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Sobre a SBMz

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A **SBMz** tem como objetivo incentivar o estudo e pesquisa dos mamíferos, além de difundir e incentivar a divulgação do conhecimento científico desenvolvido no Brasil sobre os mamíferos. A **SBMz** também atua frente a órgãos governamentais, Conselhos Regionais e Federal de Biologia, e instituições privadas, representando e defendendo os interesses dos sócios, e atendendo a consultas em questões ligadas a mamíferos. Nossa Sociedade oferece e incentiva cursos de Mastozoologia em níveis de graduação e pós-graduação, além de conceder bolsas de auxílio financeiro para simpósios e congressos nacionais e internacionais. Além disso, ajudamos a estabelecer e zelar por padrões éticos e científicos próprios da Mastozoologia brasileira.

A **SBMz** foi fundada durante o “XII Congresso Brasileiro de Zoologia”, realizado em Campinas, em fevereiro de 1985. Desde então, a **SBMz** cresceu em número de sócios, e agora conta com congressos próprios bienais realizados nas diversas regiões do país, além do apoio e promoção de eventos regionais. Nossa sociedade conta com uma publicação própria intitulada **Brazilian Journal of Mammalogy**.

Fruto da criação e organização proporcionadas pela **SBMz** ao longo desses anos, atualmente o Brasil apresenta uma comunidade científica mastozoológica madura e conectada, que congrega profissionais trabalhando em organizações e instituições públicas e privadas por todo país.

Boletim da Sociedade Brasileira de Mastozoologia Uma publicação da SBMz

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Proechimys e *Trinomys* (Rodentia: Echimyidae): diferenças no sincrânio em dois gêneros de ratos de espinho na região Neotropical

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Resumo: As coleções científicas têm um papel importante em salvar o registro da biodiversidade. Neste estudo, utilizamos crânios e mandíbulas de roedores obtidos em três museus e uma Universidade do Brasil. O nosso objetivo foi descrever as diferenças morfológicas entre os dois gêneros de ratos de espinho *Proechimys* e *Trinomys*. Para isso, foram fotografados um total de 612 indivíduos de ambos os gêneros. Utilizamos métodos de morfometria geométrica com a plotagem de marcos anatômicos bidimensionais para descrever a forma e tamanho do sincrânio. Nossos resultados demonstraram que não há diferença estatística de tamanho do sincrânio entre os gêneros *Proechimys* e *Trinomys*. Porém, há diferença de forma: as espécies de *Trinomys* apresentaram bulas auditivas proporcionalmente menores, um processo jugal relativamente mais proeminente e um crânio relativamente mais robusto do que as espécies de *Proechimys*. Este trabalho adiciona informações referentes às diferenças já estabelecidas para os gêneros *Proechimys* e *Trinomys*. Além disso, demonstra a importância das coleções científicas para a descrição da biodiversidade.

Palavras-chave: Coleções biológicas; Hystricognathi; Morfometria geométrica; Roedores.

Abstract: *Proechimys* and *Trinomys* (Rodentia: Echimyidae): syncranial differences in two genera of spiny rats in the Neotropical region. Scientific collections have an important role in safeguarding biodiversity records. In this study, we used cranium and mandible of rodents obtained from three museums and one University of Brazil. We aimed to describe the morphological differences between the two genera of spiny rats *Proechimys* and *Trinomys*. For this, a total of 612 individuals of both genera were photographed. We use geometric morphometric methods through two-dimensional anatomical landmarks to describe the shape and size of the syncranium. Our results showed an absence of statistical difference in the size of syncranium between *Proechimys* and *Trinomys* genera. However, there is a difference in shape: *Trinomys* species had proportionally smaller auditory bulla, a relatively more prominent jugal process and a relatively more robust cranium than *Proechimys* species. This study adds information regarding the differences already established for the *Proechimys* and *Trinomys* genera. Furthermore, it demonstrates the importance of scientific collections for the description of biodiversity.

Key-Words: Biological collections; Geometric morphometrics; Hystricognathi; Rodents.

INTRODUÇÃO

Através de suas coleções científicas, os museus auxiliam no conhecimento e divulgação sobre a biodiversidade. Um dos papéis fundamentais dos museus é ampliar os conhecimentos sobre os materiais depositados em coleções biológicas, por meio da pesquisa científica básica (la Sancha *et al.*, 2017). Além disso, servem como apoio educacional e garantem a conservação do material biológico, o que possibilita um acesso rápido a uma grande quantidade de exemplares, e a espécies raras de serem encontradas na natureza (Gotelli, 2004).

Neste estudo, utilizamos crânios e mandíbulas provenientes de três museus e uma Universidade do Brasil para esclarecer aspectos da morfologia craniana de dois gêneros de roedores neotropicais. Os roedores possuem ampla distribuição geográfica, ocorrem em quase todos

os continentes, e podem ocupar diferentes tipos de habitat, o que é possibilitado por seus hábitos alimentares generalistas e por apresentarem altas taxas de reprodução (Kay & Hoekstra 2008). Dentro da infraordem Hystricognathi, encontramos a família Echimyidae onde os roedores apresentam diversas características morfológicas e ecológicas (Emmons *et al.*, 2015; Lara *et al.*, 2002). As espécies atuais de Echimyidae compartilham alguns caracteres morfológicos considerados como também presentes em seus ancestrais (Lara *et al.*, 2002). Por exemplo a subfamília Eumysopinae é um dos conjuntos de espécies que retiveram algumas características nos dentes, crânio e estruturas externas consideradas ancestrais (Fabre *et al.*, 2013; Verzi *et al.*, 1995). Dentro da subfamília Eumysopinae encontram-se os gêneros de ratos de espinho *Proechimys* (Allen, 1899) e *Trinomys* (Thomas, 1921).



Os gêneros *Proechimys* e *Trinomys* compartilham muitas características crânio-dentárias e morfológicas (Pessôa *et al.*, 2015). Por compartilharem estas características chegaram a ser considerados pertencentes ao mesmo gênero, até que, há 100 anos, em 1921 Thomas dividiu o gênero *Proechimys* em dois subgêneros, *Proechimys sensu stricto* e *Trinomys* (Thomas, 1921). Mais tarde, a combinação de dados biogeográficos e filogenéticos (Fabre *et al.*, 2013; Galewski *et al.*, 2005; Lara *et al.*, 1996) separou os gêneros *Proechimys* e *Trinomys*, que são hoje considerados representantes de linhagens evolutivas relativamente distantes entre os Echimyidae, não sendo considerados grupos irmãos (Fabre *et al.*, 2013, 2016; Galewski *et al.*, 2005). Além da distância genética, as espécies dos gêneros *Proechimys* e *Trinomys* também ocupam áreas geográficas distintas. *Proechimys* ocorre na floresta Amazônica e no Cerrado (Oliveira & Bonvicino, 2006). Já as espécies de *Trinomys* são endêmicas da Mata Atlântica, e ocorrem em área de transição com o Cerrado e a Caatinga (Lara & Patton 2000; Lara *et al.*, 2002; Oliveira & Bonvicino, 2006).

Nosso objetivo foi descrever as diferenças na morfologia do sínocrânio entre os dois gêneros de ratos de espinho *Proechimys* e *Trinomys*.

MATERIAL E MÉTODOS

Foram examinados 612 indivíduos dos gêneros *Proechimys* (7 espécies) e *Trinomys* (10 espécies) (Tabela 1)

provenientes de quatro coleções científicas do Brasil: Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN-M), Museu Nacional do Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo (MZUSP) e Universidade Federal do Espírito Santo, Vitória, ES (UFES). O tamanho amostral total variou entre estruturas morfológicas já que alguns indivíduos apresentavam estruturas quebradas, desta forma sendo desconsiderados (Tabela 1). Somente indivíduos adultos (dentição permanente erupcionada – terceiro molar) foram utilizados para as análises. A lista completa dos espécimes estudados se encontra no Apêndice S1. As localidades geográficas de cada indivíduo da amostra, conforme os dados das coleções, são indicados na Figura 1.

Os indivíduos foram fotografados nas vistas dorsal, ventral e lateral esquerda do crânio, assim como na vista lateral esquerda da mandíbula, através de uma câmera digital FUJIFILM FINEPIX S regulada no modo padrão, sem flash, função macro, com resolução de 7 megapixels (3072 × 2304) a uma distância focal padrão de 13 cm. A padronização da distância foi garantida pela utilização de um suporte portátil para a câmera sobre o qual foram apoiados os indivíduos fotografados.

A ordenação e organização da lista de fotos digitais foi realizada utilizando o programa TPSUtil versão 1.64 (Rohlf, 2013). A digitalização dos marcos anatômicos que melhor representam a morfologia do crânio e da mandíbula foi realizada com o programa TPSDig2, versão 2.22 (Rohlf, 2015). Foram digitalizados 90 marcos anatômicos, sendo 23 na vista dorsal, 34 na vista ventral, 20 na vista

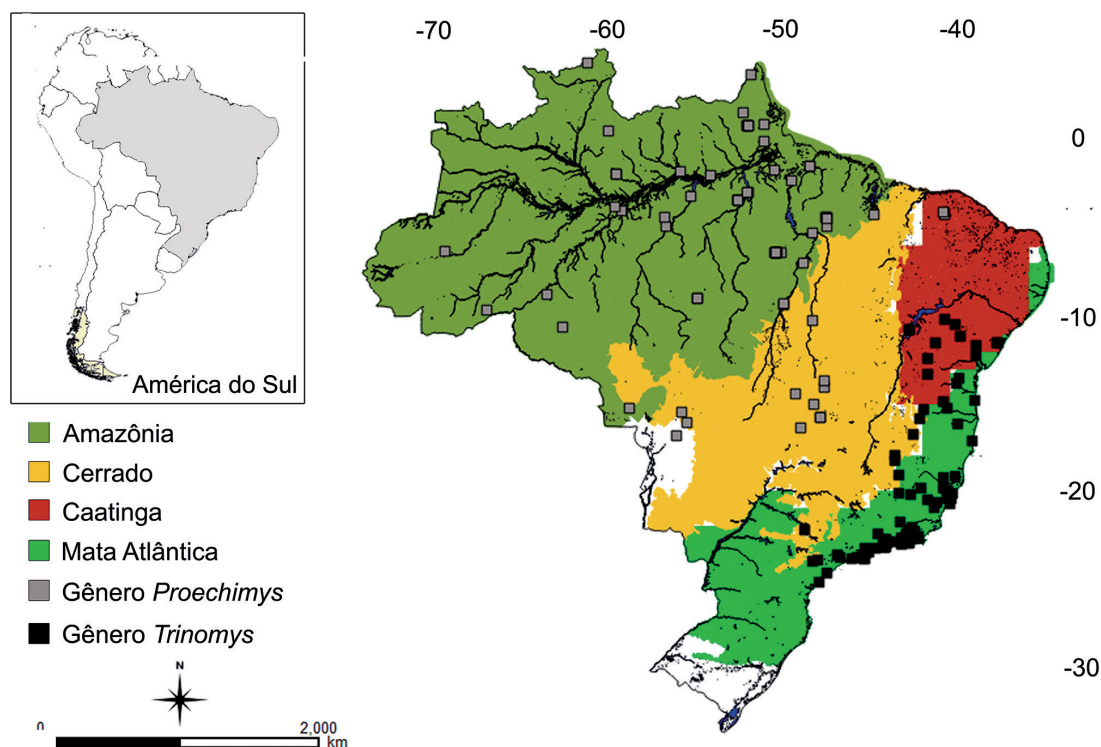


Figura 1: Mapa com os pontos amostrais dos gêneros *Proechimys* e *Trinomys*, em relação a quatro biomas brasileiros, Amazônia, Cerrado, Caatinga e Mata Atlântica, de acordo com as etiquetas do material proveniente das coleções. Fonte dos mapas (<http://www.diva-gis.org>), fonte da delimitação dos biomas (<http://mapas.mma.gov.br>). Figura gerada no programa Quantum Gis (QGis) versão 2.18.13.



Tabela 1: Tamanho amostral dos gêneros *Proechimys* e *Trinomys* analisados nesse estudo, com o total para cada espécie e para as diferentes vistas do crânio e para a vista lateral da mandíbula.

Espécies	Dorsal	Ventral	Lateral	Mandíbula
Gênero <i>Trinomys</i>				
<i>Trinomys albispinus</i>	60	55	52	55
<i>Trinomys dimidiatus</i>	32	31	28	28
<i>Trinomys eliasi</i>	5	5	5	4
<i>Trinomys gratiosus</i>	50	48	46	40
<i>Trinomys iheringi</i>	85	84	79	69
<i>Trinomys mirapitanga</i>	2	2	2	2
<i>Trinomys moojeni</i>	2	2	2	2
<i>Trinomys paratus</i>	67	67	67	65
<i>Trinomys setosus</i>	28	31	27	26
<i>Trinomys yonenagae</i>	35	34	33	30
Gênero <i>Proechimys</i>				
<i>Proechimys cuvieri</i>	22	21	21	14
<i>Proechimys goeldii</i>	23	23	24	15
<i>Proechimys guyannensis</i>	26	27	27	21
<i>Proechimys kulinae</i>	5	5	5	5
<i>Proechimys longicaudatus</i>	7	7	7	7
<i>Proechimys roberti</i>	129	127	125	70
<i>Proechimys semispinosus</i>	6	5	5	6
Total	584	574	555	459

lateral do crânio e 13 na lateral da mandíbula (Figura 2; descrição conforme Apêndice S2). Os marcos anatômicos foram similares aos propostos por Corti *et al.* (2001), Monteiro & Reis (2005) e Nicola *et al.* (2003).

As coordenadas dos marcos anatômicos foram sobrepostas com o método de sobreposição generalizada de Procrustes (GPA – *Generalized Procrustes Analysis*) (Dryden & Mardia, 1998; 2016). O método GPA remove diferenças não relacionadas à forma como escala, posição e orientação das coordenadas dos marcos anatômicos, resultando em uma matriz de variáveis de forma ou resíduos de Procrustes (Adams *et al.*, 2004; Dryden & Mardia, 1998; Rohlf & Slice, 1990).

A diferenciação no tamanho do crânio e mandíbula foi calculada a partir do tamanho do centroide que é a raiz quadrada da soma das distâncias ao quadrado entre cada marco anatômico e o centroide da forma (Bookstein, 1991). Testamos a normalidade e homocedasticidade dos dados e o tamanho do centroide foi log transformado para testar a diferença de tamanho entre os gêneros através do teste t de Student. Para explorar a variação da forma foi usada como análise exploratória a Análise de Componentes Principais (PCA – *Principal Component Analysis*) com projeção do espaço de forma nos extremos positivo e negativo dos PC1 e PC2, onde a variação de forma foi apresentada através de imagens com gradil de deformação. Para testar a diferença da forma entre os gêneros foi realizada uma análise multivariada de variância (MANOVA – *Multivariate Analysis of Variance*) e também uma análise linear discriminante (LDA – *Linear Discriminant Analysis*), com validação cruzada para acessar as porcentagens de classificação correta de espécimes entre os gêneros.

Para todas as análises estatísticas e para a geração de gráficos utilizamos a linguagem “R” na versão 3.4.3 (R Development Core Team, 2017), e as bibliotecas ape (Paradis *et al.*, 2004), geomorph (Adams *et al.*, 2017), MASS (Venables & Ripley 2002), Morpho (Schlager, 2017), Rvcg (Schlager, 2017), stats (R Core Team, 2017) e vegan (Oksanen *et al.*, 2017).

RESULTADOS

Na análise do tamanho do centroide não houve diferença de tamanho do sincrânio entre os gêneros de ratos de espinho *Proechimys* e *Trinomys* em nenhuma das vistas: dorsal ($t = 0,50$; $p = 0,61$), ventral ($t = 0,14$; $p = 0,88$), lateral ($t = 1,71$; $p = 0,08$) e lateral da mandíbula ($t = -0,23$; $p = 0,81$) (Figura 3).

Encontramos diferença na forma do crânio entre os dois gêneros de rato de espinho *Proechimys* e *Trinomys* para as vistas do sincrânio: dorsal (λ de Wilks = 0,08; $F_{(1:583)} = 308,2$; $p < 0,001$), ventral (λ de Wilks = 0,09;

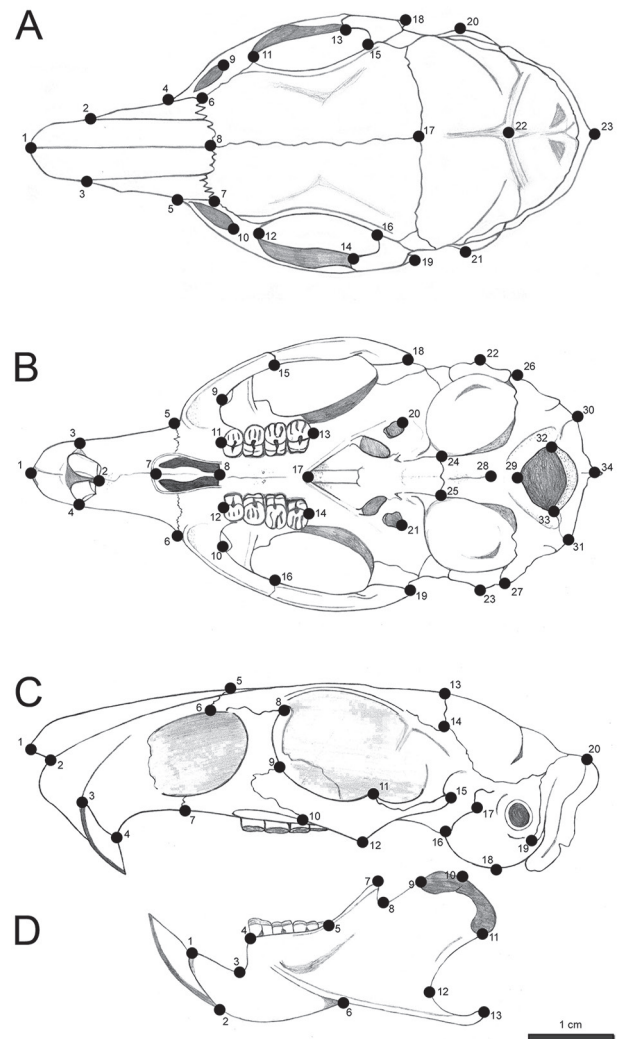


Figura 2: Posição dos marcos anatômicos no sincrânio de *Proechimys cuvieri*: nas vistas (A) dorsal, (B) ventral, e (C) lateral do crânio e (D) lateral da mandíbula.

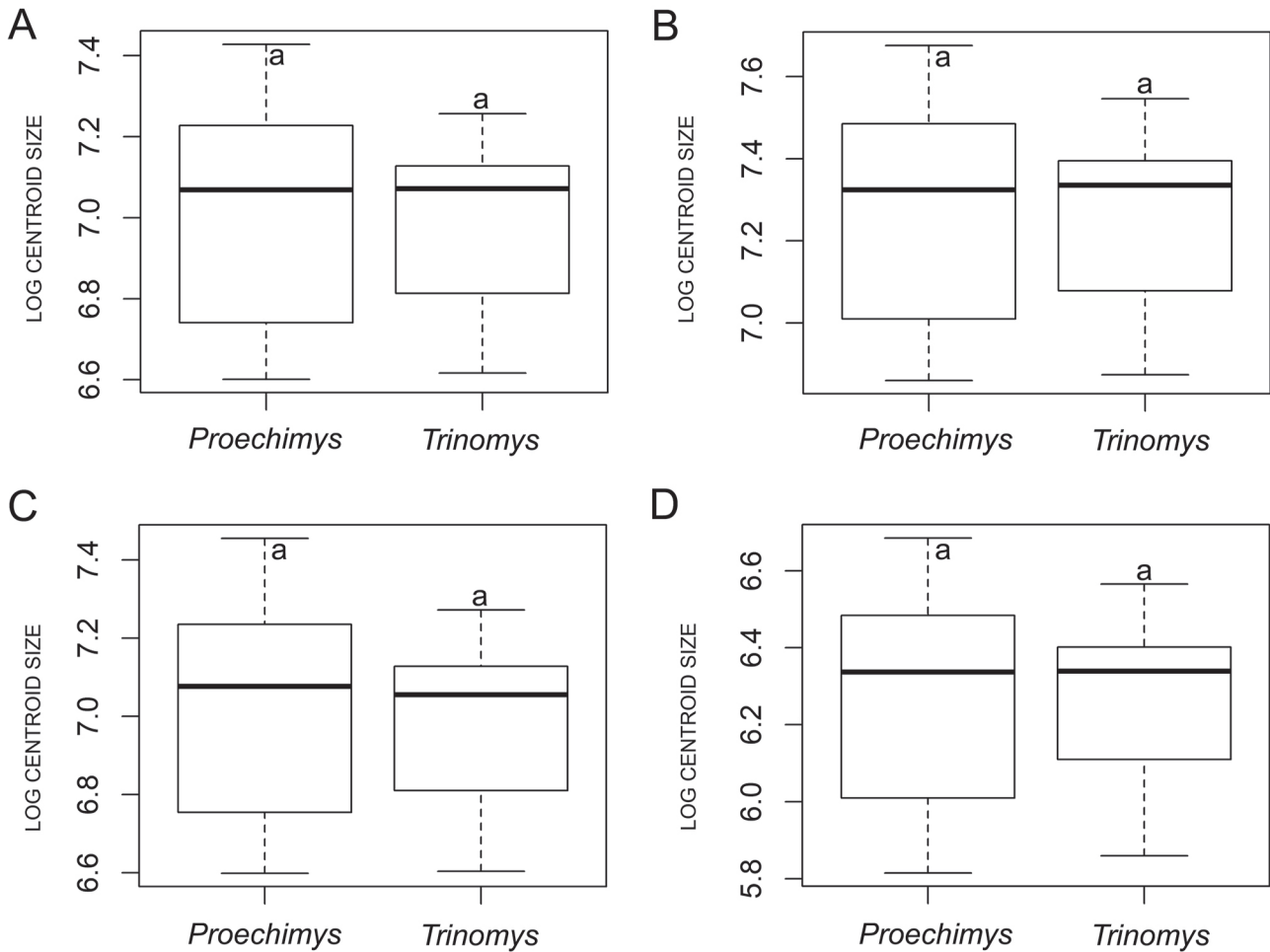


Figura 3: Boxplot da variação de tamanho do centroide entre os gêneros *Proechimys* e *Trinomys*. Para as vistas (A) dorsal; (B) ventral; e (C) lateral do crânio; e (D) lateral da mandíbula.

$F_{(1:573)} = 143,02$; $p = < 0,001$), e lateral da mandíbula (λ de Wilks = 0,11; $F_{(1:457)} = 148,08$; $p = < 0,001$), porém para a vista lateral do crânio o valor não foi significativo (λ de Wilks = 0,98; $F_{(1:553)} = 0,180$; $p = 1$). A LDA apresentou altos valores de validação da classificação correta dos gêneros para cada uma das vistas do síntrico (Tabela 2). Através da análise de componentes principais (PCA), encontramos estruturação com separação dos gêneros *Proechimys* e *Trinomys* nas vistas dorsal (Figura 4) e ventral (Figura 5) enquanto a lateral do crânio (Figura 6) e lateral da mandíbula (Figura 7) mostraram uma maior sobreposição entre os gêneros.

O gênero *Trinomys* apresenta um crânio com bulas auditivas e processo jugal mais proeminentes do que o gênero *Proechimys*, este último apresenta um crânio proporcionalmente mais alongado do que o primeiro. Para a vista dorsal do crânio o PC1 apresentou 35,09% de explicação (Figura 4), e na vista ventral, o PC1 apresentou 32,49% de explicação (Figura 5). Em ambas as vistas o gênero *Trinomys* se destaca por apresentar um crânio com bulas auditivas e processo jugal consideravelmente mais proeminentes que *Proechimys*. Na lateral do crânio o PC1 apresentou 28,74% de explicação (Figura 6), onde podemos destacar a sobreposição dos escores de

Proechimys e *Trinomys* e uma grande amplitude de variação de forma para *Proechimys*. Já a lateral da mandíbula, o PC1 apresentou 30,57% de explicação (Figura 7), destacando novamente sobreposição dos escores de *Proechimys* e *Trinomys*. Os indivíduos de *Proechimys* e

Tabela 2: Matriz de classificação dos gêneros *Proechimys* e *Trinomys* com o percentual de classificação correta da LDA.

Dorsal			
	<i>Proechimys</i>	<i>Trinomys</i>	%
<i>Proechimys</i>	218	1	99,54
<i>Trinomys</i>	0	366	100
Ventral			
	<i>Proechimys</i>	<i>Trinomys</i>	%
<i>Proechimys</i>	213	3	98,61
<i>Trinomys</i>	0	359	100
Lateral			
	<i>Proechimys</i>	<i>Trinomys</i>	%
<i>Proechimys</i>	213	1	99,53
<i>Trinomys</i>	0	341	100
Lateral da Mandíbula			
	<i>Proechimys</i>	<i>Trinomys</i>	%
<i>Proechimys</i>	134	4	97,10
<i>Trinomys</i>	4	317	98,75

alguns indivíduos de *Trinomys* apresentaram a mandíbula com o processo angular projetado para trás, com o processo condilar mais afilado, e com um processo coronoide menos saliente.

DISCUSSÃO

Neste estudo descrevemos algumas diferenças quantitativas na morfologia do crânio entre os dois

gêneros de ratos de espinho *Proechimys* e *Trinomys*. Não encontramos diferença significativa de tamanho de centroide do sincrânio entre os gêneros. Podemos inferir que isso ocorre devido a ambos os gêneros possuírem tamanho corporal similar, com as espécies de *Proechimys* variando de 180 à 300 mm (Patton & Leite, 2015) e as espécies de *Trinomys* de 152 à 246 mm (Pessôa *et al.*, 2015).

Apesar de não constarmos diferença de tamanho, a forma do crânio separa os dois gêneros claramente nas vistas dorsal e ventral do crânio. De modo

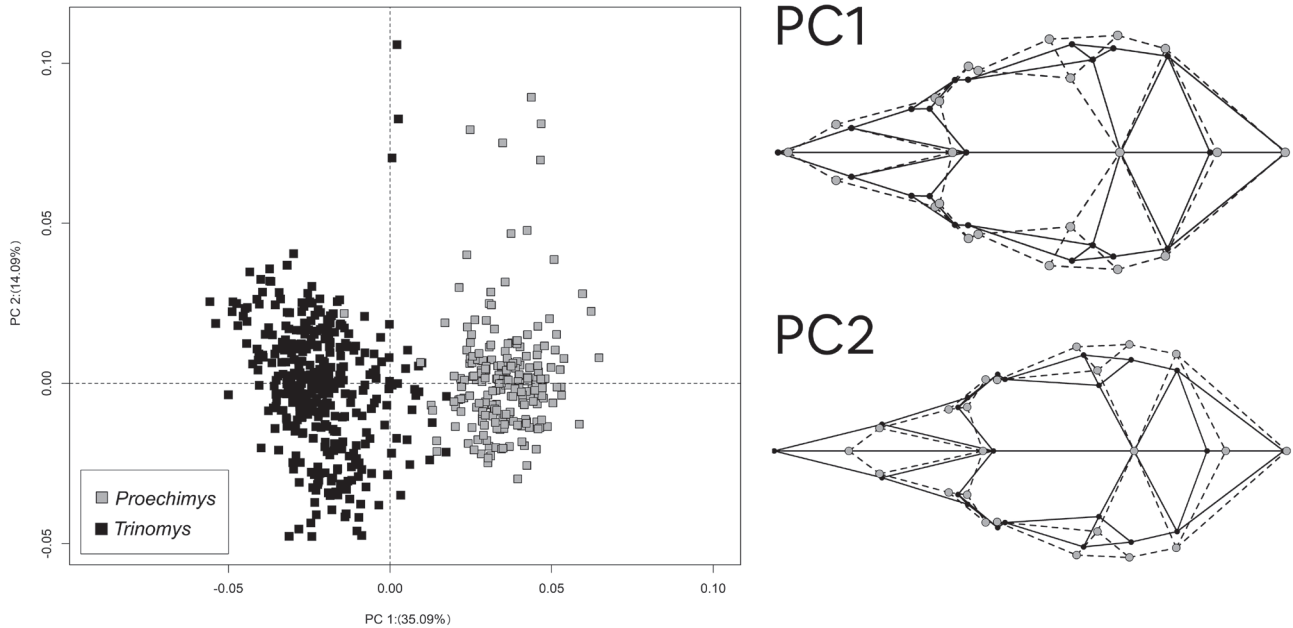


Figura 4: Análise de componentes principais mostrando os dois primeiros componentes (PC1 e PC2) para a forma do crânio de *Proechimys* e *Trinomys* na vista dorsal. Quanto a variação de forma as linhas pontilhadas representam os valores mínimos do PC e as linhas contínuas representam os valores máximos do PC, e os percentuais de explicação de cada PC são dados entre parênteses.

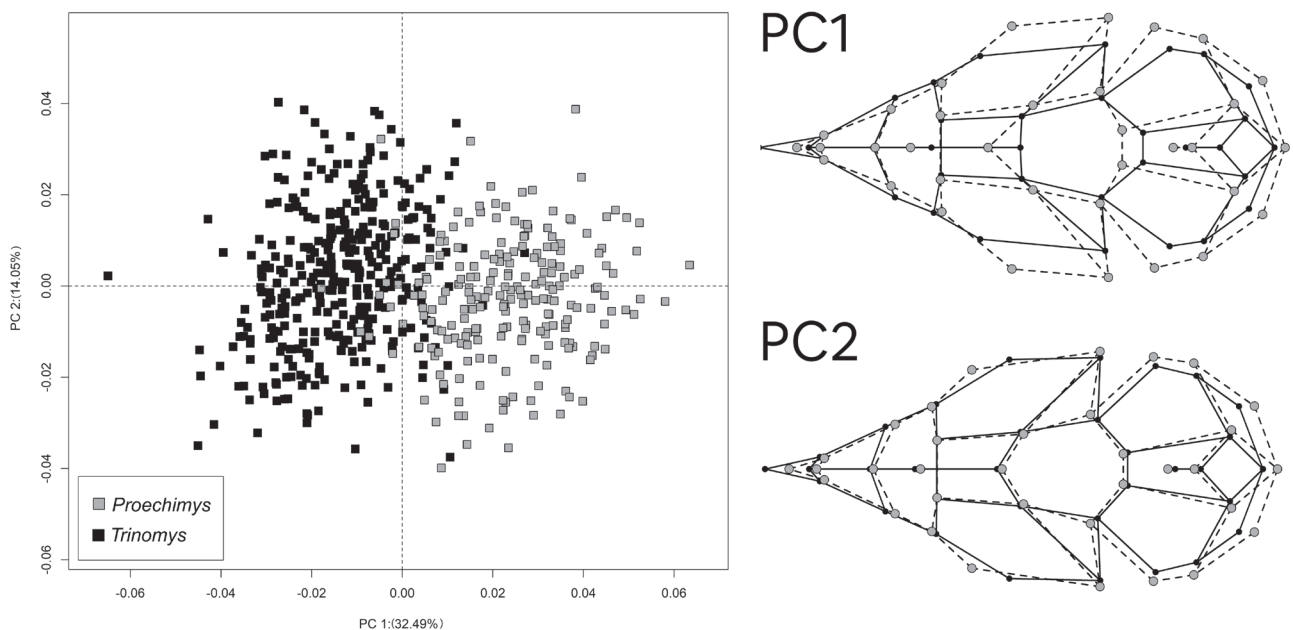


Figura 5: Análise de componentes principais mostrando os dois primeiros componentes (PC1 e PC2) para a forma do crânio de *Proechimys* e *Trinomys* na vista ventral. Quanto a variação de forma as linhas pontilhadas representam os valores mínimos do PC e as linhas contínuas representam os valores máximos do PC, e os percentuais de explicação de cada PC são dados entre parênteses.



geral, as espécies de *Trinomys* apresentam alterações nas bulas auditivas (consideravelmente maiores) e possuem processo jugal mais proeminente e um crânio mais robusto do que espécies de *Proechimys*. Já as espécies de *Proechimys* apresentam um crânio delgado e afilado, característica geralmente encontrada no gênero (Patton & Leite, 2015). A diferença de forma nas bulas auditivas já foi relatada em espécies de Echimyidae, sendo

relativamente maiores em espécies semi-fossoriais e proporcionalmente menores em espécies arbóreas e terrestres (Perez *et al.*, 2009). No gênero *Trinomys* encontramos a espécie semi-fossorial *T. yonenagae*, que possui as bulas auditivas mais proeminentes no gênero (laeger *et al.*, 2021).

No geral, as espécies terrestres da família Echimyidae são caracterizadas por uma baixa divergência

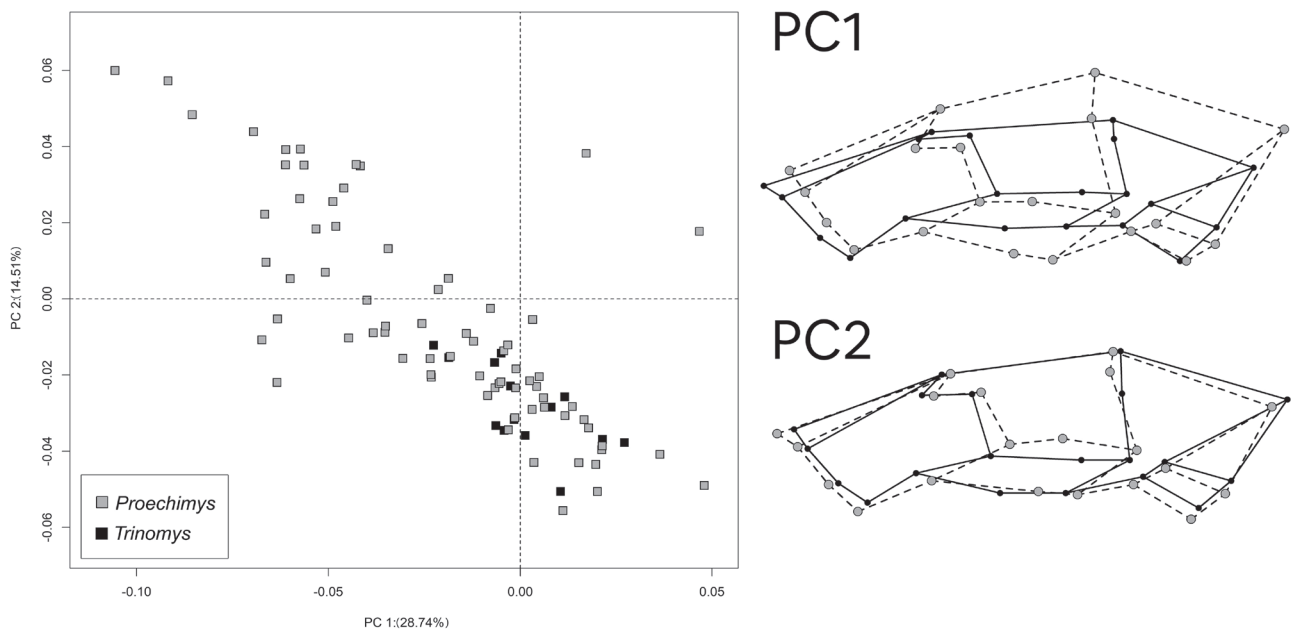


Figura 6: Análise de componentes principais mostrando os dois primeiros componentes (PC1 e PC2) para a forma do crânio de *Proechimys* e *Trinomys* na vista lateral. Quanto a variação de forma as linhas pontilhadas representam os valores mínimos do PC e as linhas contínuas representam os valores máximos do PC, e os percentuais de explicação de cada PC são dados entre parênteses.

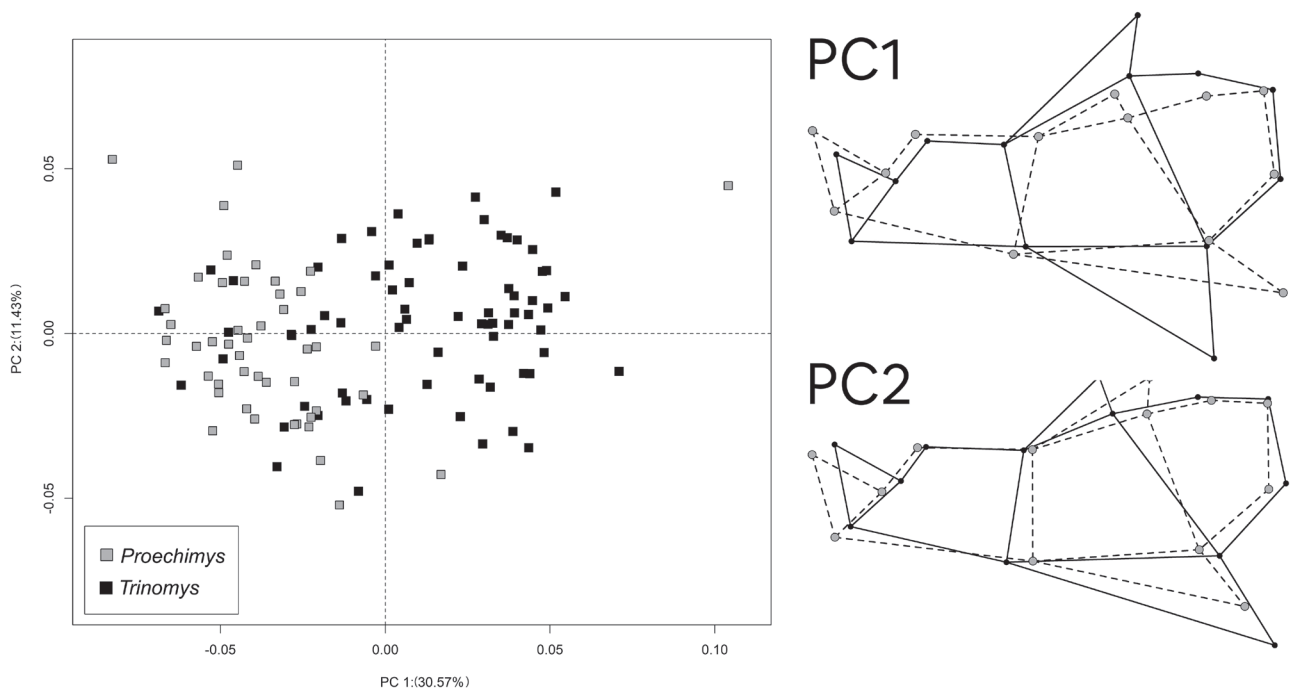


Figura 7: Análise de componentes principais mostrando os dois primeiros componentes (PC1 e PC2) para a forma do crânio de *Proechimys* e *Trinomys* na vista lateral da mandíbula. Quanto a variação de forma as linhas pontilhadas representam os valores mínimos do PC e as linhas contínuas representam os valores máximos do PC, e os percentuais de explicação de cada PC são dados entre parênteses.



morfológica do crânio, com os gêneros *Proechimys* e *Trinomys* compartilhando características crânio-dental e morfológicas (Fabre *et al.*, 2013; Pessôa *et al.*, 2015). A vista lateral do crânio e a mandíbula apresentaram sobreposição de forma entre os gêneros (Figuras 6 e 7). Sendo assim podemos considerar a vista lateral do crânio e a mandíbula como menos informativas e como estruturas que compartilham características morfológicas similares entre os gêneros *Proechimys* e *Trinomys*. A diferenciação morfológica no sincrânio das espécies do gênero *Trinomys* também se deve, em parte, à variação ambiental (laeger *et al.*, 2021). Assim, como relatado em outras espécies de roedores da família Echimyidae, que respondem às pressões ambientais (Fabre *et al.*, 2013), podemos supor que isso ocorre também no gênero *Proechimys*. Portanto, diferenças encontradas na morfologia do sincrânio entre os dois gêneros possivelmente refletem os habitats ocupados por cada um dos gêneros em algum grau. Porém, estudos subsequentes com uma amostragem maior de espécies do gênero *Proechimys* e com análises de influência ambiental explícitas são necessários para detalhar essa influência.

Este trabalho adiciona informações referentes a morfologia craniana às diferenças já estabelecidas (biogeográficas e filogenéticas) entre os gêneros *Proechimys* e *Trinomys*. Futuros estudos podem considerar diferenças entre espécies dentro e entre os gêneros, não exploradas aqui, além de adicionar outras espécie de Echimyidae. Estudos como este são possíveis graças a manutenção de coleções científicas e museus de história natural que mantem e preservam e disponibilizam para estudos o material biológico.

Informações Suplementares encontram-se em
<http://sbmz.org/publicacoes>.

APÊNDICE S1: Espécies de *Proechimys* e *Trinomys* utilizadas nas análises.

APÊNDICE S2: Descrição dos marcos anatômicos para as quatro vistas do sincrânio de *Proechimys* e *Trinomys*.

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APÊNDICE S1

Espécies de *Proechimys* e *Trinomys* utilizadas nas análises. Espécimes depositados nas coleções: Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN-M); Museu Nacional do Rio de Janeiro (MN), Museu de Zoologia da Universidade de São Paulo (MZUSP) e Universidade Federal do Espírito Santo, Vitória, ES (UFES).

Proechimys cuvieri: MZUSP26619; MN61640; MN61641; MZUSP21258; MZUSP21257; MZUSP22932; MZUSP21260; MZUSP21268; MZUSP22935; MZUSP26700; MZUSP21255; MZUSP26622; MZUSP21270; MZUSP26641; MZUSP25983; MZUSP26150; MZUSP26649; MZUSP26136; MZUSP26127; MZUSP26202; MZUSP25948; MZUSP26620; MZUSP26610; MZUSP26616.

Proechimys goeldii: MZUSP7347; MZUSP21278; MZUSP22759; MZUSP21275; MZUSP26609; MZUSP26603; MZUSP26606; MZUSP26621; MZUSP21277; MZUSP21272; MZUSP21276; MZUSP22745; MZUSP21281; MZUSP26617; MZUSP22747; MN6150; MZUSP537; MZUSP26014; MZUSP25937; MZUSP26008; MZUSP26642; MZUSP26012; MZUSP26006; MZUSP26614; MZUSP21279.

