
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO
E BIODIVERSIDADE**

**USO DO HABITAT, PADRÕES DE MOVIMENTO E GASTO ENERGÉTICO
DE MICOS-LEÕES-PRETOS (*LEONTOPITHECUS CHRYSOPYGUS*)**

GABRIELA CABRAL REZENDE

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Tese apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia, Evolução e Biodiversidade.

Orientadora: Dra. Laurence Culot

Coorientadores: Dr. Luca Börger e
Dr. Ariovaldo P. da Cruz-Neto

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TÍTULO DA TESE: USO DO HABITAT, PADRÕES DE MOVIMENTO E GASTO ENERGÉTICO DE MICOS-LEÕES-PRETO (LEONTOPITHECUS CHRYSOPYGUS)

AUTORA: GABRIELA CABRAL REZENDE

ORIENTADORA: LAURENCE MARIANNE VINCIANNE CULOT

COORDENADOR: ARIIVALDO PEREIRA DA CRUZ NETO

COORDENADOR: LUCA BÖRGER

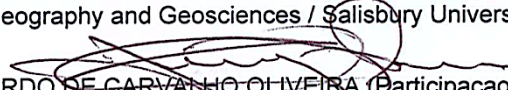
Aprovada como parte das exigências para obtenção do Título de Doutora em ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE, área: Zoologia pela Comissão Examinadora:



Profa. Dra. LAURENCE MARIANNE VINCIANNE CULOT (Participação Presencial)
Departamento de Biodiversidade / IB Rio Claro



Profa. Dra. ANDREA PRESOTTO (Participação Presencial)
Department of Geography and Geosciences / Salisbury University



Prof. Dr. LEONARDO DE CARVALHO OLIVEIRA (Participação Presencial)
Departamento de Ciências / Universidade do Estado do Rio de Janeiro

Rio Claro, 25 de agosto de 2022

Dedico à minha filha Sofia,
cujos anos de existência na presente data
coincidem com a duração desse trabalho e
a principal responsável pelo “delineamento”
dessa pesquisa.

AGRADECIMENTOS

Minha escolha de ingressar no doutorado foi um longo processo. Levei exatos quatro anos entre a defesa do mestrado e a matrícula no doutorado. Pensar que passaria “quatro anos da minha vida me dedicando a um único projeto” soava como tortura para uma geminiana. Mal sabia que esse pensamento tinha dois graves equívocos: 1. “um único projeto” era uma descrição muito leviana para todas as nuances que isso envolve; e 2. Doutorados duram “quatro anos” em CNPT (a.k.a. “Condições Normais de Pressão e Temperatura”), e não quando uma gravidez e uma pandemia resolvem dar uma dinamizada nos planos. Por fim, foram 64 meses em um projeto que de monótono não teve nada. Talvez por isso, já deixo aqui minhas desculpas se você sentir que faz parte desse processo, mas não encontrou seu nome por aqui. Foram tantas pessoas que se fizeram presentes ao longo desse processo, que me faltam palavras para agradecer e memória para lembrar de tanto.

Começo agradecendo aos micos-leões-pretos. Primeiro porque tudo isso foi feito por eles, mas também porque foram os grandes responsáveis por colocar no meu caminho a maioria dessas pessoas que mencionarei a seguir. Com eles, aprendo diariamente. Por eles, tenho trabalhado incansavelmente nos últimos 11 anos. Através deles, luto pelo meu propósito de vida. Espero que os resultados dessa tese sejam de alguma forma úteis para sua conservação.

Começando a lista de pessoas, está meu grande companheiro de todos esses anos (e hoje pai da minha filha, Sofia), Guilherme Garbino, que entrou na minha vida ainda durante o mestrado POR CAUSA dos micos. Resistimos a dois doutorados, meu e seu, com gravidezes no meio, temos uma filha maravilhosa que nos enche de orgulho e alegria a cada dia e cá estamos até hoje. Gui, obrigada pela parceria e companheirismo, por ser meu maior exemplo de cientista e me ensinar TANTO! Agradeço a paciência diária, as infinitas revisões de absolutamente todos os meus textos, manuscritos, capítulos da tese, propostas, relatórios..., a ajuda nos campos e experimentos, seja indo no meu lugar ou cuidando da Sofia na minha ausência, por ter conseguido sobreviver aos nove loongos meses longe de nós duas enquanto estivemos no Reino Unido e, por fim, por segurar as pontas em casa durante os últimos meses de escrita da tese. Enfim, poderia escrever páginas se fosse enumerar cada contribuição sua nesse trabalho. Sem dúvida, sem você, tudo isso ainda estaria no mundo das ideias.

