, ** P < 0.01 ***P < 0.001.

Continuous forest

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	1.83	3.14	2.18	6.56	3.26	6.15	3.37	6.40	5.02	9.59	2.30	3.02	-0.73	-0.66	5.23	12.89
Insect mass	1.85	**2.073***	2.03	**3.357****	1.75	**2.53***	-0.91	-0.84	-0.01	-0.01	4.91	**2.96****	0.10	0.47	0.22	0.40
Owl call	-0.20	-0.34	-0.16	-0.35	-0.37	-0.87	-1.22	-1.87	-0.12	-0.40	-0.29	-0.63	-0.18	-0.24	-0.23	-0.95
Noise	-0.16	-0.26	-0.02	-0.05	0.10	0.27	-1.38	**-2.12***	0.13	0.47	-0.89	-1.90	0.59	0.89	0.20	0.33

Fragment

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	1.11	2.15	1.15	2.70	3.16	4.82	3.08	2.44	3.00	3.29	0.45	0.46	0.18	0.46	4.26	7.20
Insect mass	-0.44	-0.57	-0.65	-0.89	0.00	0.00	2.49	1.49	1.00	1.52	1.54	1.38	-0.25	-0.59	-0.14	-1.00
Owl calling	-0.17	-0.27	-0.46	-0.78	-0.06	-0.13	-0.23	-0.22	-0.65	-1.33	0.35	0.65	-1.31	-1.75	-0.52	-1.01
Noise	0.08	0.13	0.30	0.55	0.43	0.98	-0.73	-0.79	-0.12	-0.28	1.05	2.13	-0.01	-0.02	0.07	0.14

Secondary forest

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	3.12	11.81	1.89	5.26	3.19	6.92	2.64	5.63	3.58	8.40	1.10	0.86	1.52	2.81	4.82	18.42
Insect mass	-0.83	**-2.02***	0.18	0.32	-0.02	-0.02	1.91	1.70	-0.63	-0.65	3.01	1.06	-0.98	-0.90	-0.77	**-2.88****
Owl calling	-0.56	-1.43	-0.12	-0.32	0.20	0.39	-0.20	-0.34	-0.04	-0.08	-0.02	-0.03	-1.63	**-2.51***	-0.33	-0.86
Noise	-0.66	-1.59	-0.20	-0.49	-0.10	-0.18	1.06	1.74	-0.09	-0.15	-0.61	-0.84	-1.40	**-2.07***	-0.48	-1.20

Table S7. Summary of Generalized Linear Mixed Models examining bat activity in response to insect mass, moonlight and their interaction for each habitat. Sampling night nested within research camp was specified as random effect. Bold values indicate a significant effect, '*' means P ≤ 0.05, '**' means P < 0.01 and '***' means P < 0.001.

Continuous forest

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	1.70	3.59	2.12	10.05	3.14	7.49	2.84	6.83	4.96	8.93	1.84	2.72	-0.23	-0.27	5.15	13.26
Insect mass	1.82	**2.06***	2.02	**3.43****	1.50	2.093*	0.86	1.02	0.44	0.64	4.32	**2.74****	1.28	1.14	-0.50	-0.80
Moonlight	0.21	0.53	0.32	1.14	-0.28	-0.99	0.05	0.14	-0.68	**-2.29***	0.26	0.65	-0.56	-1.24	-0.17	-0.74
Insect:Moon	0.27	0.27	0.22	0.30	-0.67	-0.80	-1.50	-1.53	-2.04	**-2.25***	2.94	1.14	-2.04	-1.33	0.80	1.23