Proechimys guyannensis: MN20427; MN20316; MN20350; MN20349; MN20359; MN20374; MN20342; MN20371; MN20444; MZUSP4660; MZUSP8994; MZUSP22353; MN20425; MN20380; MN20336; MN20352; MN20330; MN20310; MN20363; MN20366; MN20339; MN20608; MN20434; MN20446; MN20418; MN20419; MZUSP8074; MZUSP8074.

Proechimys kulinae: UFES2649; UFES2962; UFES2839; UFES2834; UFES2835.

Proechimys longicaudatus: MZUSP25837; MZUSP6346; MZUSP900; MZUSP6347; MZUSP10657; MN64694; MZUSP2005; MZUSP6346; MZUSP17562.

Proechimys roberti: MN34149; MN81717; MZUSP21271; MZUSP4498; MN34140; MN21924; MN4064; MZUSP26655; MN34168; MN34169; MN34170; MN67093; MN50209; MN50213; MN50194; MN50195; MN50199; MN76215; MN76211; UFES1390; UFES1388; MN50200; MN76750; UFES1392; UFES1395; UFES1396; UFES1397; UFES1405; UFES1398; UFES1401; 50-F-UFES1404; UFES1445; UFES1570; UFES1569; UFES1887; UFES1858; MZUSP26612; MZUSP21263; MN81718; MZUSP26693; MN21914; MN34144; MN21922; MN21923; MN4078; MN5454; MN5457; MN34174; MN50211; MN50208; MN50193; MN50196; MN75077; UFES1402; UFES1403; UFES1400; UFES1446; UFES1580; UFES1583; UFES2945; UFES1857; UFES1873; UFES1860; UFES1859; MZUSP26552; MZUSP26604; MZUSP26211; MZUSP26213; MZUSP26220; MZUSP26210; MZUSP25996; MZUSP26188; MZUSP26184; MZUSP26204; MZUSP26204; MZUSP26207; MZUSP26221; MZUSP26208; MZUSP26201; MZUSP26169; MZUSP26205; MZUSP26193; MZUSP26215; MZUSP26166; MZUSP26183; MZUSP26181; MZUSP26182; MN69846; MZUSP26214; MZUSP26195; MZUSP26055; MZUSP26110; MZUSP26134 MZUSP26115; MZUSP26209; MZUSP26133; MZUSP26112; MZUSP26198; MZUSP26219; MZUSP26089; MZUSP26117; MZUSP26111; MZUSP26035; MZUSP26090; MZUSP26116; MZUSP26026; MZUSP25979; MZUSP25984; MZUSP25913; MZUSP25954; MZUSP25930; MZUSP26029; MZUSP25945; MZUSP25944; MZUSP25912; MZUSP25922; MZUSP25947; MZUSP25957; MZUSP25943; MZUSP25991; MZUSP25997; MZUSP26034; MZUSP25941; MZUSP26175; MZUSP26023; MZUSP26167; MZUSP26057; MZUSP26122; MZUSP26118; MZUSP26065; MZUSP25981; MZUSP26135; MZUSP26114; MZUSP26191; MZUSP26130; MZUSP26124; MZUSP26206; MZUSP26216.

Proechimys semispinosus: MN27951; MN27952; MN27954; MN27950; MN27953; MZUSP2002.

Trinomys albispinus: MN9936; MN9958; MN9941; MN13759; MN13870; MN13761; MN33872; MN13764; MN13739; MZUSP2636; MN13792; MN34008; MN9939; MN9938; MN30537; MN13744; MN14026; MN13811; MN13818; MN13819; MN13952; MN33873; MN33879; MN67903; MN6454; MN13740; MN13772; MN13991; MZUSP26722.

Trinomys albispinus minor: MN44544; MN67774; MN67814; MN75883; MZUSP28887 MZUSP28940; MZUSP28885; MZUSP952; MZUSP964; MCN-M1132; MCN-M1136. MN44543; MN67763; MN75882; MN75884; MN75896; MN75873; MN75875; MN75878; MN75880; MZUSP28888; MZUSP28886; MZUSP963; MZUSP961; MCN-M726; MCN-M1050; MN67773; MN75881; MN75903; MN75923; MN75879; MN75877.

Trinomys dimidiatus: MN4943; MN42996; MN5470; MN5450; MN73778; MN70160; MN10350; MN6144; MN6157; MN10366; MN10361; MN10360; MN62269; MN62266; MN43808; MN4950; MN60209; MN4942; MN42770; MN4001; MN10344; MN73362; MN67554; MN10352; MN6147; MN6146; MN6154; MN33705; MN33704; MN6159; MN10367; MN43823; MN30521; MN62265.



Trinomys eliasi: MN42816; MN35884; MN29427; MN42868; MN29426.

Trinomys graciosus: UFES913; UFES1627; UFES1621; UFES1650; UFES1824; UFES1823; UFES1822; UFES1821; UFES1825; UFES1222; UFES1891; UFES1818; UFES1819; UFES912; UFES1652; UFES1617; UFES1835; UFES1651; UFES1817; UFES1820; UFES1839; UFES1615; UFES1889; UFES945; UFES2594; UFES3116; UFES3125; UFES3118.

Trinomys graciosus graciosus: MN43847; MN35883; MN67498.

Trinomys graciosus bonafidei: MN33517; MN43807; MN31370; MN61806; MN43821; MN75827; MN54153; MN75821; M-MN75828; MN15099; MN75826.

Trinomys graciosus panema: MN5656; MN5663; MN5767; MN5757; MN5674; MN5759; MN5772; MN33789; MN33792.

Trinomys iheringi: MN31022; MN43809; MN30520; MN30522; MN30519; MN43806; MN43829; MN31381; MN31382; MN62280; MN67500; MN69873; MZUSP2146; MZUSP28370; MZUSP28378; MZUSP27757; MZUSP10073; MZUSP10210; MZUSP11025; MZUSP27758; MZUSP1966; MZUSP1964; MZUSP1967; MZUSP26646; MZUSP26801; MZUSP11023; UFES2286; 107-F-UFES2232. MN25705; MN34388; MN30517; MN31021; MN43822; MN62281; MN62283; MN62285; MN66190; MN68927; MZUSP2095; MZUSP10071; MZUSP2145; MZUSP2096; MZUSP29409; MZUSP27432; MZUSP10211; MZUSP28381; MZUSP10209; MZUSP11022; MZUSP10212; MZUSP22809; MZUSP213; MZUSP25909; MZUSP26647; MZUSP11427; MZUSP29397; MZUSP28386; MZUSP27756; MZUSP25885; MZUSP25887; MZUSP1962; MZUSP221; MZUSP26550; MZUSP10779; MZUSP11021; MZUSP25878; UFES2231; MN43826; MN24931; MN34156; MN43845; MZUSP2525; MZUSP29410; MZUSP29400; MZUSP3201; MZUSP25900; MZUSP214; MZUSP25905; MZUSP318; MZUSP25910; MZUSP25871; MZUSP25874; MZUSP25904; MZUSP26551; MZUSP25883; MZUSP222; MZUSP25873; MZUSP25902.

Trinomys mirapitanga: MN48012; MN48013.

Trinomys moojeni: MCN-M1036. MCN-M1037.

Trinomys paratus: MN31452; MN31451; MN31407; MZUSP29420; UFES645; UFES641; UFES639; UFES638; UFES637; UFES628; UFES625; UFES654; UFES644; UFES646; UFES648; UFES658UFES659; UFES653; UFES652; UFES651; UFES650; UFES2004; UFES1487; UFES671; UFES674; UFES684; UFES662; UFES669; UFES814; UFES817; UFES815; UFES818; UFES820; UFES2809; UFES2804; UFES2818; UFES3117. MN5455; MN31406; MZUSP29419; UFES634; UFES632; UFES631; UFES630; UFES627; UFES435; UFES434; UFES642; UFES629; UFES436; UFES655; UFES656; UFES657; UFES643; UFES647; UFES649; UFES844; UFES967; UFES663; UFES673; UFES682; UFES683; UFES660; UFES661; UFES816; UFES819; UFES2798; MN67463.

Trinomys setosus: MN10473; MN30532; MN10524; MN10523; MN10997; MN33744; MN31442; UFES2043; UFES285; UFES2063; MCN-M994; MCN-M996; MN31441; MN10515; MN30528; MN30536; MN10521; MN8328; MN8327; MN8325; MN33748; UFES289; MCN-M997. MN74388; UFES2081.

Trinomys setosus elegans: MN34127; MN31448; MN34128; MN34132; MN34129; MN31449.

Trinomys yonenagae: MZUSP28936; MZUSP28941; MZUSP28911; MZUSP28930; MZUSP28913; MZUSP28928; MZUSP28945; MZUSP28944; MZUSP28897; MZUSP28901; MZUSP28900; MZUSP28903; MZUSP28912; MZUSP28883; MZUSP28902; MZUSP28917; MZUSP28920; MZUSP28915; MZUSP28884; MZUSP28943; MZUSP28934; MZUSP28925; MZUSP28935; MZUSP28904; MZUSP28923; MZUSP28933; MZUSP28927; MZUSP28929; MZUSP28899; MZUSP28898; MZUSP28918; MZUSP28919; MZUSP28909; MN44812; MN44814; MN44813.



APÊNDICE S2

Descrição dos marcos anatômicos para as quatro vistas dos sínclânio de *Proechimys* e *Trinomys*.

Vista Dorsal

1 = Extremidade do nasal na sutura entre os nasais; 2 e 3 = Extremidade anterior da sutura entre o nasal e o pré-maxilar; 4 e 5 = Extremidade anterior da raiz do arco zigomático; 6 e 7 = Sutura anterolateral entre o frontal e maxilar; 8 = Sutura sagital entre o frontal e o nasal; 9 e 10 = Extremidade posterior do forame infra orbital; 11 e 12 = Extremidade anterior do forame infra orbital; 13 e 14 = Extremidade final do processo jugal superior; 15 e 16 = Extremidade anterior da sutura entre o frontal e o esquamosal; 17 = Sutura sagital entre o frontal e o parietal; 18 e 19 = Extremidade do processo jugal posterior; 20 e 21 = Ponto de maior largura do meato auditivo externo; 22 = Sutura sagital entre o parietal e interparietal; 23 = Extremidade posterior do occipital.

Vista Ventral

1 = Extremidade anterior da sutura entre os nasais; 2 = Extremidade posterior do alvéolo incisivo; 3 e 4 = sutura entre nasal e pré-maxilar; 5 e 6 = Sutura lateral entre pré-maxilar e maxilar; 7 = Extremidade anterior do forame incisivo; 8 = Extremidade posterior do forame incisivo; 9 e 10 = Extremidade anterior do forâmen infraorbital; 11 e 12 = Margem anterior do alvéolo do 4º pré-molar; 13 e 14 = Margem posterior do alvéolo do 3º molar; 15 e 16 = Sutura entre maxilar e jugal na porção interna do arco zigomático; 17 = Extremidade posterior da sutura do palato; 18 e 19 = Extremidade do processo jugal posterior; 20 e 21 = Extremidade posterior do foramen oval; 22 e 23 = Ponto de maior largura do meato auditivo externo; 24 e 25 = Extremidade lateral da sutura entre basisfenóide e basioccipital; 26 e 27 = Extremidade lateral da apófise mastoide; 28 = Extremidade anterior da parte basilar do osso occipital; 29 = Extremidade anterior do forame magno; 30 e 31 = Extremidade lateral da crista occipital; 32 e 33 = Extremidade lateral do forame magno; 34 = Extremidade posterior do occipital.

Vista Lateral

1 = Extremidade anterior da sutura entre nasais; 2 = Extremidade anterior da sutura entre nasal e pré-maxilar; 3 = Ponto mais posterior do alvéolo incisivo; 4 = Ponto inferior do alvéolo incisivo; 5 = Sutura entre nasal e frontal; 6 = Sutura entre maxilar e frontal na borda do forame infraorbital; 7 = Ponto mais inferior da sutura entre pré-maxilar e maxilar; 8 = Ponto mais inferior da sutura entre maxilar e lacrimal; 9 = Sutura supra posterior entre maxila e jugal na borda do arco zigomático; 10 = Extremidade inferior da sutura entre maxilar e jugal; 11 = Extremidade final do processo jugal superior; 12 = Extremidade final do processo jugal inferior; 13 = Ponto superior da sutura entre frontal e parietal; 14 = Sutura entre frontal, parietal e esquamosal; 15 = Extremidade do processo jugal posterior; 16 = Extremidade anterior da sutura entre pterigoide e bula timpânica; 17 = Extremidade posterior da sutura entre pterigoide e bula timpânica próximo ao meato auditivo externo; 18 = Extremidade inferior da apófise mastoide; 19 = Sutura entre o occipital e bula timpânica; 20 = Extremidade posterior do occipital.

Vista Lateral da Mandíbula

1 = Borda anterior dorsal do alvéolo incisivo; 2 = Borda anterior ventral do alvéolo incisivo; 3 = Extremidade inferior do diastema; 4 = Borda anterior da raiz do 3º molar; 5 = intersecção posterior da raiz do molar com a superfície coronoide; 6 = Ponto dorsal da borda ventral do ramo horizontal com o corpo da mandíbula; 7 = Ponta do processo coronoide; 8 = Máximo de curvatura entre o processo coronoide e condilar; 9 = Borda anterior da superfície articular condilar; 10 = Ponta do processo condilar; 11 = Borda posterior da superfície articular condilar; 12 = Máximo de curvatura entre o processo condilar e angular; 13 = Ponta do processo angular.



The heart of a flying mammal: shared and unique features of the cardiac anatomy of the great fruit-eating bat *Artibeus lituratus*

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Abstract: The ability of true flight and the great diversity of the order Chiroptera might raise questions about the morphology and functionality of the bats' heart. Here we aimed to describe anatomical aspects of the heart of the great fruit-eating bat, *Artibeus lituratus* (Phyllostomidae, Stenodermatinae) and its functional features. Twenty-five individuals had their hearts dissected and described. We found that the *A. lituratus* heart shares general characteristics of the mammalian and Chiropteran heart, such as the bilateral anterior *vena cava*, the bulky pulmonary *conus*, the developed *venae cavae sinus*, the valve in the posterior *vena cava* and the papillary muscles attached to the right ventricle septal wall. Some features seem species-specific, like the anomalous membranous structures found in the right ventricle of some individuals, never seen before in other mammals, and also the presence of the Thebesian valve. Some of the features found might be related to flight adaptations as a highly developed set of pericardial ligaments. This complex set of ligaments has never been described before for another mammal, which probably acts by keeping the heart in position while the bat rests upside down. The pericardial ligaments have infiltrations of white fat, which, together with the deposits present on the surface of the heart, possibly act as energy reserves for the heart muscle. In this work, we suggest the presence of two anterior *venae cavae* has the function of optimizing the blood flow that returns to the heart.

Key-Words: Bats, Chiroptera; Functional anatomy; Heart anatomy; Stenodermatinae.

Resumo: O coração de um mamífero voador: características únicas e compartilhadas da anatomia cardíaca do morcego frugívoro *Artibeus lituratus*. A capacidade do voo verdadeiro e a grande diversidade da ordem Chiroptera podem levantar questões sobre a morfologia e funcionalidade do coração dos morcegos. Aqui objetivamos descrever aspectos anatômicos do coração do grande morcego das frutas, *Artibeus lituratus* (Phyllostomidae, Stenodermatinae) e suas características funcionais. Vinte e cinco indivíduos tiveram seus corações dissecados e descritos. Descobrimos que o coração de *A. lituratus* compartilha aspectos gerais tanto do coração de mamíferos quanto os característicos dos quirópteros, como a veia cava anterior bilateral, o cone pulmonar volumoso, o seio das veias cavas desenvolvido, a válvula da veia cava posterior e os músculos papilares ligados à parede septal do ventrículo direito. Algumas características parecem específicas da espécie, como as estruturas membranosas anômalas encontradas no ventrículo direito de alguns indivíduos, nunca antes vistas em outros mamíferos, e também a presença da válvula Thebesiana. Algumas das características encontradas podem estar relacionadas a adaptações ao voo, como um conjunto desenvolvido de ligamentos pericardiais. Este conjunto complexo de ligamentos nunca foi descrito antes para outro mamífero, esses provavelmente atuam mantendo o coração em posição e enquanto o morcego descansa de cabeça para baixo. Os ligamentos pericardiais apresentam infiltrações de gordura branca, que juntamente com os depósitos presentes na superfície do coração, possivelmente atuam como reservas de energia para o músculo cardíaco. Neste trabalho, sugerimos que a presença de duas veias cavas anteriores tem a função de otimizar o fluxo sanguíneo que retorna ao coração.

Palavras-Chave: Anatomia do coração; Anatomia funcional; Morcegos; Quirópteros; Stenodermatinae.

INTRODUCTION

The bats (Chiroptera, Mammalia) are the only mammals capable of true flight, showing a collection of adaptations for this extreme mode of locomotion. Much is known about the external and more conspicuous features, like the wings, grasping hind limbs and echolocation apparatus (Fenton & Simmons, 2014), but the internal structures, of equal importance for understanding the organism functioning and evolution, are poorly described, taking into account the great

diversity of the order. One of these internal structures is the heart. The mammal heart shares a common basic structure across the taxon, but several differences can be seen between orders. Also, intraspecific variation is common, regarding the heart shape, the number of the great vessels and their branches, the number and composition of valve leaflets, the chamber wall texture and the presence of certain structures like the moderator band and the *ductus arteriosus* (Amoroso *et al.*, 1942; Barnett *et al.*, 1958; Hyde, 1891; Navaratnam, 1980; Rowlatt, 1968; 1990; Stephenson *et al.*, 2017; Truex &



Copenhaver, 1947; Truex & Warshaw, 1942). Many authors described the heart anatomy of flying foxes. They are large bats with big hearts, easy to dissect (Alcock, 1898; Alijani & Ghassemi, 2016; Rowlatt, 1967; 1980). This was important to give the first insights regarding the anatomy of the Chiropteran heart and the inter and intraspecific variations.

A few authors dissected the heart of small bats, belonging to the families Emballonuridae, Molossidae, Natalidae, Phyllostomidae, Thyropteridae and Vespertilionidae (Gupta, 1966; Park, 1954; Rowlatt, 1980), giving a glimpse at the circulatory system in this latter group. However, many of these papers don't bring detailed descriptions of each contemplated species' hearts, focusing on one aspect of the organ or bringing a general description of more than one species. The Neotropical bat fauna is still a rich field to explore in this area, the great diversity of its nine families brings many questions about the morphology, variability and functionality of their organs and structures, including the heart (Fenton & Simmons, 2014).

The great diversity of bats and its unique mode of locomotion among mammals can bring questions about the morphology, variability and functionality of their hearts. These animals present some characteristic features, like bilateral *venae cavae*, a well-developed pulmonary *conus*, smooth walls of the right ventricle, a large right auricle and papillary muscles attached at the right ventricle's septal wall (Alcock, 1898; Alijani & Ghassemi, 2016; Rowlatt, 1967; 1980). Some of these features possibly have functional importance, for example, since bats experience a large venous return during flight compared to resting activity, the well-developed pulmonary *conus* possibly protects the pulmonary vasculature against the effects of rapid increase in blood flow during takeoff and the larger right auricle could act as a blood reservoir in these conditions (Rowlatt, 1967; 1980). The smooth walls of the right ventricle, an unusual feature for mammals, can act decreasing resistance against blood flow (Rowlatt, 1967).

Thereat, in this paper we will describe the heart of the great fruit-eating bat, *Artibeus lituratus*, as a whole, comparing it with other bats described in the literature. *Artibeus lituratus* belongs to the subfamily Stenodermatinae, weighing between 65 and 82 g. This bat feeds primarily on fruits, complementing its diet with insects, leaves, pollen and nectar (Kalko *et al.*, 1996; Reis *et al.*, 2013). This is a common phyllostomid, found in many Central and South America cities and rural landscapes (Kalko *et al.*, 1996; Reis *et al.*, 2013). We expected that *A. lituratus* heart has the typical mammalian anatomy, showing chiropteran features, but we intend to describe characteristics poorly studied for the family Phyllostomidae, or not described at all, like the pericardium, the pericardial ligaments, the internal cavities and the heart valves, accessing its functional properties.

MATERIALS AND METHODS

Twenty-five adult individuals were captured using mist nets. The bats were overdosed with isofluran until respiratory arrest, and death was confirmed by cardiac arrest (CONCEA, 2015). The specimens were frozen until the time of dissection. The dissected hearts of all animals were kept immersed in 70% alcohol.

Before dissection, 14 animals were formalized in buffered formaldehyde solution-salt 10% and 11 were kept frozen. The differentiation in the preservation method was effective for observing the structures of the hearts of these animals, since the fixation in formalin stiffens certain structures facilitating their differentiation and separation from other tissues, while freezing allows the removal of blood from inside the chambers after defrosting and the visualization of more delicate parts. This heart preservation protocol was developed for this work.

The dissection used a protocol developed for this work. First, a cut was made below the diaphragm, above the manubrium and on each side of the body, cutting the ribs and clavicles, in order to remove the entire frontal portion of the rib cage and have access to the intact internal organs. The *in situ* position of the heart, lungs and diaphragm was described. Second, the heart and lungs were removed together from the rib cage for a more detailed description of the heart's conformation with the lungs. Third, the lungs were separated from the heart at the point where the pulmonary arteries and veins enter these organs, and the heart's external aspects were described. Fourth, the heart was opened cutting along the interatrial, interventricular and atrioventricular limits, in order to expose the internal structures with as little damage as possible, and the cavities were described as to its shapes and structures. The heart examination was made using a Nikon C-FMBN stereoscope microscope and the specimen photographs were taken with a 48 MP, 1.6 μm Quad Pixel smartphone cam. The procedures were authorized by the ethics committee on the use of animals for laboratory research (CEUA-UFMG), under the protocol number 267/2018, and by the Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio under license number 12989-3.

RESULTS

The heart of *Artibeus lituratus* is entirely surrounded by a transparent pericardium that merges with the mediastinal pleura in its cranial portion. The parietal lamina is translucent, thicker on the lateral aspects, where it presents a reddish and opaque color (Figure 1). The visceral lamina is thin and transparent, lines the muscle tissue and coronary vessels, and it is not detachable from the muscle. Between the two pericardial layers, the pericardial cavity surrounds the entire

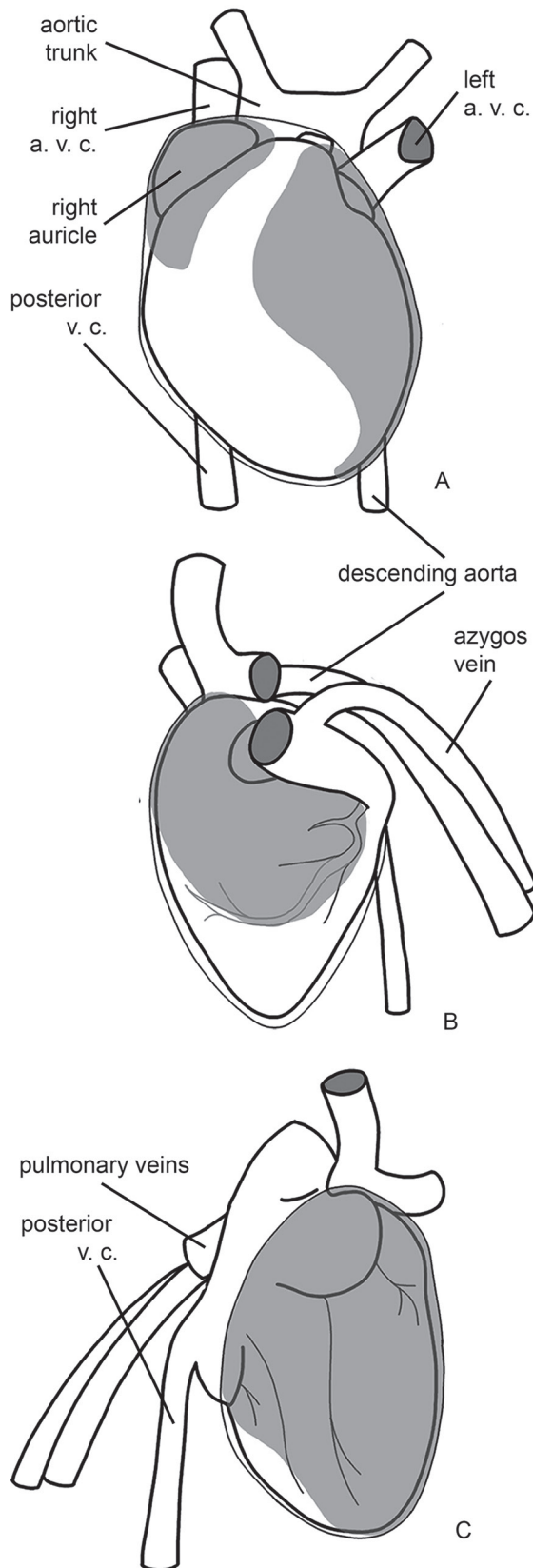


Figure 1: Schematic drawing of the opaque areas of the parietal pericardium. The parietal pericardium is represented as a thin line surrounding the heart, the opaque areas as the darkened regions, left translucent in order to show what structures these areas cover in the heart. (A) frontal view, (B) right lateral view, (C) left lateral view. a. v. c. = anterior *vena cava*; v. c. = *vena cava*.

organ, whose limits are found at the base of the heart around the insertion of the great vessels. The orifices of the *venae cavae* and the auricles are located inside the pericardial cavity, surrounded by the parietal lamina, while the orifices of the aortic and pulmonary trunk are located outside the cavity. The thickest and opaque areas of the parietal lamina are found on the lateral aspects of the heart and on the frontal aspect, carrying the pericardial blood vessels.

The heart is supported in the chest cavity by a series of membranous ligaments. The sternopericardial ligament is a strip of transparent tissue located in the anterior mediastinum, which connects the frontal aspect of the parietal pericardial lamina to the sternum and to the diaphragm (Figures 2B and 3A). The cranial border attaches to the upper mediastinum, cranial to the manubrium and medial to the clavicles, while the caudal border connects to the caudal limit of the sternum body and to the diaphragm, where there is a white fat deposit (Figures 2B-C and 3A). The dorsal border connects to the upper mediastinum and runs along the frontal aspect of the heart, while the frontal border connects to the median axis of the sternum dorsal surface and follows its entire length. A blood vessel travels from the cranial to the caudal borders of this ligament, and there may be an linear infiltration of white fat following its length. The sternopericardial ligament is better seen from both the thoracic cavity's lateral views.

In its caudal portion, the sternopericardial ligament becomes the pericardiophrenic ligament that begins in the central tendon of the diaphragm, over the frontal aspect of the posterior *vena cava*, curving frontally and then dorsally, extending to the spine (Figures 2 and 3A). Therefore, in the dorsal portion of the rib cage, the pericardiophrenic ligament forms a pouch with the lumen facing dorsally, closed cranially by the caudal aspect of the heart and caudally by the diaphragm. The left lateral aspect of this ligament supports, in the frontal-dorsal direction: esophagus, descending aorta and azygos vein (Figures 2 and 3A). This ligament and its pouch are better seen from the thoracic cavity's right lateral view. Dorsally and continuously with the pericardiophrenic ligament is the pericardiovertebral ligament, a band of tissue that connects the heart and the dorsal aspect of the superior mediastinum to the entire thoracic extension of the spine (Figure 3A). This extensive set of pericardial ligaments completely divides the thoracic cavity into two halves, one lung on each side, with no connections between them. The pericardiovertebral ligament is better seen from both thoracic cavity's lateral views.

The heart of *A. lituratus* is located in the center of its rib cage, dorsal to the sternum, the apex facing left (Figure 2A). The heart is longer than wider and the apex is round. The left auricle is smaller than the right, has a triangular or discoid shape and wrinkled outer surface and edges, with a constriction at the point where it connects to the heart (Figures 3C and 4A). The right auricle is visibly

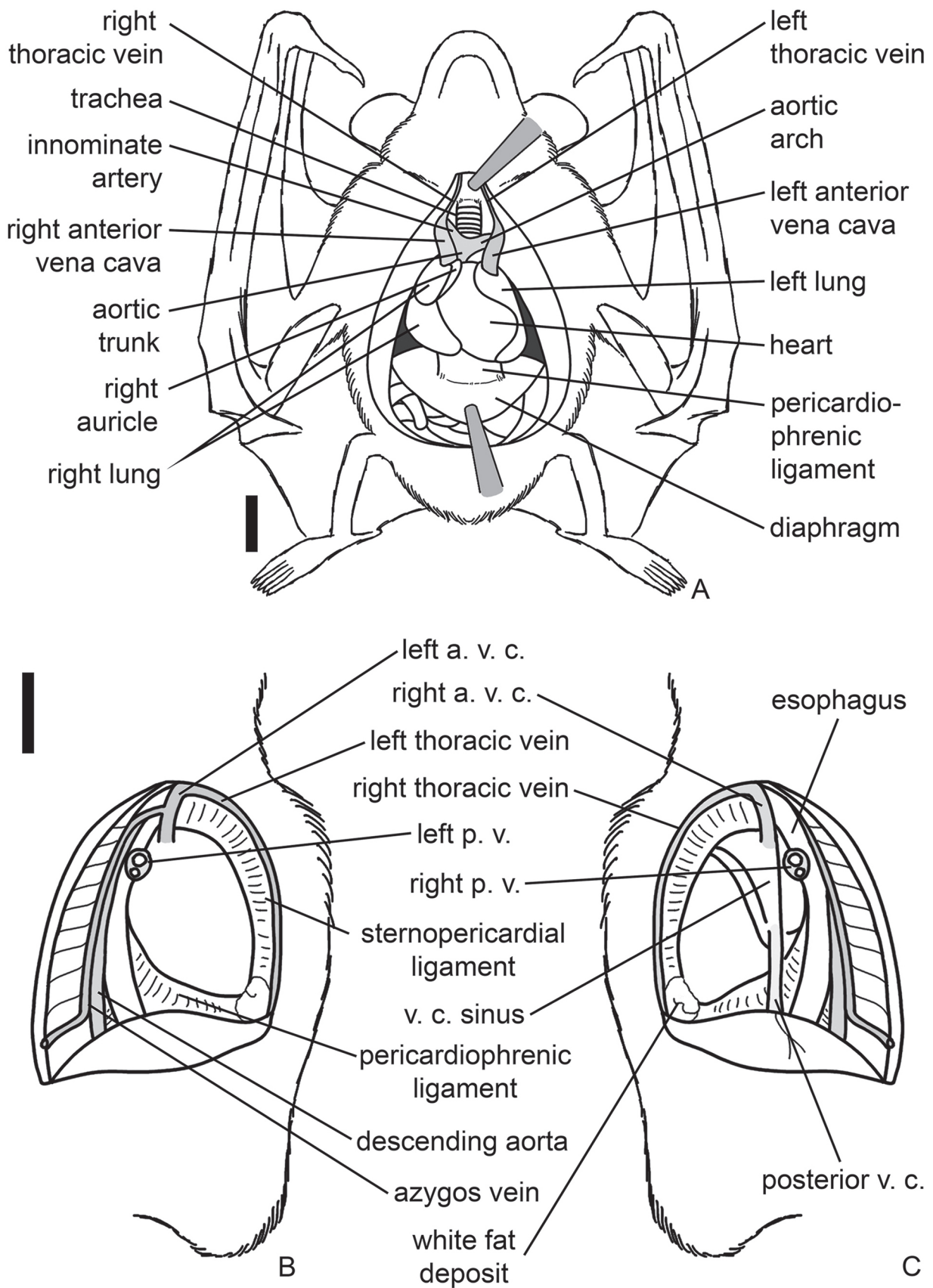


Figure 2: Schematic drawings of the thoracic cavity. (A) frontal view; (B) right lateral view; (C) left lateral view. The black bars correspond to 1 cm. a. v. c. = anterior *vena cava*; p. v. = pulmonary vein; v. c. = *vena cava*.

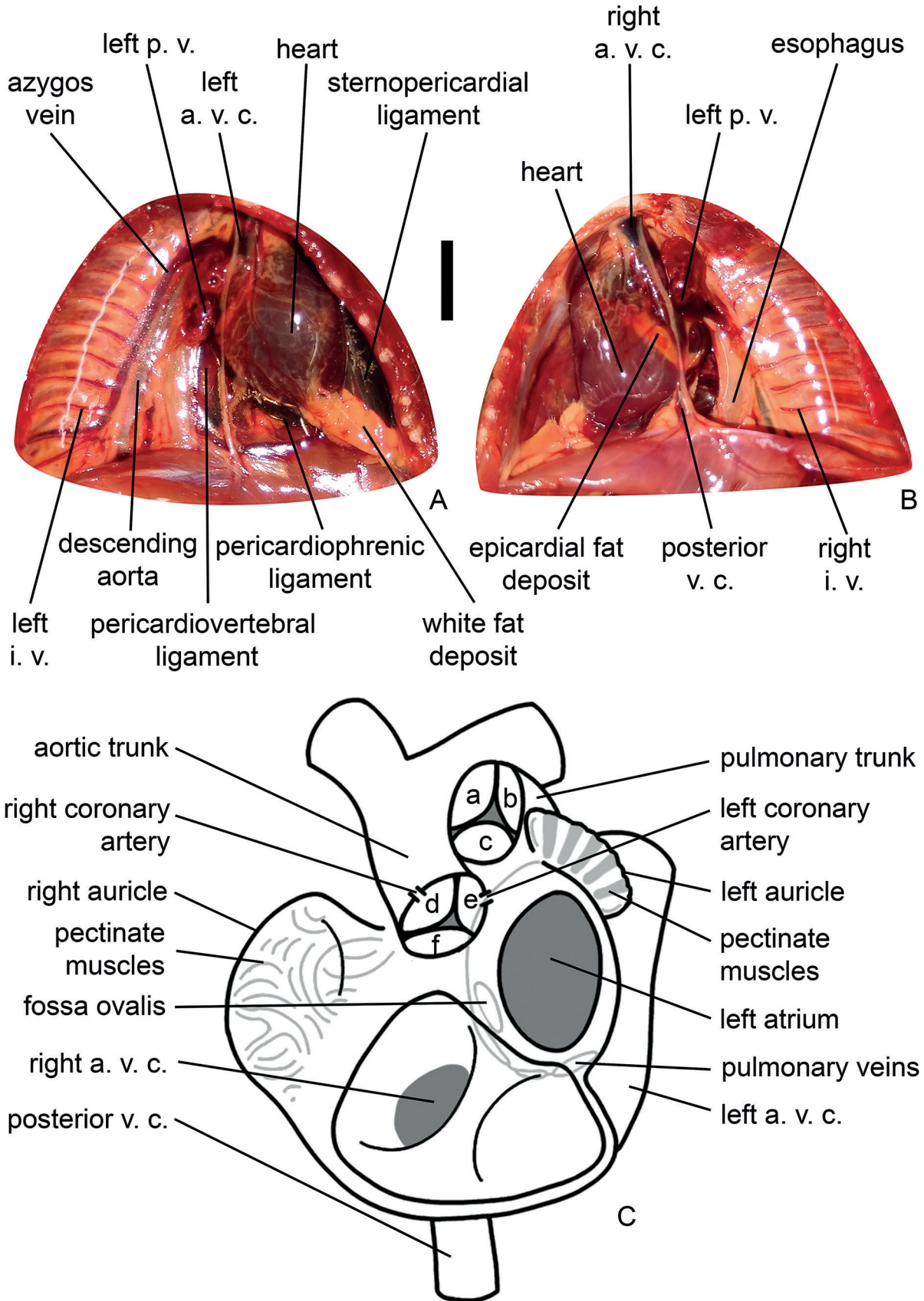


Figure 3: (A) Photo of the right lateral view of the thoracic cavity; (B) photo of the left lateral view of the thoracic cavity; (C) schematic drawing of the left and right atria caudal view, a cross section at the level of the atrioventricular valves. (a) right ventral pulmonary valve leaflet, (b) left ventral pulmonary valve leaflet, (c) dorsal pulmonary valve leaflet, (d) ventral aortic valve leaflet, (e) left dorsal aortic valve leaflet, (f) right dorsal aortic valve leaflet. The black bar corresponds to 1 cm. a. v. c. = anterior *vena cava*; p. v. = pulmonary vein; v. c. = *vena cava*; i. v. = intercostal vein.

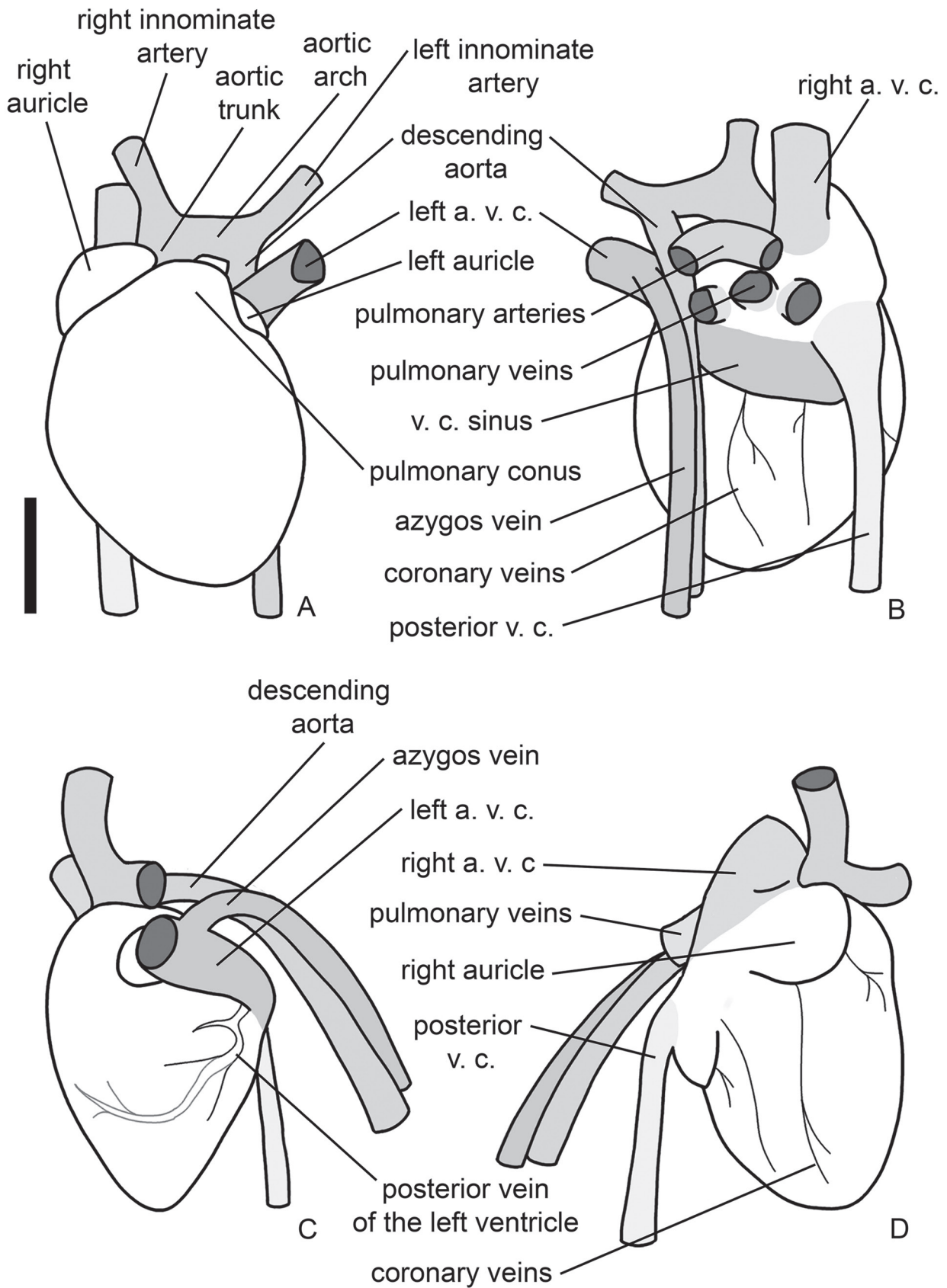


Figure 4: Schematic drawing of the *Artibeus lituratus* heart. (A) frontal view; (B) dorsal view; (C) right lateral view; (D) left lateral view. The black bar corresponds to 0.5 cm. a. v. c. = anterior vena cava; v. c. = vena cava.



larger than the left, has a slightly triangular shape with wrinkled external surface and edges (Figures 3C and 4A). It is located frontal to the opening of the right anterior *vena cava*, and curves over the frontal aspect of the aortic trunk orifice (Figures 1A, 2A and 4A). The interventricular groove may or may not be visible from the frontal surface of the heart and contains the great cardiac vein. The atrioventricular groove is not distinct.

The aortic trunk arises from the left ventricle, from the base of the heart, medial to the right anterior *vena cava* and pulmonary trunk (Figures 1A and 4A). The aortic trunk is short and protrudes cranially, dividing into two branches of similar caliber. The right branch is the right innominate artery and curves to the right, while the left branch is the systemic aorta, which curves to the left (Figure 4A). The systemic aorta forms the aortic arch, which runs parallel to the heart cranial plane and gives origin to the descending aorta, which follows in the caudal direction, forming a right angle with the aortic arch (Figures 1A-B and 4A-C). The descending aorta curves dorsally and then caudally, passing medial to the pulmonary trunk left branch and left anterior *vena cava*. This vessel runs through the dorsal aspect of the heart, over the median plane of the body, frontal to the azygos vein and dorsal to the esophagus, until it pierces the diaphragm (Figure 4A-C). The aorta and its branches are better seen from the frontal view of the heart.