Ah, Sofia, se você soubesse o quanto tem de você em cada uma dessas páginas. Espero que um dia seja capaz de compreender o real sentido de a mamãe ter se ausentado, seja estando em campo com os macaquinhos ou mesmo no cômodo ao lado, sem poder estar juntinho de você, brincando, por estar trabalhando nessas linhas todas. Saiba que você esteve presente em todos esses momentos nos meus pensamentos e que tudo isso é para que saiba que todas nós, mulheres, deveríamos ter a liberdade e o privilégio de poder correr atrás de nossos sonhos. Obrigada por me acompanhar nos primeiros campos, na nossa aventura além-mar, por ser minha grande companheira durante os nove meses que passamos em Swansea, e minha melhor amiga, pelos abraços para me acalmar e pelos “tá tudo bem, mamãe”, no auge da sua empatia, sensibilidade e maturidade de uma criança de três anos de idade. Isso tudo é por você! Para que possa também sonhar grande, minha pequena, e principalmente, realizar!

Mas se hoje tenho eles ao meu lado é porque existe um alicerce que suporta tudo isso, chamado família, sem o qual eu não seria nada. Meus pais, Noedy e Mary, que sempre me deram apoio incondicional para que eu pudesse correr atrás dos meus sonhos e meus maiores exemplos de amor, humildade e determinação; às minhas irmãs (e segundas mães) Cláudia e Eliane, irmãos (e segundos pais) Luciano e Carlos, e cunhados Adilson e Henrique, minhas maiores inspirações quando se trata de realizar sonhos e o/as melhores tio/as que a Sofia poderia ter; às minhas sobrinhas-irmãs, melhores amigas e companheiras da vida, Isabella, Isadora, Laura, Carol, Beatriz e Helena, e meu sobrinho-neto e afilhado Lucca, hoje o melhor companheiro da Sofia; aos meus sogros José Garbino e Lucia, por cuidarem da Sofia em tantos momentos cruciais para o desenvolvimento dessa pesquisa e por todo apoio de sempre; e aos meus avós (*in memoriam*), tio/as e primo/as (incluindo os que aqui nos olham de um lugar para o qual todos um dia iremos), nossa grande e amada família. Poderia escrever longos textos agradecendo a cada um, mas por agora expresso aqui minha enorme e eterna gratidão e amor. Se hoje sou quem eu sou e se cheguei aonde estou, é porque tenho vocês comigo sempre!

Também ganhei na loteria com o time que escolhi para me orientar ao longo desse processo. Um time de peso, cada um com sua especialidade e contribuição para que eu conseguisse chegar até aqui. Mais do que os acadêmicos que escolhi para me orientar, essas quatro pessoas se tornaram grandes amigos e conselheiros da vida:

A minha orientadora Dr.^a Laurence Culot. Ela, que antes de orientadora, já era parceira de trabalho. Acreditou nas minhas ideias e me deu todo suporte para seguir em frente, mesmo em meio a tantas tempestades que encontrei no caminho ao longo desse tempo. Lo, muito obrigada pela amizade, compreensão, paciência e por ser um exemplo de pesquisadora, a quem eu escolhi me espelhar. Quando fui atrás de um doutorado, muito além do título, buscava me desenvolver academicamente e me qualificar enquanto cientista, para melhorar a qualidade das minhas pesquisas. Não poderia ter tido uma orientadora melhor para esse longo e árduo percurso que é fazer ciência no Brasil. Aprendi e aprendo muito com você.

