INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Sons, cidades e sauins: efeitos do ambiente acústico no comportamento de comunicação do Sauim-de-Coleira (*Saguinus bicolor*)

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Manaus – AM

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PÓS-GRADUAÇÃO EM 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.

Aos 03 dias do mês de Novembro do ano de 2021, às 09h00min, por videoconferência. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Thiago Bicudo Krempel Santana**, do Instituto Mamirauá, a Dra. **Marina Duarte**, da Pontifícia Universidade Católica de Minas Gerais - PUCMG, a Dra. **Cintia Cornelius Frische**, da Universidade Federal do Amazônas – UFAM, a Dra. **Valentina Zaffaroni Caorsi**, da Fundação Edmund Mach, e a Dra. **Bruna Bezerra**, da Universidade Federal de Pernambuco – UFPE, tendo como suplentes o Dr. Pedro Ivo Simões, da Universidade Federal de Pernambuco – UFPE e a Dra. Mariane Bosholn, da Universidade Federal de Roraima, sob a presidência do orientador, a fim de proceder a arguição pública do trabalho de **TESE DE DOUTORADO** da **TAINARA VENTURINI SOBROZA** , intitulado: **"SONS, CIDADES E SAUINS: EFEITOS DO AMBIENTE ACÚSTICO NO COMPORTAMENTO DE COMUNICAÇÃO DO SAUIM-DE-COLEIRA (SAGUINUS BICOLOR)"**, orientada pelo Dr. Adrian Paul Ashton Barnett, do Instituto Nacional de Pesquisas da Amazônia – INPA e Co-orientada pelos Drs. Marcelo Gordo e Dr. Jacob Charles Dunn.

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

☒ APROVADO (A) ☐ REPROVADO (A)

☒ 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. THIAGO BICUDO KREMPEL SANTANA ThiagoBicudoK.Santana
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DRA. BRUNA BEZERRA Bruna Bezerra
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Sinopse: Nesta tese investigou-se o efeito do ambiente acústico sobre diferentes aspectos do comportamento de comunicação do sauim-de-coleira (*Saguinus bicolor*). Foram analisados sons de sauins-de-coleira simpátricos ao congênere sauim-de-mãos-douradas (*Saguinus midas*) e inseridos em ambiente ruidoso da cidade de Manaus, onde os níveis de ruído foram estimados e mudanças comportamentais identificadas.

Palavras-chave: Deslocamento de caracteres; Competição; Poluição acústica; Paisagem acústica; Comportamento

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Já dizia Raul Seixas, "Sonho que se sonha só é só um sonho que se sonha só, mas sonho que se sonha junto é realidade". Sem dúvida, muitas cabeças criativas fizeram esta tese sair do plano das ideias e, portanto, registro aqui meus agradecimentos.

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“Mas o que salva a humanidade

é que não há quem cure a curiosidade”

Tom Zé

RESUMO

Sons produzidos por espécies animais frequentemente são moldados pelo ambiente físico e acústico em que estão inseridos. Tanto sons de origem biológica quanto antrópicas podem induzir modificações em sinais acústicos de determinadas espécies. O sauim-de-coleira (*Saguinus bicolor*) é um primata criticamente ameaçado, com uma pequena distribuição geográfica. Ao norte de sua distribuição ele interage com o congênere sauim-de-mãos-douradas (*Saguinus midas*), enquanto o centro de sua distribuição é localizado em parte na cidade de Manaus. Nesta tese foi investigado como a paisagem acústica afeta o comportamento de comunicação do sauim-de-coleira. Ao analisar os chamados (sons territoriais) de 15 grupos de *S. midas* e *S. bicolor* identificou-se que populações de sauim-de-coleira que estão em áreas de alopatria, não apresentam diferenças significativas em seus sons se comparados com sons de populações de áreas de simpatria com *S. midas*. Por outro lado, *S. midas* em áreas de simpatria e alopatria apresentaram um deslocamento dos caracteres acústicos no sentido de tornar os sons mais similares aos sons de sauins-de-coleira. A convergência observada pode ser atribuída ao comportamento em que o som é emitido, uma vez que sons parecidos seriam mais efetivos em informar o contexto de territorialidade em áreas de simpatria. O deslocamento observado ocorreu apenas em áreas de mata primária e não em áreas de mata secundária, o que pode estar relacionado à diferença de forças seletivas para propagação do som nesses ambientes. Nesta tese também foi testado o efeito de ruído da cidade de Manaus no comportamento de comunicação de nove grupos de sauins-de-coleira. De forma geral, os sauins não aumentaram ou diminuíram o número de vocalizações de chamado em resposta ao ruído, porém, a ocorrência (1= ocorreu; 0= não ocorreu) dessas vocalizações aumentou. É possível que diante do ruído intenso algum indivíduo do grupo emita apenas uma vocalização e coordene o grupo para um local mais quieto, mas não necessariamente vocaliza mais vezes para isso. O número de vocalizações emitidas foi mais influenciado por aspectos sociais, como o tamanho dos grupos e a distância da borda de seus territórios (um proxy para interação com grupos vizinhos). Além disso, não houve mudança no padrão temporal de emissão de vocalizações ao longo do dia em resposta ao ruído, porém em uma escala mais fina, como o das vocalizações de chamado, encontramos que os chamados tem o padrão de repetição de sílabas (número de sílabas/ duração) alterado sendo que os chamados ficam mais lentos. Quanto ao restante dos parâmetros acústicos (de duração, frequência mais baixa e frequência com maior energia), não houve relação significativa com o ruído. Outra estratégia provavelmente utilizada para contornar o ruído da cidade é que os sauins-de-coleira fazem mais marcações de cheiro em ambientes ruidosos. Apesar disso, eles não reduzem os comportamentos de acústicos, portanto, não há uma troca de modalidades de comunicação, mas provavelmente uma complementação da informação contida em sinais de diferentes canais sensoriais. Por fim, este estudo aponta que sons de origem antrópica (ruído), mas não a interação com sauins-de-mãos-douradas, afetam os padrões de comunicação do sauim-de-coleira.

Sounds, cities and “sauins”: the effect of environment acoustic on the communication behavior of the pied tamarin (*Saguinus bicolor*)

Abstract

Sounds produced by animal species are often shaped by physical and acoustic environments in which they occur. Both biological and anthropogenic sounds can induce changes in acoustic signals of certain species. The pied tamarin (*Saguinus bicolor*) is a Critically Endangered primate with a narrow geographic distribution. To the north of its distribution, the pied tamarin interacts with the congeneric species red-handed tamarin (*Saguinus midas*). In contrast, the core of its distribution lies partly within the city of Manaus. This thesis investigated how the acoustic environment affects the communication behaviour of the pied tamarin. Analysis of the long calls (territorial sounds) of 15 groups of *S. midas* and *S. bicolor* reveled that the pied tamarin populations in sympatric areas did not show significant differences in vocalization compared to those that are in alloparty. On the other hand, sound character displacement was evident when comparing vocalizations of *S. midas* from sympatry and allopatry. The shifts involved had the effect of making the emitted sounds more similar to those of pied tamarins. The observed convergence can be attributed to the behaviour associated with the emission of the sound is, since similar sounds would be more effective in conveying information relating to between-species vocal territorial boundary marking in sympatric areas. Furthermore, the observed displacement occurred only in areas of primary, and not in secondary forests, which may be related to the difference in selective forces for sound propagation. This thesis also reports the effects of Manaus city noise on the communication behaviour of nine groups of pied tamarins. Pied tamarins did not increase or decrease the abundance of long calls in response to noise. However, the occurrence (1= occurred; 0= did not occur) of these vocalizations increased. It is possible that, when faced with intense noise, some of the group individuals emit a single long call to coordinate the group to move to quieter areas but not necessarily vocalise more often to do so. The abundance of emitted vocalisations was more influenced by social aspects, such as group size and distance from their territorial boundaries (a proxy for the interaction with neighbouring groups). In addition, there was no shift in the temporal pattern of vocalization emissions across the day in response to noise. However, at a finer scale, that of a long call, we found that the syllable repetition rate (number of syllables/duration) of long calls altered with calls being slower in noisier areas. As for the other acoustic parameters (duration, lower frequency, and frequency with higher energy), there were no significant relation with noise. Another strategy used probably to circumvent city noise is that pied tamarins scent mark more often in noisy environments. Despite this, they do not reduce their vocal behaviour; therefore, there is no evidence for multimodal communication shift, but probably complementation of the information contained in signals from different sensory channels. In summary, this shows that sounds of anthropic origin (noise), but not interaction with the red-handed tamarin, affect pied tamarin communication patterns.

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Figure 4 Differences of acoustic features of pied and red-handed tamarins relative to effects of habitat type (red=primary forest and blue=secondary forest) based on the Generalized Linear Mixed Model (GLMM). Each point represents A) PC 2 and B) PC 3 scores of long calls (n=275); lines represent predicted means for each group of observations. Plots use partial residuals of the response variable and thus show the effect of a given variable while controlling for the effects of remaining predictors.

Capítulo 2

Figure 1. Home range of pied tamarin (*Saguinus bicolor*) groups (1-9) (small maps) followed in the urban area of Manaus, Brazil (larger map) from November 2018 to December 2019.

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INTRODUÇÃO GERAL

Sons produzidos por espécies animais frequentemente são moldados pelo ambiente físico e acústico em que estão inseridos. A presença de sons de origem biológica (biofonias), por exemplo, pode induzir modificações em sinais acústicos de determinadas espécies (Wilkins et al. 2013) sendo o deslocamento de caracteres um dos padrões mais comuns (Pfennig and Pfennig 2012). O deslocamento de caracteres, ou seja, diferenças exageradas dos traços de populações em simpatria, se comparada a populações em alopatria, pode gerar tanto padrões de divergência quanto convergência quando esses traços são relacionados à interferência comportamental entre espécies (Grether et al. 2017). Em espécies territoriais, por exemplo há casos em que as espécies divergem seus sons de modo a reconhecer e evitarem-se, ou convergem seus sons de modo que o contexto comportamental é reconhecido e o território mais efetivamente assegurado (Laiolo 2012, Kirschel et al. 2020).

Além dos sons de origem biológicas, sons de origem antropogênica (antropofonias/tecnofonias) podem induzir diversas mudanças comportamentais nas espécies. Esses sons frequentemente têm altas amplitudes e podem mascarar sons utilizados pelas espécies para comunicação (Brumm and Slabbekoorn 2005). Para contornar esse problema espécies utilizam estratégias para otimizar e garantir a propagação ou detecção de seus sons (Brumm and Slabbekoorn 2005). Uma das estratégias empregadas por alguns animais é alterar os parâmetros acústicos de seus sons como frequências, amplitude, taxa de repetição e duração de sílabas para evitar a sobreposição acústica com os ruídos ou aumentar a redundância de seus sinais (Slabbekoorn and Peet 2003, Brumm et al. 2004, Derryberry et al. 2020). Além disso, os animais também podem aumentar a atividade vocal diante de ruídos para melhorar as chances de que o sinal chegue até o receptor (Injaian et al. 2021). Por outro lado, algumas espécies não mudam o tempo despendido nas atividades de comunicação vocal, mas alteram os horários do dia em que vão vocalizar, para evitar momentos mais ruidosos (Gil et al. 2015). Algumas espécies de aves diurnas, por exemplo, podem passar a vocalizar durante a noite ou alterar seu ritmo circadiano de vocalizações para evitar a sobreposição com antropofonias (Fuller et al. 2007, Gil et al. 2015).

Outra possibilidade para contornar os efeitos da antropofonia seria complementar ou mudar completamente para outro canal de comunicação como a olfativa e\ou visual (Partan and Marler 1999, Partan et al. 2010). A comunicação multimodal (i.e. uso de mais de um canal de comunicação) pode ter uma série de funções, como chamar atenção do receptor ou agir como um sinal de “backup” em meio a ambientes ruidosos (Hebets 2005, Dunlop et al. 2010). Esses sinais provenientes de diferentes canais sensoriais podem trazer informações complementares que ajudariam no contexto de comunicação em ambientes ruidosos (Akçay and Beecher 2019). Apesar do número de pesquisas envolvendo comunicação multimodal ter crescido substancialmente nos últimos anos, pouco se sabe sobre deslocamentos multimodais (*multimodal shift*) relacionados a mudanças rápidas no ambiente, como a adição de ruídos antropogênicos (Partan 2017).

Primatas são predominantemente sociais, portanto, a comunicação é fundamental para a coordenação de suas atividades diárias. Porém, estudos que investiguem padrões de deslocamento de caracteres sonoros e efeito de antropofonias em primatas são insipientes (mas veja Duarte et al. 2011, 2018, Santos et al. 2017, Lineros et al. 2020). Os primatas neotropicais apresentam uma ampla gama de sinais acústicos, visuais e olfativos (Oliveira and Ades 2004, Santana et al. 2012, Snowdon and Ziegler 2020) o que lhes configura uma potencialidade para modificações multimodais em resposta a alterações ambientais. Ainda, primatas são altamente vulneráveis a perda e modificação do habitat (Estrada et al. 2018) e provavelmente também às suas consequências como o maior contato com ruído antropogênico ou alterações dos padrões de interação com outras espécies (Goosem 2007, Buchmann et al. 2013).

O sauim-de-coleira, *Saguinus bicolor* (Figura 1), é um calitriquídeo com uma pequena distribuição geográfica na Amazônia Central brasileira. Sua distribuição atual abrange um total de 7.500 km^2 de área de florestas de terra firme, boa parte inserida em áreas urbanas e peri-urbanas (Gordo et al. 2013, 2017). Em áreas rurais, geralmente limítrofes de sua distribuição, o sauim-de-coleira interage e possivelmente compete com o congênere sauim-de-mãos-douradas (*Saguinus midas*) que parece ter um comportamento mais flexível (Ayres et al. 1982, Röhe 2006, Gordo et al. 2017, Sobroza et al. 2021*a,b,c*). Por outro lado, na área *core* de sua distribuição, a urbanização vem restringido grupos de sauim-de-coleira à fragmentos isolados, o que tem ocasionado a perda de indivíduos da população através de atropelamentos e acidentes por eletrocução (Gordo et al., 2017, 2013). Tal cenário implica no status de criticamente ameaçado da espécie (Gordo et al. 2019).

Figura 1. Indivíduo de sauim-de-coleira (*Saguinus bicolor*) de um dos grupos acompanhados no presente estudo.

O Sauim-de-coleira é uma espécie social, portanto utiliza diferentes formas de comunicação para suas atividades comportamentais diárias. A espécie possui um repertório vocal com pelo menos doze tipos de vocalizações utilizadas em contextos de alarme, interações afiliativas, interações agressivas e alimentação (Sobroza et al. 2017). Além disso, o chamado, ou *long call*, é uma vocalização bastante importante para a espécie, já que funciona tanto para comunicação intra quanto intergrupo para coordenação de movimentação e territorialidade dos grupos respectivamente (Sobroza et al. 2017) (Figura 2). Essa vocalização geralmente é constituída por múltiplas sílabas com frequência entre 6 e 9 kHz (Sobroza et al. 2017). Não se conhece ao certo as capacidades auditivas do sauim-de-coleira ou qualquer outro sauim do gênero *Saguinus* spp. (Ramsier e Rauschecker 2017), mas outros callitriquídeos como o sagui-comum (*Callithrix jacchus*) tem limites auditivos que vão de 125 Hz a 36 kHz com pico de sensibilidade em torno de 7 kHz (Osmanski e Xiaoqin 2011). O sauim-de-coleira também possui glândulas especializadas na produção de substâncias químicas utilizadas na comunicação olfativa (Epple et al. 2002). Em um comportamento conhecido como “marcação-de-cheiro” (*scent marking*), tanto machos quanto fêmeas de sauins friccionam suas glândulas em substratos, com o intuito de depositar os compostos químicos no ambiente (Wormell e Feistner 1992). Em calitriquídeos, os compostos contidos nas glândulas são complexos e podem conter múltiplas informações (Snowdon e Ziegler 2020) incluindo informar sobre o status social e reprodutivo dos animais, bem como delimitar território (Lazaro-Perea et al. 1999, Roberts 2012, Poirier et al. 2021).