The aortic arch also gives origin to two more vessels, the left common carotid artery, which goes cranially and the left subclavian artery, which goes to the left in relation to the aortic arch. In one individual these vessels were observed to emerge from a short artery trunk that arises from the aortic arch with the descending aorta, the left innominate artery (Figure 4A). The right innominate artery also gives origin to two branches, the right common carotid artery, which goes cranially and the right subclavian artery, which runs to the right in relation to the right innominate artery. In two individuals, the presence of a reminiscent of the *ductus arteriosus* was observed, connecting the left branch of the pulmonary trunk and the descending aorta, presenting a narrow lumen with closed ends, not being a functional duct (Figure 6C). The aortic trunk and its vessels have thick, stiff walls, which are visually thicker than those of the pulmonary arteries and all the veins. The diameter of the aortic trunk lumen and its branches is visually smaller than that of the veins.

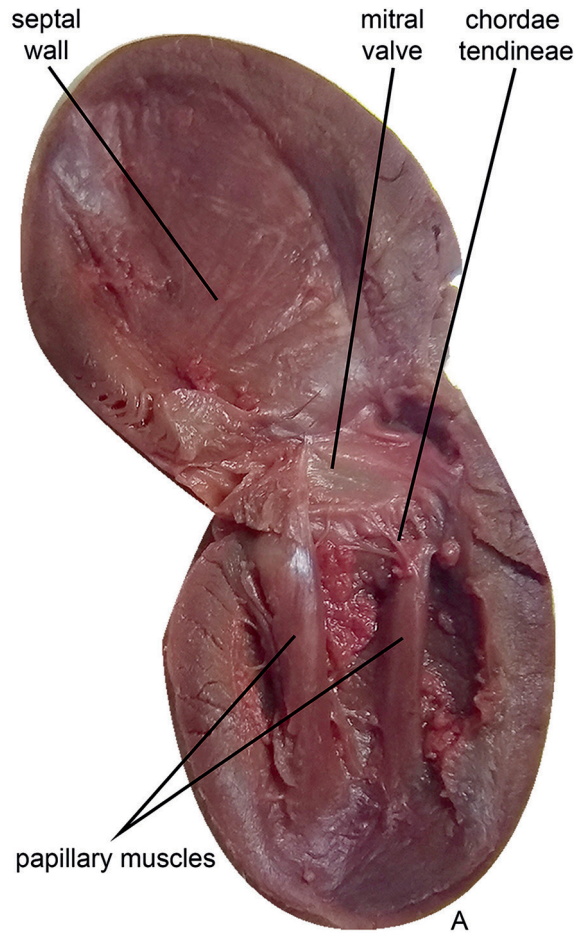
The pulmonary trunk orifice is located to the left of the aortic trunk, in the dorsal aspect of the conspicuous pulmonary *conus* (Figure 4A-B). The pulmonary trunk is short and goes dorsally, perpendicular to the aortic trunk. The pulmonary trunk gives origin to two pulmonary arteries, the right pulmonary artery and the left pulmonary artery (Figure 4B). The walls and diameter of the pulmonary trunk and arteries are similar to the aortic vessels. The pulmonary trunk and its branches are better seen from the cranial view of the heart.

There are three *venae cavae*, the left anterior *vena cava*, which reaches the heart from the left and is dorsal to the left auricle, the right anterior *vena cava*, which reaches the heart from the right and is dorsal to the right auricle, and the posterior *vena cava*, which reaches the heart caudal to the right anterior *vena cava* (Figures 1A-C, 3A-B and 4). The anterior *venae cavae* have a visually larger caliber than the arteries and also thin, malleable and collapsible walls. The posterior *vena cava* has a visually smaller caliber than the previous ones and similar wall consistency. The right anterior *vena cava* empties directly into the right atrium, the left forms a large arc-shaped *sinus* that connects to the atrium (Figure 4B). In this paper, we call this structure the *venae cavae sinus*. The posterior *vena cava* enters this *sinus* caudal to the right anterior *vena cava* (Figure 4B and D), and its orifice is guarded by a bicuspid valve, or Eustachian valve. This vessel reaches the heart parallel to the median axis of the body, curving frontally before entering the heart (Figure 3B-C). Each anterior *venae cavae* receives an internal thoracic vein that runs the entire length of the sternum dorsal surface (Figure 2B-C). The orifices of these vessels are located in the frontal aspect of their respective *vena cava*, at the point where they arise from the cranial surface of the chest cavity. There is an azygos vein that follows the spine, receiving the intercostal veins, and it enters the dorsal aspect of the left anterior *vena cava*. It has a visually smaller diameter than the other veins and thin, malleable and collapsible walls as well (Figures 1B, 2B, 3A and 4B-C). The *venae cavae sinus*, the *venae cavae* and the azygos vein are better seen from the dorsal view of the heart.

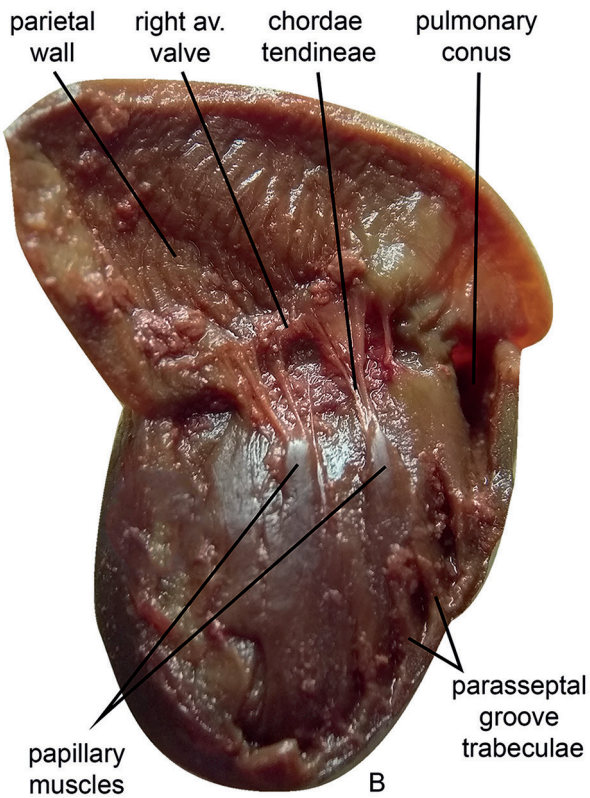
The pulmonary veins enter the heart cranial to the *venae cavae sinus*, medial to the anterior *venae cavae* (Figure 4B). There are two sets of pulmonary veins, one for each lung, ranging up to two or three orifices. These veins give origin to vessels that enter the lungs cranial to the insertion of the bronchi. They are short, having a visually larger caliber than the arteries and thin walls similar to the *venae cavae*. The pulmonary veins are better seen from the dorsal view of the heart.

The atria have visually thinner walls compared to the thick and muscular walls of the ventricles. The left atrium is formed by the atrium itself and the left auricle, the pulmonary veins flow into its parietal wall (Figure 3C). The shape of the cavity is oval and flat in the cross section. The left auricle has parallel pectinate muscles that connect the cranial and caudal walls, originating at the edges of the auricle cavity until near the orifice, dividing the cavity into open compartments (Figure 3C). The septal wall of the atrium has a *fossa ovalis* close to its dorsal border (Figure 3C). It is formed by an oval area of thin and translucent tissue, bordered by the limbic bands.

The right atrium is formed by the atrium itself, the right auricle and the *venae cavae sinus* (Figure 3C). The atrium internal walls are smooth, the lumen is free of



A



B

Figure 5: Photographs of the left and right ventricles longitudinal sections. (A) left ventricle, (B) right ventricle. a. v. = atrioventricular.

trabeculae and the cavity has a triangular shape in longitudinal section and an oval shape in cross section. The orifice of the right auricle is located caudal to right anterior *vena cava* orifice. The internal walls of this appendix are covered by well-marked interdigitated pectinate muscles (Figure 3C). Both atria discharge into their respective ventricles through wide oval atrioventricular orifices, guarded by the atrioventricular valves (Figure 5).

The ventricles have much thicker and more muscular walls than the atria. The left ventricle is circular in cross-section and conical in longitudinal section (Figure 5A). The parietal wall is visually thicker than that of the right ventricle, internally has thin and longitudinal grooves. The septal wall shows a slight roughness. Two thick papillary muscles originate from the caudal portion of the cavity, running along the lateral edges of the walls and ending near the atrioventricular orifice, being connected in all their extension with the parietal wall (Figure 5A). Several *chordae tendineae* arise from their cranial portion, not directly from the tip, and support the two leaflets of the left atrioventricular valve (mitral valve), one papillary muscle at each side of the valve (Figure 5A). The aorta orifice is located cranial and frontal to the leaflets of this valve.

The right ventricle is formed by the ventricle itself and the pulmonary *conus* (Figure 5B). The ventricle has a half moon shape in cross section, with the concavity facing the center of the heart and surrounding the left ventricle cavity. The texture of the internal walls is smooth, there are no developed *trabeculae* or deep grooves, with the exception of the paraseptal groove (Figure 5B). The ventricular cavity itself is located in the dorsal and right lateral aspect of the heart, but it curves frontally giving origin to the pulmonary *conus*, which forms a chamber continuous to the rest of the ventricle and empties into the pulmonary trunk (Figure 5B). Internally, the *conus* has smooth walls and is bordered by the supraventricular crest and the paraseptal groove, the latter marked by deep *trabeculae* perpendicular to the direction of blood flow (Figure 5B).

One individual presented a single membranous band connecting the septal and parietal walls of the right ventricle, in the same anatomical position as the moderator band, which was not seen in the heart of any other individual (Figure 6A). One individual presented a membranous and laminar structure, located at the entrance of the pulmonary *conus*, consisting of tissue similar to that of the atrioventricular valves and attached to the walls by filaments similar to the *chordae tendineae* (Figure 6). There are several leaflets forming a net-like structure, with free spaces where the blood flowed.

The septal wall of the right ventricle has two to four papillary muscles, which originate in the middle of the wall and proceed in the cranial direction, ending in a rounded tip (Figure 5B). They are connected to the septal wall only at their caudal end, being detached

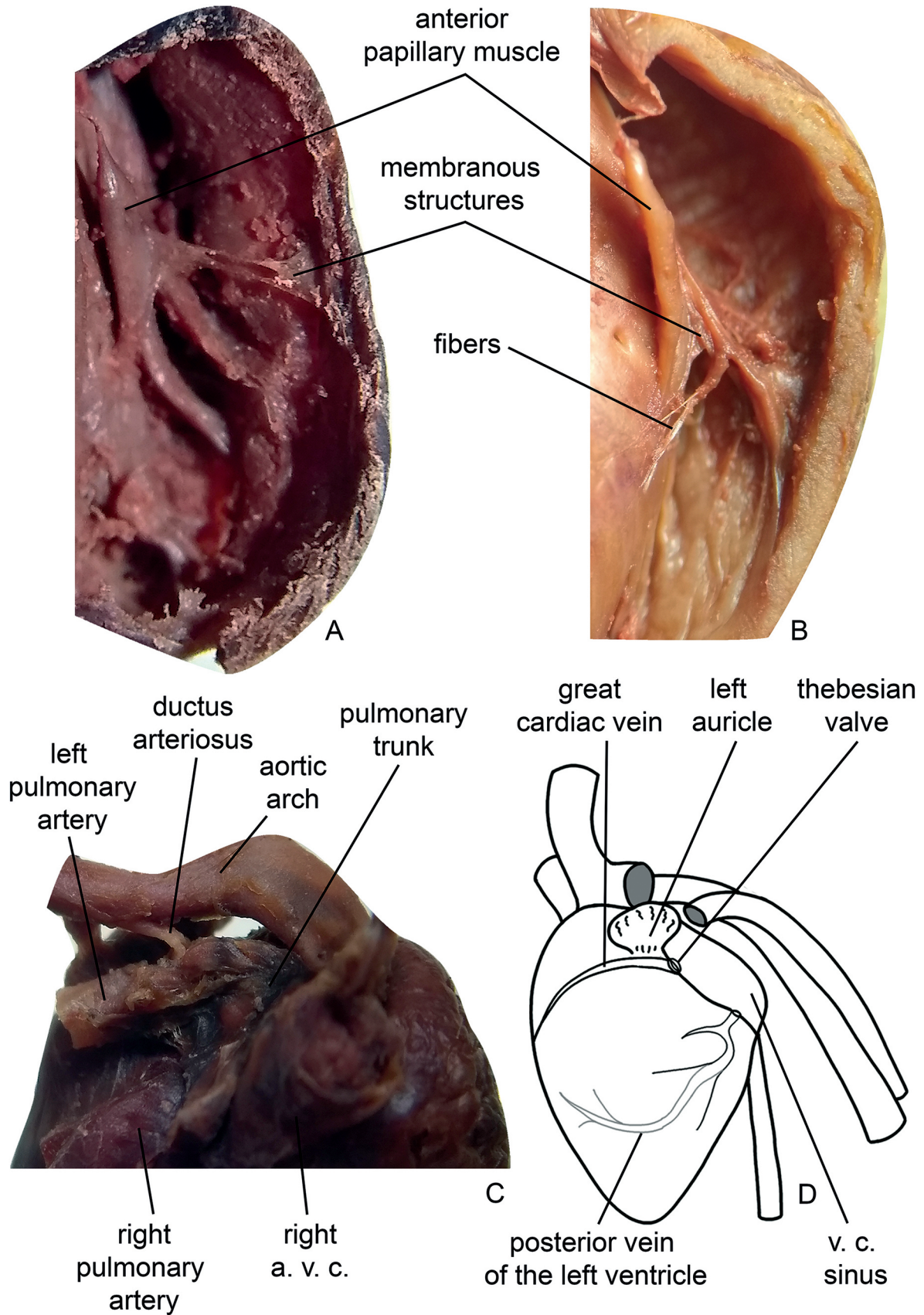


Figure 6: Exceptional structures in the heart of *Artibeus lituratus*. (A) detail of the right ventricle indicating a membranous structure connecting the caudal end of the anterior papillary muscle to the parietal wall; (B) view of the pulmonary *conus* interior indicating a membranous structure associated with fibers similar to *chordae tendineae*; (C) cranial view of the heart indicating the ductus arteriosus; (D) schematic drawing of the path and location of the great cardiac vein and its orifice. a. v. c. = anterior *vena cava*; v. c. = *vena cava*.



from it along its length. From the free end of each muscle comes a bundle of *chordae tendineae* that support the single leaflet of the right atrioventricular valve (Figure 5B). In the same heart, these structures may have different lengths, the right (anterior) papillary muscle is normally the most developed. The shape, number and conformation of the right ventricular papillary muscles vary between bats, and several morphologies have been observed. In some individuals, certain papillary muscles were small elevations over the ventricular wall, while in others, well-developed structures were observed, wider and with a double tip, as if two papillary muscles were fused, each tip with its own bundle of *chordae tendineae*. In some cases, bundles of *chordae tendineae* were attached directly to the septal wall.

The semilunar and atrioventricular valves are located in the cardiac skeleton. The aortic semilunar valve is formed by three equal leaflets with the shape of a bag, there is a ventral, a left dorsal and a right dorsal leaflet (Figure 3C). The pulmonary trunk semilunar valve also has three equal leaflets, a dorsal, a left ventral and right ventral leaflet (Figure 3C). The atrioventricular valves leaflets consist of thin and elastic tissue, with a semicircular or half-moon shape (Figure 5). The left atrioventricular orifice is guarded by a bicuspid (mitral) valve, consisting of two equal leaflets. The aortic leaflet attaches to the orifice septal edge, dividing the flow between the atrioventricular orifice and the aortic orifice, and the parietal one attaches to the parietal edge of the atrioventricular orifice. There is a well-defined *pars membranacea*, which is the extension of the mitral valve aortic leaflet to the aortic valve ventral leaflet. The right atrioventricular valve has a single leaflet that attaches to the parietal edge of the orifice (Figure 5B).

The coronary arteries orifices are located in the *sinuses* of Valsalva. The left coronary artery orifice is guarded by the left dorsal leaflet of the aortic valve, while the right coronary artery orifice is guarded by the ventral leaflet (Figure 3C). The number of orifices for each coronary artery varied between individuals. Coronary arteries cannot be seen from the surface of the heart, but the coronary veins are visible. The great cardiac vein travels through the interventricular groove, passing under the left auricle and opening up in the right atrium (Figure 6D). Two more calibrated coronary veins flow into the caudal edge of the *venae cavae sinus* through separate orifices, one vessel on each side of the dorsal surface, traversing the muscle perpendicular to each other. Both receive minor branches. Other shorter veins also flow directly into the caudal border of the *sinus* medial to the two largest. The posterior vein of the left ventricle runs through the left lateral aspect of the heart, ending at the proximal end of the left anterior *vena cava* (Figures 4C and 6D).

The orifice of the great cardiac vein is located medial to the *venae cavae sinus* wall and the left anterior *vena cava*, dorsal to the left auricle. It is guarded by a

bicuspid valve, the Thebesian valve, whose leaflets are shaped like a half moon, are membranous and translucent, oriented parallel to the median axis of the body (Figure 6D). Therefore, the heart of *A. lituratus* does not have a coronary *sinus*, only the great cardiac vein flows into the atrium, and the other coronary veins are open individually at the caudal edge of the *venae cavae sinus*.

DISCUSSION

Artibeus lituratus presents a well-developed set of pericardial ligaments. Only Rowlatt (1967, 1980) describes a sternopericardial ligament similar to that observed in the present study for the Straw-colored fruit bat, *Eidolon helvum* (Kerr, 1792) and the Indian flying fox, *Pteropus medius* (Temminck, 1825). We suggest an explanation for the function of these three extensive ligaments, they possibly share the work of supporting the weight of the heart. As the bat's natural resting position is upside down, if there were no pericardial ligaments or only few anchoring points, the heart would move by gravity to the cranial portion of the rib cage, pressing and collapsing the great vessels. The diaphragm contraction would be compromised, since it would be pulled cranially, and the large vessels that pierce this muscle would stretch under the weight of the heart. In addition, when positioning the heart in the center of the thoracic cavity, such ligaments would prevent the organ from rotating on its transverse axis, pressing on the pulmonary veins. Unfortunately, there are few studies describing the mammal pericardium and many of them focus only on the description of parietal and visceral lamina (Michaëls-son & Ho, 2000; Sisson, 1975). Therefore, to support this hypothesis, studies focusing on the mechanical role of the pericardial ligaments of bats and other mammals in supporting the heart are needed.

The caudal portion of the *A. lituratus* sternopericardial ligament has a white fat infiltration, and deposits of white adipose tissue can be seen on the surface of the heart. The first case, according to Marchington *et al.* (1989), corresponds to the pericardial deposits, which are formed in the parietal pericardium, and the second to the epicardial deposits, which are formed in the visceral pericardium, also called the epicardium. Other authors described similar pericardial deposits for flying foxes, as well as the presence of fat along the vessels that supply the pericardium, between the great vessels and epicardial deposits on the cardiac apex (Alijani & Ghassemi, 2016; Rowlatt, 1967; 1980). The epicardial adipose tissue in mammals has specific morphological and biochemical characteristics that relate to the energetic needs and physiological balance of the heart muscle (Marchington *et al.*, 1989). Unlike the deposits present in the skeletal muscle, which are separated from the muscle fibers by a collagenous fascia, the epicardial deposits are closely related to the myocardium (Marchington *et al.*, 1989).



The epicardial adipose tissue also has a high capacity for releasing fatty acids, and the cardiac muscle uses fatty acids and ketone bodies in preference to glucose, especially during fasting, intense exercise and high ingestion of lipids (Marchington *et al.*, 1989). In addition, this tissue possibly acts as a local “buffer” that absorbs excess fatty acids in the blood, keeping the concentration in the local bloodstream below toxic levels (Marchington *et al.*, 1989). Bats consume a large amount of energy during the flight, some species reach maximum heart rates of around 1000 bpm (Carpenter, 1985; O’Mara *et al.*, 2017; Thomas & Suthers, 1972; Thomas, 1975). Thus, the presence of fat in the parietal and visceral pericardium can act as a local energy source (Marchington *et al.*, 1989). O’Mara *et al.* (2017) noted that the Tent-making Bat, *Uroderma bilobatum* Peters, 1866 replaces all of its energy reserves, such as lipids and glycogen, in three days, which could lead to potential famine periods. This can be extrapolated to *A. lituratus*, also frugivorous, whose diet is rich in sugars (Kalko *et al.*, 1996; O’Mara *et al.*, 2017). Therefore, cardiac fat deposits could supply the heart’s energy requirements at those times when *A. lituratus* does not feed.

The right auricle larger than the left was an expected feature. Rowlatt (1980) describes the right auricle of *Pteropus medius* as having walls capable of great distension, suggesting that it is an adaptation to the great differences in blood volume that the heart of the bat experiences. *Artibeus lituratus* presents the aortic trunk and its branches anatomy similar to that observed for Pteropodidae, however, the flying foxes have two innominate arteries (Alcock, 1898; Rowlatt, 1967; 1980). The specimens included in the present study do not have a left innominate artery, with the exception of one individual, indicating an intraspecific variation. In general, for *A. lituratus* the left common carotid and left subclavian originate directly from the distal end of the transverse arch, which is consistent with the description of Park (1954) and Gupta (1966) for phyllostomid bats, the last one included also eleven species from six Neotropical families, besides Phyllostomidae. The presence of a vestigial, non-functional *ductus arteriosus* in some individuals seems to be a common feature in bats (Gupta, 1966; Park, 1954; Rowlatt, 1967; 1980).

Bilateral anterior *venae cavae* was observed in all individuals. These vessels are present in the early stages of embryonic development of all mammals, and frequently these vessels persist in the adult. In several taxa, however, anastomoses appear between both embryonic anterior *venae cavae* and finally the left regresses, leaving only the right one (Amoroso *et al.*, 1942; Barnett *et al.*, 1958). The presence of bilateral *venae cavae* seems to be a common feature for bats (Alcock, 1898; Alijani & Ghassemi, 2016; Amoroso *et al.*, 1942; Gupta, 1966; Park, 1954; Rowlatt, 1967; 1980). Retention of bilateral anterior *venae cavae* in bats allows some inferences regarding their function in the organism. One

of the factors required to sustain the high metabolism of flight is a short whole-body circulatory time (Maina, 2000). Since these animals are dependent on bulky flight muscles, as well as having to circulate blood through the wide wing patagia, optimizing circulation in the thoracic portion of the body is essential. The blood flow (Q), measured in volume per time, is directly proportional to the diameter of the vessels, and inversely proportional to the vessel resistance to the passage of blood (Secomb, 2016). Thus, the presence of two vessels in *A. lituratus*, one draining each side of the chest, can be a way to optimize the blood return to the heart, reducing resistance, rather than just one vessel where all flow should converge. Bats have a high hematocrit, which allows for greater oxygen uptake, on the other hand, increases blood viscosity (Hillman *et al.*, 1985). The ability to carry oxygen grows linearly with the hematocrit, but viscosity grows exponentially (Hillman *et al.*, 1985). This means that more energy is spent to move the fluid, which decreases cardiac output, oxygen consumption and aerobic scope (Maina, 2000). Since Q is inversely proportional to viscosity, adaptations that increase the flow are essential to overcome the detrimental side effects of a high hematocrit (Secomb, 2016).

On the other hand, a higher Q results in a lower blood pressure, and the venous circulation is already less pressurized (Secomb, 2016). The blood needs to return to the heart from the bulky flight muscles and the wide wing patagia, so only the pressure exerted by the heart may not be enough to guarantee this return. However, the venules of the bat’s wing membranes can actively pump blood through peristalsis, relying on valves that prevent the return of the flow, and possibly the cyclic movement of the flight muscles also acts pumping the blood, as is seen in the human hind limbs (Dongaonkar *et al.*, 2011; Secomb, 2016). The larger volume of the right atrium and *venae cavae sinus* cavities combined, including a distending auricle, agrees with the hypothesis that the presence of two *venae cavae* decreases the resistance to the blood that goes to the heart, thus, the greater blood flow that returns during the flight is supported by this wide space. Additionally, the bat’s large lungs, which have a great volume of blood in the pulmonary capillaries, are adapted to receive this increased flow (Jürgens *et al.* 1981; Maina, 2000).

Artibeus lituratus presents a single azygos vein, which empties into the dorsal aspect of the left anterior *vena cava*, which is also observed in other phyllostomids and other small bat families (Gupta, 1966; Park, 1954). Pteropodid bats show this vessel draining into the left anterior *vena cava* or have bilateral azygos veins (Alcock, 1898; Rowlatt, 1967; 1980). Most mammals have a larger right azygos vein and a left hemiazygos that runs along the midline of the body (Barnett *et al.*, 1975).

The *venae cavae sinus* found in *A. lituratus* right atrium is called *sinus venosus* and the pulmonary *conus* found in the *A. lituratus* right ventricle is called the



conus arteriosus by some authors, but they aren't in fact these structures. The true *sinus venosus* and *conus arteriosus* regress during the embryonic development of all mammals, being absent in adults (Bettex *et al.*, 2014; Moorman & Christoffels, 2003; Stephenson *et al.*, 2017). The *venae cavae sinus* of adult bats and other adult mammals with bilateral *venae cavae* is a chamber dorsal to the atrium which receives the three *venae cavae* (Alcock, 1898; Alijani & Ghassemi, 2016; Rowlatt, 1967; 1980) and the pulmonary *conus* is a distinct portion of the right ventricle that show common characteristics to all bats described (Alcock, 1898; Alijani & Ghassemi, 2016; Rowlatt, 1967; 1980). Therefore, we suggest the use of the names "*venae cavae sinus*" and "*pulmonary conus*", respectively, for these structures present in adult bats and other mammals.

Armour *et al.* (1970) demonstrated in dogs that, when the right ventricle is stimulated to contract more vigorously, the pulmonary *conus* acts as a resistor against the increased pressure, possibly protecting the pulmonary vasculature. Bats experience a wide variation in heart rate when they take off, (Canals *et al.*, 2011; Carpenter, 1985; O'Mara *et al.*, 2017; Thomas & Suthers, 1972) so the venous return to the heart also increases. The developed pulmonary *conus* of bats, including that of *A. lituratus*, may have a similar function in protecting the pulmonary vasculature. In one of the examined bats a membranous structure was found forming a network over the entrance of the *conus*, a structure not registered for any other bat in the literature.

Artibeus lituratus presents papillary muscles attached to the right ventricle septal wall, which seems to be a common feature among bats (Alcock, 1898; Alijani & Ghassemi, 2016; Rowlatt, 1967; 1980; 1990). In other mammal taxa, including man, these structures are attached on the parietal wall (Rowlatt, 1990; Truex & Copenhaver, 1947). The intraspecific variation in the number of papillary muscles was also observed, which is registered for Pteropodidae (Alcock, 1898; Alijani & Ghassemi, 2016; Rowlatt, 1967). Gupta (1966) did not find papillary muscles nor *chordae tendineae* for several small bat families, which could be misinterpreted due to the fixation effect in these structures, whose blood inside the cavities hardens into firm clots during the formaldehyde fixation process. By removing these clots during dissection, many delicate structures are damaged, including papillary muscles, *chordae tendineae* and valves.

No specimens analyzed had a moderator band, which agrees with previous records for many bats (Alcock, 1898; Rowlatt, 1967; 1980; 1990). However, in one individual, a membranous structure was found in the same position as a moderator band, connecting the ventricular walls. It consists of a strip of fragile translucent tissue, which tears easily, not being similar to any of the forms of moderator bands found in other mammals (Truex & Copenhaver, 1947; Truex & Warshaw, 1942).

The semilunar valve anatomy is similar to that described in the literature for other bats (Alcock, 1898; Gupta, 1966; Rowlatt, 1967; 1980). The right atrioventricular valve has a single parietal leaflet in *A. lituratus*, while pteropodid bats shows one or two leaflets, and in the second case the septal one is smaller and less developed (Alcock, 1898; Rowlatt, 1967; 1980) The left atrioventricular valve is similar to other mammals (Alcock, 1898; Alijani & Ghassemi, 2016; Rowlatt, 1967; 1968). A well-defined *pars membranacea* was visualized in *A. lituratus*. Rowlatt (1980) describes the structure for *Pteropus medius* and mentions that it may be partially covered by muscle, which is not the case for the species contemplated in the present study.

In *A. lituratus* two coronary arteries arise from orifices located in the walls of the *sinuses* of Valsalva as in most mammals (Rowlatt, 1968). These arteries can present supernumerary orifices in some individuals, characteristics also observed in bats and other mammals (Alcock, 1898; Rowlatt, 1967; 1968; 1980). The coronary *sinus* absence in *A. lituratus* agrees with the description of Gupta (1966) for six families of small bats. Park (1954) describes a coronary *sinus* for phyllostomid bats, while Rowlatt (1967) also describes this structure for *Eidolon helvum*. The orifice of the coronary *sinus*, in humans and other mammals, is guarded by a semilunar valve, or Thebesian valve (Hyde, 1891). A bicuspid valve is present in the orifice of the great cardiac vein in *A. lituratus*, a structure not found in other bats.

The heart of *A. lituratus* presents the anatomical characteristics common to all mammals, with some specific differences in relation to other bats and non-flying mammals described in the literature. Mammals show a conserved cardiac anatomy, which indicates their efficiency in promoting blood circulation in these animals with high metabolism and a diverse range of lifestyles (Rowlatt, 1968; 1990). There are punctual variations between taxa, in relation to the shape and presence of certain elements, but not to the structure and general conformation of the heart (Rowlatt, 1968; 1990). Some of these differences are adaptations to different lifestyles, while others are unrelated to functionality, often remnants of embryonic development and the evolutionary trajectory of the organ (Rowlatt, 1968; 1990). Bats are important examples as flight shows high energy requirements, just punctual adaptations in the cardiac anatomy optimize their blood circulation. *A. lituratus* presents intraspecific variations, a common phenomenon for bats and other mammals. These variations are found in the number of right papillary muscles, the number of orifices in the pulmonary veins, the number of orifices in the coronary arteries, the presence of a left innominate artery, and the presence of a remnant of the ductus arteriosus. The presence of the Thebesian valve guarding the orifice of the great cardiac vein was registered only for *A. lituratus*, as well as the extensive system of pericardial ligaments, never seen before in any mammal,



which is possible related with the upside down resting position. We also suggest that the retention of bilateral *venae cavae* in bats play a role in optimizing blood circulation by counteracting the resistance effects of the bat's blood high viscosity. It is also the first time to observe anomalous membranous structures present inside the pulmonary *conus* in bats. This work added knowledge in bat cardiovascular biology, opening up research possibilities in other fields such as histology, cell biology, physiology, biochemistry, and embryology of this mammal heart. The enormous diversity of bats is still a vast field to be explored within this area.

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New locality records for poorly known species of Andean sigmodontine rodents (Rodentia: Cricetidae) from Northwestern Argentina

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Abstract: The Sigmodontinae is a highly diverse subfamily of rodents that represents almost 30% of the mammalian species present in northwestern Argentina. However, the distribution of several species is delimited on the basis of scarce records. We add new localities for four poorly known species of rodents (*Abrothrix andina* Philippi 1858, *Abrothrix jelskii* Thomas 1824, *Neotomys ebriosus* Thomas 1894, *Auliscomys sublimis* Thomas 1900) in the High Andes of Jujuy and Salta provinces. We duplicate the number of known localities for *A. jelskii* in Salta, including the lowest known elevation record in Argentina and added the second known locality for Jujuy province. Furthermore, we add four new localities for *A. sublimis*, including the westernmost locality in Argentina, and reported for the first time this species at a departmental political division in NWA. Finally, we report the first departmental record for both *A. andina* and *N. ebriosus* in Valle Grande.

Key-Words: Biodiversity; Geographic distribution; High Andes; Small mammals.

Resumo: Novos registros de localidade para espécies incomuns de roedores sigmodontinae (Rodentia: Cricetidae) do noroeste da Argentina. Sigmodontinae é uma subfamília altamente diversa de roedores que representa quase 30% das espécies de mamíferos documentadas no noroeste da Argentina. Não obstante, a distribuição de várias espécies é delimitada com base em registros escassos. Neste estudo, adicionamos novas localidades para quatro espécies de roedores (*Abrothrix andina* Philippi 1858, *Abrothrix jelskii* Thomas 1824, *Neotomys ebriosus* Thomas 1894, *Auliscomys sublimis* Thomas 1900) nos Altos Andes das províncias de Jujuy e Salta. Duplicamos o número de localidades conhecidas para *A. jelskii* em Salta, incluindo o registro de menor altitude conhecido na Argentina, e também adicionamos a segunda localidade conhecida para Jujuy. Além disso, adicionamos quatro novas localidades para *A. sublimis*, incluindo a localidade mais ocidental da Argentina, e relatamos pela primeira vez esta espécie em uma divisão política departamental do NOA. Por fim, reportamos o primeiro registro de *A. andina* e *N. ebriosus* no departamento de Valle Grande.

Palavras-Chave: Altos Andes; Biodiversidade; Distribuição geográfica; Pequenos mamíferos.

INTRODUCTION

Mountainous regions are characterized by complex topography and steep environmental gradients that act as barriers to dispersal for populations of several species, leading to isolation and eventually, speciation. This is why mountain environments frequently host great species richness and endemism (Badgley, 2010; Grenyer *et al.*, 2006).

The North West of Argentina (NWA) is a region that comprises several physiographic and biogeographic unities. This area is a transition zone between both tropical and temperate biomes. Because of the latitudinal location and the abrupt altitudinal gradient, a succession of savannah, rain forests, deciduous forests, grassland and high altitude deserts take place in a relatively small area (Morrone, 2015; Morrone & Ezcurra, 2016). Therefore, there is a great diversity of both environmental and biotic changes with a unique species assembly promoted

by historic and ecological variations typical of a biogeographic transition zone (Ferro & Morrone, 2014). This region is also a hotspot of species richness and turnover for South American rodents, particularly for the sigmodontine, a highly diverse subfamily of rodents that represent almost 30% of the mammalian species present in NWA (Ferro & Barquez, 2008; 2014; Formoso & Teta, 2019; Jayat *et al.*, 2011a; Maestri & Patterson, 2016; Urquiza *et al.*, 2021; 2022).

However, there are still poorly studied regions in NWA, especially the High Andes area. Indeed, only few localities of the sigmodontine rodents' records are above 3,000 meters above sea level (m a.s.l.), and there are practically no records in the 4,750-5,500 m a.s.l. interval (Jayat *et al.*, 2011a; Storz *et al.*, 2020). In addition, most surveyed localities are located in close proximity to roads and in anthropogenically altered areas, with few studies in relatively pristine habitats (Jayat *et al.*, 2011a). Therefore, our knowledge of many highland



small mammals' taxa inhabiting NWA comes from very few locality records and affected by sampling bias. Furthermore, our understanding of the taxonomy and distribution of most species of sigmodontine in NWA is still incomplete (Jayat *et al.*, 2018).

In this paper, we report the results of fieldwork designed to fill this gap of distribution knowledge and add new localities for presumably rare High Andean sigmodontine rodent species in NWA.

MATERIAL AND METHODS

We conducted this study in highland localities placed in Jujuy and Salta provinces, Argentina, between 2016 and 2022. The study area belongs to the Puna, High Andes, and the mist grassland ecoregions (Brown & Pacheco, 2006). We surveyed 25 highland localities between 2,700 and 4,700 m a.s.l.

To sample rodent communities in each site, we used Sherman traps baited with a mixture of peanut butter, fat and oat. Generally, we set 40 traps in each site for three consecutive nights. We calculated trapping effort as trap-night, that is the number of traps multiplied by the number of nights they remained open. The trapping success is the number of captures divided by the number of trap-night (Wilson *et al.*, 1996).

We follow standardized protocols for mammal collection summarized in Barquez *et al.* (2021). We sexed, weighted and measured total length, tail length, hindfoot length (with claws), and ear length for each individual and preserved specimens as skin and skeleton or in alcohol 70%. We identified every species by comparison of morphological characters with specimens deposited in Colección Mamíferos Lillo and using specific bibliography (Patton *et al.*, 2015; Teta & Jayat, 2021). We recorded all captured specimens in the personal catalogue of two authors (AM and JHU). The voucher specimens were deposited at Colección Biológica de Vertebrados of Instituto de Biología de Altura (INBIAL-CV) Universidad Nacional de Jujuy and Colección Mamíferos Lillo (CML) Universidad Nacional de Tucumán. We followed the ethical guidelines of the American Society of Mammalogists (Sikes, 2016) during the capture and euthanization of the specimens.

All samples were authorized by the Secretary of Biodiversity, Ministry of Environment of the Jujuy province under file Nº 0257-393-V of permits granted to Dr. Marcos Vaira (Res. Nº 171/2015-DPB, extension request:

Res. Nº 040/2017-SB), and by Secretary of Environment, Ministry of Environment and Sustainable Production of the Salta province under file Nº 0090227-219363/2016-0 of permits granted to José Humberto Urquizo.

RESULTS

We captured 353 individuals with a trapping effort of 7044 trap-night, representing 13 genera and 19 species in the 20 localities where we have captured at least one individual. The total capture success was 4.98%. The morphometric measures for the specimens reported in this paper are detailed below in Table 1.

We recorded new localities for four sigmodontine species which are listed below with their known distribution and their diagnostic features. The localities added in this report are listed below and mapped in Figures 1 and 2.

Family Cricetidae Fischer, 1817 Subfamily Sigmodontinae Wagner, 1843 Tribe Abrotrichini D'Elía *et al.*, 2007

Abrothrix andina (Philippi, 1858)

Description. Small species (adults 15.5 g, total length 141.5 mm \pm 14.5 mm) with long, soft, grayish brown pelage. Black snout, distinctive whitish postauricular patches and long covered nails. The tail is shorter than the body (53.88 \pm 4.9) (Figure 3A).

Distribution. Mainly in highland grasslands of Puna and High Andes above 3,500 m a.s.l. in NW and central eastern Argentina (with records from 950 to 5,000 m a.s.l.), in the provinces of Jujuy, Salta, Catamarca, Tucumán, La Rioja, San Juan and Mendoza (Ferro & Barquez, 2008; d'Hiriart *et al.*, 2021; Jayat *et al.*, 2018; Patterson *et al.*, 2015; Teta *et al.*, 2006; Urquizo *et al.*, 2021).

New records. Jujuy: Depto. Humahuaca, Abra Azul, 35 km O de Santa Ana, 23°14'S; 65°02'53"O; 4496 msnm (INBIAL-CV 00330). Depto. Humahuaca, Abra Colorada, 23°13'52"S; 65°2'23"O; 4520 msnm (INBIAL-CV 00384 – INBIAL-CV 00387). Depto. Valle Grande, Laguna Verde, 23°17'43"S; 65°1'15"O; 4378 msnm (INBIAL-CV 00356) (Figure 1A).

Table 1: List of the four rodent species including data on number of individuals (n), mean weight (MW, g), mean total length (MTL, mm), mean tail length (MT, mm), mean hindfoot length (MF, mm), mean ear length (ME, mm) and sex ratio (sr, male:female) recorded during this study. For each measure we included the standard deviation.

Species	n	MW	MTL	MT	MF	ME	sr
<i>A. andina</i>	4	17.25 \pm 3.12	141.5 \pm 14.5	53.88 \pm 4.9	19.62 \pm 0.75	12.38 \pm 1.97	1:3
<i>A. jelskii</i>	4	32.5 \pm 7.4	183 \pm 6.37	81 \pm 4.11	24.5 \pm 2.08	18.12 \pm 0.25	2:2
<i>N. ebriosus</i>	2	47 \pm 4.24	197 \pm 11.3	82 \pm 4.6	24 \pm 0	18.5 \pm 2.12	2:0
<i>A. sublimis</i>	6	30.8 \pm 13.8	149 \pm 40.7	52 \pm 10.8	21 \pm 2.34	19.8 \pm 6.05	2:4

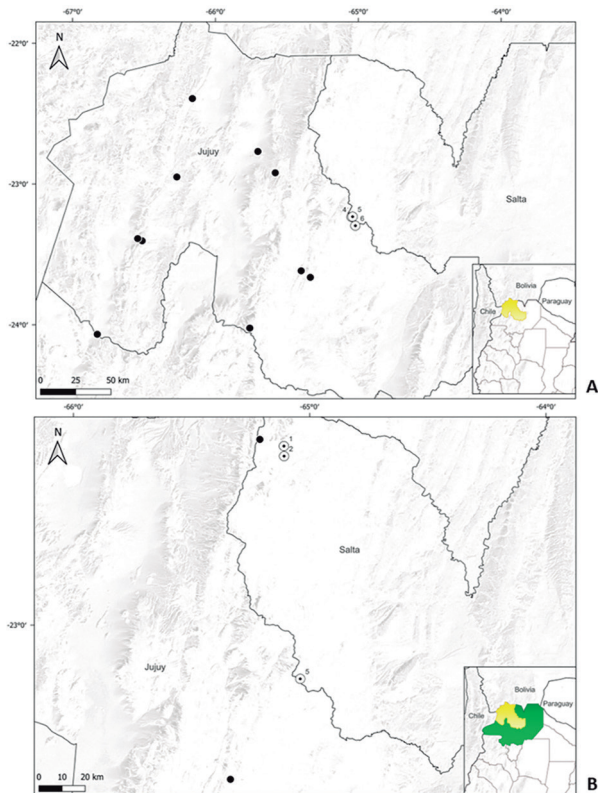


Figure 1: (A) Recorded localities for *Abrothrix andina* in Jujuy province. Black dots indicate previously published records and white dots the new localities (4 = Abra Azul, 5 = Abra Colorada, 6 = Laguna Verde). (B) Recorded localities for *Abrothrix jelskii* in Jujuy and Salta provinces. Black dots indicate previously published records and white dots the new localities (1 = Lagunas del Cerro Campanario, 2 = Curva dos, 5 = Abra Colorada).

Comments. The localities are placed in High Andes environments, characterized by cold, windy, and dry climatic conditions. The sparse vegetation, rock outcrops and sand dunes are represented by grasslands of *Poa*, *Festuca* and *Stipa* genera and woody plants such as *Azorella compacta* with compact and underground growth habitats. In Abra Azul we only captured one individual of *A. andina* and a male of *A. sublimis*, with a low trapping success (1.6%). In Abra Colorada we captured three females of *A. andina*, one of them lactating so it was released. In this locality we also captured two individuals of *A. jelskii*, with a trapping success of 4.16% in this locality. Finally, in Laguna Verde this species was captured together with *Akodon boliviensis*. The localities reported for *A. andina* in Jujuy province are placed in High Andes and Puna environments, all of them above 3300 m a.s.l.