Meu (co)orientador e supervisor do Estágio de Pesquisa no Exterior (BEPE), Dr. Luca Börger, o italiano-alemão mais internacional que conheço. Ele também, além de orientador, virou um grande parceiro, que embarcou nas minhas ideias que muitas vezes soavam impossíveis, me ajudou a buscar soluções para as perguntas que eu queria responder e me deu todo o suporte necessário para chegarmos aonde chegamos com esse trabalho (e sei que ainda dá para ir longe). Luca, grazie per la tua ospitalità e amicizia, per aver risposto ai miei messaggi a qualsiasi ora del mattino, pomeriggio, notte, alba, nel tuo pazzesco fuso orario di lavoro, per aver fatto le scelte sbagliate a volte, ma soprattutto quelle giuste, nei nostri sondaggi, insegnandomi a comprendere i miei dati e a fare di tutto per spiegarmi le “model fit”. Infine, per avermi accolto così bene a Swansea e aperto le porte di SLAM – Swansea Laboratory for Animal Movement in modo che potessi svolgere le mie analisi.

Meu também (co)orientador, Dr. Ariovaldo Cruz-Neto, que mergulhou de cabeça nesse projeto e trouxe a pitada de fisiologia que meus dados ecológicos precisavam. Parceiro de boas conversas e discussões sem fim sobre nossas metodologias e resultados, e sempre que possível acompanhadas das melhores cervejas. Neto, agradeço pela paciência em me explicar conceitos fisiológicos e pela disposição em ajudar como pode ou me aconselhar, especialmente quando a água batia no pescoço; por me apresentar a água duplamente marcada e trazer a parceria com o grande John Speakman e a Universidade de Aberdeen para viabilizar nossas análises.

Por fim, Dr. Milton Cezar Ribeiro, ele que não me orientou oficialmente, mas acompanhou cada etapa desse projeto, desde sua concepção e delineamento, participou da avaliação do meu projeto, da minha qualificação e sempre aberto a me apoiar e orientar. Miltinho, me faltam palavras para expressar a admiração que tenho

por você. Obrigada por me apoiar e incentivar desde o primeiro minuto, quando tudo isso não passava de ideias ambiciosas.

Ao reingressar numa universidade pública após oito anos de formada na graduação, e com financiamento público, compreendi novamente o privilégio que é estar num centro que produz ciência de excelência, a partir de pessoas apaixonadas pelo que fazem, enfrentando todas as dificuldades do caminho, com a única finalidade fazer seu campo do conhecimento evoluir. Sim, a ciência é feita a partir de pessoas, de mentes pensantes, movidas pela curiosidade e que, juntas, inclusive, conseguem ir mais longe. Por isso, agradeço aos professores, mestres e doutores que cruzaram meu caminho durante esse tempo e despertaram e alimentaram em mim essa curiosidade. Mas ciência também é feita de cooperação e de convivência, que muitas vezes é proporcionada pelos ambientes dessas universidades. Assim, agradeço a oportunidade de ter frequentado três laboratórios ao longo do doutorado, dentro dos quais encontrei mais do que parceiros de trabalho, mas grandes amigos:

Ao Laboratório de Primatologia (LaP/UNESP), liderado pela nossa querida Lo, agradeço pelas amizades, ajuda no campo e momentos de troca de ideia sobre os nossos tão amados micos: Olivier Kaisin, Lica Fuzessy, Felipe Bufalo, Rodrigo Amaral, Anne-Sophie Silva, Debora Tomiatti, Mayara Mulato, Raissa Sepulvida, Lucas Pereira... Não poderia deixar de agradecer especialmente ao Edu Zanette, que surgiu no meio da pandemia e se tornou um grande amigo, confidente, construtor de ideias e revisor de capítulos; e às minhas queridas orientandas, Catarina Cibim e Marina Souza, que toparam embarcar nessa pesquisa e tanto me apoiaram e me ensinaram nesse processo.