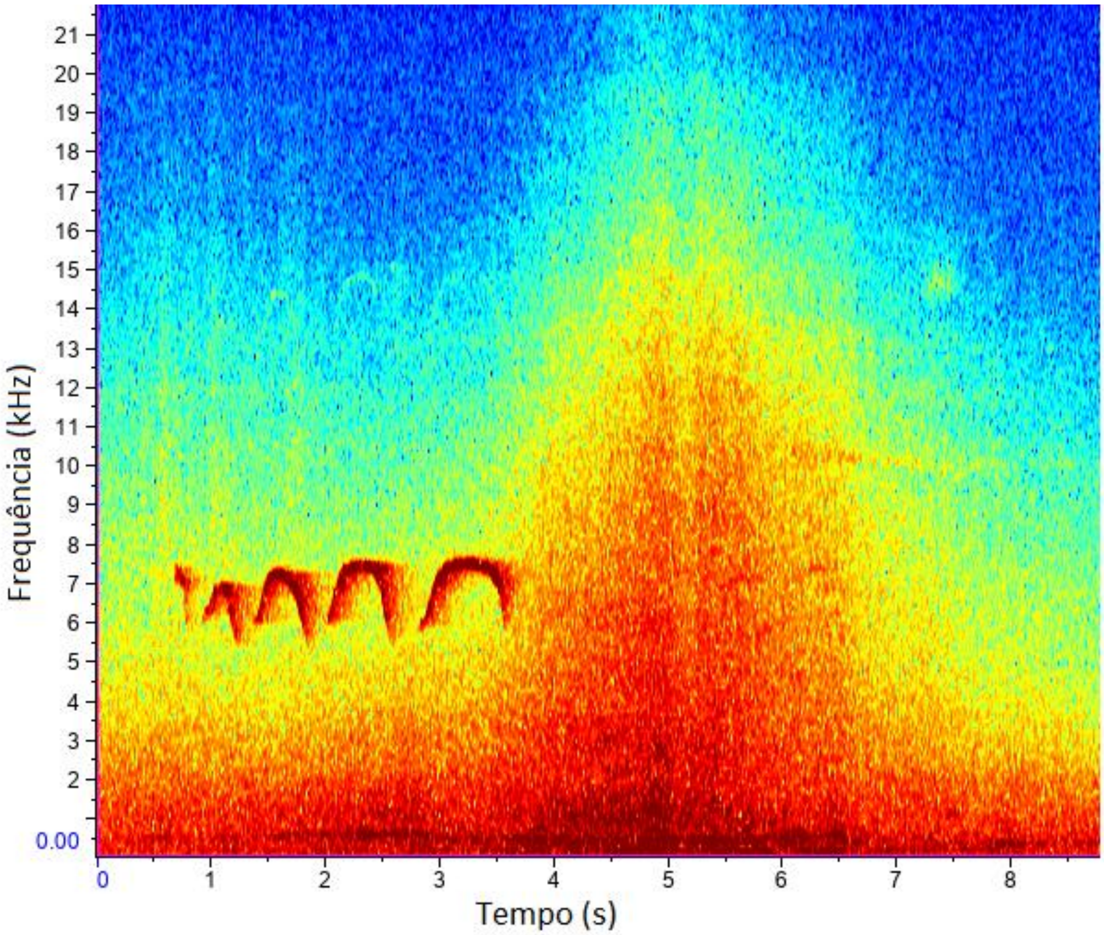

Figura 2. Espectrograma de uma vocalização de chamado de sauim-de-coleira (*Saguinus bicolor*) (entre 0,5 e 3,7 s) seguido de ruído típico de ambiente urbano (passagem de uma motocicleta) cobrindo uma ampla faixa de frequências do ambiente acústico.

A fim de reduzir o status de ameaça do sauim-de-coleira, um Plano de Ação Nacional (PAN) para a conservação do sauim-de-coleira foi criado e uma série de sugestões foram feitas para garantir a sobrevivência de populações viáveis da espécie. Uma das propostas do PAN inclui o desenvolvimento de novas pesquisas que elucidem como se dá a interação com o sauim-de-mãos-douradas (*Saguinus midas*), o que possivelmente perpassa pela comunicação interespecífica (Sobroza et al. 2017). Outra das sugestões do PAN foi a criação de corredores ecológicos urbanos e rurais que conectem diferentes fragmentos urbanos e grandes maciços florestais (Barr 2016). Depois de diversos esforços acadêmicos e articulações políticas, uma proposta de corredor ecológico foi aceita pela prefeitura da cidade de Manaus e hoje constitui a Área de Proteção Ambiental (APA) Sauim-de-Manaus (Manaus 2018). Mesmo que essa conexão física entre áreas garanta uma população viável numericamente, ainda não se sabe a real viabilidade da conexão quando considerado o comportamento da espécie, o que inclui a seguridade da comunicação efetiva entre grupos. Dentro desse contexto do corredor ecológico do sauim, torna-se importante avaliar se o ruído urbano altera os padrões de emissão das vocalizações de chamado, já que elas são importantes para a coordenação da movimentação dos grupos e a garantia dessa movimentação é justamente um dos objetivos da criação do corredor ecológico.

OBJETIVOS

O objetivo desse estudo é investigar como o ambiente acústico afeta o comportamento de comunicação do sauim-de-coleira (*Saguinus bicolor*). Para tanto, testaremos a hipótese de que diante de som de origem biológica (sauim-de-mãos douradas) e antrópicas (ruído) o sauim-de-coleira modifica seus comportamentos em termos de parâmetros espectro-temporais do som (i.e. frequências e durações), ou número de vocalizações e padrão temporal de emissão diária de sons. Também testaremos se o canal de comunicação olfativo serve como canal compensatório em áreas mais ruidosas.

Capítulo 1. Testar se os sauins-de-coleira e de mãos douradas apresentam sons com parâmetros acústicos convergentes em áreas de simpatria.

Capítulo 2. Testar se os sauins-de-coleira 1) aumentam sua atividade vocal em áreas ruidosas; 2) modificam seu padrão de atividade vocal diário em ambientes mais ruidosos; e 3) alteram os parâmetros físicos dos sons emitidos em ambientes mais ruidosos.

Capítulo 3. Testar se os sauins-de-coleira suprimem sua atividade vocal e realizam mais marcações odoríferas em ambientes ruidosos.

CAPÍTULO 1

Convergent character displacement in sympatric tamarin calls (*Saguinus* spp.)

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Convergent character displacement in sympatric tamarin calls (*Saguinus* spp.)

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Abstract

Character displacement, or a shift in traits where species co-occur, is one of the most common ecological patterns to result from interactions between closely related species. Usually, character displacement is associated to divergence in traits, though, they might be convergent, especially when used for aggressive interference between species. In the context of animal communication, territorial calls are predicted to converge in order to increase context recognition and decrease the costs of ecological interference competition. However, such signals might also be adapted to characteristics of the shared environment. In this study, we used data from 15 groups of two parapatric tamarins, *Saguinus midas* and *S. bicolor*, to test for similarities in long calls among sympatric and allopatric groups. We hypothesized that calls would converge in sympatric areas, as it would be mutually beneficial if both species recognize territorial contexts, but that convergence would depend on forest type due to acoustic adaptation. As predicted, long calls converged in sympatry, with *S. midas* shifting its calls towards *S. bicolor'*s acoustic pattern. However, this shift only occurred in primary forest. In sympatric areas, *S. midas* produced sounds with narrower bandwidths in primary than in secondary forest, consistent with optimization of sound propagation while both species produced longer calls in primary forests independently of geographic location (i.e. sympatry and allopatry). Our results suggest that both social and environmental pressures are important in shaping tamarin sounds. As their effects can interact, analyses which assume these ecological pressures act independently are likely to miss important patterns.

Keywords: character displacement, acoustic adaptation hypothesis, trait divergence, long call, Amazon *Saguinus midas*, *Saguinus bicolor*.

Introduction

Selection for reducing niche overlap often drives character displacement, i.e. exaggerated differences between species populations in sympatry relative to those in allopatry (Pfennig and Pfennig 2009; Weber and Strauss 2016; Grether et al. 2017; Stuart et al. 2017). Any morphological, ecological, physiological or behavioural trait can follow such a pattern, either through local adaptation or phenotypic plasticity (Brown and Wilson 1956; Grant 1972; Pfennig and Pfennig 2012; Allen et al. 2014; de Moura Bubadué et al. 2016). Traits related to reproductive interference (i.e. sexual interactions between species including courtship and other displays) are more likely to be divergent as pressure for mate recognition and hibridization avoidance is high (West-Eberhard 1983; Okamoto and Grether 2013).

Meanwhile, traits related to resource competition and aggressive interference can be convergent or divergent depending on the costs of the interaction between species, their relative abundance, and the evolutionary timeframe of interaction between the species (Grether et al. 2017, 2020; Germain et al. 2018). In fact, when analysing multiple traits, some pairs of species can have both convergent and divergent displacement pattens depending on trait function (Miller et al. 2019; Grether 2020). Regardless, evidence for both divergent and convergent character displacement often requires that traits are displaced in areas where species co-occur, independently of other factors (Schluter 2001; Wilkins et al. 2013).

Many species have calls that are used as a defensive response to territory intrusions from conspecifics and heterospecifics (McGregor 1993; Peiman and Robinson 2010; Christensen and Radford 2018). Such calls may be considered fitness-related traits, since behavioural interference can affect the rate of population growth (Chesson 2000; Grether et al. 2017, 2020). Therefore, selection can favour convergence of such fitness-related traits in sympatry to minimize competitive asymmetries, when competitors engage in direct conflicts (Germain et al. 2018). Accordingly, many bird species have convergently evolved sounds that facilitate the recognition of the competitive context (Laiolo 2012; Tobias et al. 2014; Kirschel et al. 2019). Also, some pairs of frogs species have convergent territory and release calls, which are traits related to aggressive or “neutral” contexts (Leary 2001; Freitas and Toledo 2020; Grether 2020; Grether et al. 2020).

Similar environmental characteristics can also promote trait convergence in ecological communities, independently of species interactions (Cardoso and Price 2010). Animal sounds, for instance, are often well-adapted for propagation in the habitats in which the emitting individuals occur (BradBury and Vehrencamp 1998). The acoustic adaptation hypothesis posits that in woody forests, high-pitched calls of short duration will degrade quickly, whereas calls that are long, low-pitched, and with narrower bandwidths, will propagate more effectively (Morton 1975; Dabelsteen et al. 1993; Holland et al. 1998). This hypothesis has been tested by numerous studies and corroborated by some (Ey and Fischer 2009), although little or no effect has been found by others (birds: Bicudo et al. 2016; felids: Peters and Peters 2010; marmots: Daniel and Blumstein 1998; howler monkeys: Holzmann and Areta 2020; and gorillas: Hedwig et al. 2015). Many of the studies that did not find support for the acoustic adaptation hypothesis have suggested that social aspects (mainly intraspecific) are also important in shaping acoustic features, although few have tested both factors together (Kirschel et al. 2019, 2020).

The acoustic adaptation hypothesis may be particularly important in understanding the impacts of land use change in human-modified landscapes, as it suggests that habitat modification creates differences in selection pressures for sound propagation optimization. For instance, the significant conversion of tropical forests into secondary forests over the last 50 years (Chazdon 2014; Crist et al. 2017) has increased environmental heterogeneity in these landscapes, with remaining forests varying widely in terms of plant species richness, composition, microclimate and above-ground biomass (Guariguata and Ostertag 2001; Montgomery and Chazdon 2001; Rozendaal et al. 2019). Old-growth (primary or pristine) forests, on the other hand, tend to be more complex in terms of canopy stratification, having larger and taller trunks and more closed canopy (Montgomery and Chazdon 2001), all of which could affect sound propagation.

Neotropical primates are a useful system for investigating the effects of habitat modification on acoustic adaptation and character displacement given that: 1) primates are generally thought to produce innate calls, and there is little evidence for plasticity in their vocalisations (Egnor and Hauser 2004; Snowdon 2017a); 2) vocal flexibility may be an important aspect in social signal convergence (Laiolo 2012); and 3) primates have suffered significant and ongoing modification of their natural tropical forests (Estrada et al. 2018). In Central Amazonia, the red-handed tamarin (*Saguinus midas*) and the pied tamarin (*S. bicolor*) are two closely related primates with parapatric distributions and a narrow sympatric zone (Röhe 2006; Rylands et al. 2016). While *S. midas* occurs over much of the northeastern portion of the Amazon region, *S. bicolor* has one of the smallest ranges of any primate in the world (~7500 km²) (Gordo et al. 2017), being restricted to the interfluvial region between the Amazon, Negro, and Urubu rivers, and much of its range lying within the largest urban area of Amazonia – the city of Manaus (Fig 1; Gordo et al. 2013). *S. bicolor* is currently classified as Critically Endangered by the International Union for the Conservation of Nature (IUCN) (Gordo et al. 2019a) due to fragmentation and habitat loss, as well as possible competition with *S. midas*, and is among the 25 most endangered primate species in the world (Gordo et al. 2019b). Additionally, over the last 30 years, the range of *S. bicolor* has decreased, while that of *S. midas* has not only increased, but it has encroached upon that of *S. bicolor* (Röhe 2006; Gordo et al. 2017). Pied and red-handed tamarins are considered potential competitors since both species have very similar body sizes (Hershkovitz 1977), niches (i.e. use of spaces with similar climate, relief, and vegetation types) (Röhe 2006), and they show asymmetrical territorial responses to each other’s calls in sympatric areas (Sobroza et al. 2021).

Tamarin long calls have an important territorial function (Snowdon 1989, 2017a, b), therefore we hypothesized that acoustic parameters of pied and red-handed tamarin long calls would converge in sympatry after accounting for potential acoustic adaptation to human-driven habitat heterogeneity (primary or secondary forest). Accordingly, the two species should converge in long call acoustic parameters in sympatry as it would be beneficial if both recognize the territorial context, in order to reduce the probability of interference competition. However, we expected frequency convergence to be stronger (or occur only) in primary forests, assuming that populations occurring in older and/or less disturbed forests are more likely to show acoustic adaptation, since frequency features are more prone to be constrained by morphology and genetics (Riede et al. 2005; Kitchen et al. 2019). In contrast, temporal parameters should converge in both forest types, as these traits tend to be more plastic (Janik and Slater 1997; Kitchen et al. 2019). We also predicted that, independently of geographic condition (i.e. sympatry and allopatry), both species would produce longer and lower-pitched calls in primary forests compared to secondary forests, as predicted by the acoustic adaptation hypothesis.

Material and methods

Study site

We carried out the study in the Brazilian Central Amazon, which included allopatric and sympatric areas in the ranges of *S. bicolor* and *S. midas* (Fig. 1). Topography in the region includes an alternation between drainage catchments and plateaus (ca. 60 – 120 m a.s.l.). Native vegetation cover is tropical humid *terra firme* forest in both primary and secondary stages of succession, with patches of white sand scrub forest (*campina* and *campinarana*) (Oliveira et al. 2008). Within this region, we chose four sites where the two primates were in allopatry, and four sites in sympatry, for a total of eight sites. We determined the geographic condition (sympatry or allopatry) of groups, based on evidence from previous studies (Ayres et al. 1982; Röhe 2006), data from long-term projects (Pied Tamarin Project and Tropical Ecology, Assessment and Monitoring Network), and co-occurrence modelling (Röhe 2006). Simultaneous observation of both species at the same site, mixed groups, or hybrids (at least those physically evident, e.g. Gordo et al. 2017) were never recorded during this study. All sampled areas contained forests with both primary and secondary growth, but forest cover was continuous in all cases. We categorized the location where the groups were detected as primary or secondary forest based on field observation of structural characteristics of the forest, and the presence of trees commonly found in Amazonian secondary forests such as *Cecropia* spp., *Vismia* spp. and *Bellucia* spp. (Mesquita et al. 2001).