Abrothrix jelskii (Thomas 1824)

Description. Medium size body (adults 32.5 g, total length 183 mm \pm 6.37 mm). Typical striking coloration, with a strong contrast between grey dorsal and white ventral parts and ferruginous tone in the nose, ears, feet and tail, and a white spot behind the ears. The tail is shorter than the body (81 \pm 4.11 mm) (Figure 3B).

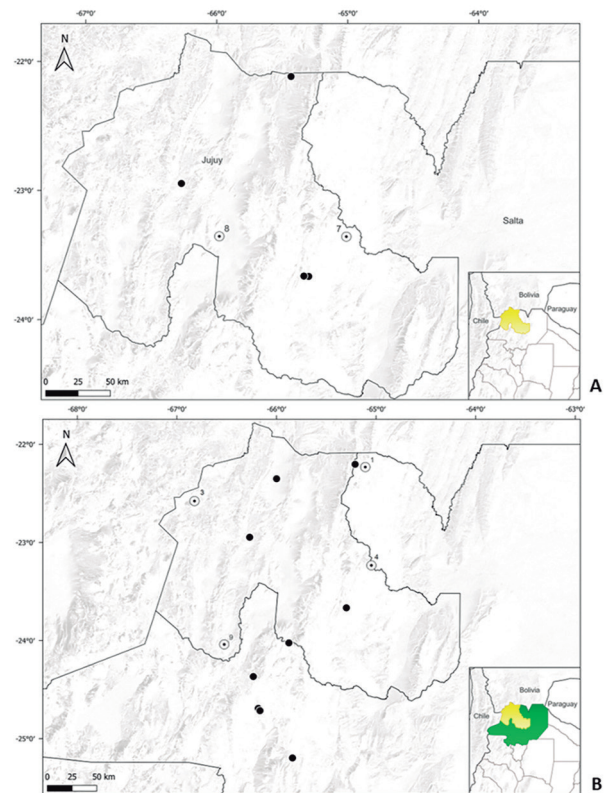


Figure 2: (A) Recorded localities for *Neotomys ebriosus* in Jujuy province. Black dots indicate previously published records and white dots the new localities (7 = Doblunzo, 8 = Abra del Valle). (B) Recorded localities for *Auliscomys sublimis* in Jujuy and Salta provinces. Black dots indicate previously published records and white dots the new localities (1 = Lagunas del Cerro Campanario, 3 = Laguna de Vilama, 4 = Abra Azul, 9 = Juguetería).

Distribution. It inhabits highland environments of the Central Andes above 3,500 m a.s.l. In Argentina was previously recorded in only two localities of Salta and Jujuy provinces (Jayat *et al.*, 2013; Sanborn, 1947).

New records. Jujuy: Depto. Humahuaca, Abra Colorada, 23°13'52"S; 65°2'23"O; 4520 msnm (INBIAL-CV 00385 – INBIAL-CV 00386). Salta: Depto. Santa Victoria, curva dos, R.P. 7 km 43, 28.3 km de Santa Victoria Oeste, 22°16'26"S; 65°6'31"O; 3936 msnm (INBIAL-CV 00329). Depto. Santa Victoria, Lagunas del Cerro Campanario, a 43 km SO de Santa Victoria Oeste, 22°13'51"S; 65°06'33"O; 4443 msnm (INBIAL-CV 00327) (Figure 1B).

Comments. In Lagunas del Cerro Campanario we recorded three individuals of *A. jelskii* and collected as a voucher specimen only one of them. We caught this species together with two species of sigmodontine rodents, two individuals of *A. sublimis* and one of *Phyllotis cf. rupestris*. In Curva dos locality, we captured one individual of *A. jelskii* with 4 individuals of *Akodon boliviensis*. The trapping success was also low: 0.33% and 0.42% for the two places respectively. The only previous record for Salta province was approximately 13 km W of the new localities, also placed in High Andes ecoregion and in similar rocky



Figure 3: Photograph of the captured specimens. (A) *Abrothrix andina* (male, INBIAL-CV 00330); (B) *Abrothrix jelskii* (male, INBIAL-CV 00329); (C) *Neotomys ebriosus* (male, INBIAL-CV 00355); (D) *Auliscomys sublimis* (male, INBIAL-CV 00320). Pictures taken by AM (A, D) and Miguel Cura (B, C).

outcrops environments and captured together with the following species: *Akodon albiventer*, *A. boliviensis*, *A. sublimis*, *Calomys musculus*, *C. lepidus*, *Phyllotis cf. rupestris*, *Andinomys edax*, *Octodontomys gliroides* and *Galea leucoblephara* (Jayat *et al.*, 2013). During one of the sampling sessions, a female was released and recaptured approximately 300 m from where it had been captured the previous day. In Abra Colorada (Jujuy) we captured a male and a female. The female was pregnant with four embryos. The only previous reproductive data was published in 1999 (Eisenberg & Redford), reporting two females captured in Perú with three embryos each one.

Tribe Euneomyini Pardiñas *et al.*, 2015

Neotomys ebriosus Thomas, 1894

Description. Medium size body (47 g, total length 197 ± 11.3 mm) with an overall greyish color with a strongly rufous muzzle, the base of the ears, the rump (Figure 3C). The tail is shorter than the body (82 ± 4.6 mm) and the hindfeet present its plantar surface entirely naked.

Distribution. This species is endemic of Central Andean highlands, associated with the presence of peatlands

(locally known as “vegas”) and dense grasses vegetation cover. Although this species has been mentioned as a mammal typical from the Altiplano, inhabiting elevations above 3,000 m a.s.l. (e.g., Pearson 1951), in the southern part of its range it occurs at lower elevations (as low as 2,700 m a.s.l.), well outside the limits of Puna and related cloud grassland on the eastern Andean slopes (Ferro & Barquez, 2017; Jayat *et al.*, 2008; Ortiz & Jayat, 2015). This species was previously recorded in Jujuy, Salta, Catamarca, San Juan, La Rioja and Tucumán provinces (Argentina) (Ferro & Barquez, 2017; d’Hiriart *et al.*, 2021; Jayat *et al.*, 2008, 2011b; Ortiz & Jayat, 2015; Pardiñas & Ortiz, 2001).

New records. Jujuy: Depto. Valle Grande, Doblونzo (Pueblo Viejo), 7 km O de Santa Ana, $23^{\circ}21'25''S$; $65^{\circ}0'40''O$; 3617 msnm (INBIAL-CV 00331). Depto. Valle Grande, Abra del Valle, Santa Ana, $23^{\circ}21'15''S$; $65^{\circ}58'51''O$; 3383 msnm (INBIAL-CV 00355) (Figure 2A).

Comments. The previous reported localities for Jujuy province were all placed in High Andes and Puna environments. We captured two males in cloud highland grasslands environments at 3300-3600 m a.s.l. We recorded three species in Doblونzo locality (*N. ebriosus*, *A. boliviensis*, *P. tucumanus*) and five in Abra del Valle (*N. ebriosus*, *A. boliviensis*, *P. tucumanus*, *Necromys*



lactens and *Oxymycterus paramensis*), with a trapping success of 1.83% and 2.5% respectively.

Tribe Phyllotini Vorontsov, 1959

Auliscomys sublimis (Thomas, 1900)

Description. Medium size body (adults 30.8 g, total length 149 mm \pm 40.7 mm). Long, soft, fine and bicolored pelage, grayish dorsally with yellowish tips and some black hairs. The hairs of the venter are whitish. An evident suede-colored line from the cheeks to the haunches is noticeable. Feet covered with abundant white hair. Tail is short and thick (52.5 mm), covered with fine white hair both dorsal as ventrally, and lacking tuft at tip. Short ears covered with fine yellowish hair and postauricular patches often present (Figure 3D).

Distribution. Present in High Andes and Puna environments, between 3,200 to above 5,000 m a.s.l. (Salazar-Bravo, 2015). It was previously registered in eight localities in Jujuy and Salta provinces (Díaz *et al.*, 2006; Jayat *et al.*, 2013; d'Hiriart *et al.*, 2021; Urquizo *et al.*, 2021).

New records. Salta: Depto. Santa Victoria, Lagunas del Cerro Campanario, a 43 km SO de Santa Victoria Oeste, 22°13'51"S; 65°06'33"O; 4443 msnm (INBIAL-CV 00320, INBIAL-CV 00328). Jujuy: Depto. Humahuaca, Abra Azul, 35 km O de Santa Ana, 23°14'S; 65°02'53"O; 4496 msnm (INBIAL-CV 00341). Depto. de Rinconada, Laguna de Vilama, refugio de Guardaparque, 22°34'41"S; 66°49'27"O; 4562 msnm (CML 14170). Depto. Susques, Juguetería, 1 km S de las piletas de Agua Termal, 24°02'21"S; 66°31'33"O; 4369 msnm (INBIAL-CV 00357, INBIAL-CV 00358) (Figure 2B).

Comments. All captures for this species in this study were near stream and peatlands, in coincidence with Diaz and Barquez (2007), these data suggest that this species lives in open places, below rocks, and along the banks of streams. In Juguetería (Susques department) two females with breeding conditions were captured during November, in the southern hemisphere summer.

DISCUSSION

In the present paper we explored high mountain rodent fauna of Jujuy and Salta provinces, one of the least known mammal communities in the NWA. Our results show a community composition characteristic of High Andean and cloud highland grasslands environments with capture rates consistent with previous results (Jayat *et al.*, 2008; Urquizo *et al.*, 2022). However, despite a relative low level of trapping effort we recorded new

localities for four species which are considered rare or uncommon in the study area.

Perhaps the least remarkable is *Abrothrix andina* that was recorded several times in NWA (*e.g.*, Díaz & Barquez, 2007; Ferro & Barquez 2008, 2014; Jayat *et al.*, 2011b, 2018; d'Hiriart *et al.*, 2021; Urquizo *et al.*, 2021). In Jujuy province seven localities were reported, all of them above 3,500 m a.s.l. The new localities are placed above 4300 m a.s.l. In addition, this is the first record of this species in Valle Grande department (Laguna Verde).

On the contrary, *A. jelskii* is one of the least known species in this genus (Jayat *et al.*, 2013; Patterson *et al.*, 2015). In Argentina, it was recorded only in two localities, one in Salta province and one in Jujuy province. In Salta, *A. jelskii* was recorded for the first time by Jayat *et al.* (2013) in Lizoite. Here we added two new localities from Salta province, including the lowest elevation record for this species in Argentina at 3,936 m a.s.l. and the second known locality for Jujuy province. In Laguna del Cerro Campanario (Salta) this species was captured with an individual of *Phyllotis cf. rupestris*. Recent research (Ojeda *et al.*, 2021; Teta *et al.*, 2022) recognized the "*P. posticalis* – *P. rupestris*" clade corresponding to highland environments of northern Jujuy and Salta provinces. Besides, the taxonomy of the species belonging to the *P. xantopygus* group needs further multidisciplinary analysis in this region.

A. jelskii is categorized as "Data Deficient" by the Red List of Mammals in Argentina (Jayat *et al.*, 2019) due to the lack of basic information about its populations. Despite the fact that the distribution of *A. jelskii* is drawn as a continuum polygon, our results suggest that the real distribution might be patched, associated with accumulation of glacial till rocks on mountain slopes. In correspondence with previous records (Ferro & Barquez, 2014; Jayat *et al.*, 2018; Teta *et al.*, 2006), this species seems to be related with rock glacier environments as those described by Martini (2016) for NWA.

Neotomys ebriosus is a monotypic genus that was considered "incertae sedis" until it was included in a new tribe, Euneomyini (Pardiñas *et al.*, 2015). This species is known by few specimens and localities, so there is much about distribution patterns and natural history still poorly understood (Ferro & Barquez, 2017; Ortiz & Jayat, 2015). It was previously recorded in two localities in Salta and three in Jujuy (Jayat *et al.*, 2008, 2011b; Pardiñas & Ortiz, 2001). Here we add two new localities for the species in Jujuy province and the first record of *N. ebriosus* from Valle Grande department. In Abra del Valle this species was captured with an individual of *Oxymycterus paramensis*, which distribution corresponds mostly with Yungas ecoregion. *N. ebriosus* was reported for Puna and High Andes environments in Argentina. However, we captured this species in cloud grassland environments, while it was not caught in the High Andes environments surveyed localities for this study.



Until this report, *Auliscomys sublimis* was recorded for eight localities in NWA. In Salta province, there were four registered localities for this species (Jayat *et al.*, 2013; Ortiz *et al.*, 2010). Here we added Lagunas del Cerro Campanario as a new locality, placed in High Andes at 4,443 m a.s.l. In Jujuy this species was previously recorded in four localities (Díaz & Barquez, 2007; Jayat *et al.*, 2011a; Ortiz *et al.*, 2010; Urquiza *et al.*, 2021). Here we added three new localities for the species in this province. Abra Azul represents the first record for Humahuaca department at 4,496 m a.s.l. Finally, we added the first record for Rinconada department and the westernmost register from Argentina in Laguna de Vilama. This locality is within approximately 80 km of other places where the species was previously recorded.

Despite the fact that the knowledge about composition and diversity of sigmodontine rodents in NWA has increased in the last years, it is still incomplete (Ferro & Barquez, 2014; Jayat *et al.*, 2011a, 2018). Our work certainly witnesses this asseveration, and our results agree that the High Andes and Puna ecoregions are among less surveyed environments in NWA (see Jayat *et al.*, 2011a, 2018). In fact, with a rather small sampling effort we add valuable new information for four largely unknown species of the region which can be used for further studies, providing better interpretations of the biogeography of these poorly known region and species. In the current context of climate change, it is necessary to resolve these information gaps, especially considering the vulnerability if these environments and species.

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Pequenos mamíferos (Didelphimorphia, Chiroptera e Rodentia) em egagropilos de *Tyto furcata* (coruja-das-igrejas) (Aves, Tytonidae) em uma área de floresta estacional do Sul do Brasil

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Resumo: Egagropilos de aves de rapina representam uma fonte importante de material para o levantamento de pequenos mamíferos em um tempo curto e a um custo baixo. Para o presente estudo foi analisado o material craniomandibular e dentes de pequenos mamíferos encontrados em egagropilos de *Tyto furcata* provenientes de uma área de floresta estacional na parte sul da Mata Atlântica, no município de Coronel Freitas, oeste do Estado de Santa Catarina, Sul do Brasil. Foram registrados 342 indivíduos de 10 espécies, sendo um marsupial (Didelphidae; 0,29% dos indivíduos), um quiróptero (Vespertilionidae; 0,29%) e oito roedores (Cricetidae e Muridae; 99,42%). *Oligoryzomys* sp. foi o táxon mais comum na amostra (51,17%), seguido por *Mus musculus* (25,15%) e *Akodon montensis* (12,28%). A amostra incluiu ainda espécies com poucos registros em áreas de floresta estacional, como *Cryptonanus guahybae*, *Brucepattersonius iheringi* e *Calomys tener*. O predomínio de roedores nos egagropilos de *Tyto furcata* em Coronel Freitas segue o padrão observado em outras áreas do Sul do Brasil. A ocorrência de espécies de ambientes abertos (*Calomys tener* e *Necromys lasiurus*) e florestais (*Akodon montensis* e *Brucepattersonius iheringi*) reflete os diferentes usos do solo localmente, enquanto a presença de murídeos e a grande frequência de *Oligoryzomys* são associadas ao impacto antrópico na área de estudo.

Palavras-Chave: *Akodon*; *Mus*; *Oligoryzomys*; Pelotas; Santa Catarina.

Abstract: Small mammals (Didelphimorphia, Chiroptera and Rodentia) in *Tyto furcata* (Barn Owl) (Aves, Tytonidae) pellets from a seasonal forest in southern Brazil. Birds of prey pellets provide an important source of specimens for small mammal surveys in a short time and at a low cost. Here we analysed craniomandibular material and teeth of small mammals obtained from *Tyto furcata* pellets from an area of Seasonal Forest in the southern part of the Atlantic Forest, in the municipality of Coronel Freitas, western Santa Catarina State, southern Brazil. We recorded 342 individuals of 10 species: one marsupial (Didelphidae; 0.29% of individuals), one chiropteran (Vespertilionidae; 0.29%) and eight rodents (Cricetidae and Muridae; 99.42%). *Oligoryzomys* sp. were the most frequent taxon in the sample (51.17%), followed by *Mus musculus* (25.15%) and *Akodon montensis* (12.28%). The sample also included species with few records in Seasonal Forest areas, such as *Cryptonanus guahybae*, *Brucepattersonius iheringi* and *Calomys tener*. The dominance of rodents in barn owl pellets from Coronel Freitas follows the pattern observed in other areas of southern Brazil. The occurrence of species from open (*Calomys tener* and *Necromys lasiurus*) and forested (*Akodon montensis* and *Brucepattersonius iheringi*) environments reflects the different uses of the soil locally, while the presence of murids and the high frequency of *Oligoryzomys* are associated with the anthropic impact in the study area.

Key-Words: *Akodon*; *Mus*; *Oligoryzomys*; Pellets; Santa Catarina State.

INTRODUÇÃO

Os egagropilos ou pelotas de aves de rapina têm sido amplamente utilizados como fonte de material osteológico e dentário de pequenos mamíferos, podendo fornecer uma grande quantidade de material em um curto prazo e a um custo baixo (Avenant, 2005; Formoso *et al.*, 2016; Heisler *et al.*, 2016). Dentre essas aves, *Tyto furcata* (Temminck, 1827), a suindara ou coruja-das-igrejas, é de particular interesse, pois pequenos mamíferos compõem parte significativa de sua alimentação e o material regurgitado pode se preservar por muito tempo, visto que essa ave nidifica em locais abrigados, como

cavernas e construções humanas (Heisler *et al.*, 2016; Sick, 2001). Apesar dos desafios para a identificação de algumas espécies de pequenos mamíferos com base em material fragmentado, os resultados desses estudos têm demonstrado a importância da análise de egagropilos, seja pela riqueza de espécies ou pelo registro de espécies pouco amostradas por métodos convencionais de captura (*e.g.*, Brito *et al.*, 2015; Fernández *et al.*, 2012; Lemos *et al.*, 2015; Mancini *et al.*, 2018; Rocha *et al.*, 2015; Teta *et al.*, 2010).

A Mata Atlântica representa a segunda maior formação florestal na América do Sul (Marques *et al.*, 2021). Considerada uma das regiões mais biodiversas



no mundo e com uma alta taxa de endemismos (Myers *et al.*, 2000), atualmente encontra-se extremamente fragmentada e reduzida a 28% da extensão original (Rezende *et al.*, 2018). Essa perda de habitat é particularmente notável na floresta estacional, um dos principais tipos vegetacionais da Mata Atlântica na região Sul do país (Carlucci *et al.*, 2021; Vibrans *et al.*, 2012). Esta formação ocupa áreas de altitude média no interior do continente, associadas a temperaturas altas e pluviosidade sazonal, que determinam um grau variável (20 a 50%) de deciduidade foliar (Carlucci *et al.*, 2021).

Apesar dos impactos, a parte sul da Mata Atlântica ainda abriga uma mastofauna diversificada, composta, por exemplo, por 17 espécies de marsupiais e 51 de roedores (Graipel *et al.*, 2017). Nos últimos anos, os estudos com egagropilos de coruja nessa parte do bioma têm aumentado e permitido ampliar o número de locais de registro de pequenos mamíferos, como *Cryptonanus guahybae* (Tate, 1931), *Calomys tener* (Winge, 1887) e *Wilfredomys oenax* (Thomas, 1928) (*e.g.*, Cherem *et al.*, 2018; Peters *et al.*, 2013; Pontes *et al.*, 2021; Silveira *et al.*, 2021). No entanto, esses estudos estão concentrados em áreas de floresta ombrófila, enquanto os dados para áreas de floresta estacional estão restritos a apenas duas localidades no estado do Rio Grande do Sul, nos municípios de Alpestre (Cherem *et al.*, 2018) e Venâncio Aires (Scheibler & Christoff, 2007). Neste sentido, o presente estudo tem por objetivo apresentar os resultados da análise de pequenos mamíferos registrados em egagropilos de *T. furcata* procedentes de uma área de floresta estacional na Mata Atlântica do Estado de Santa Catarina, Sul do Brasil.

MATERIAL E MÉTODOS

Os egagropilos foram coletados em 13 de maio de 2020 dentro de uma construção humana utilizada como abrigo por *T. furcata*, no município de Coronel Freitas (26°54'20"S, 52°48'22"O, Datum WGS-84; 345 metros de altitude), oeste do estado de Santa Catarina, sul do Brasil (Figura 1). Essa área está inserida na floresta estacional, bioma Mata Atlântica (Carlucci *et al.*, 2021; Leite, 2002). Atualmente, conforme observado em campo, a vegetação local encontra-se muito alterada, com predomínio da agropecuária, além de áreas de silvicultura de *Pinus*. A cobertura florestal nativa está em grande parte restrita a pequenos fragmentos e à mata ciliar.

Os egagropilos foram triados manualmente, a seco, com o auxílio de pinças (Muñoz-Pedrerros & Rau, 2019). Os ossos e dentes encontrados foram depositados na Coleção de Fragmentos Ósseos do Laboratório de Paleontologia, Centro de Filosofia e Ciências Humanas, Universidade Federal de Santa Catarina, Florianópolis, estado de Santa Catarina, sob o número UFSC-CF 98.

A identificação dos pequenos mamíferos foi feita por comparação com material depositado na Coleção de Mamíferos do Departamento de Ecologia e Zoologia da

UFSC (Apêndice) e com base na literatura (*e.g.*, Barquez *et al.*, 1999; Gardner, 2008; Gonçalves *et al.*, 2007; Hader *et al.*, 2016; Patton *et al.*, 2015; Stutz *et al.*, 2017). Os comprimentos das séries molares ao nível da coroa e dos alvéolos de marsupiais foram obtidos com lupa milimetrada com precisão de 0,01 mm. As demais medidas foram tomadas com paquímetro com precisão de 0,05 mm (Barquez *et al.*, 1999; Voss, 1991). O número mínimo de indivíduos (NMI) por espécie foi determinado pela contagem do elemento mais comum na amostra, considerando-se mandíbulas ou maxilares, direitos ou esquerdos (Beisaw, 2013). A nomenclatura e o ordenamento taxonômico seguiram Abreu *et al.* (2021a).

RESULTADOS

Nos egagropilos de *T. furcata* provenientes de Coronel Freitas foram registrados 972 fragmentos cranianos e mandibulares de 10 espécies de pequenos mamíferos (NMI = 342), sendo uma espécie de Didelphimorphia (família Didelphidae), uma de Chiroptera (Vespertilionidae) e oito de Rodentia (seis de Cricetidae e duas de Muridae). A amostra foi composta predominantemente por roedores (80% dos táxons e 99,42% dos indivíduos) e, dentre esses, pela família Cricetidae (60% e 73,10%, respectivamente). Apenas um indivíduo de uma espécie de marsupial e um de quiróptero foram registrados nos egagropilos (0,29% do total de indivíduos em cada caso). As espécies mais frequentes foram *Oligoryzomys* sp. (NMI = 175; 51,17%) e *Mus musculus* Linnaeus, 1758 (NMI = 86; 25,15%) (Tabela 1; Figura 2).

O material referido a *Cryptonanus* inclui dois maxilares, um direito e um esquerdo (Figura 2A), e uma

Tabela 1: Número Mínimo de Indivíduos (NMI) de pequenos mamíferos registrados em egagropilos de *Tyto furcata* no município de Coronel Freitas, estado de Santa Catarina, sul do Brasil.

Táxon	NMI	Porcentagem (%)
Ordem Didelphimorphia		
Família Didelphidae		
<i>Cryptonanus guahybae</i> (Tate, 1931)	1	0,29
Ordem Chiroptera		
Família Vespertilionidae		
<i>Myotis</i> sp.	1	0,29
Ordem Rodentia		
Família Cricetidae		
<i>Akodon montensis</i> Thomas, 1913	42	12,28
<i>Akodon paranaensis</i> Christoff <i>et al.</i> , 2000	4	1,17
<i>Bucepattersonius iheringi</i> (Thomas, 1896)	7	2,05
<i>Necomys lasiurus</i> (Lund, 1840)	19	5,55
<i>Oligoryzomys</i> sp.	175	51,17
<i>Calomys tener</i> (Winge, 1887)	3	0,88
Família Muridae		
<i>Mus musculus</i> Linnaeus, 1758	86	25,15
<i>Rattus rattus</i> (Linnaeus, 1758)	4	1,17
Total	342	100,00



Figura 1: Localização do ponto de coleta dos egagropilos de *Tyto furcata* no município de Coronel Freitas, estado de Santa Catarina, sul do Brasil.

mandíbula direita. Este gênero diferencia-se de *Gracilianus* pela ausência de fenestra maxilar no palato; de *Monodelphis* pela presença da cúspide estilar "C" nos molares superiores, especialmente no M1 e no M2, e de ambos os gêneros pela presença do cingulo anterior estreito e completo no M3 (Silveira *et al.*, 2021; Voss & Jansa, 2009; Voss *et al.*, 2005). O comprimento da série molar superior esquerda (5,16 mm) está um pouco acima

da variação registrada por Silveira *et al.* (2021) para *C. guahybae* (4,58-4,98 mm), enquanto o comprimento alveolar da série molar inferior (5,40 mm) está dentro da variação obtida por esses autores (4,20-5,56 mm), permitindo a atribuição específica.

A família Vespertilionidae está representada por um crânio incompleto (Figura 2B) e uma mandíbula direita, assinalados ao gênero *Myotis* pelas pequenas

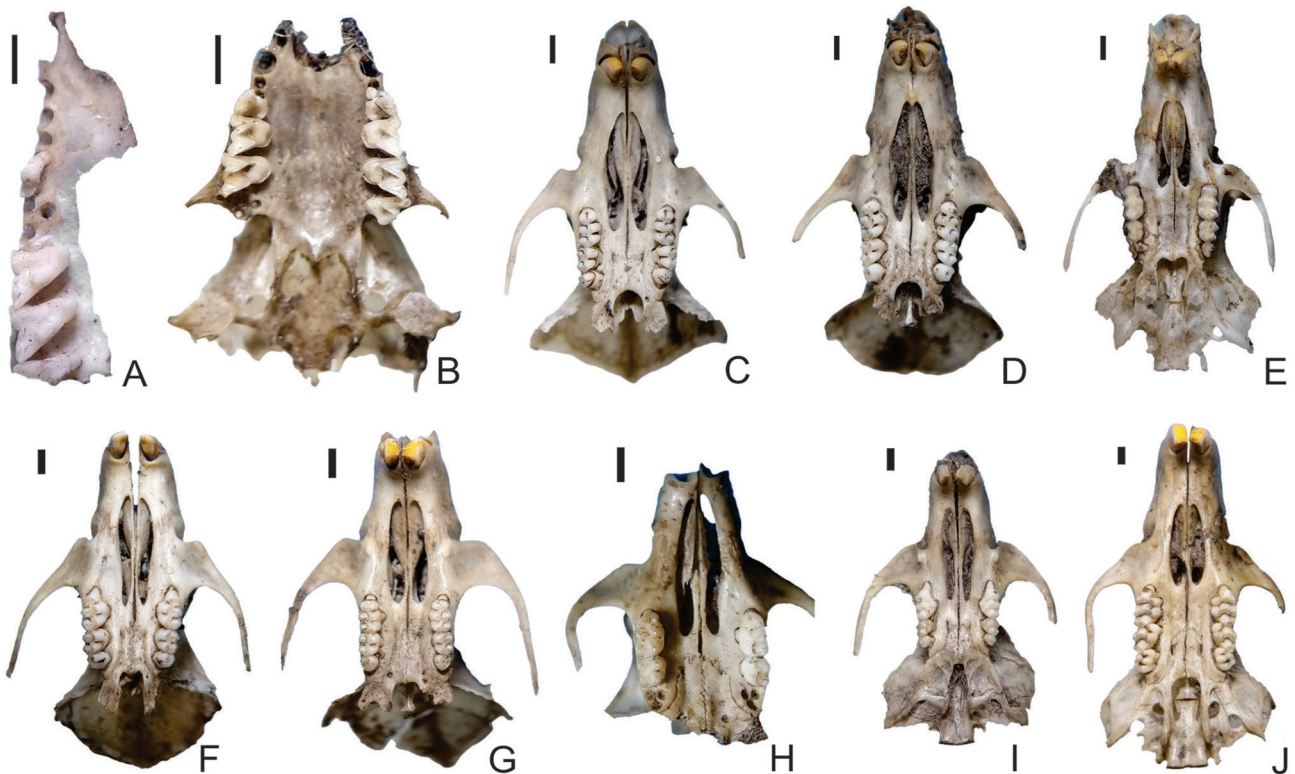


Figura 2: Pequenos mamíferos registrados em egagropilos de *Tyto furcata* em uma área de floresta estacional, em Coronel Freitas, Santa Catarina, sul do Brasil. A, *Cryptonanus guahybae*; B, *Myotis* sp.; C, *Akodon montensis*; D, *Akodon paranaensis*; E, *Brucepattersonius iheringi*; F, *Necromys lasiurus*; G, *Oligoryzomys* sp.; H, *Calomys tener*; I, *Mus musculus*; J, *Rattus rattus*. Escala = 1 mm.



dimensões (comprimento do palato = 5,60 mm; constrição pós-orbital = 3,64 mm; série molar superior = 3,14 mm; comprimento da mandíbula = 9,38 mm) e por sua fórmula dentária: I2/3, C1/1, P3/3, M3/3 (Barquez *et al.*, 1999; Miranda *et al.*, 2013; Moratelli *et al.*, 2011). No entanto, a fragmentação do material e a consequente ausência de caracteres morfológicos diagnósticos impossibilitaram a identificação da espécie.

O gênero *Akodon* inclui 46 indivíduos, caracterizados por uma constrição interorbital pouco evidente; crista supraorbital ausente; forâmen incisivo longo, estendendo-se posteriormente até o nível do protocone do M1; palato curto, não alcançando a margem posterior do M3; mandíbula baixa; flexo/ídeo anteromediano presente, exceto nos espécimes com maior desgaste dentário; e mesolofó/ídeo pequeno (Anderson & Olds, 1989; Pardiñas *et al.*, 2015a; Stutz *et al.*, 2017). Com base no comprimento da série molar superior (Gonçalves *et al.*, 2007), duas espécies estão presentes nessa amostra: *Akodon montensis* Thomas, 1913 (M1-M3 = 3,70-4,20 mm; n = 36; Figura 2C) e *Akodon paranaensis* Christoff *et al.*, 2000 (M1-M3 = 4,55-4,60 mm; n = 5; Figura 2D).

Os espécimes referidos a *Brucepattersonius* apresentam crânio baixo com rostro longo; placa zigomática curta (anteroposteriormente) e comparativamente mais inclinada posteriormente; região interorbital ampla e levemente bicôncava; crista supraorbital ausente; forâmen incisivo longo, estendendo-se posteriormente até o nível do procíngulo do M1; palato curto; séries molares relativamente longas (M1-M3 = 4,30-4,65 mm; n = 4); mandíbula baixa e longa; processos angular e condilar alongados; flexos/ídeos amplos (Figura 2E; Cherem *et al.*, 2018; Massoia, 1963). Flexo/ídeo anteromediano, anterolofó/ídeo e mesolofó/ídeo estão presentes em espécimes com pouco desgaste dentário. Duas espécies do gênero, *Brucepattersonius iheringi* (Thomas, 1896) e *Brucepattersonius soricinus* Hershkovitz, 1998, ocorrem no sul do Brasil (Abreu *et al.*, 2021b). Dias (2016) registrou apenas *B. iheringi* para localidades próximas à área de estudo. Além disso, em dois espécimes estudados que preservam os nasais, sua margem lateral é retilínea (não *trumpet-shaped* de *B. soricinus*; conforme Vilela *et al.*, 2015). Dessa forma, o material analisado é atribuído a *B. iheringi*.

Os espécimes identificados como *Necomys lasiurus* (Lund, 1840) possuem crânio relativamente alto, com constrição interorbital e crista supraorbital bem evidentes; forâmen incisivo longo; palato curto; incisivos ortodontes; molares tetralofodontes e com coroa alta; M1/m1 com contorno ovalado; flexo/ídeo anteromediano discernível apenas em espécimes com pouco desgaste dentário (Figura 2F; Anderson & Olds, 1989; Pardiñas *et al.*, 2015b).

O gênero *Oligoryzomys* está representado por 175 indivíduos. Esse material possui tamanho pequeno, forâmen incisivo longo, por vezes estendendo-se posteriormente à margem anterior do M1; palato longo,

estendendo-se posteriormente ao nível das margens posteriores dos M3, exceto em alguns espécimes jovens; mandíbulas com processo angular, condilar e coronoide curtos; M1/m1 com flexo/ídeo anteromediano e molares com mesolofó/ídeo, exceto nos espécimes com maior desgaste (Figura 2G; Gomes *et al.*, 2020; Weksler & Bonvicino, 2015).

Dois espécies, *Oligoryzomys flavescens* (Waterhouse, 1837) e *Oligoryzomys nigripes* (Olfers, 1818), ocorrem no sul do Brasil e apresentam grande similaridade na morfologia craniodentária (Machado *et al.*, 2011; Weksler & Bonvicino, 2015). Na amostra estudada, o comprimento da série molar superior variou de 3,1 a 3,8 mm (n = 75). Em vista lateral, o forâmen frontal (= suprafrontal de Machado *et al.*, 2011) varia de diminuto a comparativamente grande e, por vezes, duas ou mais aberturas estão presentes; raramente está ausente. Sua posição em relação aos molares variou desde na altura do M2 a posterior ao M3, eventualmente diferindo entre os lados de um mesmo indivíduo. Esses dados sugerem que ambas as espécies podem estar presentes na amostra (ver Machado *et al.*, 2011). No entanto, dada a ausência de uma distinção clara entre os espécimes estudados, a amostra foi referida como *Oligoryzomys* sp.

Calomys representa um dos menores roedores encontrados (M1-M3 = 3,20 mm – n = 1; m1-m3 = 3,15 mm – n = 2). Apresentam forâmen incisivo muito longo, estendendo-se posteriormente ao anterocone do M1; palato longo, estendendo-se posteriormente ao M3; quatro alvéolos para as raízes do M1/m1 e molares tetralofodontes (Figura 2H). A margem supraorbital distintamente saliente, a projeção capsular conspícua e o m3 em forma de “S” permitiram atribuir os espécimes a *C. tener*, conforme Salazar-Bravo (2015).

A família Muridae inclui duas espécies na amostra estudada, caracterizadas pelos molares superiores com três séries longitudinais de cúspides (Moojen, 1952). *Mus musculus* é uma das menores espécies de roedores encontrados nos egagropilos. Possui forâmen incisivo muito longo; fossa mesopterigoidea estreita; tubérculo massetérico presente na base da placa zigomática; mandíbula com crista massetérica ventral longa e conspícua; e processo capsular pouco desenvolvido (Figura 2I; Cherem *et al.*, 2018; Ronez & Pardiñas, 2021).

Rattus rattus (Linnaeus, 1758) é a maior espécie da amostra (Figura 2J; m1-m3 = 6,06-6,32 mm; n = 6). Diferencia-se de *R. norvegicus* (Berkenhout, 1769) por possuir cristas paralelas sobre a sutura frontoesquamosal, séries molares mais curtas e uma cúspide anterolabial menos reduzida no M1 (Catzefflis, 2018; Massoia & Fornes, 1969; Moojen, 1952). Além disso, *R. rattus* apresenta uma pequena cúspide labial posterior (*sensu* Musser, 1981) independente no m2, a qual está fusionada ao hipoconídeo em *R. norvegicus* (Cherem *et al.*, 2018). Essa cúspide independente está presente em todas as mandíbulas da amostra, exceto em uma. Sua ausência também foi verificada em alguns espécimes de *R. rattus*



utilizados para comparação (Apêndice), incluindo o m2 direito de UFSC 2394 e ambos os m2 de UFSC 2395. Além disso, essa cúspide está ausente no m2 direito de UFSC 2392, mas, neste caso, pode ser devido ao grande desgaste dentário.

DISCUSSÃO

Levantamentos mastofaunísticos com base na análise de pelotas de coruja têm fornecido dados inéditos sobre as assembleias de pequenos mamíferos para muitas localidades ou complementado as listas previamente disponíveis (e.g., Lemos *et al.*, 2015; Peters *et al.*, 2013; Stutz *et al.*, 2020). No presente estudo, os dados obtidos fornecem a primeira contribuição aos pequenos mamíferos da floresta estacional catarinense com base em pelotas de coruja e incluem espécies, como *C. guahybae*, *B. iheringi* e *C. tener*, que possuem poucos registros em áreas de floresta estacional na porção sul da Mata Atlântica (Abreu *et al.*, 2021b; Dias *et al.*, 2016; Salazar-Bravo, 2015).

A riqueza de pequenos mamíferos e o tamanho da amostra registrados na área de floresta estacional em Coronel Freitas (10 espécies, NMI = 342) está dentro da variação obtida em outros estudos realizados com egagropilos de *T. furcata*. Por exemplo, Brandão (2021) identificou três espécies em uma pequena amostra (NMI = 13) do Pantanal do Mato Grosso do Sul, enquanto Mancini *et al.* (2018) reportaram 26 espécies (NMI = 1.161) em sete cavernas na Caatinga da Bahia e de Sergipe, com uma variação de três a 20 espécies por caverna. Variação similar é observada em estudos com *T. furcata* na porção sul da Mata Atlântica (seis a 16 espécies, NMI = 41 a 2.087; Cherem *et al.*, 2018; Peters *et al.*, 2010; Pontes *et al.*, 2021; Scheibler & Christoff, 2007; Silveira *et al.*, 2021).

Especificamente em relação aos estudos em floresta estacional, a riqueza obtida em Coronel Freitas foi menor do que a de Alpestre (Cherem *et al.*, 2018; 11 espécies, considerando a presença de duas espécies de *Akodon*, NMI = 80) e Venâncio Aires (Scheibler & Christoff, 2007; 16 espécies, NMI = 2.087). Para áreas próximas, em floresta ombrófila mista, valores comparativamente altos também foram registrados, como por Cherem *et al.* (2018; 15 espécies e NMI = 621 em Lages, 16 espécies e NMI = 323 em São Mateus do Sul) e Silveira *et al.* (2021; 14 espécies e NMI = 364 em Campos Novos). Todas essas áreas estão inseridas em paisagens com florestas fragmentadas em uma matriz de ambientes antropizados. A riqueza comparativamente baixa de Coronel Freitas pode estar em parte associada ao tamanho de sua amostra, indicado pelo NMI, haja vista as maiores riqueza e tamanho da amostra em Lages e Venâncio Aires. No entanto, algumas amostras semelhantes resultaram em riquezas maiores (vide São Mateus do Sul), indicando que outros fatores também podem estar envolvidos,

como a disponibilidade e a vulnerabilidade das presas localmente (Bellocq, 1998; Bonvicino & Bezerra, 2003; Sick, 2001), além do grau de fragmentação e do estado de conservação dos ambientes florestais em torno dos pontos de coleta de egagropilos (Bovendorp *et al.*, 2019; de la Sancha *et al.*, 2020).

Apesar disso, os dados de Coronel Freitas, obtidos em um dia de campo, demonstram o potencial da amostragem com pelotas de coruja em comparação com levantamentos de pequenos mamíferos em áreas de floresta estacional através de métodos convencionais (armadilhas de arame ou chapas de alumínio e armadilhas de interceptação e queda). Por exemplo, em três áreas próximas do rio Uruguai, Cherem *et al.* (2021) registraram de duas a seis espécies por área em amostragens com armadilhas dispostas em grade (três noites durante 10 campanhas por área) e de seis a 13 espécies por área com armadilhas de queda (pelo menos nove noites durante oito campanhas por área). Além do esforço de campo e custo baixos e da riqueza e abundância altas das amostras obtidas com pelotas de *Tyto*, Scheibler & Christoff (2007) e Peters *et al.* (2010) também apontaram a complementariedade dos resultados por pelotas e armadilhas, obtendo-se um quadro mais completo da assembleia de pequenos mamíferos quando ambos os métodos de amostragem podem ser aplicados (Bonvicino & Bezerra, 2003).

Em relação à composição taxonômica, os gêneros *Akodon* e *Oligoryzomys* foram registrados tanto na amostra de Coronel Freitas quanto nos demais estudos com *T. furcata* na porção sul da Mata Atlântica (Cherem *et al.*, 2018; Peters *et al.*, 2010; Pontes *et al.*, 2021; Scheibler & Christoff, 2007; Silveira *et al.*, 2021). Esses roedores estão entre os mais comuns nas assembleias de pequenos mamíferos do bioma (Grazzini *et al.*, 2015; Melo *et al.*, 2011; Umetsu & Pardini, 2007). Por outro lado, *Oxymycterus* sp. e *Sooretamys angouya* (G. Fischer, 1814) não foram registrados no presente estudo, apesar de estarem representados em muitas localidades amostradas a partir de egagropilos de *Tyto* (e.g., Cherem *et al.*, 2018; Silveira *et al.*, 2021) e possuírem ampla distribuição na Mata Atlântica (Oliveira & Gonçalves, 2015; Percequillo, 2015).

Outras espécies registradas no presente estudo estão variavelmente representadas na dieta de *T. furcata* na porção sul da Mata Atlântica. Por exemplo, *C. tener* e *N. lasiurus* são roedores associados a ambientes abertos naturais ou modificados, como bordas de campos cultivados e áreas de plantio abandonadas (Pardiñas *et al.*, 2015b; Umetsu & Pardini, 2007). Considerando as áreas de floresta ombrófila mista ou estacional, *C. tener* ou *C. laucha* (G. Fischer, 1814) e *N. lasiurus* também foram registradas por Cherem *et al.* (2018), Peters *et al.* (2010), Scheibler & Christoff (2007) e Silveira *et al.* (2021). No entanto, esses roedores não estiveram presentes nas amostras em Floresta Ombrófila Densa (Cherem *et al.*, 2018; Pontes *et al.*, 2021).