Fragment

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	0.94	2.80	1.16	3.87	3.01	4.86	2.82	2.36	2.64	3.16	0.85	0.91	0.44	1.51	4.08	7.16
Insect mass	-0.56	-0.74	-0.48	-0.66	-0.18	-0.22	2.46	1.44	0.88	1.56	1.67	1.44	0.83	1.48	0.08	0.44
Moonlight	-0.63	**-1.93***	0.03	0.09	-0.49	-1.62	0.17	0.24	-0.12	-0.52	-0.25	-0.97	-0.04	-0.18	-0.27	-1.21
Insect:Moon	-0.32	-0.41	0.50	0.65	-0.30	-0.33	0.56	0.36	0.94	1.11	-2.02	-1.59	1.60	**2.48****	-0.27	-1.32

Secondary forest

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	2.84	13.83	1.87	9.09	3.19	8.66	3.23	7.42	3.57	7.18	-0.33	-0.17	0.91	1.60	5.00	36.01
Insect mass	-0.58	-1.27	0.51	0.93	-0.10	-0.12	2.62	**2.19***	-1.02	-0.59	-1.87	-0.30	-0.04	-0.04	-0.57	**-2.11***
Moonlight	0.03	0.11	0.02	0.10	0.29	0.96	0.64	1.34	0.80	1.71	-0.58	-0.57	0.47	1.11	0.29	1.87
Insect:Moon	-0.01	-0.01	-1.36	**-2.02***	0.79	0.85	1.83	1.49	1.43	0.90	-6.55	-1.16	1.48	1.00	0.66	1.85

Table S8. Summary of Generalized Linear Mixed Models examining bat activity in response to owl calling, noise treatment, moonlight and interaction between treatments and moonlight for each habitat. Sampling night nested within research camp was specified as random effect. Bold values indicate a significant effect, '*' means $P \leq 0.05$, '**' means $P < 0.01$ and '***' means $P < 0.001$.

Continuous forest

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	1.63	2.61	1.87	4.56	2.84	5.46	3.47	6.06	4.84	7.50	1.46	2.07	-0.80	-0.83	5.80	23.27
Owl call	-0.07	-0.12	-0.07	-0.14	-0.13	-0.29	-1.17	-1.64	-0.09	-0.22	-0.24	-0.48	-0.04	-0.06	-0.19	-0.80
Noise	-0.31	-0.48	-0.15	-0.29	0.10	0.25	-1.58	**-2.25***	0.17	0.41	-0.62	-1.25	0.79	1.29	-0.16	-0.70
Moonlight	0.77	1.27	0.25	0.52	-0.16	-0.50	0.72	1.11	-0.41	-1.23	-0.20	-0.54	-0.57	-1.12	-0.20	-0.98
Owl: Moonlight	-1.06	-1.43	0.00	0.01	-0.20	-0.46	-0.18	-0.22	-0.31	-0.67	0.45	0.81	0.26	0.38	-0.10	-0.42
Noise: Moonlight	-0.60	-0.84	0.20	0.36	0.07	0.18	-0.66	-0.80	0.58	1.41	-0.04	-0.09	0.77	1.11	0.07	0.32

Fragment

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	0.91	1.94	1.10	2.62	2.76	3.92	1.43	1.37	1.85	1.41	0.26	0.27	0.22	0.59	4.05	6.72
Owl calling	0.16	0.25	-0.20	-0.34	0.20	0.41	-0.23	-0.28	-0.97	-1.38	0.09	0.17	-1.34	-1.88	-0.29	-0.58
Noise threatment	0.22	0.35	0.46	0.84	0.64	1.30	0.10	0.12	-0.58	-0.86	0.86	1.68	-0.33	-0.57	0.28	0.56
Moonlight	-0.71	-1.70	-0.50	-1.33	-0.67	-1.91	0.18	0.31	-0.24	-0.52	0.40	0.87	0.20	0.60	-0.27	-0.80
Owl: Moonlight	0.78	1.26	1.02	1.79	0.66	1.56	-0.27	-0.34	0.16	0.24	-0.74	-1.29	0.01	0.02	0.24	0.49

Noise: Moonlight	-0.20	-0.33	0.33	0.63	0.20	0.44	-0.49	-0.64	-0.20	-0.30	-0.85	-1.55	-0.95	-1.74	-0.33	-0.69