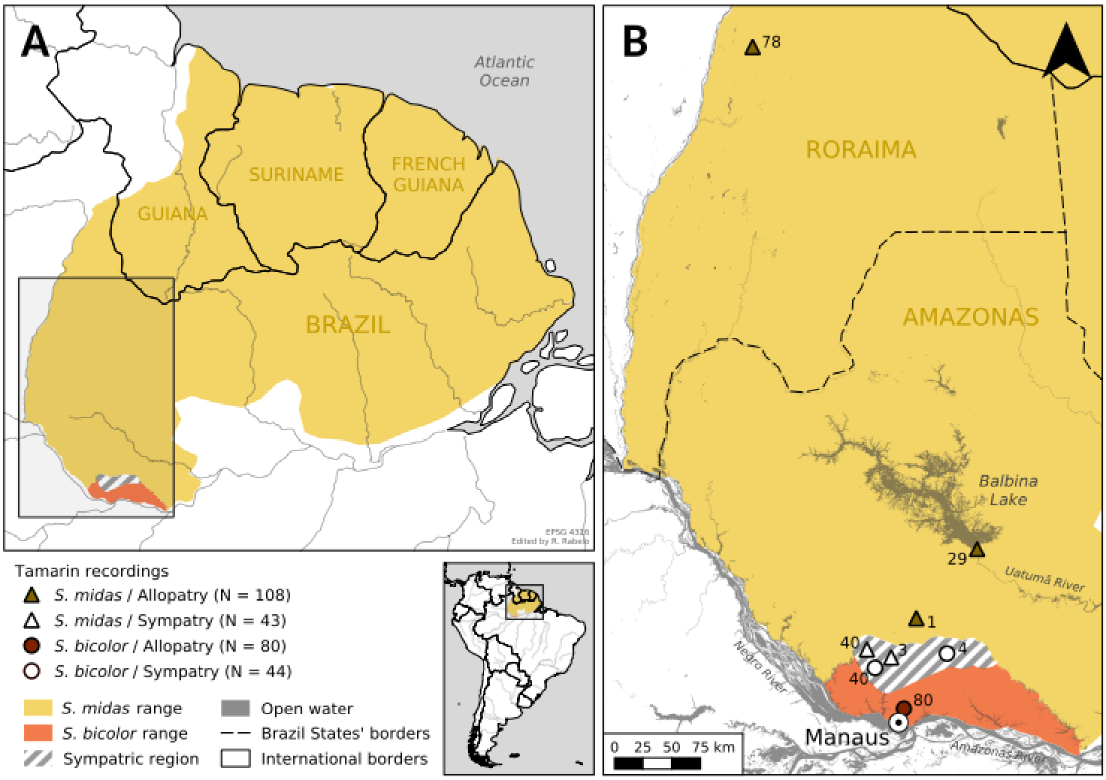

Fig. 1 Species distribution ranges and location of sampling sites. A) Map of *Saguinus midas* and *S. bicolor* ranges and putative sympatric area (based on Röhe 2006). B) Sampling sites of *S. bicolor* and *S. midas* in areas of sympatry and allopatry

Data collection

Fieldwork was carried out over nine field visits from June 2014 to February 2015 and consisted of recording tamarin long calls following standardized playback trials. A total of 275 calls were recorded in a sampling effort that comprised 690 km walked over 97 days distributed across the eight sites, with around nine consecutive sampling days at each site. Data collection was carried out between 06:30 and 16:30, the period when tamarins show the greatest activity (Day and Elwood 1999; Gordo et al. 2017). We used existing trails and roads to survey each area until we found a tamarin group. Once this occurred, we marked the encounter location with a Garmin GPS and characterized the group according to the number of adult individuals. Different sightings at a given site were considered as belonging to the same group when we consistently observed the same number of individuals and the distance between sightings did not exceed 400 m. Although the annual home range size of pied tamarins' group may reach up to 100 ha (Gordo et al. 2008), at smaller time scales such as nine days, they rarely exceed 40 ha (Day and Elwood 1999; Monteiro-Neto 2015, TVS and MG pers. obs.). Such small home range sizes are common among callitrichids (Garbino and Martins-Junior 2018), thus supporting the 400 m threshold used here. We considered as independent only those groups separated from each other by at least one km.

We recorded tamarin calls for 10 minutes immediately following playback trials (see details at Sobroza et al. 2021). This duration was chosen because the animals were not habituated to the observers and rarely stayed longer than this at the same place. During these trials, once we encountered a tamarin group, we broadcasted long calls from non-neighbouring pied or red-handed tamarins. The sounds used during the playbacks were composed of long calls from both allopatric and sympatric areas, and we presented these to the species in a balanced way across species and geographic condition (i.e. sympatric and allopatric areas). Individual groups were played recordings of long calls from both species (with a minimum interval of one hour) and their responses were recorded. We recorded tamarins with .wav files using a HTDZ HT-81 microphone (Frequency response: 1-16.0 kHz) attached to a Zoom H1 recorder (16-bit, 44 kHz). It was not possible to record data blindly because our study involved focal animals in the field.

Acoustics analysis

We analysed pied and red-handed tamarin long call recordings in Raven 1.4 (Cornell University Laboratory of Ornithology 2010). Long calls are either emitted as a territorial signal during intergroup encounters or as part of intragroup communication and cohesion (Sobroza et al. 2017). Since we recorded the calls after broadcasting playbacks, the behavioural context in which they were engaged was predominantly territorial. We defined a long call as a signal composed of variable number of syllables (not more than 8) with $\cap -$ shaped spectral signature and relatively constant interval between syllables (mean = 0.129 s, SD = 0.045 s). For each call, we analysed nine acoustic parameters (Table 1). We measured temporal parameters from oscillograms and spectral parameters of the first (fundamental) harmonic by analysing power spectra (Sobroza et al. 2017) built with the following configuration: DFT size = 1024 samples, overlap = 80%, window size = 20 ms, window type = *Blackmann*.

Data analysis

The analysed data consisted of acoustic parameters (Table 1) of individual long calls (*S. midas*, N = 151; *S. bicolor*, N = 124) clustered by tamarin group (N = 15) and sampling site (N = 8) (one to three groups per site). Since most acoustic parameters were correlated, data were ordinated using Principal Components Analysis (PCA). We applied the *broken stick* test (Peres-Neto et al. 2005) to separate meaningful information and choose how many PC axes to use in additional analysis. The test identified the first two axes as significantly informative, but we added the third axis, which contained most of the information on the temporal aspects of sound. The first axis captured 31.7 % of the data variability, and the second and third 27.9% and 14.59%, respectively. Therefore, we used PC1, PC2 and PC3 to summarize tamarin sounds and analysed each axis separately as a response variable in Generalized Linear Mixed-effects Models (GLMMs) with Gaussian distribution (Zuur et al. 2009). In all models we tested for the three-way interaction between predictors that were: species (two levels: *S. midas* or *S. bicolor*), geographic condition (two levels: sympatry or allopatry) and forest type (two levels: primary and secondary forests). Group and site identities were used as random factors to account for potential autocorrelation among calls from the same group and groups from the same site. All analyses were performed in R software version 4.0 (R Development Core Team 2020), using packages *nlme*, *vegan* and *vireg* (Dixon 2003; Breheny and Burchett 2017; Pinheiro et al. 2018).

Results

According to the PCA, the red-handed tamarin had a relatively wider acoustic niche, while the pied tamarin appeared to form a nested subgroup within the red-handed tamarin acoustic niche (Fig. 2, Table 2, 3). We found that bandwidth mainly contributed to PC1, frequency features to PC2, and duration and entropy features to PC3 (Table 2). We found that allopatric populations of *S.midas* and *S.bicolor* in primary forests were statistically different in their PC1 scores, with sounds of *S. midas* in allopatric/primary forested areas differing markedly from *S. midas* in sympatric/primary forested areas, and from *S. bicolor* in any condition (Table 4, Fig. 3). In sympatric areas, *S. midas* sounds were more similar to those of *S. bicolor* sounds. Thus, *S. midas* displaced towards convergence to *S. bicolor*'s acoustic niche, with higher PC1 scores (i.e. narrower bandwidths), but only in primary forest. In contrast, *S. bicolor* did not show such a pattern (Fig. 3, Table 4). Furthermore, forest type was the only significant predictor of PC2 and PC3 scores (Table 4). PC2 scores were slightly higher in secondary forests than in primary forests (i.e. lower dominant and higher frequencies), while PC3 scores were higher in primary than secondary forests (i.e. longer durations) (Fig. 4).

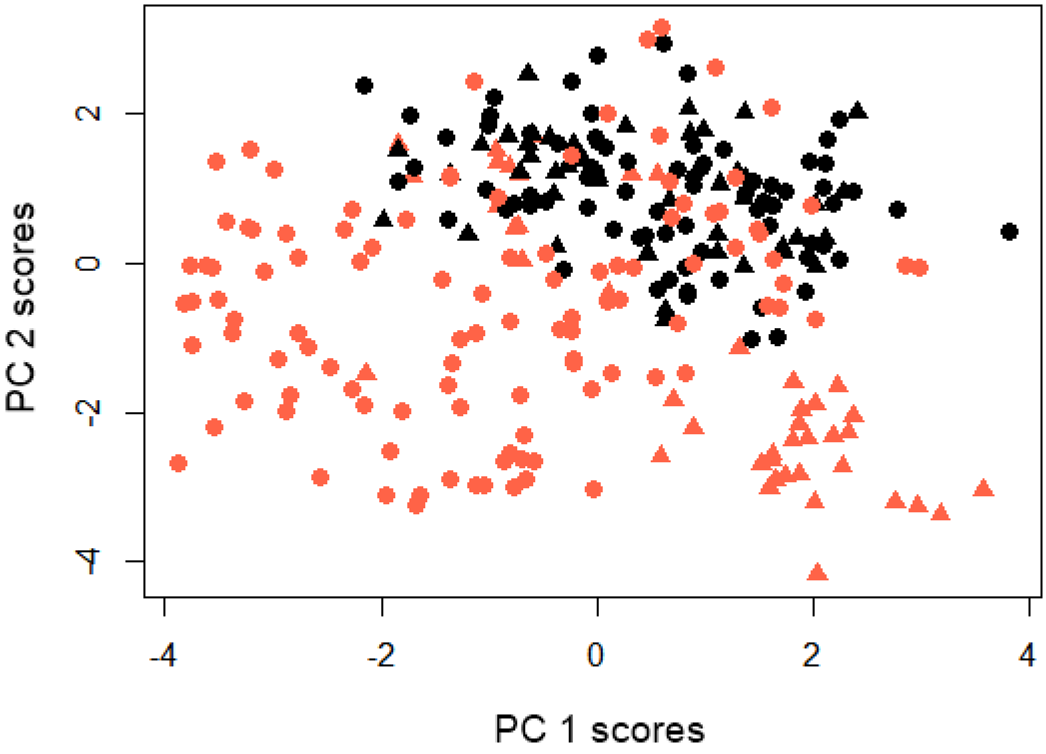

Fig. 2 Acoustic niche of pied and red-handed tamarins. The first two axes of a Principal Component Analysis (PCA) were used to represent long calls based on nine acoustic parameters. Each point in the graph represents a long call of pied tamarins (black symbols) (n=124) and red-handed tamarins (red symbols) (n=151) in sympatry (triangles) and allopatry (circles).

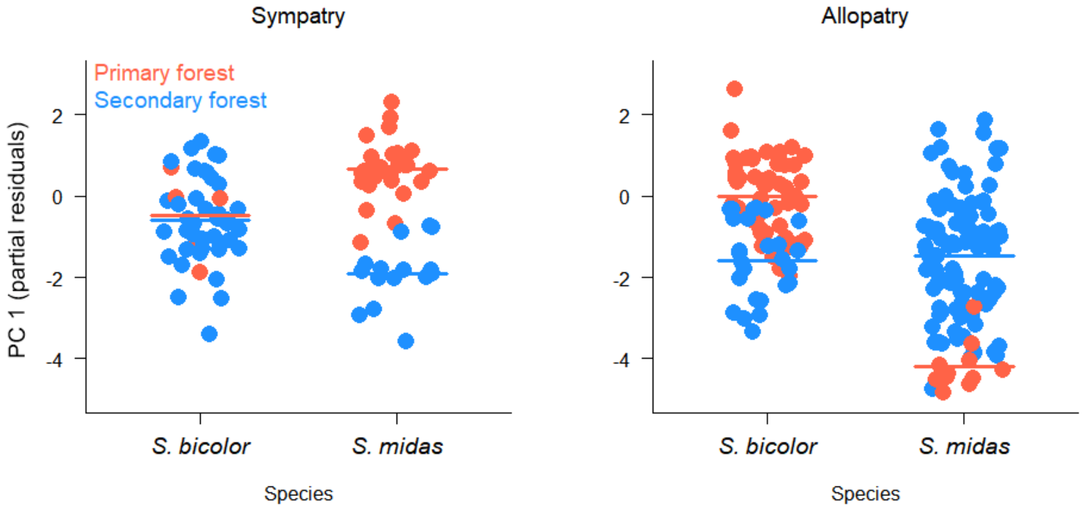

Fig. 3 Differences of acoustic features of pied and red-handed tamarins relative to interactive effects of habitat type (red=primary forest and blue=secondary forest), and geographic condition (allopatry and sympatry), based on the Generalized Linear Mixed Model (GLMM). Each point represents the PC1 score of a long call (n=275); lines represent predicted means for each group of observations. Plots use partial residuals of the response variable and thus show the effect of a given interaction while controlling for the effects of remaining predictors

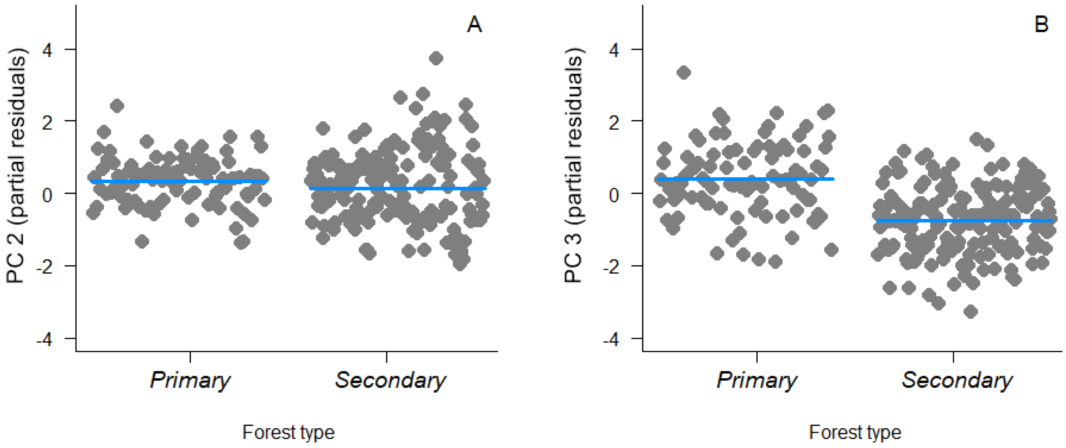

Fig. 4 Differences of acoustic features of pied and red-handed tamarins relative to effects of habitat type (red=primary forest and blue=secondary forest) based on the Generalized Linear Mixed Model (GLMM). Each point represents A) PC 2 and B) PC 3 scores of long calls (n=275); lines represent predicted means for each group of observations. Plots use partial residuals of the response variable and thus show the effect of a given variable while controlling for the effects of remaining predictors

Discussion

In this study, we tested whether selection would favour acoustic convergence of territorial calls between sympatric tamarin species, assuming this would facilitate context recognition when the risk of conflict is imminent (Laiolo 2012). Our results support this hypothesis, but only for one of the two species (*S. midas*) which showed convergent sounds in areas of sympatry. To the best of our knowledge, this is the first record of asymmetric convergent character displacement in primate social signals. Convergence in competitor recognition characters is expected when levels of interspecific aggressions are intermediate (Grether et al. 2020), whereas asymmetry in character displacement can be a result of differential success in resource holding between species (Grether et al. 2020). Indeed, *S. midas* appears to be vocally more territorial than *S. bicolor* during territory intrusion experiments (Sobroza et al. 2021*a*). Nevertheless, the fact that the shift we observed in *S. midas* calls only occurred in primary forests suggests that multiple and interacting selective forces might be shaping tamarin sounds, as observed in birds and rodents (Campbell et al. 2010; Tobias et al. 2014). Secondary forests contain more food resources for tamarins (Gordo 2012) therefore, competition would be reduced and character displacement less likely.

Many neotropical primates display long calls, which are sounds with multiple functions (Snowdon et al. 1983, Oliveira and Ades 2004). Both pied and red-handed tamarins make long calls that are used for intra- and intergroup communication to aid in group cohesion, movement coordination, and spacing during territorial contexts (Day and Elwood 1999; Snowdon 2017b; Sobroza et al. 2017). In other primates, long calls may also function in mate defence (Snowdon 1989, Wich and Nunn 2002), but we have no evidence supporting such hypothesis for the pied and red-handed tamarins, and only weak evidence for callitrichids, in general. For instance, if long calls also have a reproductive function, we would expect an asymmetric sex ratio during call emission and responses. In captive colonies of tamarins (*Saguinus oedipus*), results are inconsistent: sometimes males and sometimes females respond more to the opposite sex (McConnell and Snowdon 1986, Scott et al. 2006), while in the field, there are recordings of both males and females of *Saguinus* spp. emitting long calls during group encounters (Garber et al. 1993, Garber 1997). Therefore, while the territorial function of long calls is relatively well accepted and widespread among callitrichids, the hypothesis that it has a possible reproductive function (e.g. mate attraction or mate-guarding) remains poorly supported. When characters have multiple functions, directions of displacement may be less obvious (Grether et al. 2009), though, our results are under what is expected for territorial signals (Drury et al. 2020).