Espécies associadas a ambientes florestais, como *A. montensis* e *B. iheringi*, também foram registradas na presente amostra. Para a Mata Atlântica no Sul do Brasil, a cobertura do dossel, a densidade da vegetação herbácea e a presença de pequenas samambaias têm sido apontadas como as variáveis mais importantes do microhabitat para *A. montensis* (Dalmagro & Vieira, 2005; Melo *et al.*, 2013). No caso de *B. iheringi*, os dados disponíveis indicam que a espécie é mais frequentemente registrada em áreas florestais com cobertura herbácea e serapilheira densa (Vilela *et al.*, 2015). Outras espécies florestais, como *Gracilinanus microtarsus* (Wagner, 1842) e *S. angouya*, foram registradas em estudos semelhantes no sul do país (*e.g.*, Cherem *et al.*, 2018; Silveira *et al.*, 2021). Sua ausência na presente amostra pode refletir a redução e a alteração dos fragmentos florestais locais (Bovendorp *et al.*, 2019; de la Sancha *et al.*, 2020).

De um modo geral, roedores são comumente registrados como o grupo mais representativo nas pelotas de *T. furcata* (*e.g.*, Bellocq, 1998; Bonvicino & Bezerra, 2003). Isso também foi verificado na amostra de Coronel Freitas, onde os roedores representaram quase a totalidade dos indivíduos (99,42%). Em particular, *Oligoryzomys* sp. (51,17%) e *M. musculus* (25,15%) foram as espécies mais comuns dessa amostra. *Oligoryzomys* tem sido registrado como o pequeno mamífero mais frequente na dieta de *T. furcata* em muitas localidades, incluindo tanto áreas em floresta estacional (Cherem *et al.*, 2018 – Alpestre), quanto em floresta ombrófila densa (Cherem *et al.*, 2018 – Garuva e Siderópolis) ou mista (Cherem *et al.*, 2018 – São Mateus do Sul; Pontes *et al.*, 2021; Silveira *et al.*, 2021). *Mus musculus* também tem sido identificado como a espécie mais frequente em algumas localidades, como Venâncio Aires (Scheibler & Christoff, 2007) e UHE Quebra Queixo (Cherem *et al.*, 2018). A alta proporção de *Oligoryzomys* e *Mus* está relacionada com a ocorrência de áreas antropizadas e florestas secundárias em estágios iniciais de sucessão (Catzeflis, 2018; Melo *et al.*, 2011; Pardini & Umetsu, 2006; Scheibler & Christoff, 2007) e presumivelmente corresponde à abundância das presas nos ambientes em torno do ninho da coruja (Andrade *et al.*, 2016).

Morcegos, por outro lado, são raramente registrados em egagropilos de *Tyto* (*e.g.*, Yalden & Morris, 1990). Estudos conduzidos na parte sul da Mata Atlântica também têm indicado sua ausência (*e.g.*, Lages e Garuva em Cherem *et al.*, 2018) ou baixa representatividade nas amostras, como verificado por Scheibler & Christoff (2007; duas espécies; NMI = 7), Cherem *et al.* (2018; Araquari – três espécies; NMI = 5) e no presente estudo (uma espécie; NMI = 1). Isso contrasta com algumas amostragens realizadas em outras áreas, como a Toca dos Ossos (nove espécies; NMI = 293; Jesus & Oliveira, 2017) e a caverna de Salamanta (oito espécies; NMI = 47; Mancini *et al.*, 2018), ambas na Caatinga do Nordeste do Brasil. Nesses casos, a maior quantidade de morcegos na dieta de *T. furcata* tem sido atribuída a

condições locais específicas, como a ocorrência de colônias de morcegos e a facilidade de captura pela coruja (Mancini *et al.*, 2018; Roda, 2006).

Como corroborado pelo presente estudo, a análise de egagropilos de corujas é uma excelente ferramenta para o levantamento de pequenos mamíferos de grandes áreas com baixo custo e rapidez (Avenant, 2005; Formoso *et al.*, 2016; Heisler *et al.*, 2016). Apesar de a fragmentação do material ser um fator que dificulta a identificação das espécies de pequenos mamíferos (Stutz *et al.*, 2020), para a amostra de Coronel Freitas foi possível obter-se uma identificação confiável dos espécimes, ainda que o material atribuído a *Oligoryzomys* não pudesse ser identificado ao nível de espécie. Como refletido na composição e na proporção das espécies nessa amostra, a conversão das florestas estacionais em áreas rurais tem sido intensa (Vibrans *et al.*, 2012), a ponto de serem consideradas as florestas mais ameaçadas da Mata Atlântica no Sul do Brasil (Carlucci *et al.*, 2021). Neste sentido, espera-se que trabalhos com egagropilos sejam cada vez mais frequentes na literatura, ampliando o conhecimento sobre a distribuição e a conservação dos pequenos mamíferos, bem como sobre o monitoramento de suas populações, através de coletas periódicas do material regurgitado pelas corujas.

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APÊNDICE

Lista dos espécimes depositados na Coleção de Mamíferos do Departamento de Ecologia e Zoologia da Universidade Federal de Santa Catarina (UFSC) utilizados na comparação com os espécimes dos egagropilos.

Cryptonanus guahybae: UFSC 4465, 4589, 4854, 5197, 5234, 5434. *Gracilinanus microtarsus*: UFSC 3851, 4857, 5951, 5893. *Monodelphis dimidiata*: UFSC 3778, 4823, 4861, 5740. *Monodelphis iheringi*: UFSC 3797, 4585, 4607, 5436. *Monodelphis scalops*: UFSC 3780, 3915, 4056. *Akodon montensis*: UFSC 222, 288, 3481, 3701, 3702, 3804, 4068, 4073, 4683, 5090-5096, 5098-5101, 5103, 5104, 5109, 5110, 5628. *Akodon paranaensis*: UFSC 3628, 3631, 3721, 4064, 4086, 4686, 5138, 5154, 5160, 5161, 5627, 5685. *Brucepattersonius iheringi*: UFSC 3425, 4925. *Brucepattersonius soricinus*: UFSC 4692, 4810. *Calomys tener*: UFSC 5166, 5490. *Necomys lasiurus*: UFSC 3599, 3600, 3876, 4714. *Oligoryzomys flavescens*: UFSC 60, 3643, 4133, 4138, 4400, 4548, 4694, 4695, 5036, 5043, 5048-5050, 5639, 5891. *Oligoryzomys nigripes*: UFSC 498, 501, 502, 510, 3638, 4537-4540, 4544-4547, 5357, 5640, 5641, 5736, 5837, 5838. *Oxymycterus nasutus*: UFSC 955, 5892, 5934. *Rattus norvegicus*: UFSC 428, 2687, 4343, 4729, 4730, 5456, 5743. *Rattus rattus*: UFSC 2391-2395, 5080, 5565, 5744-5749.



Mammals from biodiversity-rich protected areas in the Brazilian Discovery Coast

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Abstract: The collection and quality of primary data on species occurrence and distribution are paramount to subsidizing evidence-based conservation initiatives. Here, we monitored medium and large-sized mammals in two protected areas in the Southern portion of the Atlantic Forest of Bahia, Brazil, the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB). We aimed to update and complement the species lists, and discuss species occurrence in the region. We conducted camera trapping from 2018 to 2021 (four campaigns) and recorded 31 species (RPPNEV = 26, PNPB = 31). Adding previous records, the aggregated overall richness increased to 36 species (RPPNEV = 30, PNPB = 34), with 36% of them considered regionally threatened. *Dasyprocta leporina*, *Dasyurus novemcinctus*, and *Mazama* sp. were the most abundant species in RPPNEV, and *D. novemcinctus*, *Dicotyles tajacu*, and *Mazama* sp. in PNPB. Even with a substantial sampling effort (16,057 trap-days), richness estimators indicate that more species can be recorded in both areas. Compared to other forest remnants in Southern Bahia (N = 70), the study areas stand out as two of the richest concerning mammalian diversity, with PNPB being the richest remnant to date, and reinforcing their role as strongholds for biodiversity in human-modified landscapes. Besides maintaining an elevated species richness, the study areas safeguard mammals sensitive to habitat loss and large-sized ones, being comparable to some of the richest sites in the Atlantic Forest. Moreover, both areas endured several economic cycles since Brazilian colonization, and still represent beacons of hope for biodiversity conservation in this megadiverse part of the biome.

Keywords: Atlantic Forest; Camera trap; Inventory; Relative abundance; Threatened species.

Resumo: Mamíferos de duas áreas protegidas na Costa do Descobrimento, Brasil. A coleta e a qualidade de dados primários sobre a ocorrência e distribuição das espécies são essenciais para subsidiar iniciativas de conservação. Nesse estudo, monitoramos mamíferos de médio e grande porte em duas áreas protegidas na porção sudoeste da Mata Atlântica da Bahia, a RPPN Estação Veracel (RPPNEV) e o Parque Nacional do Pau Brasil (PNPB), com o objetivo de atualizar as listas de espécies e discutir a sua ocorrência na região. Conduzimos o armadilhamento fotográfico entre 2018-2021, registrando 31 espécies (RPPNEV = 26, PNPB = 31). Adicionando registros anteriores, a riqueza total agregada foi ampliada para 36 espécies (RPPNEV = 30, PNPB = 34), com 36% delas ameaçadas regionalmente. *Dasyprocta leporina*, *Dasyurus novemcinctus* e *Mazama* sp. foram as espécies mais abundantes na RPPNEV, e *D. novemcinctus*, *Dicotyles tajacu* e *Mazama* sp. no PNPB. Apesar do esforço amostral substancial (16.057 armadilhas-dia), os estimadores de riqueza indicaram que mais espécies podem ser registradas em ambas as áreas. Comparadas a outros remanescentes florestais no sudoeste da Bahia (N = 70), as áreas de estudo estão entre as mais ricas em diversidade de mamíferos, sendo o PNPB a área mais rica até o momento, reforçando seu papel como áreas fonte para a biodiversidade em paisagens modificadas. Além da elevada riqueza de espécies, essas áreas abrigam mamíferos sensíveis à perda de habitat e de grande porte, comparáveis a algumas das áreas mais ricas da Mata Atlântica. Ambas as áreas resistiram a diversos ciclos econômicos desde a colonização do Brasil, e continuam representando uma esperança para conservação da biodiversidade nessa parte megabiodiversa do bioma.

Palavras-chave: Abundância relativa; Armadilhas fotográficas; Espécies ameaçadas; Inventário; Mata Atlântica.

INTRODUCTION

Primary data on species occurrence and distribution are required to subsidize evidence-based conservation initiatives. Moreover, the amount and quality of this kind of information are also needed for a more assertive application of financial resources aiming to develop strategies and actions toward biodiversity conservation. The Neotropical region has enormous biodiversity, but many knowledge gaps on species occurrence and distribution need attention (Oliveira *et al.*, 2016). Among the several biodiversity hotspots located in the Neotropics, the Atlantic Forest in South America stands out as one of

the most threatened ecosystems in the world (Rezende *et al.*, 2018), safeguarding impressive levels of biodiversity and endemism (Joly *et al.*, 2014).

Overall, the Atlantic Forest was one of the largest tropical and subtropical forests on Earth but has now been reduced to only 28% of its original coverage (Rezende *et al.*, 2018). Despite being considered biodiversity-rich, the Northeast portion of this biome has most of its forest cover replaced with anthropogenic land uses, with only 1-2% of the original forests remaining (Cl *et al.*, 2001; Costa & Guerra, 2012). This region is also underrepresented concerning the number of protected areas in comparison to the South and Southeast



portions of the Atlantic Forest, with the current network of protected areas composed of small and isolated areas (Cl *et al.*, 2001).

A key region in the Northeast portion of this biome is the Central Corridor of the Atlantic Forest (*Corredor Central da Mata Atlântica*), which covers an area of 21.3 Mha, from the Espírito Santo to the south of Bahia states in Brazil (Lamas *et al.*, 2015), encompassing two centers of endemism for terrestrial vertebrates (Costa *et al.*, 2000; Kinzey, 1982; Silva *et al.*, 2004). The continental portion of this region (13.3 Mha) is also of special relevance to conservation because it shares several taxa (fauna and flora) with the Amazon (Aguiar *et al.*, 2005). It is also the main locality of *florestas de tabuleiro* physiognomy (MMA *et al.*, 2006), a type of ombrophilous dense forest virtually restricted there.

The Southern coast of Bahia state harbors most of the Atlantic Forest remnants of northeast Brazil (Ayres *et al.*, 2005), including large and strictly protected areas. Due to its historical and ecological relevance, including its importance as an area where the European colonization first took place in Brazil (Dean, 1997), Southern Bahia is considered a priority region for conservation (BRASIL, 2018). On top of that, the region is recognized by UNESCO as a Natural World Heritage site (Brazilian Discovery Coast; UNESCO, 1999) and is considered a hotspot of biodiversity within the entire biome (Martini *et al.*, 2007).

Despite the paramount importance of the Atlantic Forest of Southern Bahia, its fauna is still poorly known, and a substantial part of the existing knowledge on vertebrate species, such as mammals, is not available. A total of 321 mammal species are expected to occur in the entire Atlantic Forest, with 65.4% (210) occurring in the Northeast portion of the biome (Graipel *et al.*, 2017). Mammals perform a wide range of ecological functions and ecosystem services in tropical forests (Bogoni *et al.*, 2020; Magioli *et al.*, 2021a), being therefore fundamental for ecosystem functioning. In the Atlantic Forest of Bahia state, 60 species of medium and large-sized mammals potentially occur, of which 26 are locally threatened, most classified as Endangered or Critically Endangered (Cassano *et al.*, 2017). Some of these species have a few known recent records, such as the Northern muriqui (*Brachyteles hypoxanthus*) in Alto Cariri National Park, the jaguar (*Panthera onca*) in Private Natural Heritage Reserve Estação Veracel, and the white-lipped pecary (*Tayassu pecari*) in Descobrimento National Park, while others are virtually extinct [*e.g.*, giant anteater (*Myrmecophaga tridactyla*), giant armadillo (*Priodontes maximus*), and bush dog (*Speothos venaticus*)] (Magioli *et al.*, 2021b).

Here, we aimed to update and complement the list of medium and large-sized mammals of two protected areas in the megadiverse Atlantic Forest hotspot of Southern Bahia, Brazil, and to discuss the occurrence of the species recorded in the region.

MATERIAL AND METHODS

The protected areas are located in the extreme south of Bahia state in Brazil (Figure 1), within the Bahia biogeographical sub-region of the Atlantic Forest, of which 85% of all forest fragments are smaller than 50 ha, indicating high levels of fragmentation and isolation (Ribeiro *et al.*, 2009). The region is relatively well-preserved, where over 50% of the land is covered by forested mosaics, including primary and secondary forests, and shade cacao plantations (Landau *et al.*, 2008). The main economic activities of the region are cattle ranching, small agriculture (cocoa and coffee plantations), planted forests (particularly *Eucalyptus* spp.), and tourism (Landau *et al.*, 2008; MMA *et al.*, 2006). According to the Köppen classification, the climate is hot and humid without a dry season, with a mean annual temperature of 24°C, and annual rainfall averaging 2,000 mm/year (Thomas *et al.*, 1998).

The Private Natural Heritage Reserve Estação Veracel (RPPNEV; 16°20'45"S, 39°08'26"W, Datum WGS84) is a protected area of sustainable use located in Porto Seguro and Santa Cruz Cabrália municipalities. This private protected area totals 6,069 ha and belongs to Veracel Celulose S.A., created in 1999 aiming to protect rare and threatened species such as the lowland tapir (*Tapirus terrestris*) and the harpy eagle (*Harpia harpia*). The Pau Brasil National Park (PNPB; 16°30'07"S, 39°16'03"W, Datum WGS84) is a strictly protected area with 19,027 ha managed by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) of the Brazilian Environmental Ministry (MMA). Created in 1998, this park aimed to protect the local biodiversity (also including the harpy eagle and lowland tapir) and one of the few remaining native populations of the Pau-Brasil tree (*Paubrasilia echinata*), an overexploited product during the Brazilian colonization, which names the park. These protected areas are ~5 km distant from each other in a straight line. The landscape between and surrounding these areas is composed of private properties and human settlements, and the main land uses are pastures, planted forests (*i.e.*, *eucalyptus*), and small forest remnants (Figure 1).

To sample mammals, we employed camera trapping during four periods: 1) from August to November 2018; 2) from April to June 2019; 3) from August to October 2019, and 4) from August to November 2021. Our study design followed the TEAM Protocol (TEAM, 2011), using 30 sampling stations with a single camera trap (Bushnell Trophy Cam HD, Model 119876) per area placed inside the forest remnants and in animal trails, and considering a distance of 1.4 km between stations. We also placed additional camera traps on dirt roads and trails. Some trapping station locations were changed during sampling due to equipment theft; details on the location of the camera traps in each campaign per area are shown in Appendix 1 – Figures S1-S4. Camera traps were installed in tree trunks ~40 cm above the ground,

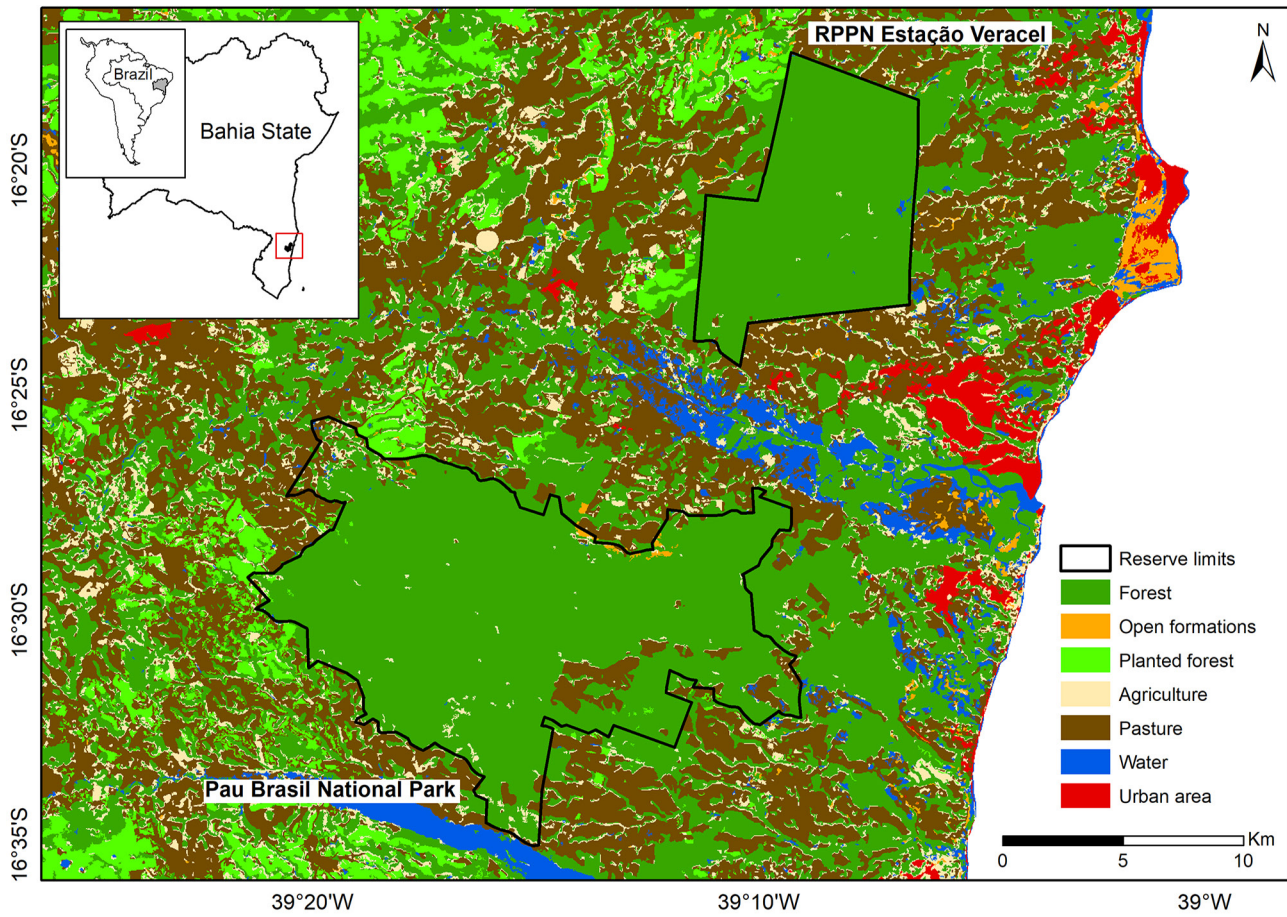


Figure 1: Location of the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB) in the Atlantic Forest of the extreme south of Bahia, Brazil, where medium and large-sized mammals were sampled.

which were active 24h/day for ~60 days per campaign; no baits were used. The number of trapping stations varied from 63 to 69 among campaigns, resulting in slightly different sampling efforts. The total sampling effort for both areas was 16,057 trap-days: 7,895 in RPPNEV (from 1818 to 2040 trap-days) and 8,162 in PNPB (from 1,838 to 2,350 trap-days).

We consulted specialized literature to identify the medium and large-sized mammal species (Becker & Dalponte, 2013; Borges & Tomás, 2008; Emmons & Feer, 1997; Oliveira & Cassaro, 2006). We considered medium-sized mammals those weighing from 1 to 7 kg (Chiarello, 2000), whereas species weighing over 7 kg were considered large-sized (Emmons & Feer, 1997). We also included some species weighing less than 1 kg in our list because they are commonly included in medium and large-sized mammal inventories (e.g., *Guerlinguetus brasiliensis*, *Callithrix* spp.). Species nomenclature followed Abreu *et al.* (2021), and we assigned threat categories per species (i.e., Vulnerable, Endangered, and Critically Endangered) following regional (Bahia, 2017), national (BRASIL, 2022), and international levels (IUCN, 2022). We considered exotic species those that occurred outside their natural range, as defined in Falk-Petersen *et al.* (2006).

To compose the species list, we also included records from visualizations, vocalizations, and tracks obtained during sampling, but these were not included in the analyzes. We complemented our species list with records from previous studies (compiled in Magioli *et al.*, 2021b). To organize and help with the identification process of the photos from camera traps, we used the Wild.ID 1.0 program (<https://github.com/ConservationInternational/Wild.ID>). For data organization and exploration, we used the R package camtrapR (Niedballa *et al.*, 2016). We considered independent records those taken with at least an one-hour interval between records of the same species in each trapping station. For each area, we calculated the species accumulation curve and estimated the richness using the 1st order Jackknife and Bootstrap estimators, implemented by the R package vegan (Oksanen *et al.*, 2022). We calculated a proxy of the species' relative abundance using the capture rate of each species weighted by the sampling effort (number of individual records * 100/sampling effort). To highlight the relevance of the study areas in the regional context, we compared the overall richness and the richness of threatened species of RPPNEV and PNPB with other protected and unprotected forest remnants in the Atlantic Forest of Southern Bahia (N = 70), compiling information



from the dataset available in Magioli *et al.* (2021b). All analyzes were performed in R 4.2.1 (R Core Team, 2022), and we used the R package ggplot2 (Wickham, 2016) for graphical implementation. Camera trapping was authorized by SISBIO permit #60641.

RESULTS

Considering the records from camera trapping and direct and indirect evidence of mammalian presence, we recorded 31 species of medium and large-sized mammals, 26 in RPPNEV, and 31 in PNPB (Table 1, Figure 2). We recorded the presence of two domesticated species, the domestic dog (*Canis lupus familiaris*) and the domestic cat (*Felis catus*). Adding records from previous studies (compiled in Magioli *et al.*, 2021b), the overall aggregated richness increased to 36 species (RPPNEV = 28; PNPB = 34), including the seven-banded armadillo (*Dasybus septemcinctus*), the white-lipped peccary (*T. pecari*), northern brown howler monkey (*Alouatta guariba guariba*), the ocelot (*Leopardus pardalis*), and the jaguar (*Panthera onca*), totaling nine orders and 23 families; the order Carnivora was the richest (N = 15 species). Thirteen species are threatened in Bahia, 10 in Brazil, and six worldwide. The greater naked-tailed armadillo (*Cabassous tatouay*) is considered data deficient nationally. The record of the maned wolf (*Chrysocyon brachyurus*) is the northernmost for the region. Poachers were detected in 16 trapping stations in RPPNEV and 12 in PNPB, with a total of 15 camera traps stolen during the sampling period (RPPNEV = 7; PNPB = 8). Domestic dogs were recorded in 18 trapping stations in RPPNEV and seven in PNPB.

Accounting for camera trap data only, the most abundant species in RPPNEV were the red-rumped

agouti (*Dasyprocta leporina*), the nine-banded armadillo (*Dasybus novemcinctus*), and the brocket deer (*Mazama sp.*) (Figure 3A), while for PNPB were the nine-banded armadillo, the collared peccary (*Dicotyles tajacu*), and the brocket deer (Figure 3B). For RPPNEV, the richness estimators' 1st order Jackknife and Bootstrap predicted 25.9 ± 1.4 and 24.4 ± 1.0 species, respectively, showing a deacceleration from the 100^o sampling day, but not reaching asymptote (Figure 4A). For PNPB, the estimators' 1st order Jackknife and Bootstrap predicted 37.9 ± 2.9 and 32.4 ± 1.5 species, respectively, not showing signs of deacceleration (Figure 4B). Compared to other forest remnants of Southern Bahia (N = 70), both study areas presented elevated overall richness, with PNPB being the richest area to date in the entire region and RPPNEV the third (Figure 5A). The pattern is reinforced concerning the richness of threatened species, with both areas being among the richest remnants of the region (Figure 5B), with PNPB as second and RPPNEV as fourth.

DISCUSSION

The study areas, RPPNEV and PNPB, stand out as two of the richest forest remnants in Southern Bahia concerning mammalian diversity, together accounting for 60% of all species expected to occur in the Atlantic Forest of the state. Moreover, 36% of the recorded species are regionally threatened, stressing the role of these protected areas as refuges for mammals sensitive to habitat loss and large-sized ones, such as the lowland tapir (*T. terrestris*), which have recent records in only three areas of Southern Bahia (Magioli *et al.*, 2021b). Even with a substantial sampling effort achieved

Table 1: Medium and large-sized mammals recorded at Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB), extreme south of Bahia, Brazil, including threat categories at regional (Bahia, 2017), national (BRASIL, 2022), and international levels (IUCN, 2022). ¹ Magioli *et al.* (2021b); C = camera trap; Vi = visualization; Vo = vocalization; F = feces; L = literature; * Domestic species; † Historical record; ‡ Possibly misidentified.

Taxon	Common name	RPPNEV	PNPB	Threat category		
				Bahia	Brazil	World
DIDELPHIMORPHIA						
DIDELPHIDAE						
<i>Didelphis aurita</i> (Wied-Neuwied, 1826)	Black-eared opossum	C	C			
PILOSA						
BRADYPODIDAE						
<i>Bradypus variegatus</i> Schinz, 1825	Brown-throated sloth	Vi	Vi			
MYRMECOPHAGIDAE						
<i>Tamandua tetradactyla</i> (Linnaeus, 1758)	Southern tamandua	C	C,Vi			
CINGULATA						
CHLAMYPHORIDAE						
<i>Cabassous tatouay</i> (Desmarest, 1804)	Greater naked-tailed armadillo	C	C			DD
<i>Euphractus sexcinctus</i> (Linnaeus, 1758)	Six-banded armadillo	L ¹	C			
DASYPODIDAE						
<i>Dasybus novemcinctus</i> Linnaeus, 1758	Nine-banded armadillo	C,Vi	C,Vi			
<i>Dasybus septemcinctus</i> (Linnaeus, 1758)	Seven-banded armadillo		L ¹			



Taxon	Common name	RPPNEV	PNPB	Threat category		
				Bahia	Brazil	World
PERISSODACTYLA						
TAPIRIDAE						
<i>Tapirus terrestris</i> (Linnaeus, 1758)	Lowland tapir	C,F	C,F	EN	VU	VU
ARTIODACTYLA						
CERVIDAE						
<i>Mazama</i> sp. (Erxleben, 1777)	Deer	C	C,Vi			
TAYASSUIDAE						
<i>Dicotyles tajacu</i> (Linnaeus, 1758)	Collared peccary	C	C,Vi			
<i>Tayassu pecari</i> (Link, 1795)	White-lipped peccary		L ¹⁺	EN	VU	VU
PRIMATES						
ATELIDAE						
<i>Alouatta guariba guariba</i> (Humboldt, 1812)	Northern brown howler monkey		L ⁺	CR	CR	CR
CALLITRICHIDAE						
<i>Callithrix geoffroyi</i> (Humboldt, 1812)	Geoffroy's tufted-ear marmoset	C,Vi,Vo	C,Vi,Vo			
CEBIDAE						
<i>Sapajus robustus</i> (Kuhl, 1820)	Crested capuchin	C,Vi,Vo	C,Vi,Vo	EN	EN	EN
PITHECIIDAE						
<i>Callicebus melanochir</i> (Wied-Neuwied, 1820)	Black-handed titi	Vi	Vo	VU	VU	VU
CARNIVORA						
CANIDAE						
<i>Canis lupus familiaris</i> *	Domestic dog	C,Vi,Vo	C,Vi,Vo			
<i>Cerdocyon thous</i> (Linnaeus, 1766)	Crab-eating fox	C	C			
<i>Chrysocyon brachyurus</i> (Illiger, 1815)	Maned wolf		C	EN	VU	
FELIDAE						
<i>Felis catus</i> *	Domestic cat		C			
<i>Herpailurus yagouaroundi</i> (É. Geoffroy, 1803)	Jaguarundi	C	C	VU	VU	
<i>Leopardus guttulus</i> (Schreber, 1775)	Southern tiger cat	C	C	EN	VU	VU
<i>Leopardus pardalis</i> (Linnaeus, 1758)	Ocelot	L ¹⁺		VU		
<i>Leopardus wiedii</i> (Schinz, 1821)	Margay	C	C	EN	VU	
<i>Panthera onca</i> (Linnaeus, 1758)	Jaguar	L ¹		CR	VU	
<i>Puma concolor</i> (Linnaeus, 1771)	Puma	C,T,F	C,T,F	VU		
MEPHITIDAE						
<i>Conepatus semistriatus</i> (Lichtenstein, 1838)	Striped hog-nosed skunk	Vi	C,T			
MUSTELIDAE						
<i>Eira barbara</i> (Linnaeus, 1758)	Tayra	C	C,Vi			
<i>Galictis cuja</i> (Molina, 1782)	Lesser grison		C,T			
<i>Lontra longicaudis</i> (Olfers, 1818)	Neotropical otter		C	VU		
PROCYONIDAE						
<i>Nasua nasua</i> (Linnaeus, 1766)	South American coati	C,Vi	C			
<i>Potos flavus</i> (Schreber, 1774)	Kinkajou		C			
<i>Procyon cancrivorus</i> (G. Cuvier, 1798)	Crab-eating raccoon	C	C			
LAGOMORPHA						
LEPORIDAE						
<i>Sylvilagus brasiliensis</i> (Linnaeus, 1758)	Tapeti	C,Vi	C			
RODENTIA						
CAVIIDAE						
<i>Hydrochoerus hydrochaeris</i> (Linnaeus, 1766)	Capybara	C	C			
CUNICULIDAE						
<i>Cuniculus paca</i> (Linnaeus, 1766)	Lowland paca	C	C,T			
DASYPROCTIDAE						
<i>Dasyprocta leporina</i> (Linnaeus, 1758)	Red-rumped agouti	C,Vi	C			
ERETHIZONTIDAE						
<i>Coendou insidiosus</i> (Lichtenstein, 1818)	Bahia hairy dwarf porcupine	C	C			
SCIURIDAE						
<i>Guerlinguetus brasiliensis</i> (Thomas, 1901)	Brazilian squirrel	C,Vi	C			
Total (only native species)	36 (3 ⁺)	30 (1 ⁺)	34 (2 ⁺)	13	10	6



Figure 2: Photographic records of the medium and large-sized mammals recorded in the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB), extreme south of Bahia, Brazil. A. *Didelphis aurita*; B. *Bradypus variegatus*; C. *Tamandua tetradactyla*; D. *Cabassous tatouay*; E. *Euphractus sexinctus*; F. *Dasypus novemcinctus*; G. *Tapirus terrestris*; H. *Mazama* sp.; I. *Dicotyles tajacu*; J. *Callithrix geoffroyi*; K. *Sapajus robustus*; L. *Cerdocyon thous*; M. *Herpailurus yagouaroundi*; N. *Leopardus guttulus*; O. *Leopardus wiedii*; P. *Puma concolor*; Q. *Conepatus semistriatus*; R. *Eira barbara*; S. *Galictis cuja*; T. *Lontra longicaudis*; U. *Nasua nasua*; V. *Potos flavus*; X. *Procyon cancrivorus*; W. *Sylvilagus brasiliensis*; Y. *Hydrochoerus hydrochaeris*; Z. *Cuniculus paca*; A1. *Dasyprocta leporina*; B1. *Coendou insidiosus*; C1. *Guerlinguetus brasiliensis*.



(16,057 trap-days), the richness estimators indicate that more species can be recorded in both areas, strengthening their role as strongholds for biodiversity in heavily

human-modified landscapes. We highlight the presence of species associated with and tolerant to open habitats, such as the striped hog-nosed skunk (*Conepatus*

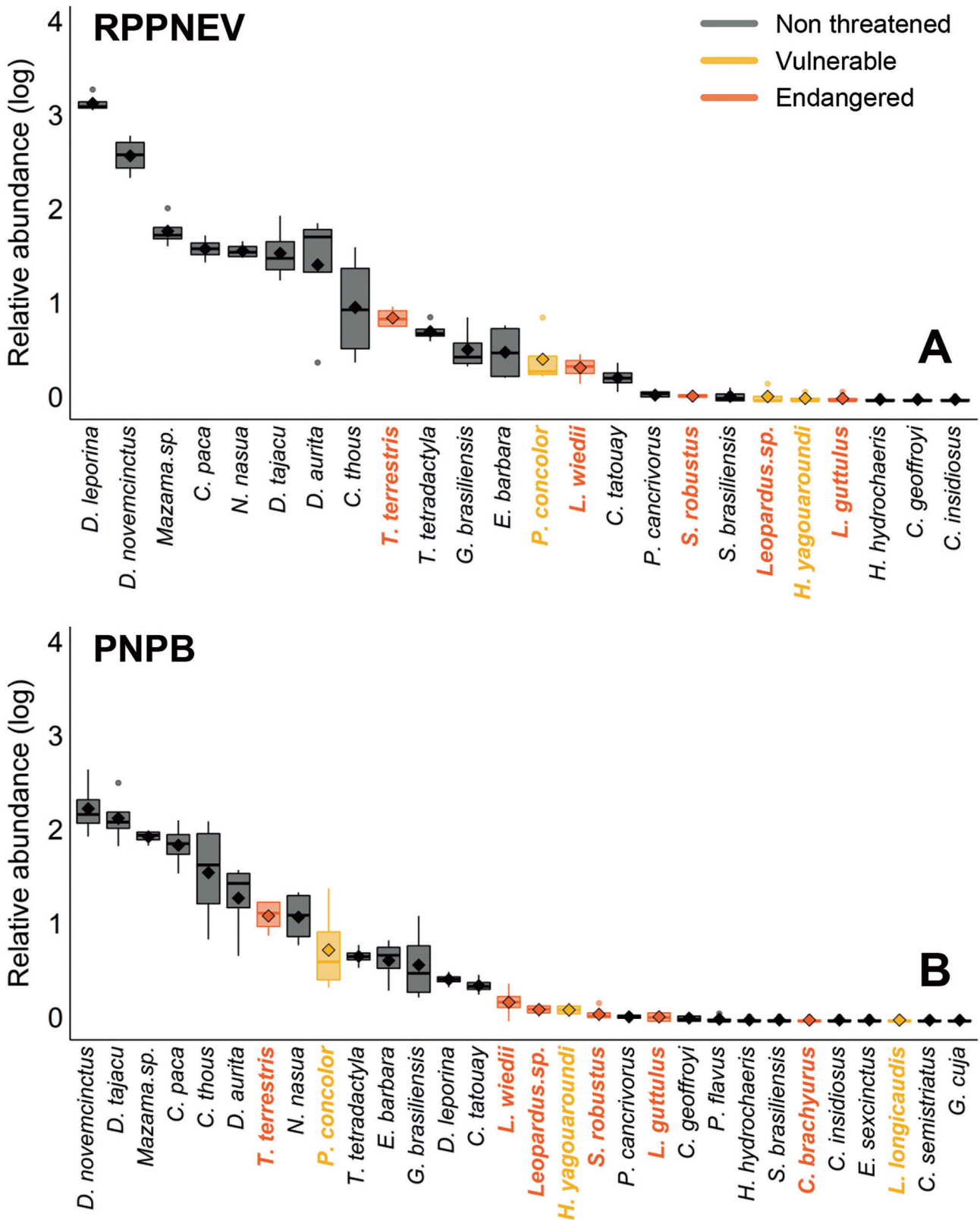


Figure 3. Relative abundance (log-transformed) of medium and large-sized mammals sampled with camera trapping in the Private Natural Heritage Reserve Estação Veracel (RPPNEV; A) and Pau Brasil National Park (PNPB; B) in the extreme south of Bahia, Brazil. Boxplots show means (diamonds), medians, quartiles, and outliers. Species listed in Bahia state red list (Bahia 2017) are highlighted according to the threat category.

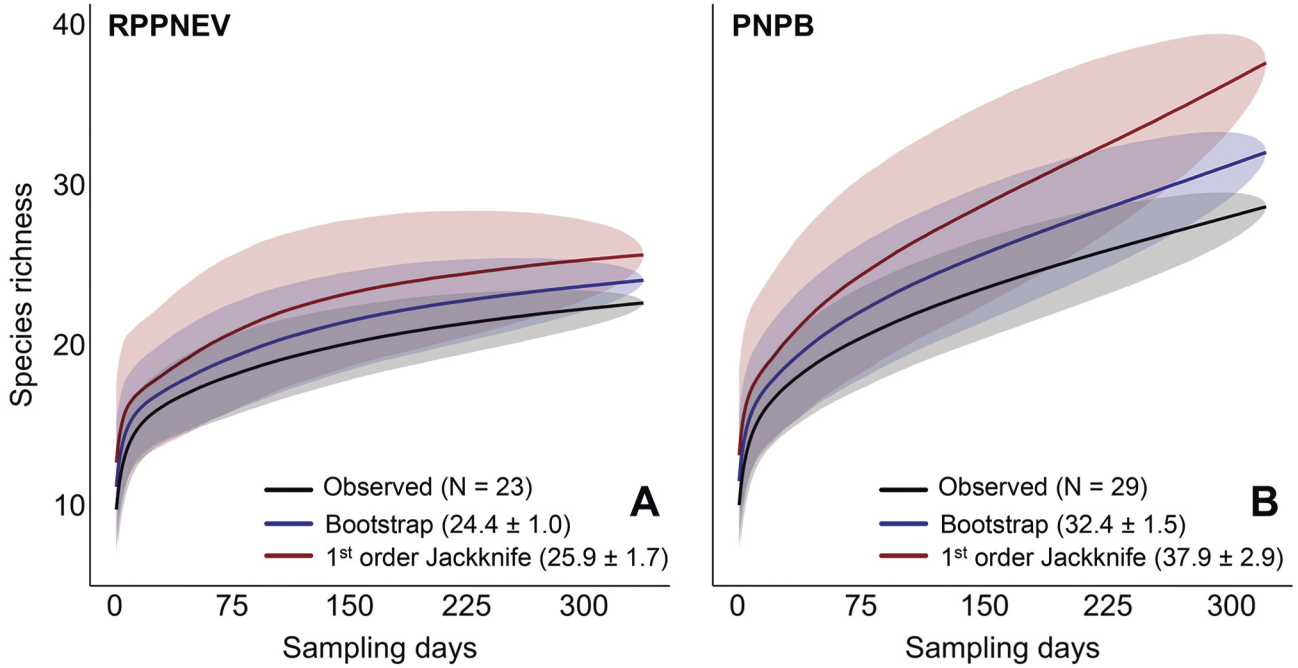


Figure 4. Species accumulation curve and richness estimators (1st order Jackknife and Bootstrap) of medium and large-sized mammals sampled with camera trapping in the Private Natural Heritage Reserve Estação Veracel (RPPNEV; A) and Pau Brasil National Park (PNPB; B) in the extreme south of Bahia, Brazil. Shaded areas represent the 95% confidence intervals.