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Minha gratidão enorme também ao IPÊ – Instituto de Pesquisas Ecológicas, minha segunda casa, a instituição que me acolheu durante toda minha vida profissional e que ofereceu todo o apoio e condições para que esse projeto alçasse seus voos. No começo de tudo, Claudio Valladares Padua, pioneiro nas pesquisas de campo com o mico-leão-preto e idealizador do projeto cuja continuidade e liderança me foram confiadas há dez anos. Meu grande mentor, conselheiro e amigo, responsável pelo meu ingresso e crescimento na primatologia, que acreditou e acredita no meu potencial (às vezes mais do que eu mesma) e que nunca mediu esforços para me fazer alcançar todos os meus objetivos. Nunca terei palavras para te agradecer o suficiente. Em seguida, aos meus “pais do mato”, eles, sem os quais nenhum desses micos teria sido estudado: José Wilson Alves (ou Wilsinho), André Albuquerque e Cícero José da Silva Filho (ou Cicinho, *in memoriam*), essas páginas são resultado de suas décadas de experiência acompanhando os micos na floresta. Obrigada por toda paciência e persistência em fazer essa (e outras) pesquisa(s) acontecer(em), por me ensinarem a usar um facão, a andar e (tentar) ficar em silêncio no mato, e por serem os melhores professores sobre ecologia e biologia de mico-leão-preto.

Outra pessoa que embarcou nessa pesquisa desde o começo e nunca mediu esforços para que ela acontecesse foi Daniel Felippi, nosso vet, que participou e acompanhou todas as capturas (desde as primeiras, quando ainda falhávamos miseravelmente nas coletas de dados) e agora, oficialmente veterinário do Programa de Conservação do Mico-leão-preto (PCMLP/IPÊ), segue fazendo com que os processos de captura de micos continuem dando saltos gigantescos em qualidade e

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Desde o começo, eu sonhei grande nesse projeto e fiz o que pude para não precisar ter “plano B” (apesar de algumas mudanças e adaptações no caminho). Foram muitas pessoas envolvidas na coleta de dados em campo e no cativeiro, às quais não poderia deixar de listar e agradecer, algumas delas pela segunda vez: à equipe de campo do IPÊ ao longo desses anos: Daniel, Vinícius, André, Wilsinho, Francy, Leonardo Silva, Frederico Mazziero e mais alguns voluntários que se juntaram a essa empreitada; ao pessoal do LaP/UNESP: Marina, Catarina, Rodrigo, Olivier, Edu, Felipe, Francisco e Gabriel Sabino (nosso botânico agregado); e aos que realizaram o experimento no Centro de Primatologia do Rio de Janeiro (no meu último mês de gravidez): Gui, Luca, Neto e, em especial, Silvia Bahadian e Dr. Alcides Pissinatti, por terem aberto as portas do CPRJ para nós. Foram ao menos 22 pessoas

envolvidas na coleta desses dados, sem as quais, sem dúvida, essa pesquisa não teria acontecido da forma que aconteceu.

Mas esse projeto, de fato, só pode acontecer porque, além dessas pessoas, tivemos apoiadores e parceiros superimportantes, que garantiram que cada etapa pudesse ser implementada, mesmo com tantos imprevistos. O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001, que me concedeu bolsa durante os primeiros 25 meses do doutorado (sendo 4 de licença maternidade) e o auxílio financeiro PROAP para a realização do experimento no CPRJ; da Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), que me concedeu a bolsa no país (Processo 2017/11962-9) e a bolsa estágio de pesquisa no exterior (BEPE - Processo 2020/10617-9) durante todos os 41 meses restantes do meu doutorado, e os Auxílios via Projeto Jovem Pesquisador da Dr. Laurence Culot (Processo 2014/14739-0) e Projeto de Auxílio à Pesquisa do Dr. Ariovaldo Cruz-Neto (Processo 2014/16320-7). Agradeço também o apoio do DLW Resource Centre, do Departamento de Zoologia da University of Aberdeen (Scotland), em especial a John Speakman e equipe, que realizou as análises de água duplamente marcada; da Swansea University, com o apoio institucional durante a minha estadia no SLAM para a BEPE; e da Universidade Estadual Paulista (UNESP Rio Claro), com a oferta de toda infraestrutura e suporte institucional, em especial aos funcionários da Seção Técnica de Pós-Graduação.

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Centro de Primatologia do Rio de Janeiro (CPRJ/INEA) e Zoológico Municipal Quinzinho de Barros (Sorocaba/SP).