Secondary forest

	P. alitonus		*P. rubiginosus*		*S. bilineata*		*S. leptura*		*C. maximiliani*		*C. brevirostris*		*P. kappleri*		Total activity	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	3.30	13.37	1.94	8.06	3.21	6.73	2.70	8.19	3.55	8.81	-0.79	-0.34	1.54	2.56	4.75	18.11
Owl calling	-0.36	-1.08	-0.22	-0.68	0.23	0.47	-0.47	-1.14	0.14	0.30	0.68	0.80	-1.42	**-2.56****	0.01	0.02
Noise threatment	-0.57	-1.55	-0.37	-1.02	-0.12	-0.23	-0.38	-0.75	0.01	0.01	-0.41	-0.41	-1.35	**-2.30***	-0.42	-1.05
Moonlight	-0.02	-0.06	-0.16	-0.59	0.12	0.33	0.10	0.33	0.32	0.84	-0.07	-0.10	0.18	0.47	0.23	0.80
Owl: Moonlight	-0.61	-1.72	0.40	1.12	-0.24	-0.48	-0.43	-1.08	-0.41	-0.81	-0.16	-0.19	-0.55	-0.88	-0.40	-1.00
Noise: Moonlight	0.46	1.35	1.19	**3.26****	0.24	0.47	0.71	1.49	0.63	1.20	1.56	1.60	0.79	1.27	0.52	1.33

Table S9. Results of Kolmogorov-Smirnov 2-sample tests comparing the distribution of hourly activity between control nights and nights with owl calls for each forest type (continuous forest, fragments and secondary forest). Bold values indicate $P \leq 0.05$.

Species	Continuous forest		Fragments		Secondary forest	
	D	P-value	D	P-value	D	P-value
Pteronotus rubiginosus	0.21	0.9	0.21	0.9	0.14	0.99
Pteronotus alitonus	0.21	0.9	0.14	0.99	0.42	0.15
Centronycteris maximiliani	0.21	0.9	0.28	0.63	0.28	0.61
Cormura brevirostris	0.14	0.99	0.28	0.61	0.07	1
Saccopteryx bilineata	0.35	0.33	0.14	0.99	0.42	0.15
Saccopteryx leptura	0.14	0.99	0.35	0.33	0.28	0.61
Peropteryx kappleri	0.21	0.9	0.05	0.06	0.42	0.15
Total activity	0.5	**0.050**	0.21	0.9	0.57	**0.021**

CONCLUSÕES

Atividade de morcegos insetívoros aéreos em resposta a luminosidade lunar, distúrbio do habitat, condições climáticas e interação presa-predador em florestas preservadas e alteradas da Amazônia Central

Os resultados obtidos nessa tese de doutorado demonstram a importância do monitoramento acústico para melhor compreensão da ecologia dos morcegos insetívoros aéreos da Amazônia. Baseado em um estudo conduzido na Reserva Ducke e uma revisão de levantamentos conduzidos em toda a Amazônia, observei no **primeiro capítulo** que o uso dos gravadores de ultrassom resulta na melhor amostragem dos morcegos insetívoros aéreos, não necessitando utilizar outro método complementar. Para estudos ecológicos e de distribuição ao longo de gradientes ecológicos das espécies de morcegos insetívoros aéreos, não recomendo usar dados de redes-de-neblina pois a distribuição pode ser

subestimada com a baixa amostragem em relação aos gravadores. No entanto, se o objetivo do estudo é amostrar a riqueza local de morcegos na Amazônia, eu recomendo o uso complementar dos gravadores de ultrassom junto com as redes-de-neblina.