As expected, frequency shifts (see PC1 and PC2, Table 2) occurred mainly in primary forests, and were accompanied by shifts in temporal features (PC3, Table 2). Such acoustic changes are only partially following the acoustic adaptation hypothesis, which predicts that in areas with woody vegetation (e.g. primary forest), signals that are longer, lower-pitched and with a narrow bandwidth would be selected (Morton 1975). We found that *S. midas* presented narrower bandwidths in primary forests, in accordance with the acoustic adaptation hypothesis, but mainly in sympatric areas. Sounds with narrower bandwidths propagate better in closed habitats because the intensity is concentrated in specific frequency bands (Morton 1975). One possible explanation for the asymmetry in the displacement is that in areas where a possible competitor is present, *S. midas* emits sounds with narrower bandwidths, and higher amplitude to achieve longer distances, which could also imply an advantage during territorial defence (Ritschard et al. 2012). Even if the effect was not strong, both species produced slightly higher dominant frequencies in primary forests independently of geographic condition. Higher frequencies tend to degrade quickly in closed habitats. So, other strategies that enhance sound propagation may be used by tamarins such as site-selected perching, as occurs in other callithrichids (Sabatini and Ruiz-Miranda 2010). As predicted, both species presented longer calls in primary than in secondary forests, and our findings agree with the idea that frequency features are less plastic than temporal features (Janik and Slater 1997); the strongest effect on frequency features was more evident in primary forests. Amplitude and temporal features are more likely to be modulated in a shorter period through phenotypic plasticity, due to simpler mechanisms of production (Janik and Slater 1997). Plasticity provides an important mechanism that facilitates resource partitioning (Pfennig et al. 2006), but the extent to which the observed acoustic differences reflect plasticity vs. local adaptation is unclear.

Whatever mechanism is behind the acoustic variation that we observed, tamarin calls did not differ significantly between species in secondary forests. If long calls also play a role in sex recognition in pied and red-handed tamarins as is suggested for other callitrichids (Weiss et al. 2001, Miller et al. 2004), this may be related to recognition errors that could result in maladaptive mating and hybridization. During the last three decades, the city of Manaus has been growing rapidly, and new roads have been created in areas where the pied and the red-handed tamarins co-occur, thereby increasing the likelihood of hybridization

(McFarlane and Pemberton 2019). Hybridization often causes convergence in physical and behavioural aspects of parapatric species (Brockelman and Schilling 1984; Long et al. 1998; Secondi et al. 2003; Kitchen et al. 2019). As the physical appearance of *S. midas* and *S. bicolor* hybrids can be similar to parental species, or a mix of characteristics of parental species (Gordo et al. 2017), it is not possible to rule out the possibility that we recorded individuals that are phenotypically similar to one of the parental species but are hybrids. Many bird species tend to show convergent traits and intense interspecific territoriality when hybridization occurs in sympatric areas (Drury et al. 2020; Cowen et al. 2020), which may also be the case for pied and red-handed tamarins. There is no data available on the actual magnitude of gene flow between the red-handed and the pied tamarin hybrids. If the behavioural dominance of *S. midas* (Sobroza et al. 2021) also implies differences of gene flow, this could cause the absence of differentiation between species calls and asymmetrical character displacement (Yikweon 2008). Sound signal similarities can be the cause and consequence of hybridization, and the origin or extent to which both processes are occurring in this system remains to be tested.

Sobroza et al. (2021) found that red-handed tamarins responded with more territorial calls when listening to pied tamarin calls than to its own species in sympatric areas; while pied tamarins did not respond differently when listening to its species or the congener. Hence, despite the major pattern of convergence in acoustic features recorded here, such sounds must not be functionally interpreted equally by both species. Not only signal production can be susceptible to character displacement, but also its perception (Seddon and Tobias 2010), if pied and red-handed tamarins use different acoustic features as cues for species recognition or are different in terms of tuning capacity (e.g. Curé et al. 2012; Pasch et al. 2017), this may also be related to the asymmetries found in responses to the playback. Even closely related species can have asymmetrical cognitive and recognition capacities, and some species are capable of detecting specific signals with minimal variance (Seddon and Tobias 2010; Grether 2011; Pasch et al. 2017). It is worth mentioning that in the previous playback experiments Sobroza et al. (2021) did not present congeneric sounds from all possible combinations (i.e. sympatric\primary forest; sympatric\secondary forest; allopatric\primary forest, and allopatric\secondary areas), which may be a non-biological explanation related to their findings of asymmetrical responses.

Generally, character displacement and competitor recognition are phenomena involving many signal components, sensory modalities and genes (Ortiz-Barrientos et al.

2004; Grether 2011; Pureswaran et al. 2016). Therefore, even if acoustic signals are convergent and can be influenced by hybridization, species discrimination can still be possible if this function is retained in at least one signal. Many animals are flexible enough to quickly shift communication modalities when the signal transmission is impaired (*sensu* Partan 2017). Secondary forests usually have a more open canopy, fewer obstacles such as large trunks and lower relative humidity, features that might favour visual and chemical long-distance communication (Müller-Schwarze 2006; Sicsú et al. 2013). Thus, we cannot underestimate the recognition capacity of pied and red-handed tamarins in sympatric areas based only on our acoustic results.

It is instructive to consider the extent to which other factors not linked to forest structure could affect our results. For instance, some gregarious species have sounds that are group-specific (Crockford et al. 2004; Zaccaroni et al. 2012; Mumm and Knörnschild 2017). If tamarins also have sounds that act as group identifiers and the density of tamarins in secondary forest is higher, then acoustic diversity related to group identity may be increased. Indeed, red-handed tamarins are known to occur at higher densities in secondary forests than in primary forests (Lenz et al. 2014). Our statistical analysis included the identity of the groups as a random factor – therefore our results are unlikely to be related to group identity. Primary and secondary forests will also have a distinct composition of vocally-active species other than tamarins (e.g. birds, anurans and insects), such as, creating a local soundscape that might also drive acoustic divergence and sound diversification (Naugler and Ratcliffe 1994; Snowdon and de la Torre 2002; Gasc et al. 2013; Bicudo et al. 2016). Finally, secondary forests themselves can be highly variable in terms of acoustically-relevant structural properties (Wiley and Richards 1978; Montgomery and Chazdon 2001), though, it does not explain the observed displacement among sympatric and allopatric areas. Accounting for all these potential effects is logistically challenging, but our findings provide a template upon which more detailed hypotheses can be elaborated.

In summary, *S. midas* seems to have a wider acoustic niche and greater vocal flexibility than *S. bicolor*, responding both to the presence of the congener and forest type. In allopatric areas and primary forest, both species have a unique sound structure. Yet, this structure is consistent with the acoustic adaptation hypothesis, suggesting it optimizes sound propagation in these habitats. In contrast, in sympatric areas, the major pattern of variation in the acoustic features converge, consistent with selection for enhanced context recognition and, thus, reduce interference competition. Our results suggest that both social and physical constraints interact asymmetrically to shape the sound produced by parapatric tamarins. Thus, analyses that account for these pressures independently are likely to miss important patterns in ecological systems of co-occurring species.

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Tables

Table 1 Definitions of acoustic parameters measured in pied and red-handed tamarin long calls

Parameter	Definition
Low frequency (kHz)	Lowest frequency from the call
High frequency (kHz)	Highest frequency from the call
Dominant frequency (kHz)	Frequency with the highest energy
Bandwidth (kHz)	Difference between high frequency and low frequency of the long call
Bandwidth of the first syllal (kHz)	Difference between lower and upper frequency of the first syllable of the long call
Bandwidth of the last syllal (kHz)	Difference between lower and upper frequency of the last syllable of the long call
Average entropy (u)	Average of the entropy values in each spectrogram time slice of the vocalization
Delta time (s)	Time elapsed between initiation and ending of the vocalization
Number of syllables	Number of elements of one call

Table 2 Loadings and percent of variance explained by Principal Components extracted from *Saguinus bicolor* and *S. midas* long calls. Highest loadings ($r > 0.5$) are in bold

Acoustic feature	**PC1**	**PC2**	**PC3**
Low frequency (kHz)	0.39	-0.36	0.32
High frequency (kHz)	-0.22	**-0.54**	0.20
Dominant frequency (kHz)	0.10	**-0.51**	0.37
Bandwidth (kHz)	**-0.52**	-0.18	-0.11
Bandwidth of the first syllable (kHz)	-0.19	-0.18	-0.39
Bandwidth of the last syllable (kHz)	**-0.52**	-0.15	-0.11
Average entropy (u)	-0.01	0.14	0.34
Delta time (s)	-0.27	0.25	**0.51**
Number of syllables	-0.35	0.33	0.37
% Variance explained	31.73	27.25	14.59

Table 3 Summary measurements of the acoustic structure of the vocal signals emitted by pied and red-handed tamarins (*S. bicolor* and *S. midas*) in areas of sympatry and allopatry ($\bar{x}$ = mean; SD= standard deviation). Sounds were recorded in the municipalities of Manaus and Rio Preto da Eva, Amazonas State, and Caracaraí, Roraima State, Brazil

	Saguinus midas (allopatry)		*Saguinus midas* (sympatry)		*Saguinus bicolor* (allopatry)		*Saguinus bicolor* (sympatry)	
Parameter	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Low frequency (kHz)	6477.43	702.76	7848.77	1578.37	6818.52	985.98	6515.38	855.95
High frequency (kHz)	9885.61	1065.71	10112.91	816.52	8848.68	559.69	8688.01	575.33
Dominant frequency (kHz)	8942.23	1200.79	9567.96	963.44	8531.25	583.14	8314.09	635.73
Bandwidth 90% (kHz)	2499.48	1018.33	1725.10	666.25	1497.04	489.11	1578.83	558.31
Bandwidth of the first syllable (kHz)	1388.72	700.87	1366.60	506.28	948.55	800.41	1213.80	558.86
Bandwidth of the last syllable (kHz)	3124.73	1258.63	2146.49	869.06	1945.24	944.97	2057.07	811.97
Average entropy (u)	2.65	0.59	2.31	0.59	3.44	1.37	2.56	0.62
Delta time (s)	2.28	0.76	2.26	0.97	2.46	0.77	3.05	0.76
Number of syllables	4.41	1.44	3.23	1.17	4.14	1.16	4.35	0.86

Table 4 Summary of GLMMs results on the effect of geographic condition (sympatry or allopatry) and forest type (primary or secondary) on pied and red-handed tamarins (*S. bicolor* and *S. midas*) calls. Acoustic features were summarized in PC1, PC2 and PC3 ordinations (response variable). Sounds were recorded in the municipalities of Manaus, Rio Preto da Eva and Caracaraí, Amazonas State, Brazil, from 2014 to 2015 (N=275). *Results statistically significant (P<0.05)

Response variable	Parameter	Estimate	SE	T	P
PC1	Species	-4.19	0.87	-4.80	0.0086*
	Geographic condition	-0.47	0.91	-0.51	0.6332
	Forest type	-1.60	0.27	-5.82	<0.0001*
	Species* Geographic condition	5.32	1.30	4.06	0.0153*
	Geographic condition*Forest type	1.46	0.63	2.29	0.0224*
	Species* Forest type	4.32	0.67	6.42	<0.0001*
	Species* Geographic condition* Forest type	-6.75	1.27	-5.29	0.0018*
PC2	Species	-0.82	0.99	-0.82	0.4542
	Geographic condition	-1.04	1.01	-1.03	0.3600
	Forest type	0.65	0.22	2.84	0.0047*

	Species* Geographic condition	-1.77	1.51	-1.17	0.3064
	Geographic condition* Forest type	0.39	0.53	0.73	0.4631
	Species* Forest type	-0.84	0.61	-1.38	0.1676
	Species* Geographic condition* Forest type	2.56	1.40	1.82	0.1174
PC3	Species	-0.55	0.95	-0.58	0.59
	Geographic condition	-0.04	1.03	-0.04	0.96
	Forest type	-1.54	0.23	-6.68	<0.0001*
	Species* Geographic condition	-0.63	1.34	-0.47	0.66
	Geographic condition* Forest type	0.67	0.52	1.27	0.20
	Species* Forest type	0.41	0.46	0.88	0.37
	Species* Geographic condition* Forest type	0.58	0.76	0.76	0.47

CAPÍTULO 2

Sounds, Cities and “Sauins”: Vocal responses of a Neotropical primate to environmental noise across a human-modified landscape

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Sounds, Cities and “Sauins”: Vocal responses of a Neotropical primate to environmental noise across a human-modified landscape

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Abstract

Many species significantly depend on sounds to communicate with conspecifics. Human-generated noise is often loud, and may mask acoustic signals and disrupt behavioural aspects. To circumvent this, animals may use a variety of strategies, including change in vocal activity and modification of acoustic parameters of their sounds. Here, we tested whether wild pied tamarins (*Saguinus bicolor*) change their vocal behaviour in response to city noise. We predicted that, to increase signal redundancy, both occurrence and abundance of long calls would be increased in response to loud noises. We also expected that pied tamarins would shift their vocal activity across the day to avoid noisier periods. At the finer scale, we expected that temporal parameters of tamarin sound acoustic features (e.g. syllable repetition rate) will increase with amplitude noise. We collected information on the emission of long calls of nine wild pied tamarin groups in Manaus, Brazil. We recorded their calls and estimated environmental sound levels. We found that long call occurrence increased with sound levels, though the abundance of long calls did not. Instead, the abundance of long calls was related to hour of day and distance from the border of their home ranges, a proxy for proximity from neighbouring groups. As long calls are important for group cohesion during movement, it is possible that the tamarins emit one single call with an acoustic structure that would be optimal to achieve the receptor, such as those with lower syllable repetition rate, and move to quieter areas of their ranges. Neither long call occurrence nor abundance tracked noise levels, and so did not occur more commonly during quieter periods of the day, though long calls were more likely to be emitted early in the morning, independently of sound levels. Overall, the occurrence, abundance and structure of long calls emitted by urban pied tamarins seems to be governed by both environmental and social mechanisms, such as city noise and proximity from neighbouring groups.

Keywords: sound pollution, soundscape, Amazon, primates, noise

Introduction

Many species, especially those that are social, depend significantly on sound to communicate with conspecifics about such essential daily behaviours as foraging, defense against predators, territorial activities, group cohesion and mate attraction (BradBury and Vehrencamp 1998). All these activities can be disrupted in noisy environments due to sound masking and/or distraction of individuals (Brumm and Slabbekoorn 2005, Chan and Blumstein 2011, Huet des Aunay et al. 2017, Grabarczyk and Gill 2019, Buxton et al. 2020, Allen et al. 2021). With the increase of human population, anthropogenic noise has increased around the world, imposing new selective pressures on wildlife (Slabbekoorn et al. 2010, Sih et al. 2011, Swaddle et al. 2015). Responses to such disturbances have been reported across ecological scales, from individuals to populations, communities, and the dynamics of many ecosystems (Slabbekoorn and Halfwerk 2009, New et al. 2014, Hubert et al. 2018, Barbosa et al. 2020, Soudijn et al. 2020).

Collectively, animals use a variety of strategies to either avoid or reduce noise impacts, or to improve sound propagation and its perception (Brumm et al. 2004, Brumm and Slabbekoorn 2005). For instance, species may shift their temporal pattern of activity in response to noise. Species naturally have peaks of vocal activity through the day which may be related to optimal acoustic transmissibility (Waser and Brown 1984, Pérez-Granados and Schuchmann 2021), but also reflect species circadian rhythm and physiology (Thomas 1999, Koch et al. 2017). The peaks of such activities may also be timed to avoid overlapping with periods when other species emit sounds i.e. acoustic niche (Schneider et al. 2008), or, contrarily to overlap with conspecifics in choruses that increase signal audibility (Hall and Peters 2008, Torti et al. 2013, Ravignani et al. 2014). Temporal displacement of vocal activity is a possible response to anthropogenic noise, for instance, some birds may shift and increase their vocal activity from daytime to nighttime as noise increases (Fuller et al. 2007, Gil et al. 2017).