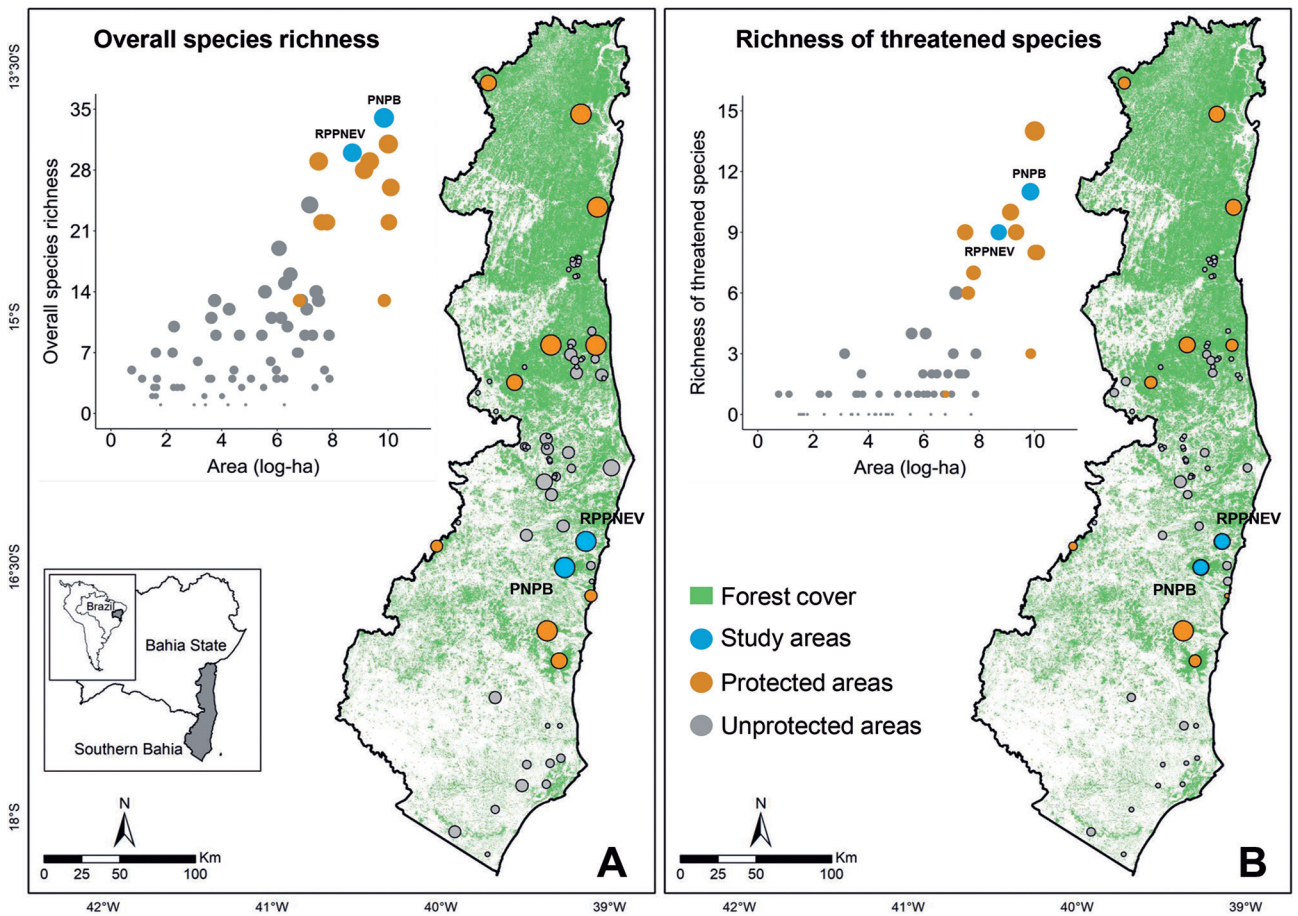


Figure 5. (A) The overall richness and (B) richness of locally threatened species (Bahia 2017) of medium and large-sized mammals in the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB) compared to protected (N = 10) and unprotected areas (N = 60) of different sizes at the Atlantic Forest in Southern Bahia, Brazil. Dot size in (A) and (B) depicts the richness of overall species and threatened species in each area.



semistriatus), the maned wolf (*C. brachyurus*), and the six-banded armadillo (*Euphractus sexcinctus*), which presence might be related to deforestation and habitat modification in the surrounding areas.

In comparison to previous studies (Falcão *et al.*, 2012; RPPN Estação Veracel, 2016), we increased the species richness in RPPNEV from 23 to 30 species, including seven new records: capybara (*Hydrochoerus hydrochaeris*), Bahia hairy dwarf porcupine (*Coendou insidiosus*), tayra (*Eira barbara*), tapeti (*Sylvilagus brasiliensis*), crab-eating raccoon (*Procyon cancrivorus*), striped hog-nosed skunk (*C. semistriatus*), and Southern tiger cat (*Leopardus guttulus*). In PNPB, compared to the previous list (ICMBio, 2016), we added another 15 species, increasing richness from 17 to 32 species: brown-throated sloth (*Bradypus variegatus*), Southern tamandua (*Tamandua tetradactyla*), greater naked-tailed armadillo (*C. tatouay*), maned wolf (*C. brachyurus*), jaguarundi (*Herpailurus yagouaroundi*), Southern tiger cat (*L. guttulus*), South American coati (*Nasua nasua*), striped hog-nosed skunk (*C. semistriatus*), lesser grison (*Galictis cuja*), Neotropical otter (*Lontra longicaudis*), crab-eating raccoon (*P. cancrivorus*), kinkajou (*Potos flavus*), tapeti (*S. brasiliensis*), capybara (*H. hydrochaeris*), and Bahia hairy dwarf porcupine (*C. insidiosus*). Another two species were added from literature to PNPB (Magioli *et al.*, 2021b), the seven-banded armadillo (*D. septemcinctus*), and the brown howler monkey (*A. guariba guariba*), totaling 34 species.

Richness estimators, considering only camera trap data, indicated that more species can be recorded in both study areas. In RPPNEV, for example, the lesser grison, the Neotropical otter, and the kinkajou were not recorded but might occur in the area. The records of the aforementioned species, and others with arboreal (*e.g.*, primates) and semi-aquatic habits (*e.g.*, capybara) are not favored by ground-level camera trap sampling, which reflects their scarce number of records during sampling in both areas. The six-banded armadillo, despite being a rather common species more associated with open habitats, occurs in forested areas closer to forest edges and secondary formations (Redford & Wetzel, 1985); the species was recorded a single time in PNPB, and it is mentioned in the management plan of RPPNEV (RPPN Estação Veracel, 2016), possibly occurring in low abundance. The records of the striped hog-nosed skunk and the maned wolf were surprising since these species are associated with more open habitats (*e.g.*, open Cerrado formations, and Caatinga), and are not expected to occur in large forest remnants. Considering that both areas are composed of dense forests (*tabuleiros* physiognomy), their records are somewhat worrisome because these species might benefit from habitat loss and habitat modification, expanding their distribution toward previously inadequate areas (*e.g.*, Magioli *et al.*, 2020).

The record of the maned wolf in PNPB is the northernmost record of the species in the Atlantic Forest of

Southern Bahia, ~120 km distant from previous records, *i.e.*, a roadkilled individual in Teixeira de Freitas municipality (Queirolo *et al.*, 2011). Lately, records of the species across the biome have become quite common as agricultural land uses, cattle ranching, and urban areas expand over natural forests, in addition to the loss of Cerrado formations, creating human-modified landscapes with open habitats that might favor the maned wolf presence (*e.g.*, Queirolo *et al.*, 2011; Bereta *et al.*, 2017). Nonetheless, our record occurred in a trapping station further inside the forest (primary formation), close to the center of PNPB and about 3.5 km from the border of the park, with the animal closely following a group of collared peccaries (*D. tajacu*). Since the species prefer open habitats and avoid densely forested ones (Paula & DeMatteo, 2015), we believe this is a vagrant individual that is exploring the landscape, and not actively using PNPB as part of its territory. Records of the species in densely forested areas, similar to ours, should be the target of studies aiming to understand behavioral and ecological aspects of the maned wolf mediated by land use changes.

From all the species recorded, the ocelot (*L. pardalis*), the jaguar (*P. onca*), the white-lipped peccary (*T. pecari*), the seven-banded armadillo (*D. septemcinctus*), and the brown howler monkey (*A. guariba guariba*) were not recorded recently. The ocelot is mentioned in the management plan of RPPNEV (RPPN Estação Veracel, 2016), being recorded a single time through tracks, while it was absent from PNPB without any previous records. We highlight that the species was recorded in only a few remnants throughout Southern Bahia and with a low number of records (Magioli *et al.*, 2021b), which suggests that the species might occur in low abundance. The jaguar was last recorded in 2017 in RPPNEV, after 20 years without records in the region (Casanova *et al.*, 2018), and with historical records only in Monte Pascoal National Park. The individual recorded in 2017 might have been dispersing, thus, moving among forest remnants in the region and not being restricted to a single area, which reduces the odds of recording it again.

The brown howler monkey, which is Critically Endangered in Bahia, was recorded by vocalization a single time in PNPB (Magioli *et al.*, 2021b), but no recent evidence was found, nor was it mentioned by the park staff or locals. The species has also historical records in other protected areas, Monte Pascoal National Park and Wenceslau Guimarães Ecological Station, but is virtually extinct from the region. The white-lipped peccary is mentioned in the management plan of PNPB (ICMBio, 2016), recorded by visualization, however, we believe it was a misidentification because no evidence was found of the presence of this species in the area, and not a single mention of the species by the park staff or locals. The species has historical records in Monte Pascoal National Park, but its presence is currently restricted to Descobrimento National Park (Magioli *et al.*, 2021b). Finally,



despite being smaller than the nine-banded armadillo, the seven-banded armadillo shares many morphological similarities (Feijó, 2020), being hard to identify and differentiate through camera trap photos. In addition, the species seems to be more associated with open habitats (Feijó, 2020), which could difficult its record in densely forested areas such as RPPNEV and PNPB.

Some other species are expected to occur, such as the maned three-toed sloth (*Bradypus torquatus*) and the thin-spined porcupine (*Chaetomys subspinosus*), both classified as Vulnerable to extinction in Bahia (Bahia, 2017), with distributions overlapping the study areas (Giné & Faria, 2018; Hirsch & Chiarello, 2012). There is evidence of the presence of the thin-spined porcupine in Porto Seguro (Giné & Faria, 2018), where both study areas are located, and a recent observation of an individual in the urban part of the city suggests that the species might be present in RPPNEV and PNPB. Conversely, the maned three-toed sloth was recorded in protected and unprotected areas in Southern Bahia (Magioli *et al.*, 2021b), with some of them close to the study areas (Hirsch & Chiarello, 2012). Species such as the giant armadillo (*Priodontes maximus*) are virtually extinct in the region and throughout the Atlantic Forest, with only a few remaining populations (Chiarello *et al.*, 2015). In Southern Bahia, there are historical records in Monte Pascoal National Park and a mention in the first version of the management plan of RPPNEV (Almeida *et al.*, 1998). Locals mentioned that the species occurred locally, but the last sightings were between the 1960s and 1970s (M. Magioli, pers. comm.). Previous studies mentioned the presence of the lesser naked-tailed armadillo (*Cabassous unicinctus*) in Southern Bahia (*e.g.*, Falcão *et al.*, 2012; Moura, 2003), but as suggested by Anacleto *et al.* (2006) and confirmed by Ribeiro *et al.* (2013), the greater naked-tailed armadillo (*C. tatouay*) is the species that occurs in the region, which was also confirmed by our study.

The most evident difference between the study areas is related to the number of records of red-rumped agouti (*D. leporina*), one of the most important seed dispersers in Neotropical rainforests (Emmons & Reid, 2016). It was the most abundant species in RPPNEV being recorded in all trapping stations while presenting an abundance 41 times lower in PNPB, occurring only from three to six stations per campaign. In the Atlantic Forest, although inhabiting secondary forests and human-modified environments (Emmons & Reid, 2016), the red-rumped agouti prefer primary forests, with its occupancy being primarily influenced by distance from water and forest edges, palm abundance (Ferreguetti *et al.*, 2018), and hunting pressure (Sousa & Srbek-Araujo, 2017). Interestingly, both study areas are very similar concerning floristic composition and conservation condition, besides being geographically close (~5 km in a straight line), but PNPB is about three-fold larger than RPPNEV. Further studies are necessary to uncover the

drivers of this pronounced difference, such as analysis of microhabitat, occupancy, and co-occurrence with other frugivore species, knowledge that will also contribute to the species conservation in the long term.

The study areas were among the richest forest remnants of Southern Bahia concerning the overall richness and the number of threatened species, with PNPB being the richest remnant in the region to date. Moreover, the aggregated richness of medium and large-sized mammals of both areas (N = 36) is comparable to some of the richest areas in the Atlantic Forest, such as the Serra do Mar Biodiversity Corridor in São Paulo (N = 39; Ferraz *et al.*, 2022), the forest block formed by Sooretama Biological Reserve and Vale Natural Reserve in Espírito Santo (N = 36; Srbek-Araujo & Kierulff, 2016), Iguaçú National Park in Paraná (N = 41; Brocardo *et al.*, 2019), and Turvo State Park in Rio Grande do Sul (N = 32; Kasper *et al.*, 2007; Meller *et al.*, 2020).

Although presenting an elevated mammalian diversity, these areas are not free from adverse factors that might jeopardize species conservation in the long term, such as the presence of poachers, domestic species, and illegal logging. We found abundant evidence of poaching spread out in both study areas, such as trails, tree stands (*esperas*), baits (fleshy fruits), handmade cannons (*trabucos*), traps (varied models), and camping sites, in addition to the theft of 15 of our camera traps. The records were made mostly in stations closer to trails, dirt roads, and forest edges, which facilitates people's dislocation and where camera traps were more exposed, eventually, being stolen. The substantial evidence of poaching can be mainly linked to elevated poverty levels in Northeast Brazil (Canale *et al.*, 2012; Castilho *et al.*, 2017; Flesher & Laufer, 2013), indicating that proximity to urban areas and human settlements are the main drivers of this increased poaching pressure (Santos *et al.*, 2018). The records of domestic dogs were also widespread, particularly in RPPNEV, being mainly associated with trapping stations in trails, dirt roads, and forest edges, and recording single individuals, pairs, and groups, or following poachers. The domestic species is responsible for competing with native carnivores for prey, persecuting and killing wildlife, and transmitting and being contaminated with diseases (Young *et al.*, 2011), stressing its negative impact on the mammalian fauna.

In conclusion, despite enduring several economic cycles since Brazilian colonization, the study areas still represent beacons of hope for biodiversity conservation in this megadiverse part of the Atlantic Forest, maintaining an elevated overall species richness and safeguarding populations of mammals sensitive to habitat loss. However, considering the current anthropogenic threats to which this region is under (*e.g.*, deforestation, poaching, agriculture, and urban expansion), the protected areas alone are not enough to contain biodiversity erosion. Therefore, is paramount to re-establish the connectivity between RPPNEV and PNPB, and with other protected



areas across Southern Bahia (e.g., Descobrimento, Monte Pascoal, Alto Cariri National Parks). To reconnect the network of existing protected areas, aiming to facilitate gene and species flux in the landscape, small and unprotected forest remnants in private properties need to be included. Moreover, knowledge of the biodiversity that inhabits these smaller remnants should be the target of future studies aiming to safeguard mammalian diversity and subsidize long-term conservation strategies.

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Supplementary material can be found at <https://sbmz.org/publicacoes>.

Appendix 1. Location of the trapping stations during each sampling campaign in the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB) in the extreme south of Bahia, Brazil (Figures S1 to S4).

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Appendix 1. Location of the trapping stations during each sampling campaign in the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB) in the extreme south of Bahia, Brazil.

Figure S1. Location of the camera trapping stations during the sampling campaign of Aug-Nov/2018 at the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB), extreme south of Bahia, Brazil.

Figure S2. Location of the camera trapping stations during the sampling campaign of Apr-Jun/2019 at the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB), extreme south of Bahia, Brazil.

Figure S3. Location of the camera trapping stations during the sampling campaign of Aug-Oct/2019 at the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB), extreme south of Bahia, Brazil.

Figure S4. Location of the camera trapping stations during the sampling campaign of Aug-Nov/2021 at the Private Natural Heritage Reserve Estação Veracel (RPPNEV) and Pau Brasil National Park (PNPB), extreme south of Bahia, Brazil.



Medium and large-sized mammals of the central region of Ceará state, Northeastern Brazil

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Abstract: Although it had been an important room for Mammalogy in the past, the state of Ceará (Northeastern Brazil) faces severe study gaps. Our goal is to fill part of this lack for the medium and large-sized mammals in the Central Region of Ceará and provide subsidies to effective conservation plans. Data were obtained between January 2017 to April 2021 through camera traps, visual records, tracks, records of roadkill, and voucher specimens from scientific collections. Human communities were interviewed in order to investigate non-recorded species and possible past occurrences. We documented 18 species belonging to 13 families and seven orders. Six species are documented as threatened in red lists and another five were cited by informants as locally extinct. Our results indicate that the Central Region of Ceará is a potential hotspot for mammals in the Caatinga biome and reveal an urgent need for further ecological research and conservation efforts.

Keywords: Brazilian Northeast, Caatinga; Conservation; Ecology; Inventory.

Resumo: Mamíferos de médio e grande porte da região central do estado do Ceará, Nordeste do Brasil. Embora tenha sido um importante palco para a Mastozoologia no passado, o estado do Ceará (Nordeste do Brasil) enfrenta graves lacunas de estudo. Nosso objetivo é preencher parte dessa lacuna para mamíferos de médio e grande porte da Região Central do Ceará e fornecer subsídios para medidas eficazes de conservação. Os dados foram obtidos entre janeiro de 2017 a abril de 2021 por meio de armadilhas fotográficas, registros visuais, rastros, registros de atropelamento e espécimes-testemunho de coleções científicas. Comunidades humanas foram entrevistadas para investigar espécies não registradas e possíveis ocorrências pretéritas. Documentamos 18 espécies pertencentes a 13 famílias e sete ordens. Seis espécies estão documentadas como ameaçadas em listas vermelhas e outras cinco foram citadas pelos informantes como localmente extintas. Nossos resultados indicam que a Região Central do Ceará é um potencial hotspot de mamíferos no bioma da Caatinga e revelam uma urgente necessidade de pesquisas ecológicas mais aprofundadas e ações de conservação.

Palavras-chave: Caatinga; Conservação; Ecologia; Inventário; Nordeste brasileiro.

INTRODUCTION

Caatinga is a semi-arid biome endemic from Brazil which involves a territory of more than 900,000 km² and reaches the states of Ceará, Piauí, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia and Minas Gerais (Silva *et al.*, 2017). It is known as a mosaic of seasonally dry and semi-deciduous forests, thorny shrubs and open fields (Albuquerque *et al.*, 2012; Leal *et al.*, 2005). This region lost approximately 90,000 km² of natural vegetation between 1990 and 2010, which means 37% of its original territory (Beuchle *et al.*, 2015). In addition, the biome is highly impacted by overhunting, fires, logging, alien species, and large areas of desertification (Albuquerque *et al.*, 2012; Silva & Barbosa, 2017; Vendruscolo *et al.*, 2021). Less than 8% of the Caatinga is inserted in protected areas and

only 1.3% is in reserves with full legal protection (Teixeira *et al.*, 2021).

On mammals, the last overview documents 183 small, medium and large sized species in this region (Carmignotto & Astúa, 2017), 30 more than that survey published five years earlier (Carmignotto *et al.*, 2012). This large difference in a short period suggests a huge lack of knowledge of the Mammalogy of Caatinga. In fact, new distribution records and even new species descriptions have been frequently published in recent years (*e.g.*, Feijó & Langguth, 2013; Gurgel-Filho *et al.*, 2015; Moratelli & Dias, 2015; Nascimento & Feijó, 2017). This biome is home to 11 endemic mammals (three bats, seven rodents and one primate), indicating a high ecological importance and complex biogeographic relationships (Carmignotto & Astúa, 2017). Mammals of the Brazilian Northeast face not only threats such as overhunting and



habitat loss (Albuquerque *et al.*, 2012; Alves *et al.*, 2016) but also a Linnean shortfall (Feijó & Langguth, 2013).

Ceará can be considered an accurate example of this scenario. This is the third most populous state of Northeastern Brazil, covered mainly by several phytoecological units of the Caatinga biome, in addition to Atlantic Forest remnants and Cerrado enclaves (Moro *et al.*, 2016; IPECE, 2021). Although it had been an important room for Mammalogy in the past, it faces severe study gaps. During decades, there was almost a total absence of research groups and large projects (see Fernandes-Ferreira *et al.*, 2014) with few exceptions (*e.g.*, Mares, 1981; Rocha, 1945; Thomas, 1910). The last few years witness an increase of scientific products which are still very focused on inventories (*e.g.*, Dias *et al.*, 2017; Fernandes-Ferreira *et al.*, 2015; Guedes *et al.*, 2000). While there are these gaps to be filled, 30 species of Ceará's mammals are locally threatened with extinction (SEMA, 2022).

Among recent publications, a state list for the terrestrial mammals was published and recorded 115 species (Fernandes-Ferreira *et al.*, 2021) but it is worth highlighting two surveys that aimed to review the taxonomy and distribution of mammals in the Brazilian Northeast. The first work includes medium and large-sized species in the states of Ceará, Paraíba, Pernambuco and Alagoas, where 40 species were documented, of which 26 were recorded in Ceará (Feijó & Langguth, 2013). The second

work surveyed 63 species of small mammals (Chiroptera, Didelphimorphia and Sigmodontinae rodents) from Ceará (Gurgel-Filho *et al.*, 2015). Both articles as well as the overview of papers published about mammals of Ceará reveal that its central portion is one of the main sampling gaps for the research of mammals. Our goal is to fill part of this lack of knowledge for the medium and large-sized species and provide subsidies to effective conservation plans.

MATERIAL AND METHODS

The fieldwork was carried out mainly in the municipality of Quixadá, Ceará, northeastern Brazil. Three localities were investigated there: Pedra dos Ventos (PV) (WGS84 05°04'26.5"S, 39°02'21.6"W), Logradouro (LO) (WGS84 05°04'44.5"S, 39°02'13.1"W) and Ouro Preto (OP) (WGS84 05°05'23.4"S, 39°05'26.5"W). The last one is located in the Natural Monument of the Monoliths of Quixadá, a state protected area. Additionally, occasional records (photographs and roadkills) were documented in rural areas of the municipalities of Ibareta (WGS84 04°49'S, 38°49'W), Quixeramobim (WGS84 05°11'S, 39°17'W), Ibicuitinga (WGS84 04°58'S, 38°38'W), Banabuiu (WGS84 05°18'S, 38°55'W), Morada Nova (WGS84 05°06'S, 38°22'W) and other localities of Quixadá. All

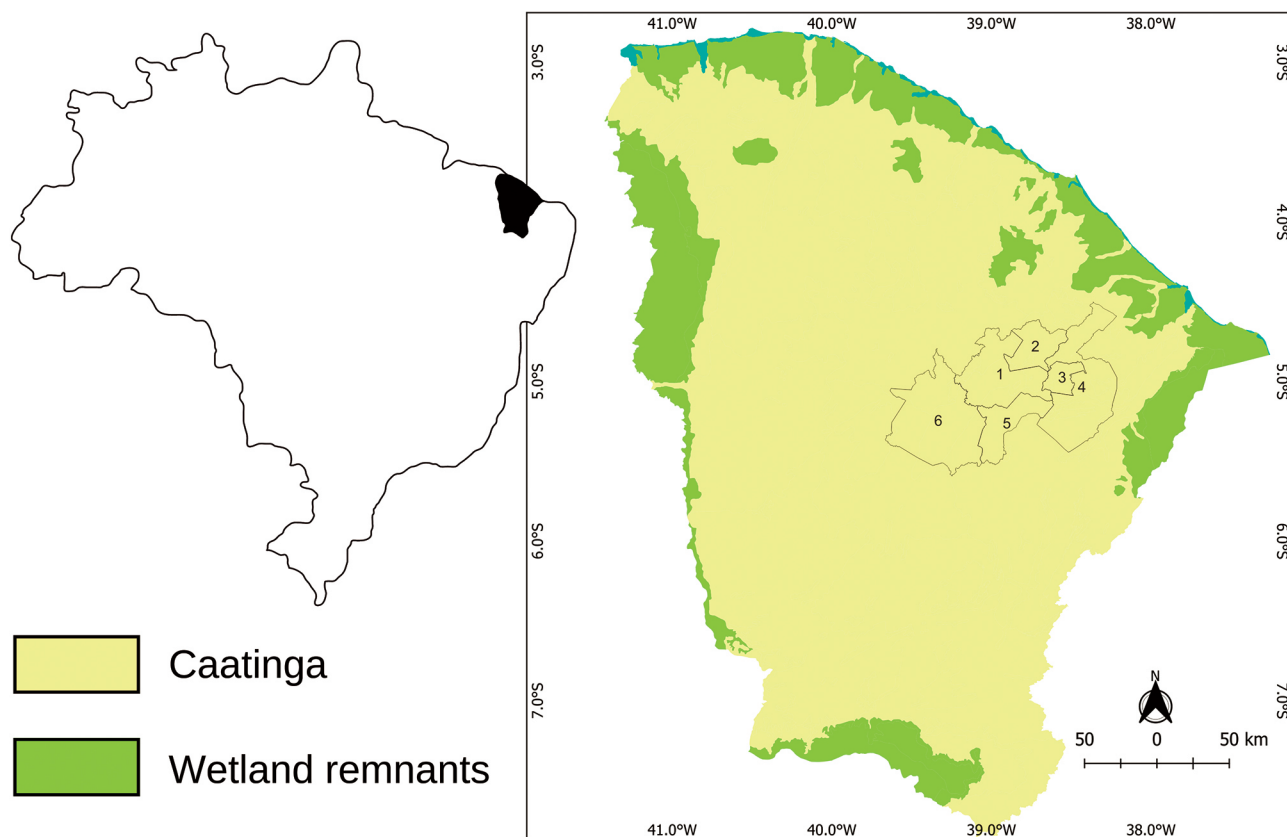


Figure 1: Study sites for the survey of medium and large-sized mammals in the Central Region of Ceará (CRC), Northeastern Brazil. 1: Quixadá. 2: Ibareta. 3: Ibicuitinga. 4: Morada Nova. 5: Banabuiu. 6: Quixeramobim. Green area: wetland regions such as coastal forests and Atlantic Forest remnants known by *brejos de altitude*. Yellowish area: Caatinga biome.



these places are located in the Central Region of Ceará (CRC), a semi-arid territory with long and severe periods of drought (Figure 1). Its rainy season generally occurs between February and April. The climate is considered Aw (Köppen-Geiger classification), annual rainfall is around 840 mm and the average temperature is between 26°C to 28°C. The relief consists mainly of depressions, residual massifs and crystalline inselbergs (monoliths). Its vegetation is typical of the Caatinga (dense shrub, close shrub and semi-deciduous dry forests) (IPECE, 2021).

In Quixadá, data on the medium and large-sized species were obtained between January 2017 to April 2021 through camera traps, visual records of live individuals, and tracks. Ten cameras (Bushnell Core 119938C, Bushnell Core DS 119977C and Bushnell HD 119537) were installed individually at each location along trails and near to water bodies with no pattern of time, position or spacing and without baits. The total sampling effort was 8,480 camera days (PV = 4,230 camera days; OP = 1,210; LO = 3,040). Opportunistic observations of mammals were recorded along the trails, as well vocalization recognition and occasional traces such as footprints, feces, skeletons, and burrows. In addition, sporadic records of roadkill on the BR-122 and CE-265 Highways in the aforementioned municipalities are added to the survey. The biological samples were photographed with scales and identified in the field or through comparison with the scientific literature e.g. Becker & Dalponte, 2013; Prist *et al.*, 2020).

The inventory was complemented by analyzing voucher specimens from the mammal collections of the Universidade Federal do Ceará (UFC) and Museu de História Natural do Ceará (MHNCE).

In order to investigate non-recorded species and possible local extinctions, people who inhabit more than 70% of their lives in rural areas of Quixadá and that interacted in any manner with wild mammals were consulted and subsequently selected to be interviewed based on this sample utilizing the “snowball” technique (Bailey, 2019). In this way, a total of 21 “local specialists” (people who consider themselves and are likewise recognized within the community to be knowledgeable on the subject) were identified (Hays, 1976). Semi-structured questionnaires were conducted with photographs of Brazilian mammals (occurring or not in the state inventory) to assess identification. Altogether, 18 men and three women between 39 and 97 years old were interviewed.

We assume as medium and large-sized mammals those species which have more than 1,0 kg and/or can not be surveyed by live traps (Feijó & Langguth, 2013). This inventory follows the taxonomy adopted by the Brazilian Society of Mammalogy (Abreu-Jr *et al.*, 2021). The global, national, and local conservation status of each species was obtained from the red lists of the International Union for Conservation of Nature (IUCN, 2023), Brazilian Environment Ministry (MMA, 2022) and Environment Secretary of Ceará State (SEMA, 2022).

RESULTS

We recorded 18 species of medium and large-sized mammals belonging to 13 families and seven orders were documented in CRC (Table 1, Figure 2). Most of the 182 records were obtained by camera trap (n = 78; 42.8%) followed by visual records (n = 50; 27.5%), roadkill (n = 36; 19.8%), tracks (n = 14; 7.7%), voucher specimens (n = 2; 1.1%), and vocalization (n = 2; 1.1%).

Carnivora and Rodentia are the most speciose orders (n = 8 and 3 spp. respectively). *Cerdocyon thous* was the most recorded species (n = 31; 17%) followed by *Kerodon rupestris* (n = 26; 14.28%) and *Euphractus sexcinctus* (n = 15; 8.24%). *Puma concolor* (n = 2; 1.1%), *Galictis cuja* (n = 2; 1.1%) and *Dasyprocta prymnolopha* (n = 3; 1.6%) obtained the least amount of records (Figure 3).

Six mammals are documented as threatened in red lists (MMA, 2022; SEMA, 2022, IUCN, 2023): *Leopardus emiliae*, *Leopardus pardalis*, *Puma concolor*, *Herpailurus yagouaroundi*, *Subulo gouazoubira* and *Kerodon rupestris* (Table 1). The last one is endemic from Caatinga biome.

All species considered extant by the informants were registered in the fieldwork and five were cited as locally extinct: *Dicotyles tajacu*, *Cuniculus paca*, *Tolypeutes tricinctus*, *Panthera onca* and *Alouatta* sp.

DISCUSSION

The richness obtained in CRC represents 44% of the medium and large-sized and 15.6% of all mammals listed in the state inventory which includes Atlantic Forest remnants (Fernandes-Ferreira *et al.*, 2021). Among the medium and large-sized species of Caatinga (Carmignotto & Astúa, 2017), this number represents 35.2%. This outcome is considered as expected when compared with other surveys in Ceará. Dias *et al.* (2017) reported 21 medium and large-sized mammals in a well-preserved private area of Caatinga in the municipality of Crateús, central-western of the state. Only *Cuniculus paca*, *Dicotyles tajacu* (both mentioned as extinct by local people in this work) and *Eira barbara* were not recorded in CRC. In a remnant of Atlantic Forest inserted in the Caatinga biome (Baturité Ridge), Fernandes-Ferreira *et al.* (2015) documented all the species surveyed in CRC, in addition to *E. barbara*, *Coendou baturitensis*, *Didelphis marsupialis* and *Speothos venaticus*. In the Ibiapaba Ridge, Guedes *et al.* (2000) recorded 20 species including *C. paca*, *E. barbara*, *Mazama americana*, *Nasua nasua* and *Alouatta ululata*. All these non-recorded species in CRC seem to be elusive and very restricted to protected wetland areas in Ceará state.

However, it is important to reveal that the mammal richness reported here is higher than that obtained by most other studies in similar areas of Caatinga. For



Figure 2: Medium and large-sized mammals recorded in the Central Region of Ceará, Northeastern Brazil. A: *Leopardus pardalis*. B: *Leopardus emiliae*. C: *Herpailurus yagouaroundi*. D: *Puma concolor*. E: *Procyon cancrivorus*. F: *Galictis cuja*. G: *Cerdocyon thous*. H: *Kerodon rupestris*. I: *Dasyprocta prymnolopha*. J: *Euphractus sexcinctus*. K: *Sapajus libidinosus*. (A, B, C, E, G, H, I: video frames of camera traps installed by H. Fernandes-Ferreira and his team. D: video frame of camera trap installed by Thiago Mendonça. F, J, K: photographs taken by Rogério Rumão).



Table 1: Medium and large-sized mammals recorded in the Central Region of Ceará (CRC), Northeastern Brazil, with the respective localities, type of records and conservation status by IUCN (2023), MMA (2022) and SEMA (2022). Pv (Pedra dos Ventos Hotel, Quixadá), Lo (Logradouro, Quixadá), Op (Ouro Preto, Quixadá), QUI (other localities in Quixadá), IBA (Ibaretama), BAN (Banabuiú), QMB (Quixeramobim), IBI (Ibicuitinga), MOR (Morada Nova), Ct (camera trap), Vr (visual record), Rk (roadkilled specimen), Vs (Voucher specimen), Tr (tracks), Vo (vocalization), LC (least concern), VU (vulnerable), EN (endangered), NE (not evaluated).

Taxon	Localities	Type of record	IUCN	MMA	SEMA
DIDELPHIMORPHIA					
<i>Didelphis albiventris</i> (Lund, 1840)	Pv, Lo, Op, QUI, IBA	Ct, Vr, Rk	LC	LC	LC
RODENTIA					
<i>Galea spixii</i> (Wagler, 1831)	Pv, Lo, Op, QMB	Vr, Rk	LC	LC	LC
<i>Kerodon rupestris</i> (Wied-Neuwied, 1820)	Pv, Lo, Op, IBA	Ct, Vr, Tr, Vo	LC	VU	LC
<i>Dasyprocta prymnolopha</i> (Wagler, 1831)	Lo	Ct	LC	LC	LC
CINGULATA					
<i>Dasybus novemcinctus</i> Linnaeus, 1758	Pv, Lo, QUI, BAN, IBI	Ct, Rk	LC	LC	LC
<i>Euphractus sexcinctus</i> (Linnaeus, 1758)	Pv, Lo, QUI, IBA, MOR	Ct, Vr, Rk	LC	LC	LC
PILOSA					
<i>Tamandua tetradactyla</i> (Linnaeus, 1758)	Pv, Lo, IBA	Ct, Tr	LC	LC	LC
CARNIVORA					
<i>Leopardus pardalis</i> (Linnaeus, 1758)	Pv, Lo	Ct, Tr	LC	LC	VU
<i>Leopardus emiliae</i> (Thomas, 1914)*	Pv, Lo, QUI	Ct, Rk, Vs	NE	NE	VU
<i>Puma concolor</i> (Linnaeus, 1771)	QUI, MOR	Tr	LC	VU	EN
<i>Herpailurus yagouaroundi</i> (Saint-Hilaire, 1803)	Pv, Lo, BAN, QMB	Ct, Rk, Vs	VU	VU	VU
<i>Cerdocyon thous</i> (Linnaeus, 1766)	Pv, Lo, Op, QUI, IBA, QMB, IBI	Ct, Vr, Rk, Vs	LC	LC	LC
<i>Procyon cancrivorus</i> (Cuvier, 1798)	Pv, Lo, IBA, QMB	Ct, Rk	LC	LC	LC
<i>Conepatus semistriatus</i> (Boddaert, 1785)	Pv, Lo, Op, BAN, IBI	Ct, Rk, Tr	LC	LC	LC
<i>Galictis cuja</i> (Molina, 1782)	Pv, MOR	Ct, Vr	LC	LC	LC
CETARTIODACTYLA					
<i>Subulo gouazoubira</i> (Fischer, 1814)	Pv, Lo	Ct, Tr	LC	LC	VU
PRIMATES					
<i>Callithrix jacchus</i> (Linnaeus, 1758)	Pv, Lo, IBA, QUI	Ct, Vr	LC	LC	LC
<i>Sapajus libidinosus</i> (Spix, 1823)	Op, IBA, MOR	Vr, Tr, Vo, Vs	LC	LC	LC

* We assume the taxonomy proposed by Nascimento & Feijó (2017) that consider *Leopardus emiliae* as a separated species from *Leopardus tigrinus*. However, MMA (2022) and IUCN (2023) follows by considering *L. tigrinus* as a single species and evaluates it as endangered (EN).

example, Bezerra *et al.* (2014) surveyed eight medium and large-sized species of the 17 mammals documented in 15 localities of the states of Bahia and Alagoas. In neighboring states, Cherem *et al.* (2019) listed 11 species of this group in Rio Grande do Norte and Delciellos (2016) reported 15 in four areas of Piauí. Previous studies published by Dias & Bocchiglieri (2016), Rocha *et al.* (2015), Beltrão-Mendes *et al.* (2020) and Freitas *et al.* (2017) documented 10, 11, 13 and 15 species respectively in semi-arid areas of Sergipe state. The diversity in CRC is even higher than that listed in 10 priority areas of conservation around Rio Grande do Norte ($n = 14$ species) for instance (Marinho *et al.*, 2018).

This pattern reveals that CRC may be an important conservation theater for Caatinga mammals. Further investigations are needed to assess why this region reaches greater richness than other areas in Caatinga. For while, some hypotheses can be raised: 1) differences in the sampling effort must be considered. Some studies applied 1,600 to 3,240 trap-nights (Freitas *et al.*, 2017; Beltrão-Mendes *et al.*, 2020) for example. However, other works used approximately 5,000 to 7,300 trap-nights (Freitas *et al.*, 2017; Marinho *et al.*, 2018), an effort only slightly less than that used in our study ($n = 8,480$).

2) inselbergs are an important environment within the Caatinga Phytogeographic Domain. They are widespread in the crystalline terrains and provide an important habitat for rupicolous plants (Moro *et al.*, 2016). Even in the dry season, areas close to these inselbergs remain humid and possibly this promotes attractive refuge zones for the wildlife. Despite this scenario and although there was no specific ecological method to assess local extinctions, the mentions of past occurrence require concern and deserve to be detailed.

Dicotyles tajacu is recorded in some areas along the Northeast region of Brazil (Dias *et al.*, 2017; Feijó & Langguth, 2013; Marinho *et al.*, 2019), including in Ceará where it is considered as Endangered (EN) (SEMA, 2022). This animal was extinct in most of the coastal region between Rio Grande do Norte and Alagoas (Pernambuco Endemism Center) (Garbino *et al.*, 2018). According to 19 informants of Quixadá, the species was extinct in the region more than 25 years ago.

Only two municipalities are known for *Cuniculus paca* in Ceará: Crateús and Granja (Dias *et al.*, 2017; Feijó & Langguth 2013). The species is listed as Endangered (EN) in the state red list (SEMA, 2022) and was mentioned as extinct in the Baturité Ridge more than



45 years ago (Fernandes-Ferreira *et al.*, 2015). A similar estimation was also pointed out by 12 interviewees in this study.

Tolypeutes tricinctus, another species cited as having disappeared 50 years ago, is considered as Vulnerable (VU) by IUCN (2023), Endangered (EN) by MMA (2023) and Critically Endangered (CR) by SEMA (2022). Eleven informants reported that the species has always been rare due to the difficulty of finding enough sandy soil to build their burrows. The occurrence of the three-banded armadillo in Ceará is almost all based on historical records and interviews (Fernandes-Ferreira *et al.*, 2021, Feijó *et al.*, 2015).

In relation to *Panthera onca*, there are no current records in Ceará. Reported as Endangered (EN) by IUCN (2023) and MMA (2022), this felid is mentioned in some historical documents for the state (see Fernandes-Ferreira *et al.*, 2014) and was listed as Probably Extinct (CR-PEX) by SEMA (2022). Reports of Baturité suggested 30 years of disappearance (Fernandes-Ferreira *et al.*, 2015) while five informants (> 85 years old) from Quixadá pointed to more than 100 years. According to them, their relatives possibly had hunted the last jaguars of CRC.

Alouatta sp. was mentioned only by three elderly interviewees (> 80 years old) who reported an extinction of more than 70 years. The word *guariba*, folk nomenclature used only for *Alouatta* species around Brazil, names a mountain ridge in Quixadá (*Serra das Guaribas*) (05°03'S, 39°07'W) and a locality in Ibaretama (04°51'S, 38°35'W). According to the local people, these names are due to the past presence of this primate. Moreover, Feijó & Langguth (2013) documented a mention of this species in Quixadá and three hunters reported to FWP that a howler monkey occurs in Milhã (05°40'S, 39°11'W), 80 km away from this municipality. The only howler monkey confirmed in Ceará is *Alouatta ululata* (Fernandes-Ferreira *et al.*, 2021) with populations concentrated in its western portion (Freire-Filho *et al.*, 2018) and listed as Endangered (EN) (MMA, 2022; SEMA, 2022). Therefore, it is possible that these past and probable current occurrences in CRC refer to this species. Nevertheless, the niche distribution modeling of *Alouatta ululata* published by Freire-Filho & Palmeirim (2019) did not indicate the study area investigated here as suitable.