Em florestas tropicais primárias, especialmente na estação chuvosa, a chuva é um fator imprevisível ao longo do tempo, enquanto a temperatura durante a noite é mais previsível e pode variar pouco. Já a luminosidade lunar segue uma variação cíclica e mais previsível, e no **segundo capítulo** apresentei que a luminosidade lunar e a temperatura possuem efeitos mais pronunciados na atividade dos morcegos insetívoros aéreos comparado com a chuva entre noites. O efeito lunar varia de espécie para espécie, e e observei que a maioria das espécies continuam respondendo a lua independente da chuva e temperatura. Apenas duas espécies (*S. bilineata* e *C. brevirostris*) responderam positivamente a temperatura e acreditamos que está relacionado com a atividade dos insetos e ao status reprodutivo dos morcegos nesse período. A chuva não interrompeu a atividade das espécies tanto entre noites como dentro de uma mesma noite, indicando que a chuva fraca não é um fator limitante para estes morcegos em uma floresta primária.

Em uma paisagem alterada, a relação dos morcegos insetívoros aéreos com a luminosidade lunar pode mudar devido a maior entrada de luminosidade do luar no interior dos fragmentos e da floresta em regeneração. No **terceiro capítulo**, eu avaliei que a luminosidade lunar modula pouco a atividade destes morcegos em paisagens alteradas. As espécies de morcegos insetívoros responderam mais ao distúrbio do habitat do que a luminosidade lunar, sendo que a maioria das espécies apresentaram baixa atividade nas florestas secundárias e algumas espécies são menos ativas nos fragmentos. Mesmo com 30 anos de regeneração, as florestas secundárias do PDBFF foram pouco atrativas para os morcegos. Em relação aos fragmentos, observei que seis espécies foram mais ativas nas noites escuras comparadas a noites claras. Isso sugere que o risco de predação provavelmente foi maior nas noites claras dos fragmentos, e que provavelmente os morcegos evitaram as bordas dos fragmentos nesse período de luminosidade lunar intensa. Quando comparei a atividade horária entre noites escuras e claras de cada habitat, observei que o efeito lunar é fraco e que os morcegos insetívoros mudam pouco a atividade dentro de uma mesma noite nos extremos de luminosidade lunar. Ainda, os resultados sugeriram, que *P. alitonus* e *P. rubiginosus* são as espécies mais sensíveis a luminosidade lunar, e que são capazes de mudar suas respostas de acordo com o habitat.

Foi visto que a atividade dos morcegos insetívoros era negativamente afetada pelo distúrbio do habitat no PDBFF, no entanto os mecanismos que explicavam esse efeito

ainda não estavam compreendidos. Como as presas e os predadores dos morcegos insetívoros aéreos podem modificar com o distúrbio do habitat também, no **quarto capítulo** quis entender como a interação presa-predador influenciada a atividade dos morcegos em cada habitat. Avaliei que o distúrbio do habitat continuava a ser um efeito negativo forte na atividade das espécies, no entanto encontrei mais espécies de morcegos com respostas negativas nos fragmentos do que na floresta secundária. Possivelmente o reisolamento dos fragmentos feito quatro anos atrás do período do monitormento intensificou as respostas com mais espécies diminuindo de atividade nos fragmentos. Além disso, indiquei que as espécies de morcegos responderam mais a massa de inseto do que o risco de predação e a luminosidade lunar tanto nas florestas preservadas como alteradas. A massa de insetos foi significativamente menor na floresta secundária do que na floresta preservada, e possivelmente a diminuição da atividade dos morcegos na floresta secundária está relacionada a esta menor disponibilidade de alimento. A luminosidade lunar continuou tendo um efeito fraco na atividade dos morcegos, mas observei que a luminosidade lunar é capaz de mudar a abundância de algumas ordens de insetos, assim é provável que quando as espécies respondem a luminosidade lunar elas estão seguindo a quantidade de alimento e não evitando o risco de predação em noites mais claras. De modo geral, florestas que contém insetos noturnos mais pesados podem ser consideradas “hotspots” de atividade dos morcegos insetívoros aéreos.