At a finer scale, species may change the parameters of their calls in all acoustic domains (i. e. spectral, temporal and amplitude). By doing this, they can potentially avoid masking, or the obscuring of signal spectral features, increase signal redundancy, as well as enhancing signal-to noise ratio and signal audibility (Slabbekoorn and Peet 2003, Brumm and Slabbekoorn 2005). Although debatable, it is suggested that some species may call at higher pitches to avoid spectral overlap with anthropogenic noise (Slabbekoorn and Peet 2003, Brumm and Bee 2016, Roca et al. 2016), that often (but not uniquely) has more energy in the lower frequencies (Gill et al. 2015, Alquezar and Macedo 2019, Caorsi et al. 2019). Such pattern may also be reversed when sound levels are extremely loud and animals became deaf or rely more on physical capacity of supposably better propagation of lower frequencies in dense habitats (Santos et al. 2017, Wolfenden et al. 2019). Some species also increase call duration and rate to increase the chances of detectability by the receptor (Brumm et al. 2004, Egnor et al. 2007, Picciulin et al. 2012, Santos et al. 2017). In contrast, other animals cease call activity to minimize energy expenditure (Kaiser et al. 2011, Duarte et al. 2019).

Responses to noise vary across taxa (Kunc & Schmidt, 2021) and studies with wild Neotropical primates are few (Duarte et al. 2011, 2018, Santos et al. 2017, Lineros et al. 2020). Primates can be specially susceptible to anthropogenic noise because of impacts of rapid and significant modification of their natural tropical forests (Estrada et al. 2018). Many primate species produce long calls, signals that have multiple functions such as group cohesion, territory, food resource and mate defense (Wich and Nunn 2002, Hopkins 2013, Snowdon 2017*b*). For example, in the southern brown howler monkeys (*Alouatta guariba*) whose vocalizations play an important role in intergroup competition, natural emission of long calls tends to be spatially structured with animals roaring more often at territory boundaries to actively defend their territories (Da Cunha and Jalles-Filho 2007). Nevertheless, the use of long calls also seems to be important during competitive events, as the increase in the abundance of long calls may well provide information on numerical odds, since they tend to be proportional to group size (Kitchen 2004). Emitting long calls may significantly impact the overall time budget of highly social animals and understanding how they may change due to sound pollution is important to allow a bigger picture to be drawn concerning how a changing selective regime may shape primate social systems and evolution.

The pied tamarins (*Saguinus bicolor),* or "*sauins*" as they are locally known, are central Brazilian Amazonian callitrichids with a highly-restricted geographic range. Its range encompasses a total of 7,500 km², much of which is in urban and peri-urban areas of Manaus (Gordo et al. 2013, 2017). Urbanization is confining groups to isolated forest fragments. In consequence, there is an intense loss of individuals to roadkill, electrocution, and attacks by domestic animals (Gordo et al. 2013, Farias et al. 2015). As the species is Critically Endangered (Gordo et al. 2019), a National Plan of Action for the pied tamarin conservation was created (Barr 2016). A key action to secure viable populations of pied tamarins is to create ecological corridors that connect otherwise isolated urban forest fragments and reserves (Barr 2016). Even if this enhanced connectivity results in populations viable in term of numbers of individuals, their viability in terms of behaviour is still unknown, since this must include continuance of those inter and intragroup communications that result in long-term population maintenance.

The objective of this study was to evaluate whether pied tamarins alter their communication behaviour in response to city noise levels. We hypothesized that both occurrence and abundance of long calls would increase in response to such noise so animals signal content would become redundant and more likely to achieve the receptor (Brumm and Slater 2006, Deoniziak and Osiejuk 2016). We also expected that pied tamarin vocal activity would interact with augmented noise levels and will shift their vocal activity throughout the day to avoid noisiest periods. At a finer scale, we also predicted that temporal parameters of the acoustic features of the tamarin vocalisations (duration, and syllable repetition rate) will increase with noise amplitude, while the dominant and lower frequencies will remain similar, as pied tamarin long calls are already high-pitched ranging from 6 to 9 kHz (Sobroza et al. 2017) and frequency features are less likely than temporal features to be modulated in primates (Janik and Slater 1997).

Material and methods

Study area

The study was conducted in the central Brazilian Amazon, in the city of Manaus, Amazonas state, Brazil (Figure1). Acordinly to the nearest station of the Brazilian Institute for Meteorology (INMET- station A101), the average temperature during the sampling period was 27.7 Cº (sd= 2.6) and relative air humidity ~73,27 % (sd=13.94). Study sites comprised five forest fragments ranging from 24 to ~700 ha managed by different social sectors (private, municipal, state, and federal - including one military area). The fragments have been isolated from between 30 to 68 years (Gontijo 2008), and each is surrounded by a paved road system. The most common anthropogenic source of noise in all areas is road traffic, though there is also air traffic, park visitors, the talking and screaming of children and university students, songs, and gunshots from military activities. In a non-forested area of Manaus noise on average varies from 64 to 86 dB and estimates correlate both day and night (Bessa, Lima & Silva-Júnior et al. 2017). Nine groups of pied tamarins were followed in five forest fragments of the city of Manaus and one continuous forested area in the peripheral area of the city (Table 1) (Figure 1).

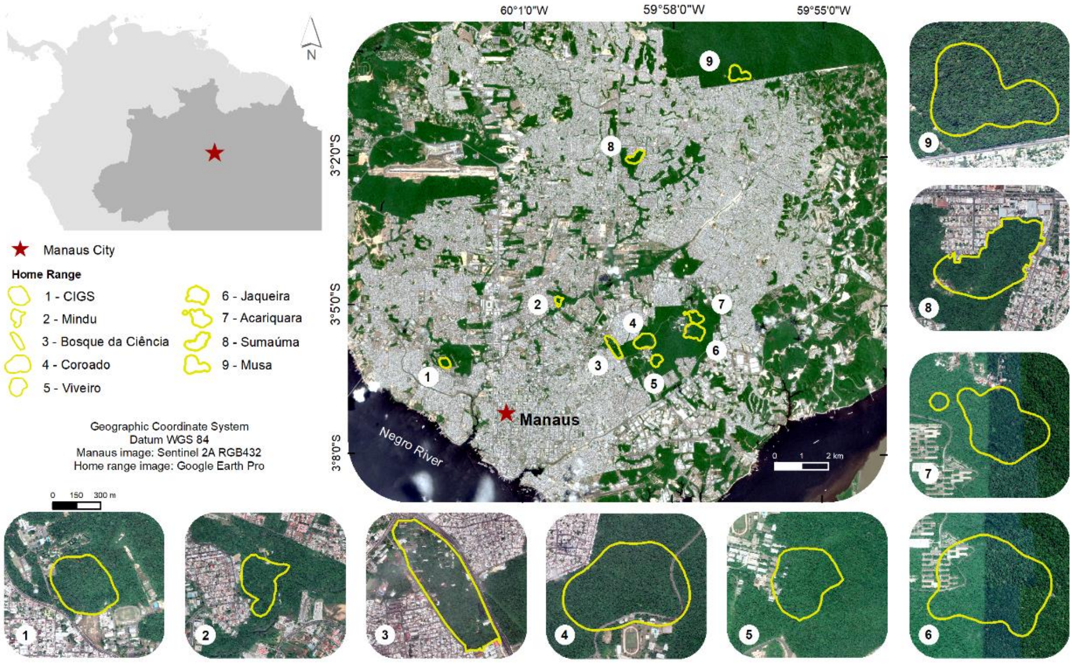

Figure 1. Home range of pied tamarin (*Saguinus bicolor*) groups (1-9) (small maps) followed in the urban area of Manaus, Brazil (larger map) from November 2018 to December 2019.

Subjects and capture proceedings

Data collection took place between November of 2018 and mid-December, 2019. We followed nine pied tamarin groups (Table 1) seven of them using radio-telemetry to facilitate location, and monitoring. To capture the groups we habituated the pied tamarins to bait (banana), then, to the traps and, capture them after one to four months of habituation. We used bated Tomahawk TH105 (10x10x40cm) live traps placed ~1.60 m above the ground. Once the animals were captured we sedated them with 0.1 ml of Ketamine® anesthetic and attached a SOM 2380 transitter (Wildlife Materials) preferably to the alpha female of each group. This protocol has been widely used by the long-term project Pied Tamarin Project (UFAM) (Lagroteria et al. 2017). The attached transmitter emited specific frequencies (164.00-164.99 MHz) that were detected with a two (H) or three (Yagi) element antenna and an ATS® receptor (164-168 MHz). Two of the collars were removed after recapture, another dropped from the target animal spontaneously. For two others we were unsuccessful in recapturing the animal carrying the radio. The planned final sample collections were interrupted by the COVID pandemic.

Data collection

A researcher and a field assistant followed each group for 10 days from ~6:30-17:00, the period of pied tamarins major activity (Egler, 1986). In the field we collected data during five-minute behavioral bouts followed by five-minute intervals (Martin & Bateson, 1993). In the five-min behavioral bout we wrote down the number of long calls (herein called abundance of long calls) emitted by all pied tamarins in the group. We also recorded the location of the group with a GPS (GPSMap 78s) and estimated noise through the day while following the tamarins.

We estimated noise via equivalent continuous sound levels (Leq; time-averaged level of sound) (dB) using a C-weighting curve. Leq was estimated based on sound pressures estimated every second during 1-minute readings. The sound level meter CEL-246 (Casela Solutions) was calibrated and manually supported 1.10 m above the ground directed to the tamarin group. The average noise in all sampled areas was 59.19 dB (sd=5.9) with a standart variation of about 5.54 dB through the day (Figure 2) ranging from a minimum of 40.2 dB to a maximum of 84.8 dB.

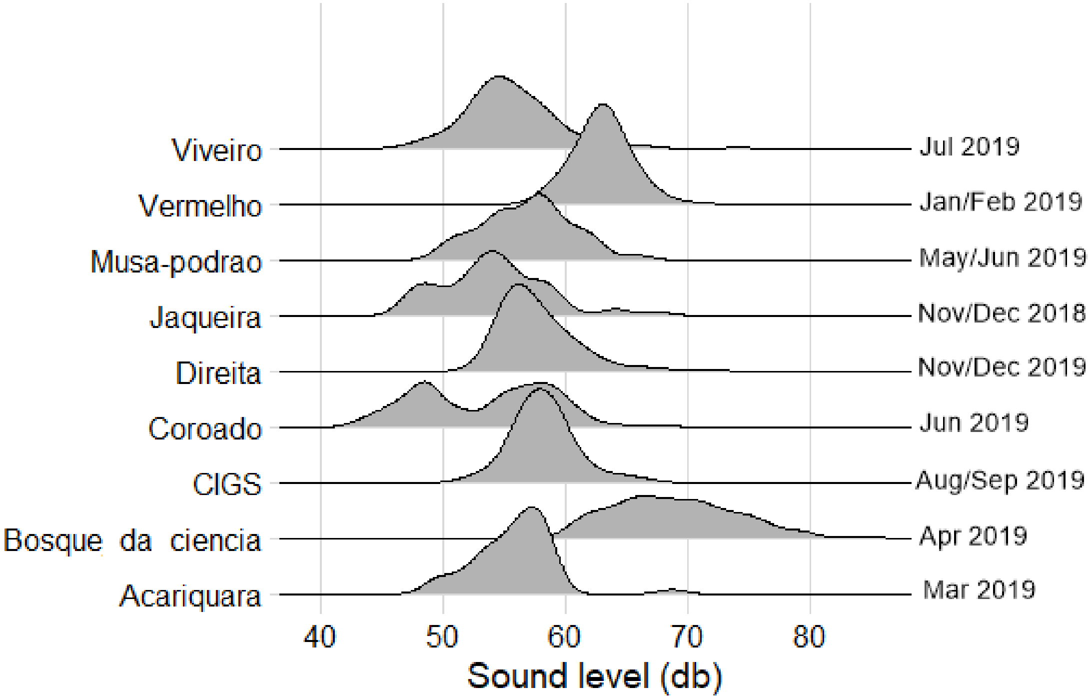

Figure 2. Distribution of city noise levels (dB) in the respective environment and sampling period for each of the nine pied tamarin (*Saguinus bicolor*) groups followed in the urban area of Manaus, Brazil. Sound levels estimated during 1-minute in each behavioural bout.

After 10 days of field data collection, in the lab, we estimated the group home ranges (HR) boundaries using all the GPS points recorded. To do so, we used a kernel density estimator with a reference smooth parameter for all groups (Worton 1989). We defined as home range the area where 95% of the points were found (Anderson 1982). To calculate HR limits, we used the *adehabitatHR* package (Calenge 2006) in R (R Development Core Team 2020). To estimate the distances from each point to the polygon of HR boundaries we used the *Near* function from ArcMap 10.5.

Acoustic analysis

We analysed the long calls using Raven 1.6 (Bioacoustics 2019) and defined a long call as a signal composed of variable number of syllables with ∩ − shaped spectral signature and relatively constant interval between syllables (Sobroza et al. 2021*b*). For each call, we analysed four acoustic parameters: dominant frequency, lower frequency, duration and syllable repetition rate (number of syllables divided by call duration). In Raven, we estimated the parameters from the first (fundamental) harmonic using the power spectra tool to select only high-quality sounds and avoid biased estimates (Zollinger et al. 2012) using a -20 dB cut relative to the frequency with maximum energy (Podos 1997). Spectrograms were built with the following configuration: DFT size = 1024 samples, overlap = 80%, window size = 20 ms, window type = *Blackmann*.

Statistical analysis

To test if the occurrence of tamarin long calls was related to environmental and spatiotemporal aspects, we used Generalised Linear Mixed Models (GLMM) (Zuur et al. 2009). In the first analysis, each behavioural bout was the sampling unit, and the occurrence of long calls was the response variable (1= occurred; 0= did not occur) (N=953), assuming binomial errors and logit link. We used as predictors: a) 1-minute sound level estimate b) hour of the day. Because the occurrence of long calls may be related to other social aspects regarding intra- and inter-group communication, we also included: c) group size and; d) distance from the border of their home ranges as predictors. We included both fragment and group identity as random factors to control for non-independence between observations of the same group and any fragment-level variation. Initially, we included an interaction factor between sound level and hour of the day to evaluate whether tamarins shift their vocal activity through the day in response to sound level. Once this was shown to be statistically non-significant (p>0.05), we removed the interacting term and reran the model.

To test if the previous predictors were related to the abundance of long calls, we used the behavioural bout as the sampling unit, using only those that contained at least one long call (N=472). We also used: a) 1-minute sound level estimate b) hour of the day; c) group size and; d) distance from the border of their home ranges as predictors. Fragment and group identity were used as random factors. As before, we initially included an interaction factor between sound level and hour of the day to evaluate whether tamarins shift their vocal activity through the day. This interacting term was statistically non-significant ($p>0.05$), thus we removed it and reran the model (Supplementary material).

Finally, to evaluate if acoustic features of pied tamarin long calls change in response to sound levels, we used a GLMM for each acoustic parameter. In this case, each long call was used as sampling unity (N=520), and the response variables were: 1) dominant frequency, 2) lower frequency, 3) duration and 4) syllable repetition rate. For all models we used the 1-minute sound level as predictor; and fragment and group identity as random factors. We used normal distributions with identity links for all models related to acoustic features, except for "syllable repetition rate" which we used the Gamma distribution with log link.

All analyses were made using R version 3.5 (R Core Team 2018), using the *lme4* and *visreg* packages (Bates et al. 2015, Breheny and Burchett 2017).

Ethical approval

The research was approved by the Ethical Committee of the Instituto Nacional de Pesquisas da Amazônia (SEI.01280.00900\2018-58). SISBIO/MMA (Ministry of Environment) granted us the necessary licenses to capture, anesthetize, manipulate, and mark the study animals (N. 60347-1). Appropriate licenses were also obtained to access the parks and military areas.

Results

We found that long call occurrence was positively related to sound levels and group size, and negatively related to the hour of the day (Fig 3), while the distance from the border of the group territory had no effect in the occurrence of long calls (Table 2). On the other hand, the distance from the boundaries of the group home range influenced the abundance of long calls — pied tamarins called more in shorter distances from the border (Fig 4). The abundance of long calls was also related to the hour of the day, with pied tamarins calling more in the early morning, but independently of sound levels or group size (Table 2) (Fig 4) (Supplementary material). When analysing specific acoustic features, we found that pied tamarin frequency features did not change in response to sound level [dominant frequency: Estimate= 7.803; (SE) = 8.31, t =0.93, P = 0.34; lower frequency: Estimate=3.09, (SE) = 6.45, t =0.48, P = 0.63]. Neither did call duration (Estimate=0.01, SE: 0.009, t= 1.19, P=0.23). However, syllable repetition rate decreased with increasing sound levels (Estimate=−0.006, SE= 0.002, t= −3.32, P<0.001) (Fig 6).