In all cases, overhunting was appointed by all respondents as the main reason for the possible local

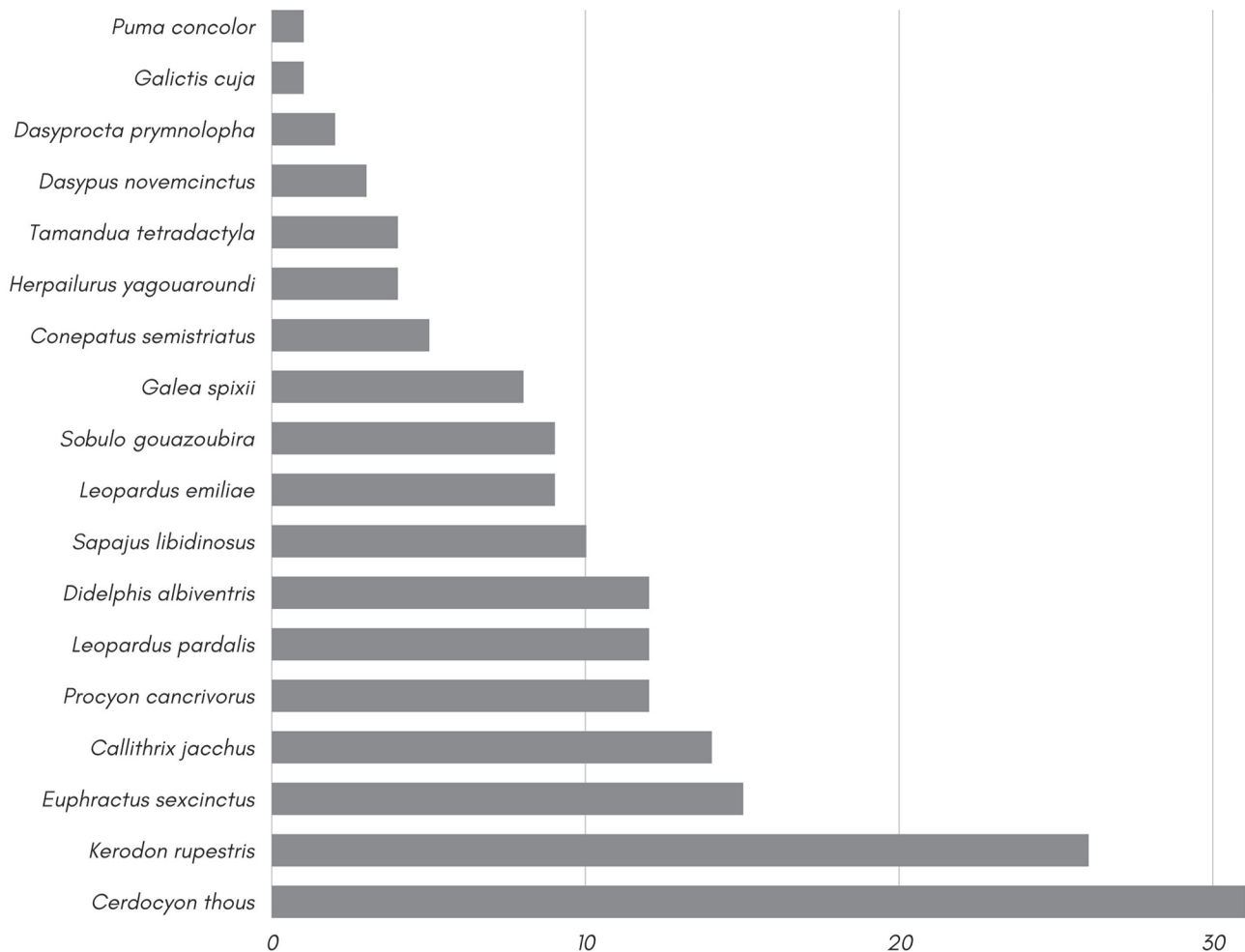


Figure 3: Number of records of medium and large-sized mammals in the Central Region of Ceará (CRC), Northeastern Brazil.



extinctions. This activity impacts 41 mammals of the Caatinga biome (Alves *et al.*, 2016). All species with more than 300 g are potentially hunted for food there (Fernandes-Ferreira, 2014) and the same pattern was observed in CRC. According to all informants, even small rodents like *Galea spixii* are highly consumed. Impoverished human communities in the Caatinga are historically dependent on bushmeat for subsistence. Nowadays, hunting is not always directly related to this dependence, sometimes being the result of the entertainment that it gives the hunters in the practice of those game activities. It is also related to zootherapy, magic-religious uses or to conflicts with carnivores that can pose risks to livestock or human life (Alves *et al.*, 2016; Barboza *et al.*, 2016; Fernandes-Ferreira, 2014).

In this context, poaching is also a continuous threat to the extant mammals of CRC. While some species such as *D. albiventris*, *E. sexcinctus*, and *G. spixii* are still highly consumed, others are more difficult to find. The few records ($n = 3$) of *D. prymnolopha* for example (Figure 3) may reflect population depletion. The presence of *Kerodon rupestris* in CRC seems to be restricted to protected areas as it occurs in other regions of Ceará (Dias *et al.*, 2017; Fernandes-Ferreira *et al.*, 2015). *Subulo gouazoubira*, *Galictis cuja* and even an abundant social species like *S. libidinosus* are virtually rare in non-protected sites. *Puma concolor* was recorded only twice and was mentioned as locally very rare by all informants. Like the Cougar, all other carnivores reported are involved in conflict with humans in CRC.

Roadkill was recorded as a constant and worrying threat for the local mammals as is the case in other regions of Brazil (Grilo *et al.*, 2018). Almeida (2019) monitored 40 km of the BR-122 Highway in Quixadá and estimated that 190 vertebrates are road-killed per kilometer every year, amounting to approximately 7,000 animals. Among the mammals (13%), 90% of the individuals recorded are *Cerdocyon thous*, corroborating our results. With approximately 15% of the Brazilian road system (IPEA, 2009), Caatinga has an extensive road network when compared to other arid regions around the world. Despite these facts, research related to road ecology is concentrated in south and southeast Brazil (Pereira *et al.*, 2018).

Habitat loss may also represent a problem to the mammals of CRC. Agriculture and livestock were established centuries ago and reached 26.28% of the territory of Quixadá (Mapbiomas, 2021). This is a pattern well known for Caatinga. Silva & Barbosa (2017) point out that at least 63.3% of the biome is composed of anthropogenic ecosystems, while less than 8% is inserted in protected areas (Teixeira *et al.*, 2021). In CRC, this scenario affects arboreal and scansorial species directly (*S. libidinosus*, *C. jacchus*, *T. tetradactyla*), in addition to specialist herbivorous such as *S. gouazoubira*.

Our results indicate that the Central Region of Ceará is a potential hotspot for mammals in the Caatinga

biome. This research fills an important gap of knowledge but also reveals an urgent need for further ecological research. In addition, the threats observed and the possibility of local extinctions call attention to the need for public policies. Conservation measures are necessary to contain threats such as installing speed control in the highways, inspection and prevention of hunting and habitat loss, in addition to environmental education and alternative income to the local communities in order to reduce the human dependence on the wild resources. Moreover, rewilding should be considered as a means of restoring environmental services lost in the past. For example, Galetti *et al.* (2017) suggested *Dicotyles tajacu* as one of the potential candidates for trophic rewilding programs for defaunated Neotropical forests. Its occurrence in other locations of Ceará (Fernandes-Ferreira *et al.*, 2021), the ease of management and monitoring can ensure a genetically and ecologically suitable population to be restored in protected areas in CRC.

Regarding scientific perspectives, long-term monitoring needs to be urgently implemented to investigate the ecological responses of mammals to the environmental changes in this hotspot. For example, a more direct approach must be conducted to properly evaluate the pressure of hunting and roadkill on local remnants.

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APPENDIX 1

List of voucher specimens of medium and large-sized mammals of the Central Region of Ceará (CRC) analyzed in scientific collections.

Cerdocyon thous (Ibaretama: MHNCE-MAM00110).
Leopardus emiliae (Quixadá: UFC M330. Ibaretama: UFC M331).
Herpailurus yagouaroundi (Quixadá: UFC M334).
Sapajus libidinosus (Fazenda Ouro Preto, Quixadá: UFC M332).



State of the art on the knowledge: a scientometric analysis of small non-volant mammals from Brazil (Didelphimorphia and Rodentia)

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Abstract: Considering the diversity of non-flying small mammals in the Neotropical region, the impact of landscape change and the lack of knowledge about the real impacts on this megagroup, we developed a scientometric analysis over a 50-year interval. The study focuses on Neotropical countries, especially Brazil, and aims to point out how these communities are structured in different environments. We searched for word combinations in the databases of the Science, Scielo and Scopus websites, resulting in 5,144 records, of which 2,941 were removed from the analysis due to their inadequacy to our topic. Of the 2,203 manuscripts that fit the objective of our study, 816 articles were carried out in Brazil, representing 46% of all publications related to the Neotropical region. The biome with the highest number of publications was the Atlantic Forest. While the knowledge gaps about the Cerrado and Amazon biomes are still evident. It is known that, in Brazil, the inequality in the concentration of investments in research is also reflected in quality scientific production. In this sense, our results highlight the need for a serious policy of investments in science and technology in the country, with partnerships between states and evaluation of the least studied biomes.

Key-Words: Brazil; Cerrado; Didelphimorphia; Landscape structure; Rodentia.

Resumo: O estado da arte sobre o conhecimento de pequenos mamíferos não-voadores (Didelphimorphia e Rodentia) do Brasil. Considerando a diversidade de pequenos mamíferos não voadores na região Neotropical, o impacto da mudança da paisagem na diversidade de espécies e a falta de conhecimento sobre os reais impactos neste grupo megadiverso, desenvolvemos uma análise cientométrica sobre o grupo nos últimos 50 anos. O estudo tem como foco os países neotropicais, especialmente o Brasil, e tem como objetivo apontar como essas comunidades se estruturam em diferentes ambientes. Buscamos combinações de palavras nas bases de dados Web of Science, Scielo e Scopus, resultando em 5.144 registros, dos quais 2.941 foram retirados da análise por inadequação ao nosso tema. Dos 2.203 artigos que se enquadram no objetivo do nosso estudo, 816 artigos foram realizados no Brasil, representando 37% de todas as publicações relacionadas à região Neotropical. O bioma com maior número de publicações foi a Mata Atlântica. No entanto, as lacunas de conhecimento sobre os biomas Cerrado e Amazônia ainda são evidentes. Sabe-se que, no Brasil, a desigualdade de concentração de investimentos em pesquisa também se reflete na produção científica de qualidade. Nesse sentido, nossos resultados evidenciam a necessidade de uma política séria de investimentos em ciência e tecnologia no país, que apoie parcerias e pesquisas realizadas em estados e biomas menos estudados.

Palavras-Chave: Brasil; Cerrado; Didelphimorphia; Estrutura da paisagem; Rodentia.

INTRODUCTION

The Neotropical region runs from Central Mexico to Southern Brazil, including Central America such as Caribbean islands and a large part of South America (Morrone, 2014; Noguera-Urbano & Escalante, 2017;). It is the most diverse biogeographic realm, comprising about 25% of mammalian diversity (Burgin *et al.*, 2018) and seven of 35 biodiversity hotspots (Williams *et al.*, 2011). However, the existing biodiversity and ecosystem services in this region are under constant threat. At least ¼ of 14,000 species from known taxonomic groups are at risk of extinction in terrestrial, freshwater, and marine environments (Joly, 2018). Neotropical species are still poorly studied or unknown, and their ecological aspects,

origin and evolutionary history are not fully understood (Antonelli & Sanmartin, 2011; Tinoco *et al.*, 2015; Turcetto-Zolet *et al.*, 2013). Within the Neotropical region, Brazil occupies almost half of South America and is home to two of the world's biodiversity conservation hotspots (Cerrado and Atlantic Forest; Myers *et al.*, 2000), as well as a large part of the Amazon rainforest.

Estimates indicate that Brazil is home to between 15% to 20% of the 1.5 million described species in the world (Lewinsohn & Prado, 2002), of which 775 species are mammals, comprising 11 orders, 51 families, and 247 genera (Abreu Jr. *et al.*, 2022; Quintela *et al.*, 2020). The most diverse orders are Rodentia (267 species), Chiroptera (182 species) and Primates (131 species). Cricetidae (Rodentia) is the most diverse family, with 155 species



(Abreu Jr. *et al.*, 2022; Quintela *et al.*, 2020). Although mammals are the best-known group of organisms, it is estimated that there are still many species to be discovered and described, mainly species of rodents, marsupials, and bats (Mendes-Oliveira *et al.*, 2015a). Despite the increase in current inventories, which are associated with a cytogenetic and molecular approach, it is still possible to find sampling gaps for species and ecosystems, especially from Cerrado, and Amazon regions (Mendonça *et al.*, 2018).

A large amount of Neotropical mammals is sensitive to human activities, which cause changes in the structural complexity and heterogeneity of habitats (Uhl & Vieira, 1989). However, habitat loss appears to have a more negative impact on species loss than the effect of fragmentation itself (*e.g.*, changes in habitat configuration and isolation; Fahrig, 2003; Fahrig *et al.*, 2019). Depending on the impact, intensity and modification, replacement and/or simplification of habitats, these changes may reflect on the availability of food resources, protection, or support, which influence the structure of biological communities in a given area (Malcolm, 1995). Community responses to habitat loss may differ according to the type of impact and the ecological characteristics of the species (Bernard *et al.*, 2011).

Small non-volant mammals, that belongs to the orders Didelphimorphia (family Didelphidae) and Rodentia (families Cricetidae, Muridae, and Echimyidae), comprises one of the most diverse groups of Neotropical mammals (Gardner, 2008; Patton *et al.*, 2015). They present diverse strategies of habitat use, including terrestrial, arboreal, scansorial, semi-aquatic, semi-fossorial, and fossorial animals (Cunha & Vieira, 2004; Dalmagro & Vieira, 2005; Merritt, 2010), and a varied diet, being omnivores, insectivores and frugivores (Paglia *et al.*, 2012; Pena & Mendes-Oliveira, 2019; Pinheiro *et al.*, 2002; Pinto *et al.*, 2009; Vieira, 2003). There are also carnivore/vermivore (some small marsupials), folivore and granivore (several small rodents) species (Verde Arregoitia & D'Elia, 2021).

The assessment of the state of the art of mammalogy in pioneering studies in Brazil, at the beginning of this century, were marked by the contributions of Alípio de Miranda Ribeiro, Hermann von Ihering, Paulo Schirch, Emilio Goeldi, G. Hagmann and Emilia Snethlage (Ávila-Pires, 1960). Currently, biodiversity is an object of study by researchers all over the world, and its main documentation relies on scientific collections (Prudente, 2003). However, in recent years, the concern with monitoring scientific production has grown, mainly due to the discovery of new species (Zaher & Young, 2003). Therefore, metric, quantitative, and qualitative studies are increasingly needed. Among the applied methods, scientometrics stands out as the area dedicated to quantitative studies of scientific activities related to the production, propagation, and use of scientific information by a given country, scientific community, or institution (Spinak, 1998).

Thus, considering the high diversity of mammals of the Didelphimorphia and Rodentia orders and the impact of landscape change on species richness and diversity, we carried out a scientometric study with small non-volant mammals from the Neotropical region. We identify the temporal and spatial patterns, and the main themes addressed in publications over 50 years (1970-2020), emphasizing the studies conducted in Brazil. With this study, we were able to answer: (i) What is the temporal trend of scientific articles regarding small non-volant mammals of the Neotropical region and Brazil? (ii) In which Brazilian biomes small non-volant mammals are more studied? (iii) What are the most studied species of small non-volant mammals in Brazil? (iv) What is the contribution of Brazilian states to the development of research with small non-volant mammals in Brazil? (v) What is the number of articles per area of knowledge/subject produced in Brazil? and, finally, (vi) What are the main landscape variables used to study the community structure of small non-flying mammals in areas with different landscape matrices in Brazil?

MATERIAL AND METHODS

We built a database reviewing all scientific articles published in indexed journals for a period of 50 years (from 1970 to 2020). We searched for studies carried out with small non-volant mammals in the Neotropical region, restricted to the Americas, in all databases of the Clarivate PLC (Web of Science – <https://clarivate.com/webofsciencelibrary/solutions/web-of-science>), Scielo (Scientific Electronic Library Online – <https://scielo.org>), and Scopus (<https://www.scopus.com>) in January 2021, comprising publications in Portuguese, English, and Spanish. The first search field was selected to include all articles related to small mammals. We used a combination of the following terms: “small mammal” OR “small mammals” OR “Rodentia” OR “rodent” OR “sigmodontine” OR “Cricetidae” OR “cricetid*” OR “Didelphimorphia” OR “Didelphidae” AND “Neotropical” OR “Neotropics”. Where retrieved from each of the databases from 1970 to 2020: 19,469 documents, of which 198 corresponded to Brazil (WOS); 10,799 documents, of which 524 corresponded to Brazil (Scopus) and 645 documents, of which 94 corresponded to Brazil (Scielo).

These combinations resulted in 5,144 records. A second stage was carried out, where 2,941 were removed from the analysis (scientometrics, meta-analyses, summaries, book chapters, monographs, dissertations, theses and reviews), as they are works that do not have wide circulation and the majority have not gone through an editorial board, which may restrict the reach of these works by researchers from other countries, as well as duplicate records. After examining the abstracts and refining the database, only articles that fitted our objectives were listed. Therefore, we proceeded with a



scientometrics on small non-volant mammals from the Neotropical region, emphasizing the studies carried out in Brazil, which resulted in a total of 2,203 articles.

Finally, each abstract was carefully read and checked against the following criteria to determine if the reference was appropriate for our assessment: article title, journal, year of publication, DOI, countries, and continent where the work was carried out. For articles that were performed in Brazil, we collected the following information: biome; search area; whether they were marsupials or rodents; which species were studied; in which Brazilian states the studies were conducted; and which articles used predictor variables (*e.g.*, environmental variables) in the study. All this information was gathered in tables using Microsoft Excel (2013). Regarding taxonomy, in order not to homogenize the names of the species mentioned in the articles, since several have undergone taxonomic revisions and changes in delimitation and nomenclature, we have reviewed and adapted the species using data compiled by several authors (Abreu Jr. *et al.*, 2022; Gardner, 2008; Patton *et al.*, 2015; Pavan, 2019; Pavan *et al.*, 2012; 2014; Quintela *et al.*, 2020).

We compared the number and percentage of articles published by each Neotropical country in the 50-year period using bar and pie charts. We also quantified the number of species included in the different IUCN red list categories per year for Brazil using Sperman's correlation analysis that considered the number of studies per year and the number of species listed by the IUCN.

We constructed the temporal trend of the number of articles for the Neotropical region (restricted to the Americas) and Brazil, investigating the number of articles published per year in Brazil; in the Neotropical region (excluding Brazil); and the number of articles published in the world. The lines of the graph represent all publications found in this study, where one line shows the number of publications from the Neotropical region (Americas without data from Brazil) that were selected by our scientometrics per year, divided by the total number of articles that were published in the world *per annum*. The second line on the graph went through the same process; however, there is a limit, but with the number of publications made in Brazil, excluding Neotropical data. For the time trend, the number of articles was transformed into relative frequency (number of articles of interest to this study divided by the total number of articles indexed in ISI, Scielo and Scopus in the year, multiplied by 100). We divided the annual article production by the total article production to eliminate the effect of the temporal increase (Nabout *et al.*, 2012).

We quantified the percentage of studies performed for non-volant small mammals in Brazilian biomes using a map with biome divisions to demonstrate our results and implemented a temporal trend analysis. To verify the number of citations that each species obtained in studies carried out in Brazil, we set up an updated table (Table S1 – supplementary material) with the taxonomy

of the species based on data compiled by Abreu Jr. *et al.* (2022); Díaz-Nieto & Voss (2016) for *Marmosops*; Gardner (2008), Patton *et al.* (2015), Pavan *et al.* (2017); for *Monodelphis*; Quintela *et al.* (2020); Voss & Jansa (2009) and Voss *et al.* (2019) for *M. myosuros*.

We categorize the contribution of Brazilian states to the development of research on small non-volant mammals by calculating the percentage of publications carried out by each state and we demonstrate the results through a map of political divisions. We identified the total number of articles developed in Brazil by the area of knowledge through a bar graph, where we plotted the most studied subject, allocating each article in only one study category. The categories of the knowledge area were defined, for example: Parasitology – Studies that assess parasites, their hosts and the relationships between them; Geographic distribution – Describes and explains the distribution of communities of living beings and their relationships with other elements of the physical and human environment; Diet – It features the ability of a species to take advantage of a more advantageous food source at a given time; Genetics – Study the mechanisms of heredity or biological inheritance; Morphometry – Way or act of measuring the body dimensions of a certain species.

Articles published in Brazil that evaluated local environmental metrics were placed together with landscape variables (Table 1) applied to study the community structure of small non-volant mammals in areas with different landscape matrices. Additionally, we implemented a hierarchy chart considering the main journals in which studies carried out in Brazil between 1970 and 2020 were published. The analyzes were performed in the R environment (R Core Team 2021) and the maps in the QGIS 3.10 program (SIG, 2013).

RESULTS

Of the 2,203 manuscripts selected regarding small non-volant mammals, 816 were carried out in Brazil, representing 37% of all works published about the Neotropical region (Figure 1). Argentina was the second country that most contributed with publications (25.2%), followed by Chile (7.2%). Countries such as El Salvador, Guatemala, Nicaragua and the Caribbean region contributed less than 5% of publications each (Figure 1).

Correlation analysis (Figure 2) showed that publications focused mainly or majority on species with conservation status of Least Threat Concern (Figure 2A – Least concern) ($p = 0,0001$; $r = 0,9275$), and critically endangered species (Figure 2B – Critically endangered) ($p = 0,839$; $r = -0,0950$) or in danger were less studied with increasing number of publications in Brazil. At the same time, species with deficient data (Figure 2C – Data deficient) ($p = 0,0001$; $r = 0,8693$) or that have not yet been analyzed because they were recently described or



Table 1: Type of landscape descriptors and analyzes of predictor variables addressed in articles on small non-volant mammals (Didelphimorphia and Rodentia) that were published in Brazil.

Landscape variables	Landscape analysis	Number of publications
Complexity and environmental heterogeneity	Correlating the heterogeneity and complexity of different phytophysiognomies with the composition, abundance, and richness of small mammals (vegetation density in vertical strata)	6
Climate changes	Effect of weather and wind; Temperature (°C); Relative humidity; El Niño effects; light intensity, wind speed and direction; ambient noise and rain; fire effect in places of different ages	13
Forest fragments	Connectivity between forest fragments and vegetation patches; vegetation corridors (corn plantations, pastures, human buildings, vegetation corridors); secondary forests in different stages of regeneration; influence of fragment size on capture success through radio tracking	7
Anthropic impact	Effect of grazing at different pressures; different management regimes; possible effects of future deforestation on mammals using the species-area relationship; clearings caused by mining that produce an edge effect on the assemblage of small mammals; amount of deforested area; construction of hydroelectricpower stations; hunting	11
Habitat and microhabitat use	Analysis of the species' meso and macro habitats; changes in microhabitat use patterns; use of the matrix of open areas and the frequency of species' movements between fragments; whether individuals actively select different diameters and slopes of branches; whether vegetation structure and availability of food resources affect functional traits; whether species tolerate habitat disturbance and trophic guild; patterns of species co-occurrence at different spatial scales; whether different habitat matrices affect the diet, locomotion, behavior and home range of species	35
Seasonality	If drought and rain are factors that contribute to population and intrapopulation variation in the breadth of the food niche; whether the area of daily activities is affected by climatic (dry and wet) and reproductive seasons	25

revalidated, do not have criteria or the data are inefficient for their assessment as a threat.

As evidenced by the time trend graph (Figure 3), in the years 1979, 1987, 1995, 2004, 2015, 2018 and 2020, Brazil surpassed other countries in the Neotropics in terms of the number of publications. Even showing the same general trend in 1996, Brazil showed a considerable drop between the years 1982, 1985, 1989, 1996 and 1998 (Figure 3). Despite the fluctuations over the years, Brazil had a peak in the number of publications in 2009 (Figure 3).

The biome with the highest number of publications was the Atlantic Forest, with 478 articles (Figure 4). The Cerrado (with 232 articles) and the Amazon (113) were

the second and third biomes with the largest number of studies carried out with small non-volant mammals in Brazil, respectively (Figure 4). The Pampa (87 articles), the Caatinga (71 articles) and the Pantanal (20 articles) were the biomes with the lowest number of documents.

According to our data, studies on the Amazon biome were first published in 1995, but the percentiles of studies increased only in 2001 (Figure 5). Although with notable “ups and downs”, the Atlantic Forest curve shows a general upward trend, from the late 1970s to the mid-2010s (Figure 5), however, the curve shows a general downward trend in the last five years studied. A similar pattern is shown by the Cerrado biome and, to a lesser extent, the Pampa biome. The Caatinga, Amazon and Pantanal biomes seem to show a more stable trend (Figure 5).

In the 816 studies carried out in Brazil, 395 of them carried out research at the species level, while 406 addressed themes in the community of species. In our study, we recorded six families, eight subfamilies, 74 genera and 261 cited species (58 marsupials and 203 rodents) (Table S1 – Supplementary material). Compared with other groups of mammals, the study with small non-volant mammals in Brazil is scarce, however, there is a significant amount of information in the literature that addresses and cites a high number of species: of the 984 citations of species, 547 were citations of rodent species and 437 of marsupial species, representing 55.5% and 44.4% of the citations, respectively (Table S1 – Supplementary material).

Of the 260 species mentioned in the works carried out in Brazil, 217 are included in some IUCN

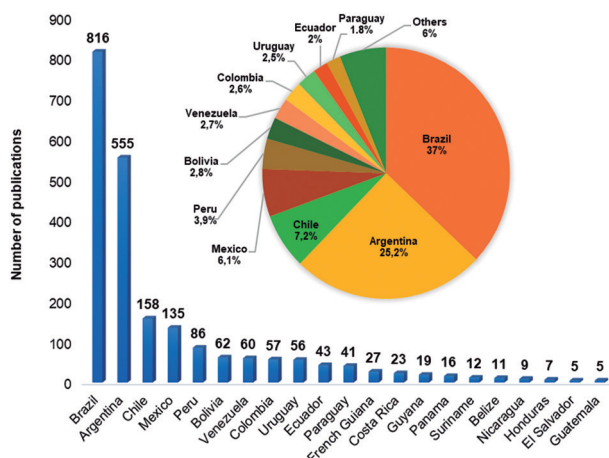


Figure 1: Number of articles on small non-volant animals (Didelphimorphia and Rodentia) by country in the Neotropics and percentage of publications by country between 1970 and 2020.

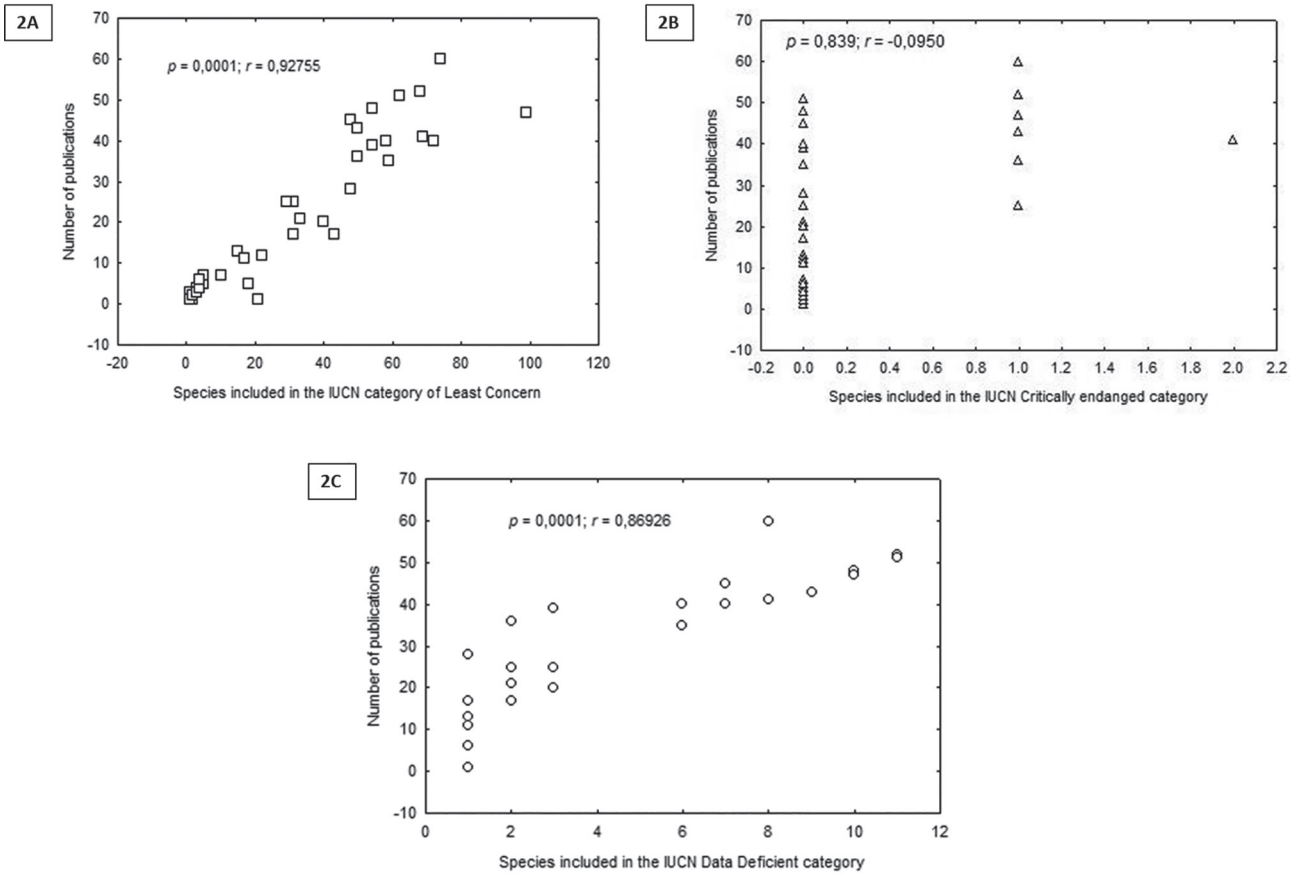


Figure 2: Representation of the number of non-volant small mammal species (Didelphimorphia and Rodentia) included in the IUCN red list for Brazil by year of publication (1970-2020).

(International List of Threatened Species) threat category (Supplementary material): 61.5% (164 species) listed as Least Concern – LC; 3% (nine species) listed as Threatened – EN; 2.6% (six species) listed as Near Threatened – NT; 1.1% (four species) listed as Critically Endangered – CR; 1.9% (six species) listed as Vulnerable – VU; and 10.7% (28 species) listed as Deficient Data for

Conservation – DD. However, there is not enough information for, for example, species like *Neacomys marajoara*, *Neacomys vossi* e *Neacomys xingu*, that have been recently described, are evaluated and validated for their threat (Semedo *et al.*, 2020). Of the Brazilian species cited in the articles, 28 are on the Red List of Endangered Brazilian Fauna (ICMBio, 2018), with 17 species classified

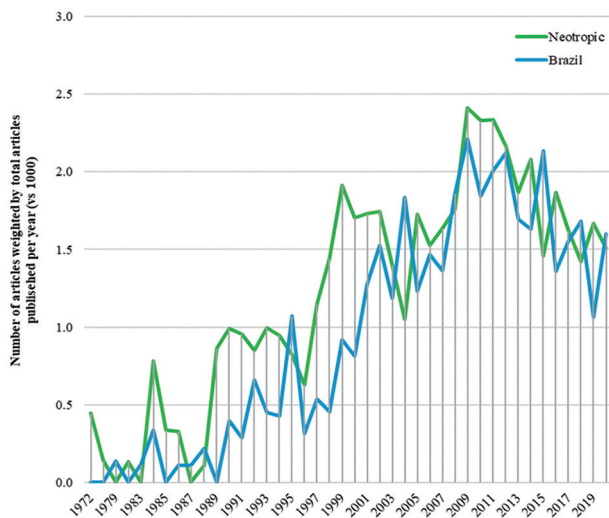


Figure 3: Temporal trend in the publication of scientific articles on small non-volant mammals (Didelphimorphia and Rodentia) in Brazil and other countries in the Neotropical region between 1972 and 2020.

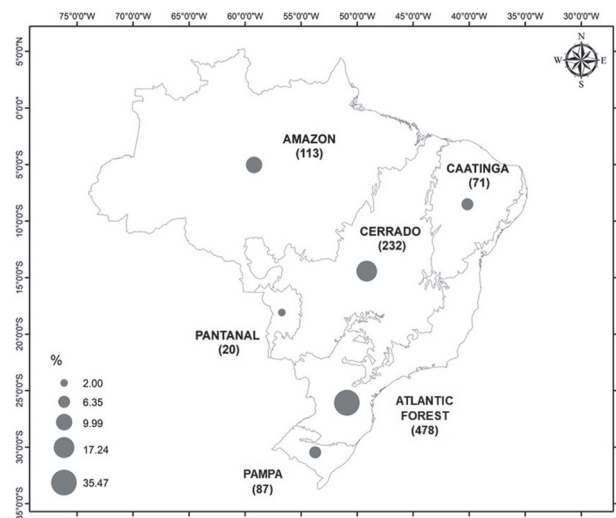


Figure 4: Map of Brazilian biomes with the total number and percentage of studies on small non-volant mammals (Didelphimorphia and Rodentia) in the last 50 years (1970-2020).

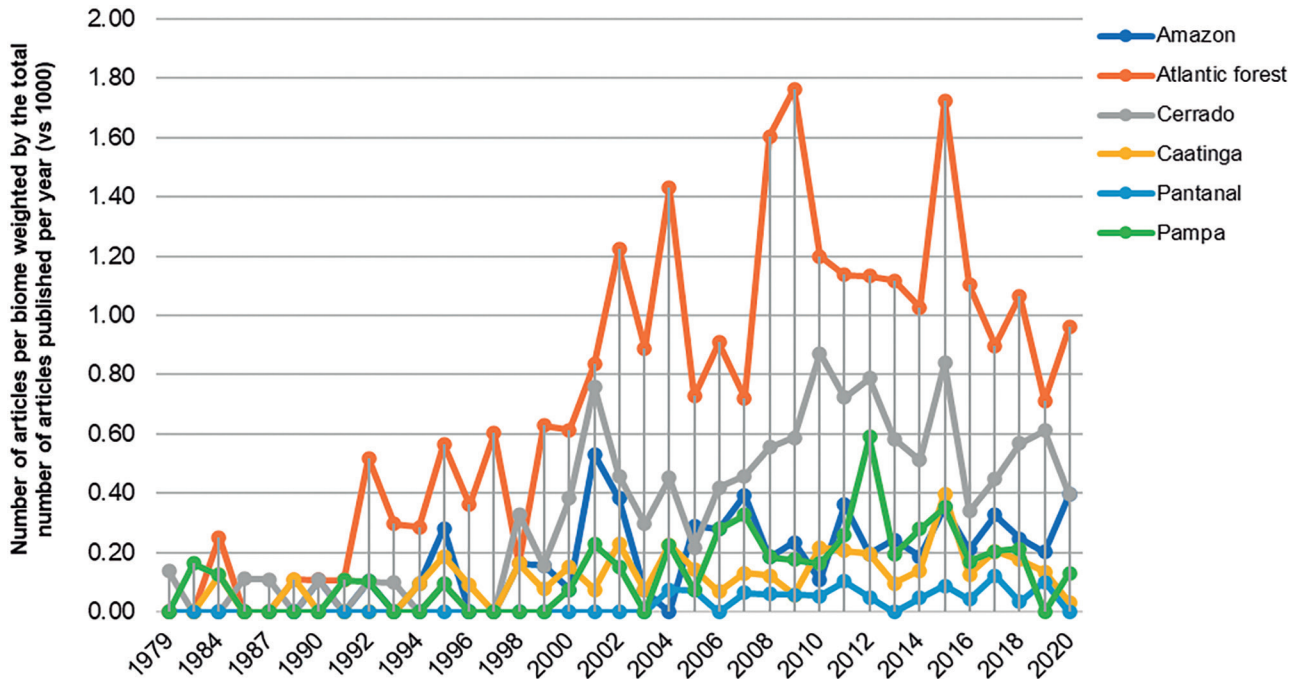


Figure 5: Temporal trend in the publication of scientific articles on non-volant small mammals (Didelphimorphia and Rodentia) in Brazilian biomes.

as Endangered – EN; eight as Vulnerable – VU and three as Critically Endangered – CR.

Among marsupials, the most cited species were *Didelphis aurita* (Wied-Neuwied, 1826) (14% of citations), *Didelphis albiventris* Lund, 1840 (13.5%), *Gracilinanus microtarsus* (Wagner, 1842) (8.8%), *Metachirus nudicaudatus* (Geoffroy, 1803) (8.2%) and *Gracilinanus agilis* (Burmeister, 1854) (7.8%) (Supplementary Material). Among rodents, the species with the highest percentage of citations were *Necomys lasiurus* (Lund, 1841) (11.7%), *Necomys squamipes* (Brants, 1827) (9.6%), *Akodon montensis* Thomas, 1913 (7.3%) and *Akodon cursor* (Winge, 1887) (7%) (Table S1 – Supplementary Material). These rodent species are classified as Least Concern – LC by IUCN (2020).

We observed a high spatial heterogeneity of scientific research activities in Brazil, where the regional pattern of publications is highly concentrated in the Southeast region (Figure 6), especially in Rio de Janeiro (198 articles), Minas Gerais (158 articles) and São Paulo (151 articles) states. Compared to other regions of the country, the North region has the lowest numbers of published articles, especially the states of Amapá (19 articles) and Roraima (nine articles).

Considering the total number of articles developed in Brazil and the subject of study (Figure 7), we observed that most publications were inventories of species (76 articles), followed by Parasitology (74), Geographical distribution (63), Diet (41), Genetics (38) and Morphometry (28) (Figure 7). It is noteworthy that we did not include some articles because they have less than ten manuscripts per area of knowledge, such as Use of Habitat (8 publications), Predation (8), Endozoochory (7) and Effect of fire (6).

Among the works published and carried out in Brazil, we identified the most used environmental variables to measure the distribution of species in the environmental gradient. Use of Habitat and Microhabitat (35 articles) was the most discussed topic to study the community structure of small non-volant mammals in areas with different landscape matrices, followed by Seasonality (25) and Climate Change (13) (Table 1).

In addition to these data, we observed that the articles analyzed in Brazil were published in 108 different journals. The journal *Mammalia* (82 articles) and the *Journal of Mammalogy* (78 articles) published the majority of studies carried out in Brazil, representing 9.9% and 9.4% of the total number of journals, followed by *Mammalian Biology* (46 articles, 5.6%) and *Neotropical Biota* (41 articles, 5%) (Figure 8).

DISCUSSION

Although the number of publications on small terrestrial mammals in Brazil is the largest for the Neotropical region, the study of the group is still restricted to some regions, ecosystems and taxa (Rossi & Bianconi, 2011) of species described for Brazil, knowledge is not linear. Brazil is a continental, developing and megadiverse country (Lewinsohn & Prado, 2002), and this greater diversity may reflect its larger area and greater diversity of environments in relation to neighboring countries. And much of this diversity, still unknown, requires a more accelerated investigative taxonomy (Quintela *et al.*, 2020) to establish future scientific measures and advances to address environmental changes that

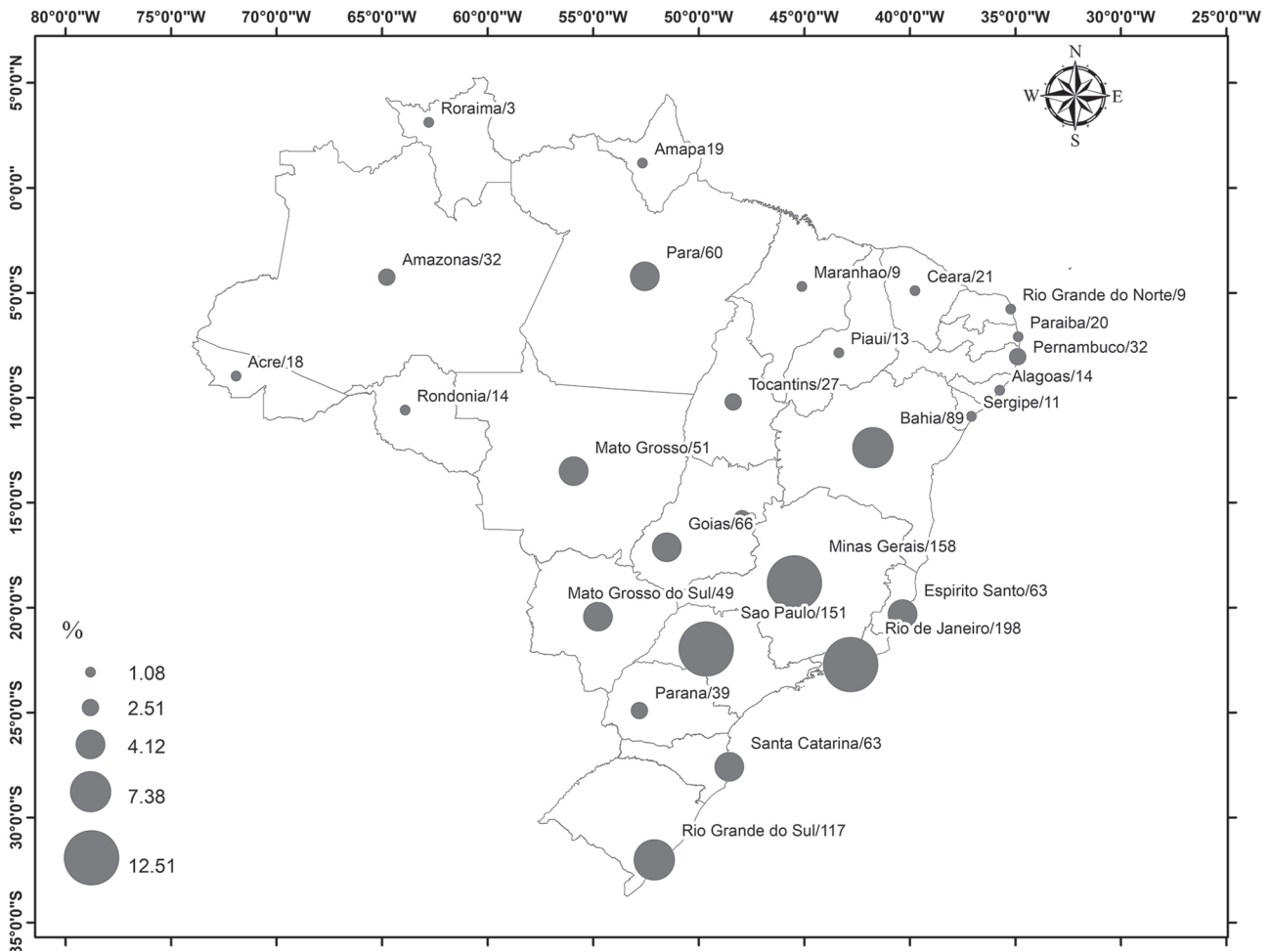


Figure 6: Map of Brazil (geopolitically divided) with number and percentage of studies on small non-volant mammals (Didelphimorphia and Rodentia).