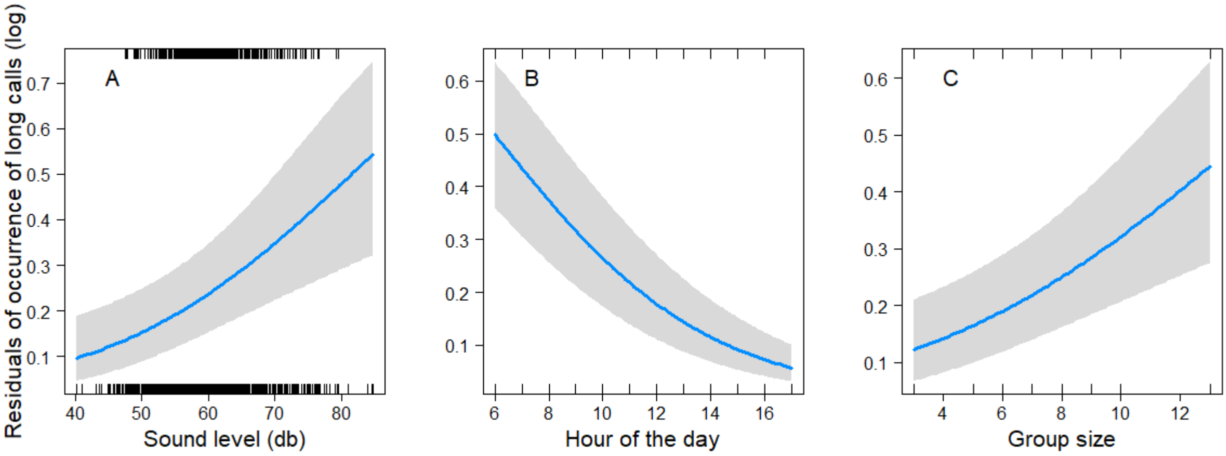

Figure 3. Relation between occurrence of pied tamarin (*Saguinus bicolor)* long calls and sound levels (dB) (a), hour of the day (b), and group size (N=953).

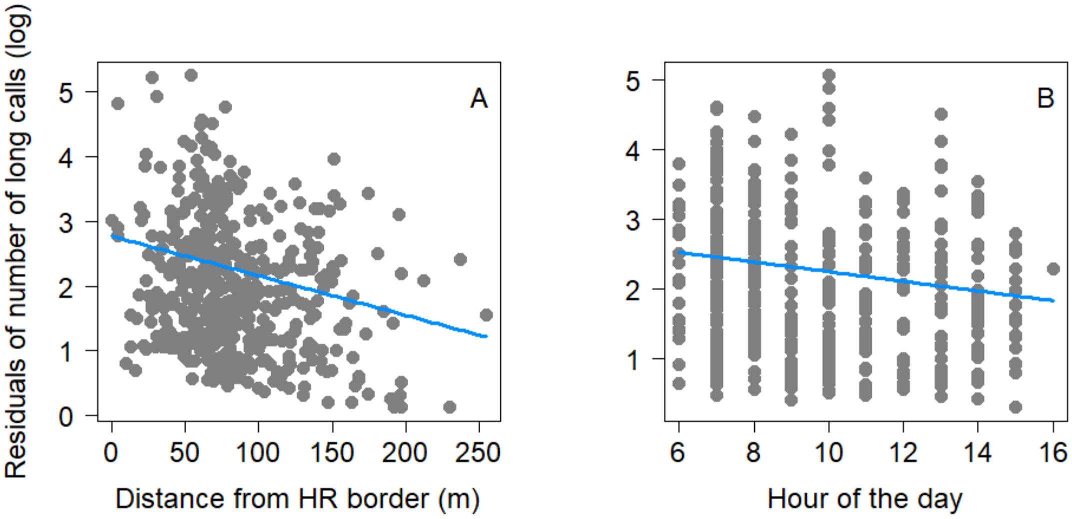

Figure 4 Relation between the abundance of long calls (i.e., number of long calls) and distance from home range border (a) and hour of the day (b). Each poin represents a behavioural bout with at least one long call (N=472).

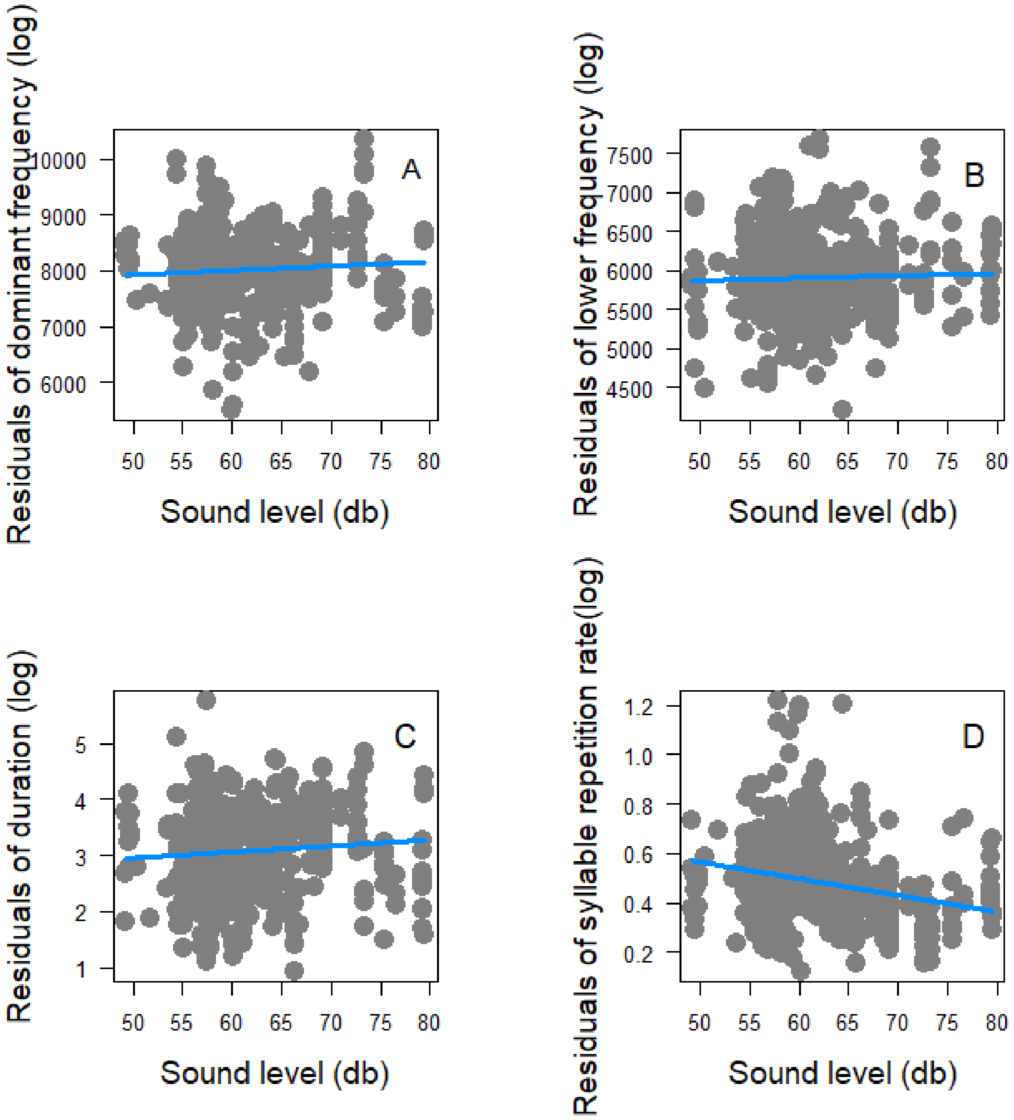

Figure 5 Relation between temporal (A-B) and frequency (C-D) acoustic features of pied tamarin (*Saguinus bicolor)* long calls and sound level (dB). Each point represents a long call (N=520).

Discussion

Here we found that the occurrence and the abundance of long calls emitted by pied tamarins in urban areas seem to be determined by environmental and social mechanisms such ambient sound level (i.e. “noise”), and putative distance from neighbouring groups. Additionally, although pied tamarins vocal activity (both in terms of occurrence and abundance of long calls) did not interacted with noise and they did not shift their vocal activity through the day in response to noise. The patterns of daily vocal activity are similar among sound levels, with tamarins calling most often early in the morning. Even if pied tamarins did not shift their temporal pattern of calling activity across the day in response to noise, fine-scale signal timing was influenced by sound level, with pied tamarins calling at a slower syllable repetition rate in noisier areas. Other pied tamarin acoustic features such as dominant frequency, lower frequency and duration of long calls did not change in response to sound levels.

We found that when sound levels were higher, the probability that pied tamarins emitted a long call increased. Long calls are used for group cohesion, and may also help in navigation (Fischer and Zinner 2011, Snowdon 2017*b*). It could well be that when sound levels surpass a discomfort threshold, pied tamarins move to quieter areas. Many studies have shown that loud noises can induce escape responses that influence patterns of both short- and long-range movements such as use of space, dispersion and migration (Duarte et al. 2011, Neo et al. 2014, Tennessen et al. 2014, Ware et al. 2015, Velasquez Jimenez et al. 2020).

Contrary to predictions, we found neither a negative or positive association between the pied tamarins abundance of calls and sound levels. This lack of correlation is a pattern that also occur in frogs (Jiménez-Vargas and Vargas-Salinas 2021). Possibly pied tamarins do not have to increase or suppress their calling activities because sound levels did not achieve a certain threshold (not addressed in this paper) that would induce a behavioural response [i.e. dose-response (Williams et al. 2014)]. Additionally, their other strategies, such as the changes in acoustic features could be sufficient to circumvent noise at least in over the short-term, such as for the duration that we analysed. We also did not corroborate the hypothesis that pied tamarins shift their vocal activity through the day in response to noise, possibly because, in most of the places studied, sound levels showed low temporal variation and were non-intermittent across the day. Such regularity may lead to habituation by the pied tamarins (Bejder et al. 2009), and be less impacting especially if the species is flexible and use other strategies to ensure communication, as seems to be the case for the pied tamarin.

In addition, we find that, in noisier places, pied tamarins reduced the syllable repetition rate, meaning that they emitted slower long calls, with either time between syllables being longer or the syllables themselves being more prolonged. A longer inter-syllable duration could allow pied tamarins to call in short periods of silence, a feature also observed with captive cotton-top tamarins and common marmosets that called amidst bursts of loud noises (Egnor et al. 2007, Roy et al. 2011). If, in pied tamarins, the syllables function as a unity of information, as in cotton-top tamarins (Miller et al. 2003), and the lower syllable repetition rate imply that the syllable is longer, this could also be advantageous as longer signals would have more chances to achieve the receptor.

As predicted, we did not find a difference in frequency features of long calls in response to sound levels, possibly because pied tamarins' sounds are already high-pitched, with dominant frequencies that can reach 11 kHz. This is different from what is found in other callitrichids that modulate frequency features rapidly (Zhao et al. 2019). Analysis of frequency contours of each syllable in relation to the spectral composition of background noise could be instructive in this context. Finally, many species increase the amplitude of their calls (Lombard effect) to boost signal to noise ratio and enhance signal transmission capacity (Brumm and Zollinger 2011). It is difficult to estimate amplitude features from the tamarins' calls due to numerous variables that can add error to the estimates in the field, including the direction from which the animal is calling, proximity of the animal to the microphone, background noise, and other physical condition of the sound propagation medium (including temperature, humidity, and vegetation density) (Zollinger et al. 2012).

In our study, we characterized noise in terms of amplitude, though, it can be more complex and variable in terms of spectral and temporal signatures (Neo et al. 2014, Gill et al. 2015, McKenna et al. 2016). We did not directly evaluate the composition of the soundscape, thus our "noise" estimates include not only anthropophonies (i.e., sounds of anthropogenic origin), but also biophonies (i.e. sounds of biological origins, such as other animals calling or moving). For instance, cicadas are an important component in tropical soundscapes, as their sounds can achieve very loud amplitudes, often occupy a large frequency band, and they can call for several minutes and even hours, affecting the overall use of the acoustic space (Aide et al. 2017). Additionally, we only followed tamarins for relatively short time periods and both biophonies and anthropofonies can be seasonal (Munir et al. 2021). Despite coverage by the current study of a broad sound level gradient (Min=40.2, Max=84.8; Fig 2), it would be potentially informative to have sampling at sites more distant from the urban matrix to understand how different soundscape components may affect their sounds. Pristine sites, for example, could function as an important behavioural and acoustic baseline.

In addition to sound levels, other environmental constrains could play a role in the pattern of vocal activity of the pied tamarins. For example, we found that individuals of this species vocalise more during the morning, as with many other species such as birds and other primates (Schneider et al. 2008, Van Belle et al. 2013). This common trend is widely-considered to occur because, during the morning, the status of such abiotic factors as temperature, humidity and wind favour sound propagation (Waser and Brown 1984). However, this is usually tested in pristine areas, and the distinct microclimate and the ubiquity of planar surfaces in urban areas could cause subtle changes to acoustic propagation (Slabbekoorn et al. 2007). An alternative hypothesis for the peaking of vocal activity during the morning relies on the dial pied tamarin behaviour: individuals usually enter their sleeping sites relatively early in the afternoon (~16:00), and begin their daily activities around 05:30 (Egler 1986, Gordo et al. 2017). After more than 12 hours of resting, individuals must be hungry, and long calls could be important to coordinate the group while browsing for fruits.

Besides the influence of sound levels, we also found that social aspects are important for both occurrence and abundance of long calls. As expected, we found that the occurrence of long calls was related to group size. Yet, the abundance of long calls had only a marginal statistical significance. Such finding is in accordance with a previous playback study which showed that, unlike to other group-living animals (Kitchen 2004, Van Belle and Scarry 2015), larger groups of pied tamarins do not emit more long calls while listening to conspecific long calls (Sobroza et al. 2021*c*). We also found a negative relation between the abundance of long calls and the distance from home range boundaries. This result relates to what is found in other territorial species that perform a regular patrolling behaviour, signalling more at the boundaries of their territories (Mitani and Watts 2005, Da Cunha and Jalles-Filho 2007). A variety of studies have shown that the emission of long calls is more related to resource distribution than range boundaries, which should also be investigated for pied tamarins (Hopkins 2013, Van Belle et al. 2013, Caselli et al. 2014, Ceccarelli et al. 2021).

In summary, pied tamarins do not increase the abundance of long calls in response to noise, but the occurrence of long calls is influenced by sound levels. As long calls are important for group cohesion during movement, it is possible that the tamarins emit one single call with a proper acoustic structure (i.e. lower syllable repetition rate and probably higher amplitude), and move to quieter areas of their ranges. Neither occurrence nor abundance of long calls are altered to so that they occur in quieter periods of the day, although, independent of sound levels, the emission of long calls is more likely to occur early in the morning. Further, the abundance of long calls is negatively related to the home range boundaries. Overall, the occurrence and the abundance of long calls emitted by pied tamarins in urban areas seem to be ruled by combination of both environmental and social mechanisms. These are exciting results from a conservation perspective as it supports the ongoing efforts to create ecological corridors in Manaus, Brazil. Once habitat connection is established, pied tamarins may be capable of coping with city noise to communicate with conspecifics, a fundamental tenet of species survival.

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Authors' contributions

TVS, APAB, MG and JC originally formulated the research topic. TVS collected data and wrote the original draft. TVS and BNM performed exploratory and current spatial analysis. TVS and PACLP, performed statistical analyses. APAB, MG, and JCD supervised. TVS raised funds. APAB and JCD checked the English. All authors contributed to the writing and reviewing.

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Tables

Table 1. Characteristics of sampling locations and pied tamarin (*Saguinus bicolor)* groups followed in urban areas of Manaus, Brazil.