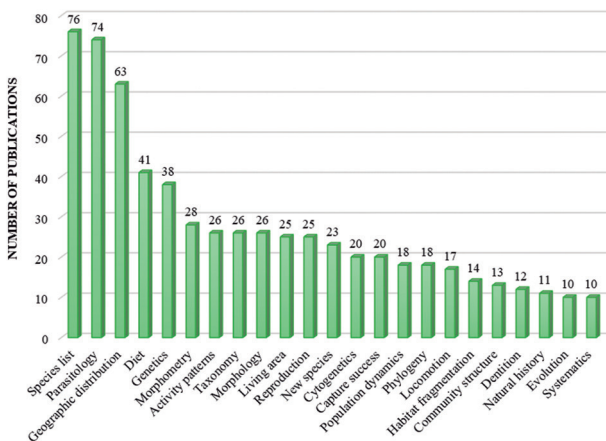


Figure 7: Number of articles published for small non-volant mammals (Didelphimorphia and Rodentia) in Brazil by area of knowledge (only more than 10 manuscripts are represented).

have a negative impact on biodiversity (Marques & Lamas, 2006).

The Atlantic Forest, which covers about 15% of the national territory and is the third biodiversity *hotspot* in the world (Mittermeier *et al.*, 2002), has only 4.7% of its total area within protected areas (CNUC, 2020).

82 Qualis B2 Mammalia	46 Qualis A2 Mammalian Biology	37 Qualis B1 Mastozologia neotropical	29 Qualis B1 Zootaxa	25 Qualis B2 Acta Theriologica
		33 Qualis B3 Oecologia Australis	25 Qualis B3 Brazilian Journal of Biology	22 Qualis B2 Zoologia
78 Qualis A2 Journal of Mammalogy	41 Qualis B2 Biota Neotropica	33 Qualis B3 Check List	20 Qualis B1 Journal of Tropical Ecology	20 Qualis B2 Studies on Neotrop... Fauna and Environ...
			20 Qualis B2 Revista Brasile... de Zoologia	17 Qualis B2 Zoologia

Figure 8: Main journals that published articles on small non-volant mammals (Didelphimorphia and Rodentia) in Brazil, between 1970 and 2020.

However, even though it is the most studied biome, as evidenced in our study (Figures 4 and 5), it has been facing intense degradation and fragmentation for decades, and this leads to a greater number of threatened species, both in richness and in absolute numbers (ICMBio, 2018). At the same time, there are still gaps in terms of geographic and taxonomic information about the group of small non-flying mammals, mainly in the Amazon biome, perhaps due to the low number of researchers in these regions, or even the difficulty of sampling in these areas (Bini *et al.*, 2006; Diniz-Filho *et al.*, 2010; Lambert



et al., 2005; Mendes *et al.*, 2011; Mendes-Oliveira *et al.*, 2015b; Nóbrega & De Marco, 2011; Rocha *et al.*, 2018; Silva *et al.*, 2013; Whittaker *et al.*, 2005).

The Cerrado biome, which has only 2.2% of its total area legally protected in federal conservation units (Cavalcanti & Joly, 2002; Françoso *et al.*, 2015), remains one of the least studied morphoclimatic domains (Oliveira & Marquis, 2002). Although highly threatened by land grabbing and the advance of grain cultivation (Aguir *et al.*, 2014; Barbosa *et al.*, 2007). Cerrado areas in the Amazon biome have been suffering similar pressures, especially in the state of Amapá, where savanna areas have been converted to grain crops (mainly soybeans and corn) in the last 20 years (Carvalho & Mustin, 2017). These regions, home to rich and unique flora and fauna, including endemic animals, remain undersampled for most taxa (Mustin *et al.*, 2017). Even so, new species records were found in the state (Costa-Campos & Freire, 2015; Silva *et al.*, 1997; 2013), increasing the possibility of better sampling in the region.

Despite the species richness of small non-volant mammals (Burgin *et al.*, 2018; Cole *et al.*, 1994; Wilson *et al.*, 1996), the Neotropical region is still poorly studied regarding the importance of these organisms to the ecosystem (Ernest & Mares, 1986; Fleming, 1975; Stallings, 1989), as these animals play an important role in the maintenance and regeneration of tropical forests, presenting vital ecological functions and being key in the structuring of biological communities (Grelle, 2003; Sánchez-Cordero & Martínez-Gallardo, 1998), in addition to being good indicators of local changes in habitat and landscape (Pardini & Umetsu, 2006).

Of the 1300 species of fauna and flora endemic to Brazilian biomes that are threatened with extinction (ICMBio, 2018), the species *Caluromysiops irrupta* Sanborn, 1951 is the only one described for the genus. It is listed in the IUCN (2020) in the Least Concern (LC) category, however, little is known about this rare species, including topics as basic as reproduction (Collins, 1973). The endemic species of the Cerrado biome, *Oligoryzomys rupestris* Weksler & Bonvicino, 2005, is evaluated as Data Deficit (DD) on the IUCN List (2020), has limited distribution, occurring only in conserved areas, and has restricted habitat use (Bonvicino *et al.*, 2002). Already the species *Kerodon rupestris* (Wied-Neuwied, 1820), restricted to the Caatinga, it is classified as Least Concern by the IUCN (2020), but the expansion of agricultural activities represents the main threat factor for these species, followed by hunting (Lapola *et al.*, 2014). Regional lists classify species as: critically endangered (CR), endangered (EN) and vulnerable (VU), respectively, reflecting these scenarios.

Although Brazil leads the production of scientific articles compared to other Latin American countries, our results highlight the spatial heterogeneity of scientific production and collaboration within the country. Even with world-renowned research institutions and

renowned researchers, according to the National Council for Scientific and Technological Development (CNPq) and the Coordination for the Improvement of Higher Education Personnel (CAPES), Brazil has been showing a drop in investments in teaching and research. Since 2015 In Brazil, 80% of science and technology research is linked to postgraduate programs at public universities (Hilu & Gisi, 2011; Van Noorden, 2014). Since the second half of 2019, due to interruptions in the payment of scholarships, there has been a technological gap in laboratories and universities that have risked several scientific programs (IPEA, 2020), and this ends up influencing the scientific production of these institutions.

As observed in this study, the survey of scientific production on small non-flying mammals, through studies on various topics, such as inventories and lists of species, carried out in Brazilian biomes, contributes to the state of the art of the group and helps in the discovery of new species and expands the knowledge about the geographic distribution of these species. Research topics such as Species Inventories, Geographical Distribution, Taxonomy, Reproduction, Diet and Genetics are extremely relevant for ecological studies of this group. However, the number of studies related to “habitat fragmentation” was low compared to other areas of knowledge. The lack of specialists in the area and the scarcity of studies on various topics and for many taxa can be one of the negative points in the search for knowledge of these organisms (Mendes-Oliveira *et al.*, 2015c). These works characterize the composition of species in the environment, contributing to the taking of measures for the delineation of areas destined for management and conservation, in addition to establishing parameters for comparison with degraded or fragmented areas (Pardini & Umetsu, 2006).

Although Brazil hosts a large number of mammal specimens in its collections, this number is far from representing the diversity of mammals in the country (one article observed in this study). Given the diversity of existing species, the geographic coverage of collections is mainly regional or national (Chiquito *et al.*, 2021). Recently, the Sociedade Brasileira de Mastozoologia included a list of Brazilian mammal species (Abreu Jr. *et al.*, 2022) that are formally described and have confirmed records in Brazil through specimens deposited in scientific collections or have documented records of occurrence in the Brazilian scientific literature.

It is known that in Brazil the assessment of science is unequal and that the inequality in the concentration of investments in research is also reflected in the production of quality science. However, even with fewer researchers compared to the global average, Brazilian scientists stand out for their relevance in cutting-edge scientific production (FAPESP, 2021; OCTI, 2021). In this sense, our results highlight the need for a better investment policy in science and technology in the country, which supports alliances and research in the least



studied states and biomes. In this way, it will be possible to address important issues for the knowledge and conservation of small mammals, such as fragmentation and habitat loss.

The survey of scientific production in Brazil on small non-Volant mammals (Didelphimorphia and Rodentia) contributes to the knowledge of the state of the art of the group, identifying the main characteristics addressed in the works. It also reflects the large number of works carried out in different areas of knowledge and in different Brazilian biomes, especially in the Brazilian Amazon. However, studies with this group should be expanded, especially in the northern states of the country, due to the scarcity of studies carried out compared to the great existing diversity.

The present study demonstrated a considerable advance in the knowledge of small non-volant mammals (Didelphimorphia and Rodentia) in the last 50 years. Despite the large number of articles on topics in ecology, it is understood that it is necessary to expand studies on the composition and inventory of species in these groups in environments, due to their importance in providing subsidies in the design of priority areas for conservation.

It is also suggested that future research on the quantitative study of small mammals be expanded, with the aim of recognizing the characteristics present in the scientific production of non-indexed articles.

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SUPPLEMENTARY INFORMATION ONLINE

Appendix S1. List of small non-volant mammals (Didelphimorphia and Rodentia) that occur in Brazil and their conservation status based on national (ICMBio 2018) and international lists of threatened species (IUCN 2019). The number of citations recorded for each species addressed in the selected articles was based on data compiled by Abreu Jr. *et al.* (2021); Díaz-Nieto & Voss (2016); Gardner (2008), Paglia *et al.* (2012), Patton *et al.* (2015), Pavan & Voss (2006); Quintela *et al.* (2020); Voss & Jansa (2009) and Voss *et al.* (2019). Acronyms: CR = Critically Endangered, DD = Data Deficient, EN = Endangered, LC = Least Concern, NT = Near Threatened, VU = Vulnerable.

Appendix S2. Final database reviewing all scientific articles published in indexed journals for a period of 50 years (from 1970 to 2020) for small non-volant mammals (Didelphimorphia and Rodentia).



Predation of *Kerodon rupestris* (Rodentia: Caviidae) by *Cerdocyon thous* (Carnivora: Canidae) in Northern Minas Gerais, Brazil

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Abstract: In this paper, we report an event of predation of the rock cavy, *Kerodon rupestris* by the crab-eating fox, *Cerdocyon thous*, in the municipality of Engenheiro Navarro, northern Minas Gerais, Brazil. Fractured bones along the rock cavy's vertebral column may be indicative of the strategy employed by the crab-eating fox to capture and kill its prey. This is the first time such interaction is reported, since there are few systematic studies on the diet of *Cerdocyon thous* in the Brazilian Caatinga and Cerrado ecosystems, where the species shares its range with *K. rupestris*.

Keywords: Crab-eating fox; Diet; Ecology; Rock cavy; Trophic relationships.

Resumo: Predação de *Kerodon rupestris* (Rodentia: Caviidae) por *Cerdocyon thous* (Carnivora: Canidae) no norte de Minas Gerais, Brasil. Reportamos pela primeira vez um evento de predação de *Kerodon rupestris* por *Cerdocyon thous*. O evento ocorreu no município de Engenheiro Navarro, norte de Minas Gerais, sudeste do Brasil. Os ossos fraturados na coluna vertebral de *K. rupestris* podem ser indicativos da estratégia utilizada por *C. thous* para capturar e matar sua presa. Esta é a primeira vez em que essa interação é reportada, mas há poucos estudos sistemáticos sobre a dieta de *Cerdocyon thous* nos ecossistemas da Caatinga e do Cerrado, onde a espécie coexiste com *Kerodon rupestris*.

Palavras-chave: Cachorro-do-mato; Dieta; Ecologia; Mocó; Relações tróficas.

The crab-eating fox, *Cerdocyon thous* (Linnaeus, 1766), is a medium-sized canid native to South America, distributed from northern Argentina and Uruguay to Colombia and Venezuela (Berta, 1982). While it is known that *C. thous* is an opportunistic omnivore, with a diet that varies seasonally and includes mostly small to medium-sized vertebrates, fruits and insects, most quantitative studies of its diet are based on methods such as fecal analysis (e.g., Bueno & Motta-Júnior, 2004; Facure, 1996; Juárez & Marinho-Filho, 2002; Pedó *et al.*, 2006; Raíces & Bergallo, 2010) or stomach content (Rocha *et al.*, 2008). Besides similar results, studies with stomach content also show consumption of gastropods, fruit pulp and human refuse by *Cerdocyon thous*. The species also eats carcasses of domestic and wild animals (Beisiegel *et al.*, 2013).

Both of these methods of assessing the diet of mammals have important limitations. For instance, both fecal and stomach content rely on the identification of fragmented material, which may be difficult. These methods are also faced with the possibility that the predator may not have ingested any identifiable parts of larger prey. Furthermore, stomach content analysis frequently depends on the accidental killing of specimens (such as roadkill, e.g., Rocha *et al.*, 2008). On the other hand, fecal analysis is limited by differential processing and digestion of the prey's body parts by mammals (Dickman & Huang, 1988). These works can

be complemented by occasional sightings of feeding behavior in the field, which, despite being unpredictable, might improve our knowledge of the diet and ecology of many species. Here we report a predation event of the rock cavy, *Kerodon rupestris* (Wied-Neuwied, 1820), by *Cerdocyon thous*.

The event was observed during fieldwork conducted on October 2018 in the rural area of Engenheiro Navarro, northern Minas Gerais (coordinates: 17°24'2.23"S; 43°58'7.21"W, Datum WGS84), southeastern Brazil. The area is characterized by dry, deciduous forest (Mata Seca), with the presence of rocky outcrops. We found an individual of *C. thous* preying upon *K. rupestris*, but the predator fled when approached, leaving the prey. The specimen of *K. rupestris* had puncture wounds along its neck and upper back, caused by bites from its predator. The specimen was prepared as skin and skeleton, had tissue samples collected and it is deposited at the Coleção de Mamíferos do Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais (CM-CCT/UFMG) under the catalog number UFMG 7059. We observed three fractured bones along the vertebral column of the *K. rupestris* specimen: the second cervical vertebra (spinous process broken at the tip); the third cervical vertebra (multiple fractures); and the fourth thoracic vertebra (spinous process broken at the tip). These fractures match the areas where skin was pierced (Fig. 1A-D).



Kerodon rupestris is a mid-sized rodent, weighing up to 1 kg, and is endemic to northeastern Brazil, with a distribution that ranges from the states of Ceará and Piauí to northern Minas Gerais (Nascimento, 2017). These animals are specialized for life in rocky outcrops that occur along its distribution, being adept climbers that forage throughout day and night (Dunnum, 2015). This species is considered a generalist herbivore, eating

leaves, bark, and other vegetative parts of plants all year long, and might be an important resource for opportunistic omnivores, such as *Cerdocyon thous*, during drier months, when insects and fruits are less readily available (Silva *et al.*, 2020; Vasconcellos *et al.*, 2010).

The rock cavy's fractured vertebrae, along with the pierced skin, point to the probable strategy employed by the crab-eating fox to capture and kill its prey. These

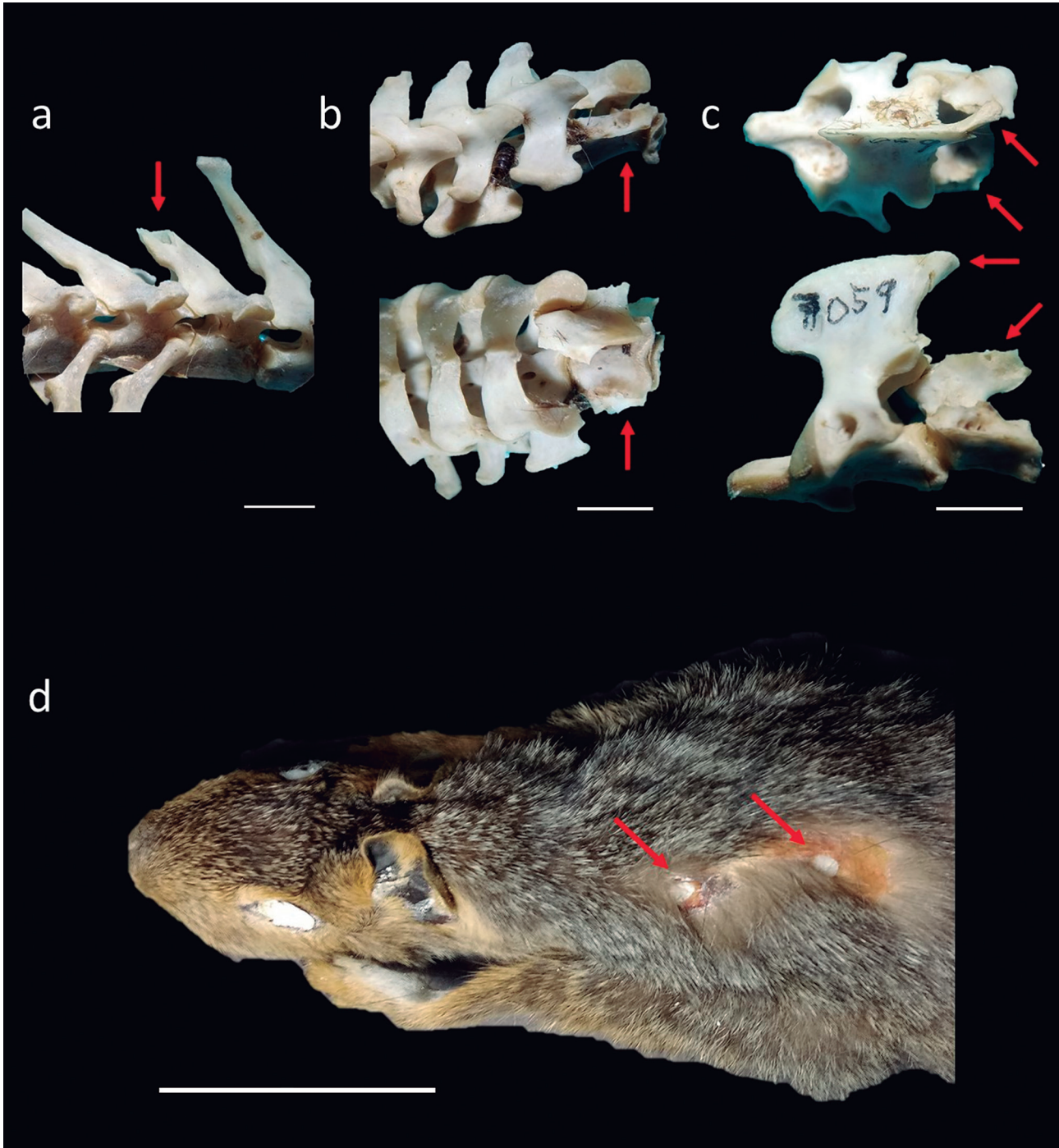


Figure 1: Specimen UFMG 7059, *Kerodon rupestris*, showing fractured bones and wounds on its skin. a) Thoracic vertebrae, left lateral view; red arrow points to the fractured spinous process of the fourth thoracic vertebra; white bar = 5 mm. Cervical vertebrae, right lateral view (upper) and dorsal view (lower); red arrow points to the left portion of the third cervical vertebra; white bar = 5 mm. c) Cervical vertebrae, left lateral view (lower) and dorsal view (upper); red arrows point to fractures on the spinous process of the second cervical vertebra and on the right portion of the third cervical vertebra; white bar = 5 mm. d) Preserved skin of the specimen; red arrows point to the wounds inflicted by the predator; white bar = 5 cm.



wounds are consistent with the capture patterns observed by Brady (1979) for *C. thous* in the Venezuelan Llanos and by Fox (1969) for coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in captivity, which involve jumping towards the prey and trapping it with the front paws, while simultaneously securing it with the teeth, which often immobilizes the prey. However, we did not observe the capture of the rock cavy. Examining skeletons of other specimens housed at scientific collections might allow determining signs of predation that could be useful for estimating trophic interactions among both extant and extinct taxa, and a thorough examination of such specimens can be an important source of information for ecological and palaeoecological studies.

This is the first documented event of predation of *Kerodon rupestris* by *Cerdocyon thous*. The few studies on the feeding ecology of *Cerdocyon thous* in the Caatinga of Northeastern Brazil have not recorded any predation event of *Kerodon rupestris*, even where the distribution of the two species overlaps (Catzefflis *et al.*, 2016; Lucherini, 2015), although other caviids such as *Galea spixii* have been identified in scats of *C. thous* (Dias & Bocchiglieri, 2016; Olmos, 1993). Other animals that have been reported as preying on *K. rupestris* are mammals such as *Sapajus libidinosus* (Freire Filho *et al.*, 2021), *Herpailurus yagouaroundi* (Oliveira, 1998), *Galictis vittata* (Larivière & Jennings, 2009), and humans (Alves *et al.*, 2016), as well as birds such as *Herpetotheres cachinnans* (Amora & Ferrari, 2014). It seems likely that the rock cavy may be as an important food item for these and other species, especially for opportunistic omnivores and carnivores. Additional systematic studies are necessary to elucidate the diet and behavior of *C. thous* in this region and the frequency and importance of the rock cavy in the diets of *C. thous* and other predators.

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First record of leucism in a crab-eating fox (*Cerdocyon thous*) from the Atlantic Forest hotspot

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Abstract: Leucism has been increasingly reported in mammals, but there are still few records for canids. Here, we report the first record of a leucistic crab-eating fox (*Cerdocyon thous*) from Atlantic Forest in the southern Brazil. The region has savanna relics immersed into the Atlantic Forest domain and is dominated by large crops. In wild canids, cases of hypopigmentation are rare and the genetic and environmental mechanisms behind these anomalous colorations are poorly studied and understood. We recommend obtaining biological samples from the leucistic crab-eating fox aiming to analyze candidate genes involved with white coat color pattern.

Key-Words: Canid; Carnivora; Coloration Polymorphism; Hypopigmentation; Neotropical Mammals.

Resumo: Primeiro registro de leucismo em cachorro-do-mato (*Cerdocyon thous*) no hotspot Mata Atlântica. O leucismo tem sido cada vez mais reportado em mamíferos, mas ainda são poucos os registros para canídeos. Nós relatamos o primeiro registro de cachorro-do-mato leucístico (*Cerdocyon thous*) na Mata Atlântica, sul do Brasil. A região possui manchas de Cerrado imersas na Mata Atlântica e é dominada por grandes lavouras. Em canídeos selvagens, casos de hipopigmentação são raros e os mecanismos genéticos e ambientais por trás dessas colorações anômalas são pouco estudados e compreendidos. Recomendamos a obtenção de amostras biológicas deste indivíduo de cachorro-do-mato leucístico com o objetivo de analisar possíveis genes envolvidos a este padrão de coloração esbranquiçada.

Palavras-Chave: Canídeo; Carnívora; Hipopigmentação; Mamíferos Neotrópicos; Polimorfismo de Coloração.

Polymorphic phenotypes occur occasionally in several taxa (Eizirik & Trindade, 2021; Krecsák, 2008; Mahabal *et al.*, 2019; Silva, 2017; Tinajero & Rodríguez-Estrella, 2010). It is caused by genetic mutations that result in excess (melanism), an absence of (albinism) or deficient (leucism and piebaldism) melanin synthesis (Eizirik *et al.*, 2003; Miller, 2005). Leucism is caused by low frequencies recessive mutations in mammals (Cho *et al.*, 2013; Xu *et al.*, 2013) and is rare in wild populations (Cronemberger *et al.*, 2018; Silva *et al.*, 2019a). Leucistic individuals may have the same coat color pattern as their conspecifics (Miller, 2005; Silva *et al.*, 2019a), but with a lack or reduction of pigmentation in most or parts of the body, except for the eyes and body extremities (Aximoff *et al.*, 2020; Mendes-Pontes *et al.*, 2020). This polymorphism commonly is considered as a disadvantage, possibly decreasing individual survival and fitness (Caro, 2005; Cronemberger *et al.*, 2018) due to greater susceptibility to predation or difficulty with camouflage, especially in the case of top predators (Abreu *et al.*, 2013; Sokos *et al.*, 2018), and can be associated visual and immunological pathologies (Grant *et al.*, 2001; Summers, 2009).

Among Neotropical mammals, rodents, chiropterans, and cetaceans have more reports of species with

polymorphic pigmentation, with leucism being the least frequent anomaly (Abreu *et al.*, 2013; Fertl *et al.*, 2004; Neves *et al.*, 2014; Silva *et al.*, 2019b; Stumpp *et al.*, 2019). Within Carnivora, records of species with leucism in the Neotropics are still few and punctual, being already reported in *Lontra longicaudis* (Olfers, 1818) (Ariaga-Flores *et al.* 2016), *Eira barbara* (Linnaeus, 1758) (Mendes-Pontes *et al.*, 2020; Srich *et al.*, 2019; Talamoni *et al.*, 2017), *Nasua narica* (Linnaeus, 1766) (Silva-Caballero *et al.*, 2014), *Puma concolor* (Linnaeus, 1771) (Cronemberger *et al.*, 2018), *Leopardus pardalis* (Linnaeus, 1758) (McBride & Giordano, 2010) and, recently, in three canids, *Lycalopex gymnocercus* G. Fischer, 1814 (Chatellenaz & Zaracho, 2021), *Canis latrans* Say, 1823 (Arroyo-Arce *et al.*, 2019) and *Cerdocyon thous* (Linnaeus, 1766) (Oliveira *et al.*, 2019). This last case of a leucistic crab-eating fox (*C. thous*) was registered in 2015 in the semi-arid Caatinga, in the Brazilian state of Pernambuco, and represents the only known record for the species throughout its geographic distribution. Thus, we report here the second record of a leucistic crab-eating fox in Brazil and the first for the Atlantic Forest hotspot domain.

The crab-eating fox is a small to medium-sized canid that inhabits a diversity of environments in South



America (Lucherini, 2015). However, the species has a clear preference for more open environments over dense forests (Beisiegel *et al.*, 2013) and can also be found along forest edges and in anthropized areas, such as crops, pastures, and suburban landscapes (Lemos *et al.*, 2011). It's a polymorphic animal naturally, being its coat from dark gray to gray-brown in color, with a darker band along the back reaching the tail, as well as dark coloring on the lower legs (Castelló, 2018), although its coloration can vary among its subspecies and throughout its distribution. The coat coloration tends to be lighter in more open and drier environments (Oliveira *et al.*, 2019), such as the Caatinga and Cerrado, while in forested environments, such as the Atlantic Forest and Amazon, it tends to be darker (Beisiegel *et al.*, 2013), which is a pattern already found in other Neotropical polymorphic carnivores (Silva *et al.*, 2016).

The record site is located in the rural area of the municipality of Indianópolis, Paraná State, southern Brazil (23°34'47"S, 52°47'34"W) (Fig. 1). The Atlantic Forest is the dominant biome in the region, but there is also the presence of natural patches of Brazilian savannah inserted along this area in the northwest of the state of Paraná (Villwock & Colavite, 2020). The area is inserted between a livestock pasture area and a sugarcane plantation, close to a small forest fragment of 40 hectares. At

06:04 a.m. on February 3, 2021, the observed individual passed by a parked farm vehicle, from which it was observed and photographed, and then moved to into the livestock pasture area.

One adult individual of crab-eating fox of indeterminate sex, presenting leucism coloration was recorded on a rural road in the southern Brazil. The coat of the individual was white throughout the entire body, with pigmentation only at the end of the tail, towards the tip of the snout and in the eyes (Fig. 2), ruling out the possibility of albinism.

In wild canids, cases of hypopigmentation are rare and the genetic and environmental mechanisms behind these anomalous colorations are poorly studied and understood (Abreu *et al.*, 2013; Arroyo-Arce *et al.*, 2019; Chatellenaz & Zaracho, 2021; Oliveira *et al.*, 2019). However, a few studies try to link hypopigmentation in mammals to inbreeding (due population isolation and a higher probability of fixing the recessive alleles), and to environmental disturbances (Aximoff *et al.*, 2020; Bensch *et al.*, 2000; Lopucki & Mróz, 2010; Møller & Mousseau, 2001).

Although this single record does not allow a conclusion regarding the possible causes of this anomalous color appearance in this individual crab-eating fox, some environmental similarities can be found in the local

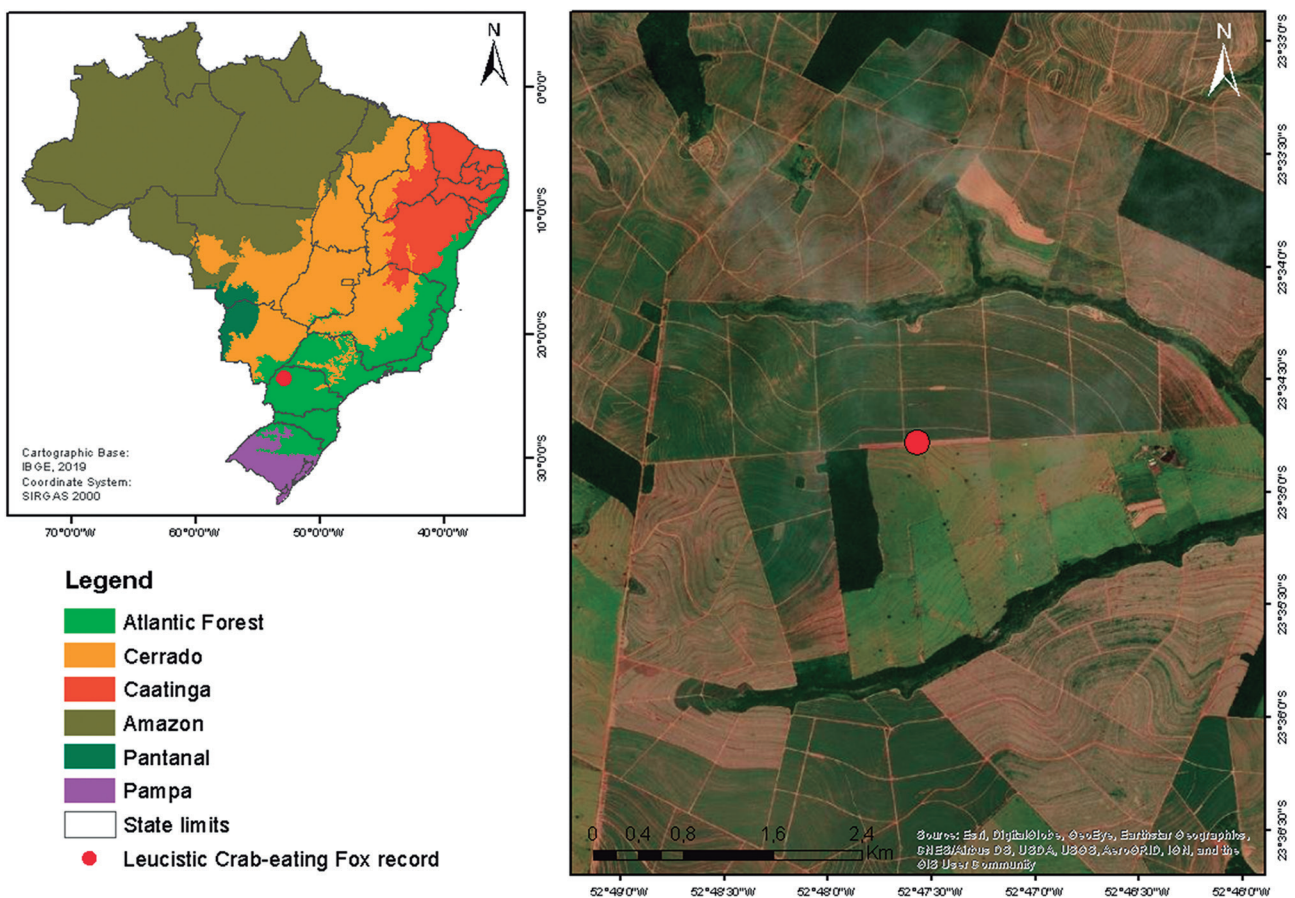


Figure 1: Location of the record of the individual crab-eating fox (*Cerdocyon thous*) with leucism in the Atlantic Forest domain, municipality of Indianópolis, Paraná State, southern Brazil.

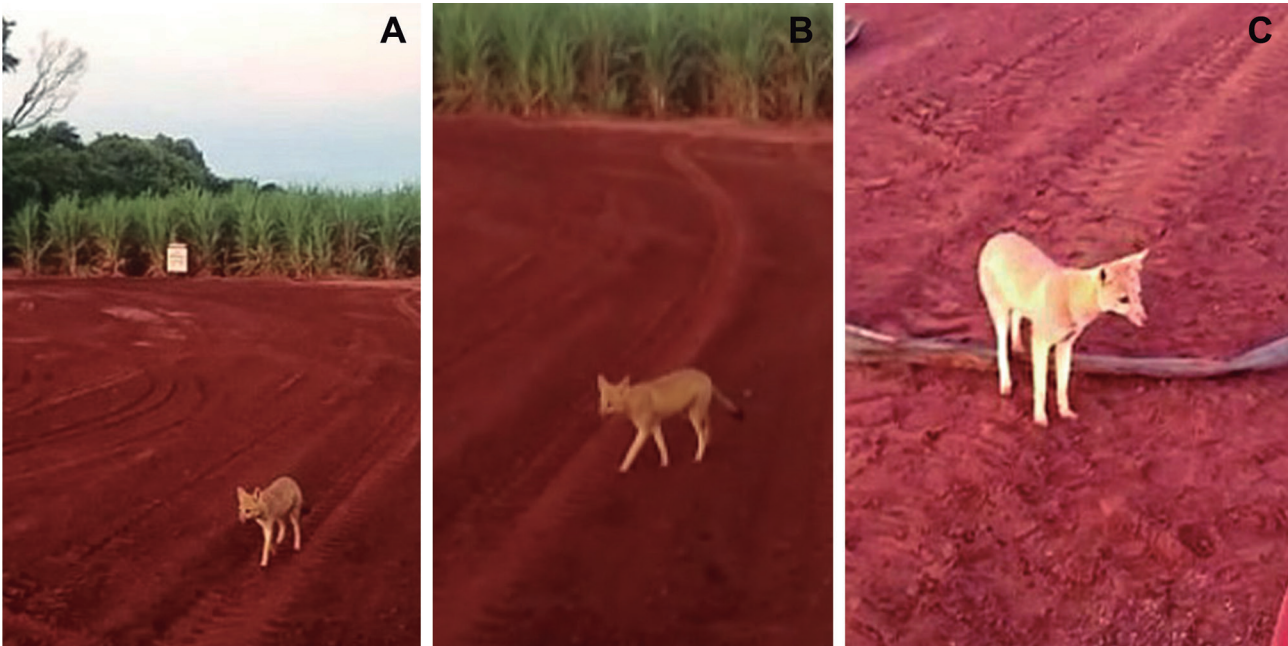


Figure 2: Leucism in a crab-eating fox (*Cerdocyon thous*) in the rural area of the municipality of Indianópolis, Paraná State, southern Brazil. Recorded on February 3, 2021. Note the white color of the coat, with pigmentation only at the end of the tail, snout and eyes.

record of another leucistic individual of this same species of canid made by Oliveira *et al.* (2019) in the Caatinga biome. Both areas are dominated by large crops, with degradation and loss of their original vegetation cover, in addition to the use of pesticides (Cunha *et al.*, 2010; Inoue *et al.*, 2003).

We recommend obtaining biological samples from the leucistic crab-eating fox aiming to analyze candidate genes involved with white coat color pattern, using the cases of tigers (Xu *et al.*, 2013) and lions (Cho *et al.*, 2013) as baseline. In this scenario, with biological samples from both animals (from Atlantic Forest and Caatinga) it would be possible to identify if leucism mutations risked independently from both biomes. In the Atlantic Forest, a high number of hypopigmentation cases are found in Brazilian mammals (Aximoff & Rosa, 2016; Aximoff *et al.*, 2020, 2021; Cronemberger *et al.*, 2018; Landis *et al.*, 2020; Silva *et al.*, 2019a; Sodre *et al.*, 2004; Souza *et al.*, 2013; Tavares *et al.*, 2020; Ventorin *et al.*, 2021), a pattern that could be related to original landscapes that can favor the adaptive relevance of leucistic individuals, or to the historic fragmentation process that reduced this biome to around a quarter of its original geographic range (Rezende *et al.*, 2018).

The crab-eating fox is a canid with high ecological plasticity (Beisiegel *et al.*, 2013), being able to survive in disturbed landscapes like the one of the current records. However, the indirect effects of anthropogenic impacts can have on the gene pool of wild populations over the long term are still unknown. Thus, studies aiming to better understanding these effects on animal coloration and the genetic diversity of wild carnivores in the Atlantic Forest region are necessary. Moreover, it can serve as baseline tools for understanding ecological processes

involved in the generation and maintenance of polymorphic phenotypes (such as leucism) in natural populations, and the adaptive relevance of coloration morphs under different ecological conditions.

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Pequenos mamíferos de uma área protegida: Explorando padrões de diversidade em uma paisagem altamente fragmentada

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RESUMOS

Entender os mecanismos que afetam os padrões de diversidade é tema de interesse para ecólogos que estudam os pequenos mamíferos, no entanto, grande parte destes trabalhos direcionam a investigação somente para o padrão de riqueza. A questão, é que a riqueza atribui pesos iguais às espécies, o que a depender do estudo, pode ser limitado. Neste trabalho, investigamos os índices de diversidade, riqueza, diversidade funcional (FD), e diversidade filogenética (PD) de uma comunidade de pequenos mamíferos e o quanto são influenciados por recursos locais, estrutura do habitat e características da paisagem em uma reserva inserida em paisagem fragmentada do Brasil Central. Dividimos a área protegida e seu entorno em 20 hexágonos, onde em cada unidade amostral, estabelecemos 10 estações de armadilhas para a captura de pequenos mamíferos. Em metade das estações, coletamos dados sobre a estrutura da vegetação e recursos alimentares, enquanto as métricas de paisagem foram obtidas por meio de imagens de satélite. Estimamos a diversidade funcional a partir de traços morfológicos, ecológicos e comportamentais das espécies capturadas. Para as relações filogenéticas, derivamos a árvore filogenética a partir da filogenia de Upham, 2019. Nenhum dos padrões de diversidade foram explicados pelos recursos alimentares. Já dentre as variáveis de estrutura do habitat, FD e PD foram explicados por arbustos, embora essa relação tenha sido negativa. FD foi explicado pelo número de lianas, e PDNTI, medida de diversidade filogenética que relaciona a co-ocorrência de espécies, também utilizada, foi explicada pela quantidade de árvores. Dentre as medidas da paisagem, PDNTI foi explicado pela distância ao curso d'água mais próximo, por meio de uma relação negativa. Em ambientes florestais, a quantidade de lianas e árvores apresentam papel importante na estruturação vertical de florestas, o que aumenta o espaço funcional para as espécies, possuindo então maior diversidade funcional e filogenética do que ambientes mais abertos, caracterizados pela maior quantidade de arbustos. Além disso, espécies mais parecidas filogeneticamente parecem ocupar ambientes com mais árvores, destacando as adaptações de espécies arbóricolas em ambiente florestal, algumas já com evidência de sinal filogenético. Com tantas mudanças na paisagem e na dinâmica da floresta causadas no último, e atual século, mais estudos são necessários para avaliar o efeito da estrutura da vegetação, entre outras variáveis, sobre a comunidade de pequenos mamíferos.



Relações entre morfometria geométrica pós-craniana e filogenias de roedores equimiídeos (Rodentia: Histicognathi: Echimyidae)

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Os roedores constituem a ordem mais rica em espécies de mamíferos. Na América do Sul, dentre os roedores caviomorfos, a família Echimyidae possui uma história taxonômica confusa e apesar de várias revisões, ainda permanecem lacunas de estudos sistemáticos para esta família que é compreendida pelos ratos-de-espinho, as hutias e o coypu. Esta família destaca-se por possuir um elevado número de espécies (ca. 100 spp.), larga variação na massa corporal e, ainda, uma grande diversidade de hábitos locomotores, os quais incluem espécies arborícolas, escansoriais, semi-aquáticas, semifossoriais e terrestres. Assim, a função esquelética dos roedores equimiídeos juntamente com a sua organização filogenética, fornecem um modelo de estudo promissor e de particular interesse para a compreensão de como fatores alométricos, ecológicos e filogenéticos afetam a evolução do esqueleto pós-craniano. Assim, o objetivo principal desta tese foi analisar a influência destes três fatores sobre a diferença da forma e do tamanho na morfologia pós-craniana em um contexto filogenético, possibilitando a compreensão da evolução e da divergência nas características morfológicas e ecológicas. Para a realização destas análises, fotografamos 186 escápulas e 181 úmeros de 38 espécies de 15 gêneros equimiídeos (ca. 37% e 54% respectivamente do total de equimiídeos). Posteriormente, para a resolução deste problema, utilizamos a morfometria geométrica, uma ferramenta de baixo custo e precisa para identificação de sutis diferenças morfológicas digitalizando 31 marcos anatômicos bidimensionais (2D) para a escápula (14 *landmarks* e 17 *semilandmarks*) enquanto para o úmero, foram utilizados 23 marcos (19 *landmarks* e 4 *semilandmarks*). A partir das coordenadas destes pontos, foi possível eliminar o efeito do tamanho das espécies possibilitando testarmos as diferenças de forma entre os grupos filogenéticos e os hábitos locomotores. A variação morfológica da escápula e do úmero mostraram uma baixa correlação com a massa e o tamanho corporal evidenciando um efeito alométrico pequeno ou desprezível. Os resultados demonstraram ainda um sinal filogenético significativo, mas baixo, para ambas as estruturas. A variação morfológica da escápula foi extensamente estruturada pela filogenia dos equimiídeos podendo tornar-se um relevante marcador taxonômico e filogenético em estudos futuros. Por outro lado, a variação morfológica do úmero foi estruturada pelos hábitos locomotores tornando-se útil para áreas de estudo como a paleontologia que buscam reconstruir hábitos locomotores sobre uma perspectiva ecomorfológica. Assim, estes resultados sugerem que estruturas pós-cranianas como escápula e úmero foram moldadas por restrições e adaptações evolutivas e por estarem envolvidas com a locomoção, estas estruturas são bem adequadas para os estudos ecomorfológicos por integrarem uma parte essencial da diversificação ecomorfológica e filogenética. Embora existam vários trabalhos com a escápula e o úmero de caviomorfos utilizando abordagens morfológicas e morfofuncionais, este é o primeiro estudo morfométrico a abordar uma ampla diversidade de gêneros equimiídeos utilizando a escápula e o úmero. Este trabalho fornece uma visão sobre a função e a evolução do sistema esquelético dos equimiídeos sugerindo ainda que a diversidade dos membros anteriores seja uma parte essencial da diversificação ecomorfológica e filogenética desta família de roedores.

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