Group	**Fragment size (ha)**	**Group Size**	**Group composition**	**Estimated home range***	**Radio-collar**	**Number of points used in kernel analysis**
Viveiro	~700 ha	8	1 F+ 2M+ 3JF+ I+ 1 UN	13.39	Yes	408
Jaqueira	~700 ha	13	3F+ 5M + 2JF +1 JM+ 1 I+ 1 UN	33.46	Yes	63
Coroado	~700 ha	7	3 M+ 1JM + 1 I+ 2 UN	33.70	Yes	93
Acariquara	~700 ha	7	2F+ 1 JF+ 1 MF+ 3 UN	18.64 ha	Dannified during the study	45
CIGS	~100 ha	5	1 F+ 2M + 1 FJ+ 1 UN	11.55	Yes	442
Mindu	~50 ha	6	2F+ 1M+ 1MJ+ 2 UN	6.30 ha	No	227
Sumaúma	~50 ha	9	3F+3M+ 1FJ + 2MJ	19.29 ha	Yes	416
Bosque da Ciência	~24 ha	3	2F+1M	24 ha	No	279
Musa	continuous	10	NA	34 ha	No	45

*Home ranges estimated with kernel 95%. Group composition: M= adult male; F= adult female; JF= juvenile female; JM= juvenile male; I=infant; UN=adults of unknown sex.

Table 2. Summary of Generalized Mixed Effects Models for different descriptors of emissions of long calls by nine groups pied tamarin (*Saguinus bicolor)* in urban areas of Manaus, Brazil.

Response variable	**Predictor**	**Estimate**	**SE**	**Z**	**p**
Occurrence of long calls	Intercept	-2.997	1.088	-2.755	<0.001
	Sound level (dB)	0.054	0.014	3.623	<0.001 *
	Hour of the day	-0.253	0.021	-11.57	<0.001 *
	Group size	0.175	0.0452	3.879	<0.001 *
	Distance from HR border	0.001	0.001	1.068	0.285
Abundance of long calls	Intercept	3.036	0.916	3.313	<0.001 *
	Sound level (dB)	-0.003	0.012	-0.289	0.772
	Hour of the day	-0.069	0.018	-3.843	<0.001 *
	Group size	0.070	0.042	1.683	0.092
	Distance from HR border	-0.006	0.001	-4.202	<0.001 *

HR= home range; * p-values significant.

Supplementary material Summary of Generalized Mixed Effects Models for different descriptors of emissions of long calls by nine groups pied tamarin (*Saguinus bicolor)* in urban areas of Manaus, Brazil.

Response variable	**Predictor**	**Estimate**	**SE**	**Z**	**p**
Occurrence of long calls	Intercept	-0.655	2.893	-0.22	0.820
	Sound level (dB)	0.015	0.047	0.32	0.748
	Hour of the day	-0.466	0.244	-1.92	0.055
	Group size	0.172	0.045	3.79	<0.001 *
	Distance from HR border	0.0018	0.001	1.11	0.262
	Sound level (dB)× Hour of the day	0.003	0.004	0.878	0.380
Abundance of long calls	Intercept	4.336	2.131	2.03	0.041*
	Sound level (dB)	-0.022	0.035	-0.64	0.516
	Hour of the day	-0.176	.0184	-0.96	0.337
	Group size	0.04	0.033	1.22	0.22
	Distance from HR border	-0.004	0.001	-3.29	<0.001 *
	Sound level (dB)× Hour of the day	0.001	0.003	0.52	0.59

HR= home range; * p-values statistically significant. ×Interaction term

CAPÍTULO 3

Pied tamarins go multimodal in response to anthropogenic noise

Sobroza, TV.; Dunn, JC; Gordo, M; Barnett, APA. Formatado para a revista *Bioloy Letters.*

“The music's too loud, and the noise from the crowd
Increases the chance of misinterpretation
So let your hips do the talking”

Kings of Convenience –
Banda indie sobre troca multimodal.

Pied tamarins go multimodal in response to anthropogenic noise

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Abstract

Sounds produced by human activities are often loud and may mask acoustic signals used by other species for communication. To circumvent this, animals may use various strategies, including shifting communication modalities completely or complementing acoustic information by also using another modality of communication. Here we tested the overlooked multimodal shift hypothesis using pied tamarins (*Saguinus bicolor*) as models. We predicted that in noisier areas the species would exhibit more scent marking behaviour (i.e., olfactory communication), while reducing the emission of long calls (i.e., acoustic communication). We collected information on vocal and scent marking behaviour in nine groups of wild pied tamarins in Manaus, Brazil. We found that scent marking occurrence increased with noise amplitude, though the number of long calls did not change. Thus, our results do not suggest a shift between channels but complementation of information, where scent marking may counteract against the compromising of the acoustic channel by the urban environment. This is an interesting result from a conservation perspective and supports ongoing efforts to create ecological corridors in Manaus, Brazil; once habitat connection is established, pied tamarins may be capable of coping with city noise to communicate with conspecifics, an important aspect for species survival.

Keywords: animal communication, urban soundscape, multimodality, Amazon, *Saguinus bicolor*.

1. Background

Many species depend on sound to communicate with conspecifics about essential behaviours such as foraging, defence, territorial activities, and mate attraction [1]. The environments in which animals reside are sometimes naturally noisy. However, humans have contributed many additional stimuli to the soundscapes that animals have evolved to cope with [2]. Sounds produced by human activities (anthropogenic noise) are often loud and may mask natural sounds. In response, animals use a variety of strategies to circumvent this, including completely shifting to a different modality or complementing acoustic communication by using another modality [3]. Humpback whales, for instance, usually display more surface-active behaviours (which may be considered both as acoustic and\or visual) when background noise is high [4]. In human speech, in what is called the “cocktail party” phenomenon, people also rely on visual cues (e.g., movement of the mouth and eye position) when the acoustic environment is too noisy, and the auditory channel is compromised [5,6].

Multimodality, or the capacity to communicate using signals in more than one sensory channel, is widespread among animal species [7–9]. These signals can contain complementary or redundant information that serves various functions, such as attracting additional attention to the signaller, or acting as a backup signal in noisy contexts [9,10]. Cues, that do not contain any intrinsic information can also enhance the detectability of signals from the main communication channel [11,12]. The ability to switch from reliance on one modality to another during communication in a noisy context is known as a *multimodal shift* [3], and is more likely to be effective if the information contained in both channels is redundant [3] – i.e., the same message can be sent using either modality. However, in the absence of signal redundancy, multimodality can still help to overcome constraints during information reception in noisy contexts, due to attention enhancement [12,13].

Many studies evaluating the impact of anthropogenic noise have been published [14,15], but among primates such investigations have been restricted mainly to captive environments and unimodal senses [16–18]. Nevertheless, multimodality has been addressed in captive and semi-captive apes, but hypothesis testing regarding communication shifts is mostly speculative [19]. Neotropical primates use a great variety of signals in communication, including visual, chemical, and acoustics modalities [20–24], and are highly susceptible to habitat loss and its consequences, such as increases in anthropogenic noise [25]. Therefore, Neotropical primates have a great potential to exhibit multimodal shifting, adding a broader perspective to theories on the evolution of multimodality across species.

The pied tamarin (*Saguinus bicolor*) is a callitrichid with a narrow geographic range in the central Brazilian Amazonia. Its range encompasses a total of 7,500 km², much of which is located in urban and peri-urban areas of the city of Manaus [26]. Urbanization is restricting individual groups to isolated forest fragments surrounded by a noisy anthropized matrix. Mainly due to fragmentation and its consequences (e.g., road-kill, electrocution, and attacks from domestic animals), the species is considered Critically Endangered by the IUCN [27]. Pied tamarins possess five main types of scent marking: sternal, suprapubic, anogenital, tailmarking, and hand marking [28,29], which can be observed both in captivity and in the wild [28,29]. In callitrichids, scent markings serve to deposit chemicals that may function both as a signal and a cue across a variety of contexts including territoriality [24]. The species also produce various sounds, including long calls that function both for territoriality and group cohesion [30,31], therefore it is likely to shift modalities in response to noise. Here we aim to test whether pied tamarins shift the use of communication modalities in response to noise. Thus, we predict that the occurrence of scent-marking behavior will increase in noisier areas to compensate for the possible compromising of acoustic-based communication. If such a shift happens, we also expect that the number of long calls will decrease in noisier areas.

2. Material and Methods

(a) Study area and subjects

The study was conducted in the Central Brazilian Amazon, in the city of Manaus, Amazonas state, Brazil (figure 1). Acordinly to the nearest station of the Brazilian Institute for Meteorology (INMET- station A101), the average temperature during the sampling period was 27.7 C^o (sd= 2.6) and relative air humidity ~73,27 % (sd=13.94). We followed nine groups of pied tamarins in different forest fragments within the city limits of Manaus (figure 1). The study area comprised five forest fragments ranging from 24 to ~700 ha, where other primate species also occur, including *Saimiri sciureus* and *Pithecia crysocephala*. The most common source of anthropogenic noise in all areas is road traffic, though there is also air traffic, park visitors, talking and screaming from children and university students, and singing and gunshots from military activities.

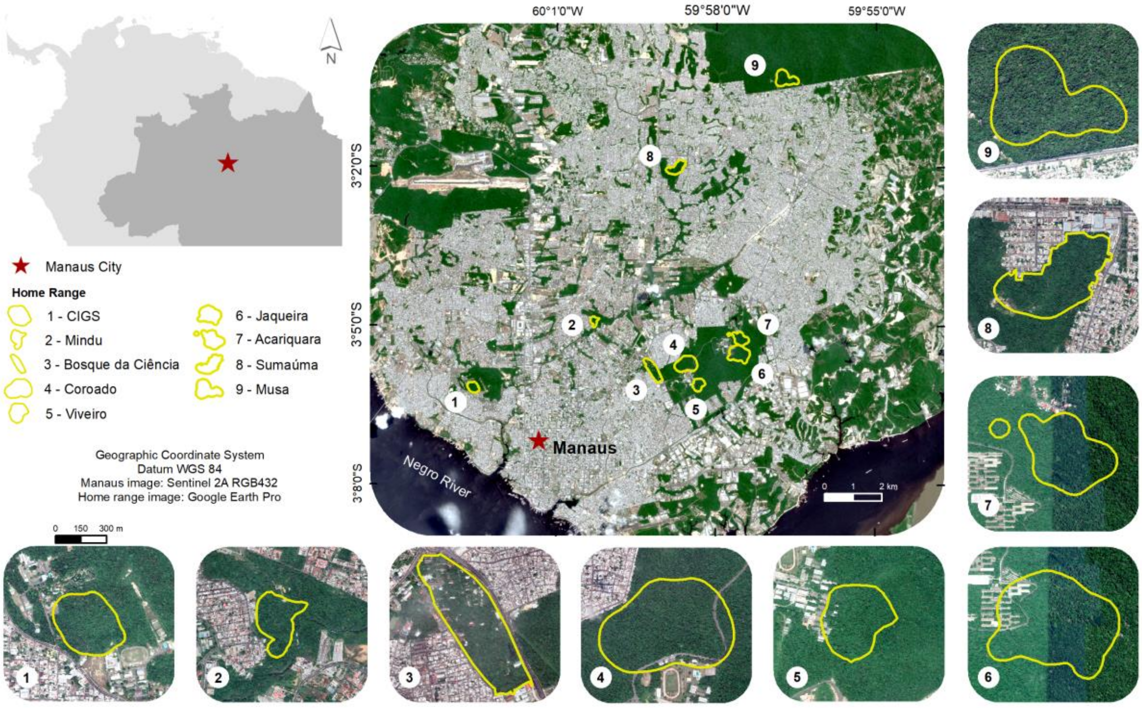

Figure 1. Home ranges of pied tamarin (*Saguinus bicolor*) groups (1-9) (small maps) followed in the urban area of Manaus, Brazil (larger map) from November 2018 to December 2019.

The studied tamarin groups varied from 3 to 13 individuals; two of these groups were relatively well-habituated to human presence due to frequent public visitation to the parks in which they occurred. We followed non-habituated groups by radio-tracking. To capture the groups we habituated the pied tamarins to bait (banana), then, to the traps and, capture them after one to four months of habituation. We captured the groups using baited Tomahawk TH105 (10 x 10 x 40 cm) live traps to attach the radio-collars onto the animals, placing the traps ~1.60 m above the ground [30]. Once we captured the animals we sedated them with 0.2 mg/kg Ketamine® anesthesia [30], and attached a SOM 2380 transmitter (164.00-164.99 MHz) (Wildlife Materials) to the alpha female of each group. The frequencies emitted by the transmitter were detected with a two or three element directional antenna and an ATS® receiver (164-168 MHz).

(b) Data collection

Data collection took place from November 2018 to December 2019. We followed each tamarin group for ten complete days from 6:00 a.m. to 5:00 p.m. In the field, we collected data during five-minute behavioral bouts (followed by five-minute intervals), observing and registering all occurrences of scent marking and counting the number of long calls emitted from all individuals in the group in each behavioral bout. During these 5 minutes, we also took a 1-minute sample of noise amplitude and calculated the equivalent continuous sound levels (LCeq; time-averaged level of sound) (dBC), using a calibrated CEL-246 sound level meter (Casela Solutions). Leq was estimated based on sound pressures estimated every second during 1-minute readings. The sound level meter was manually supported 1.10 m above the ground directed to the tamarin group. The average noise in all sampled areas was 59.19 dB (sd=5.9) with a standart variation of about 5.54 dB through the day ranging from a minimum of 40.2 dB to a maximum of 84.8 dB. Calling and scent marking activity were recorded from all nine groups, but we only detected scent-marking behaviour in five groups.

(c) Statistical analysis

To test whether pied tamarins scent mark more often in noisier areas, we used a zero-inflated Generalized Linear Mixed Model (GLMM), assuming a binomial distribution and logit link function. In this analysis, each behavioral bout was deployed as a sample unit —the occurrence of scent marking as the response variable and the noise amplitude interacting with the number of long calls as predictors. Both predictors were scaled to zero mean and unit standard deviation to facilitate parameter estimation. Once the interaction term was not statistically supported ($p > 0.05$), we removed it and refitted the model, including only noise amplitude as a fixed predictor. Additionally, we included both fragment and group identity as random factors to control for any landscape-induced variation, non-independence between observation of the same group, or different sample sizes [32]. We also ran a GLMM assuming a negative binomial distribution and log function to test whether the number of long calls diminishes in response to noise. As before, we included both fragment and group identity as random factors. We performed all analyses in R version 3.5 [33], using the *glmmTMB* and *visreg* packages [34,35].

3. Results

We observed 50 scent-marking and 490 long call events during the 801 and 1910 behavioral bouts, respectively (Supplementary material). As predicted, we found that the occurrence of scent marking was positively related to an increase in noise amplitude (figure 2, table 1). However, this change cannot be considered as multimodal shift, as the interaction between the number of long calls and noise amplitude was not a significant predictor of scent marking occurrence, and the number of long calls was not reduced significantly when noise amplitude increased (Methods; table 1).

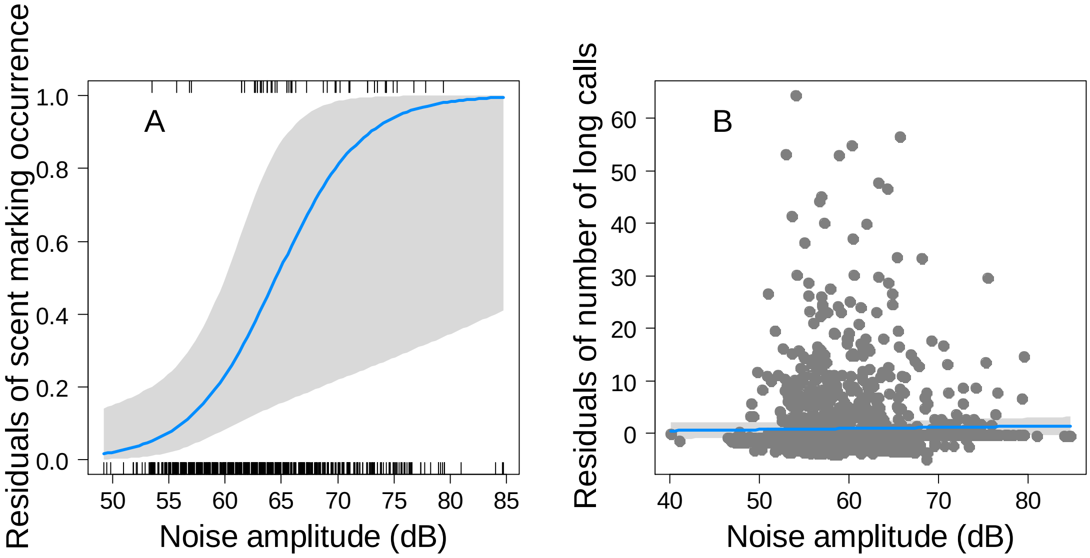

Figure 2. A) Relationship between scent mark occurrence and noise amplitude (dB) (sample unit= behavioural bout; N=801); and B) Relationship between the number of long calls and noise amplitude (dB) in wild pied tamarins (*Saguinus bicolor*) in Manaus City, Brazil. (sample unit= behavioural bout; N=1910). Lines represent the best-fitting model (Table 1).

Table 1. Summary of results from generalized linear mixed-effects models for observations of scent marking (N=801) and emission of long calls (N=1910) in response to noise amplitudes in nine groups of wild pied tamarins (*Saguinus bicolor*), Manaus, Brazil.

Response variable	**Predictor**	**Coefficient**	**SE**	**Z**	**P**

Scent marking occurrence	Intercept	-0.42	-	-	-
	Amplitude Noise (dB)	1.59	0.65	2.44	0.014*
Number of long calls	Intercept	0.93	-	-	-
	Amplitude Noise (dB)	0.11	0.11	1.00	0.31

Model for scent marking occurrences with parameters estimated with a zero-inflated single model. * Results statistically significant ($P<0.05$).

4. Discussion

Here we assessed whether pied tamarins exhibited more scent marking in noisier contexts and, as predicted, our findings upheld this hypothesis. In contrast, the number of long calls did not decline significantly in noisier areas. Therefore, our observations do not indicate a complete shift between channels but rather suggest complementation of information by using multimodal communication. Thus, it seems that scent-marking may represent a strategy to compensate for the possible compromising of the acoustic communication channel in noisy environments. In great apes, both social and ecological factors are known to affect multimodal communication [36]. Our study represents the first time an ecological effect on multimodal communication has been reported for a Neotropical Primate.

Acoustic signals are ideal for immediate communication over distance in forest environments due to their capacity to circumvent physical obstacles. One downside is that they are ephemeral, while chemical cues persist longer in the environment [1]. Also, acoustic and chemical signals have different propagation capacities, and act in long- and short-range communication, respectively, therefore, signals from these different channels are unlikely to be redundant. However, in the presence of high-intensity noise, short-range modalities may become more relevant [37] as they can function as complementary signals or be used for refinement [36]. One possibility is that pied tamarins may enhance detection and discrimination of territorial long calls in the presence of scent marks due to enhanced attention by receivers. Humans, for example, use gestural information to improve receivers' perception of speech in the presence of noise [38]. In common marmosets, neurological pathways that affect responses towards chemical signals have been found that are similar to those related to auditory perception, locomotion and decision-making [39].

Scent marking has been traditionally correlated with territoriality across mammalian taxa, and in callitrichids it may function both as a signal and a cue across a variety of contexts [24]. The territorial function of scent marking has been debated [40–44], but the refutation of the territorial role of scent marks comes primarily from unimodal studies [40,41]. If we consider the context of multiple channels being used and that the meaning of chemical signals may be learned [45], it becomes clear that the possibility that scent marking has a territorial function is still a possibility.

Group sizes and the rate of intergroup encounters may influence the frequency of communication behaviours [46]. Of the habituated groups in which we evaluated scent-marking behavior, one had three individuals and no neighboring groups in the fragment (though, three other primate species are common in the area), while the other group was composed of six individuals, and often encountered neighboring tamarin groups. Despite demographic and social differences, such a pattern of scent marking was not group-specific, suggesting that scent marking occurrence increases in response to local conditions (in this case, noise), as occurs in other mammal species [47].

Our result is also interesting in terms of conservation; as long as urban fragments where pied tamarins groups occur are functionally connected [48,49], individuals are likely to cope with city noise with strategies that use the interchanging of communication channels that possibly provide complementary information. The increase in scent-marking may be a widespread flexible response toward environmental change, as occurs in birds [12]. However, we are not aware if this exchange is reversible [50], which would be desirable if fragments are connected to pristine quieter areas [48]. Tamarins are fast breeders, and can give birth to twins at least once a year (sometimes twice) [51]. The groups that we studied, and their ancestors, have probably been in contact with a noisy urban matrix for at least twenty years (about 30 tamarins generations) [26]. Thus, it would not be impossible that our observations are related to shifts in gene expression associated with sensory channels - an event that has been observed in guppies [52]. Laboratory experiments using playback techniques could help resolve such questions.

Our study has a few limitations such as the sampling a small number of groups for a comparatively short period. Due to that, we cannot rule out the possibility that seasonality might have influenced our results since chemical composition and information content may vary across months [53]. In addition to that some species use scent marking as a displacement activity to minimize the impact of environmental stressors (e.g., noise) [54,55]. Accordingly, one possibility is that the scent marks that we observed were deposited with no communication intention but in response to stress, even though these odours could still function as a cue.

Noisier areas coincide with higher levels of physical and ecological impact on natural areas, so that large predators such as felids are less likely to be present. Felids often eavesdrop on their prey based on chemical cues, so primates may avoid using scent marking when predation pressure is high, and "relax" its use in places where native predators have disappeared, such as in fragmented landscapes [56]. The sampling areas where we detected scent-marking were fragments without natural predators, although domestic dogs and cats are often present. Even if dogs are not scansorial and as threatening as some natural predators (e.g., margay cat), they still have a powerful sense of smell and impact urban wildlife [51,57]. Thus, it is less likely that the pattern we detected is related to complete relaxation in predation pressure.

Despite possible biases, common in ecological studies of wild animals, our results show a strong ecological effect of noise on multimodal communication, which indicates complementarity of communication channels. From a conservation perspective, this is an interesting result supporting ongoing efforts to create ecological corridors for the Critically Endangered pied tamarin [48]. Further studies are still required to ascertain whether the increase in scent marking is a successful response to noise. If it does, pied tamarins may be able to deal with city noise and communicate with conspecifics, an essential requirement for its continued survival.

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Ethics

The Project was approved by the Ethical Committee of the Instituto Nacional de Pesquisas da Amazônia (SEI.01280.00900\2018-58). SISBIO/MMA (Ministry of Environment) granted us the necessary licenses to capture, anesthetize, manipulate, and mark the subjects (N. 60347-1). Appropriate licenses were obtained to access municipal and state parks and military areas.

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SÍNTESE

Nesta tese foi investigado como o ambiente acústico afeta o comportamento de comunicação do sauim-de-coleira (*Saguinus bicolor*). Em especial, focou-se na interação dos sons dos sauins diante de sons de origem biológica (sauim-de-mãos douradas) e antrópicas (ruído) considerando também o ambiente físico em que os animais estão inseridos. No primeiro capítulo foi testado se os sauins-de-coleira e o sauim-de-mãos-douradas apresentam sons com parâmetros acústicos similares em áreas de simpatria. Já no capítulo dois foi testado se os sauins-de-coleira alteram a quantidade de vocalizações emitidas ou o padrão temporal da emissão de vocalizações em ambientes mais ruidosos. Também nesse capítulo foi avaliado se os sauins-de-coleira alteram os parâmetros físicos de seus sons em ambientes mais ruidosos. Por fim, no terceiro capítulo foi testada a hipótese de troca multimodal onde testou-se a hipótese de que os sauins-de-coleira reduziriam suas atividades vocais e realizam mais marcações odoríferas em ambientes ruidosos.

No primeiro capítulo foi observado que ao comparar sons territoriais de grupos de *S.bicolor* em ambientes de alopatria e simpatria com *S.midas*, *S. bicolor* não apresentou diferenças significativas do som. Por outro lado, ao comparar os sons de *S. midas* em simpatria houve um deslocamento dos caracteres sonoros, sendo que essa modificação foi no sentido de tornar os sons mais similares aos sons de sauins-de-coleiras. Assim, o deslocamento de caracteres encontrados foi assimétrico, já que foi constatado apenas em uma das espécies. A convergência do som das espécies em área de simpatria pode ser atribuída ao comportamento em que o som é emitido, uma vez que sons parecidos seriam mais efetivos em informar o contexto de territorialidade em áreas de simpatria. Ainda, o deslocamento observado ocorreu apenas em áreas de mata primária, e não em áreas de mata secundária, o que pode estar relacionado à diferença de forças seletivas para propagação do som nesses ambientes.

No segundo capítulo, o foco foi no efeito do ruído da cidade de Manaus no comportamento de comunicação do sauim-de-coleira. De forma geral, os sauins não aumentaram ou diminuíram a abundância de vocalizações de chamado em resposta ao ruído, porém, a ocorrência dessas vocalizações sim. É possível que diante de um ruído intenso os animais emitam apenas uma vocalização para coordenar o grupo para um local mais quieto, mas não necessariamente vocalizam mais vezes para isso. A abundância de vocalizações emitidas, por outro lado, foi mais influenciada por aspectos sociais, como a distância da borda de seus territórios, um proxy para interações com grupos vizinhos. Além disso, não houve mudança no padrão temporal de emissão de vocalizações ao longo do dia em resposta ao ruído, porém em uma escala mais fina, encontramos que as vocalizações tem um padrão de repetição de sílabas (número de sílabas/ duração) alterado em relação ao ruído, sendo que os chamados ficam mais lentos. Quando os chamados tem uma taxa de repetição mais lenta, duas coisas podem estar acontecendo, ou a vocalização tem silabas maiores ou o intervalo entre silabas é maior. No primeiro caso, ao aumentar a duração da silaba, pode haver maior chance de que pelo menos parte do sinal chegue ao receptor o que seria benéfico em ambientes ruidosos. No segundo caso, com intervalos entre sílabas maiores, os animais podem estar intercalando as sílabas nas janelas de tempo mais silenciosas. Quanto ao restante dos parâmetros acústicos (duração do chamado, frequência mais baixa e frequência com maior energia), não houve relação significativa com o ruído.

Em adição a estratégias para contornar o ruído da cidade, no capítulo 3 também encontramos que a ocorrência de marcações de cheiro é maior em ambientes ruidosos. Ou seja, é possível que os sauins-de-coleira usem mais outros canais de comunicação quando o ruído atrapalha o canal de comunicação acústica. Apesar disso, eles não reduzem os comportamentos de vocalização, portanto, não há uma troca de modalidades de comunicação, mas provavelmente uma complementação da informação contida nesses sinais de diferentes canais sensoriais. De forma geral, esta tese mostra que tanto sons de origem biótica (presença de outras espécies ou tipo de floresta) quanto antrópicos (ruído) afetam os padrões de vocalização e comportamentos de comunicação do sauim-de-coleira (Figura 1).

Do ponto de vista da conservação o som pode ser uma ferramenta útil para entender a relação do sauim-de-coleira com outras espécies, como o sauim-de-mãos douradas. Desde a década de 80 suspeita-se sobre a possibilidade de competição entre *S.midas* e *S.bicolor* (Ayres et al. 1982), no entanto devido à dificuldade de encontrar ambas espécies em sintopia, o teste de hipóteses foi restrito a estudos genéticos e de distribuição geográficas (Röhe 2006, Oliveira 2014, Serfaty et al. 2017). Através do estudo de seus sons foi possível ir além e trazer novas informações sobre a dinâmica social dessas espécies (Sobroza et al. 2021 *a,b,c*). Os esforços para montar esse "quebra-cabeça" continuam e estamos longe de ter uma resposta única e clara sobre o que acontece entre essas duas espécies, mas sem dúvida essa dinâmica deve ser considerada durante o planejamento de ações para a conservação do sauim-de-coleira.

Com relação ao efeito do ruído no comportamento do sauim, encontramos que a espécie possui algumas estratégias para contornar o problema, o que é bom do ponto de vista de conservação, já que, uma vez que os animais possuam habitat suficiente, provavelmente eles ainda serão capazes de se comunicar efetivamente. No entanto, futuros estudos devem considerar outros aspectos, como a saúde e bem-estar desses animais embebidos pelo ruído urbano.

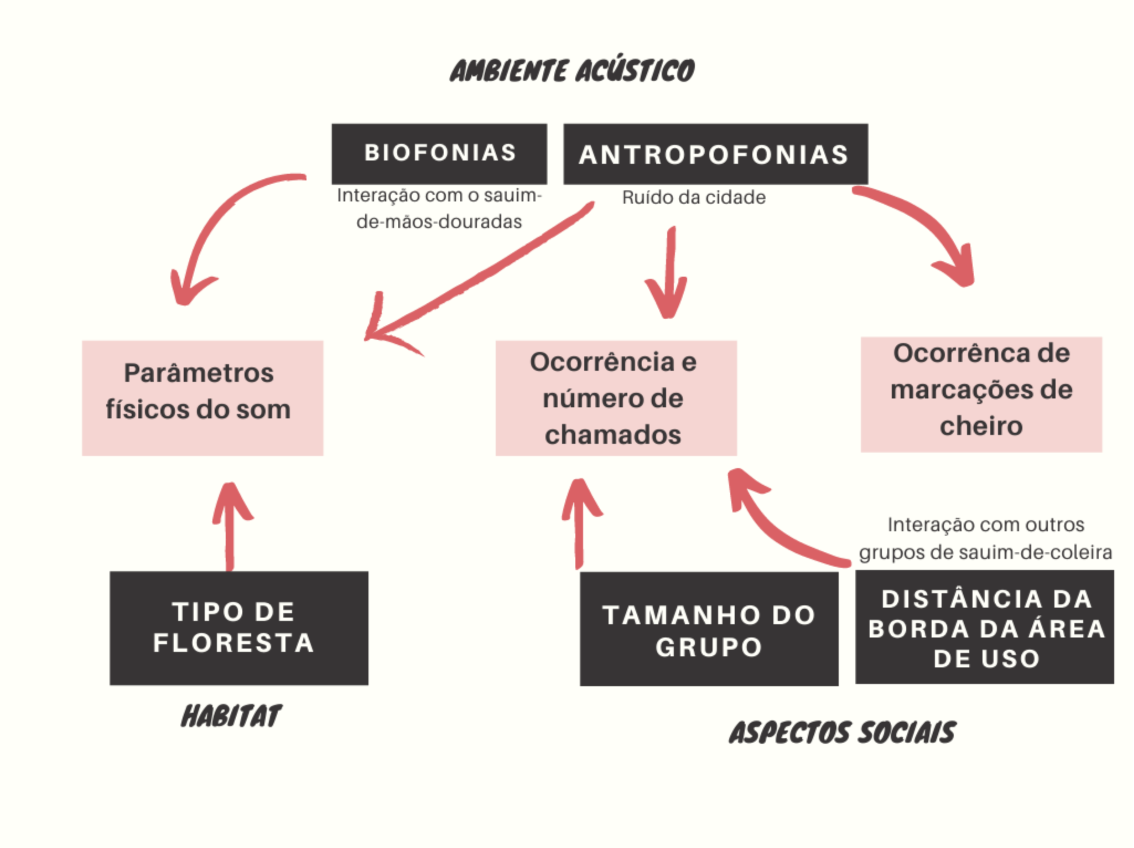

Figura 1. Síntese das relações investigadas nesta tese. As caixas rosas representam os comportamentos de comunicação do sauim-de-coleira enquanto as caixas pretas representam as variáveis preditoras desses comportamentos agrupadas em três categorias: ambiente

acústico, habitat e aspectos sociais. Setas unidirecionais representam relações estatisticamente significativas.

CONCLUSÃO GERAL

De forma geral, o comportamento de comunicação do sauim-de-coleira (*Saguinus bicolor*) é afetado pelo ambiente físico, acústico e social do local onde se encontram. Quando considerada a interação com o sauim-de-mãos-douradas (*Saguinus midas*), o sauim-de-coleira não muda os parâmetros físicos de seus sons em áreas de simpatria, mas o sauim-de-mãos-douradas quando ocorrendo em florestas primárias sim. Já na área urbana, a ocorrência das vocalizações de chamados do sauim-de-coleira é relacionado à amplitude do ruído, mas a abundância de chamados não. Esta é mais influenciada por aspectos sociais, como o tamanho dos grupos e distância da borda de seus territórios (um proxy para intensidade de interação com grupos vizinhos). Além disso, não houve mudança no padrão temporal de emissão de vocalizações ao longo do dia. Em uma escala mais fina, encontramos que as vocalizações tem um padrão de repetição de sílabas (número de sílabas/ duração) alterado em relação ao ruído, sendo que os chamados ficam mais lentos. Ainda, em ambientes ruidosos os sauins-de-coleira fazem mais marcações de cheiro como uma provável forma de uma complementação da informação contida nos sinais de diferentes canais sensoriais.

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