Chegar até aqui me fez ter certeza de que um doutorado vai muito além da pesquisa e do título em si. O doutorado é um processo que envolve muito mais nuances que podemos imaginar ao ingressar, nuances de uma coisa chamada vida. Então, desejo que essa pesquisa também vá muito além de seus resultados e inspire muitas mulheres pesquisadoras a correrem atrás de seus sonhos, sejam eles profissionais, acadêmicos, maternos, de vida...! Porque esse doutorado, além de tudo, me ensinou a ter planos mais flexíveis e a abraçar as circunstâncias que a vida traz. Então, para terminar, peço licença ao Quino para reproduzir uma tirinha da querida Mafalda que muito representa o que quis eu expressar nessas longas páginas de agradecimentos:



“The least I can do is speak out for those
who cannot speak for themselves.”

Jane Goodall

“Our education system teaches about linearity,
not about what to do when this linear pattern breaks,
not where to look for resilience,
not the art of recovery from disruption.”

Keisha Blair

“Não é sobre chegar no topo do mundo e saber que venceu
É sobre escalar e sentir que o caminho te fortaleceu
[...]

Também não é sobre correr contra o tempo pra ter sempre mais
Porque quando menos se espera a vida já ficou pra trás
Segura teu filho no colo
Sorria e abraça os teus pais enquanto estão aqui
Que a vida é trem-bala, parceiro
E a gente é só passageiro prestes a partir”

Ana Vilela

RESUMO

Alterações na estrutura das florestas decorrentes da degradação do habitat podem levar a alterações na movimentação de animais que dependem desses ambientes, afetando seu balanço energético e, em última análise, sua taxa de reprodução e sobrevivência. Portanto, compreender padrões de movimento e gasto energético de espécies em paisagens degradadas pode auxiliar no desenvolvimento de diretrizes para o manejo do habitat, de modo a aumentar a viabilidade de populações nesses ambientes. Escolhemos o mico-leão-preto (*Leontopithecus chrysopygus*), endêmico da Mata Atlântica de São Paulo e ameaçado devido à fragmentação, como modelo para compreender as consequências energéticas decorrentes da fragmentação do habitat em primatas arborícolas. Numa escala ampla, a) avaliamos como processos de diferentes escalas atuam na distribuição de uma espécie dependente de ambientes florestais; e numa escala local, b) caracterizamos e comparamos padrões de movimento e uso de habitat de micos-leões-pretos em diferentes fragmentos, e c) avaliamos como a estrutura florestal, os fatores abióticos e os padrões de movimento influenciam seu gasto energético. Inicialmente, utilizamos Modelos de Nicho Ecológico para prever a distribuição potencial de mico-leão-preto a partir do uso de variáveis de clima combinadas a de paisagem. Posteriormente, trabalhamos as questões de movimento e gasto energético dessa espécie, utilizando dados coletados remotamente a partir de dispositivos de GPS e acelerômetro. Validamos, através de um experimento em cativeiro, a utilização de acelerômetros para estimar o custo energético do movimento do mico-leão-preto em seu ambiente natural. Em seguida, monitoramos micos-leões selvagens para caracterizar seus padrões de movimento e estimar o gasto energético relativo a esse movimento. Nossos resultados mostram que a espécie está presente em menos de 1% de sua distribuição original, sugerindo um profundo efeito da fragmentação. Também identificamos áreas de alta adequabilidade climática e de paisagem para sua ocorrência e determinamos prioridades regionais em termos de estratégias de manejo visando sua conservação. A partir do monitoramento de quatro indivíduos durante 1575 horas e obtendo mais de 136 milhões de registros, encontramos que os micos-leões-pretos selvagens gastaram, em média, 100,5 ($\pm 8,4$) kcal por dia, enquanto os cativos gastaram 84,5 ($\pm 11,9$) kcal/dia. Os resultados do monitoramento em campo também sugeriram um efeito do tamanho do fragmento no uso e compartilhamento do espaço, e indicaram

que a distância percorrida e a direcionalidade do movimento, assim como a temperatura, umidade, duração do dia, e a estrutura e composição da floresta influenciaram o gasto energético dos micos. Encontramos uma relação negativa entre gasto energético e as variáveis estruturais (DAP, área basal e volume) e composicionais (riqueza) da floresta, corroborando a nossa hipótese de que os micos gastam menos energia em florestas de melhor qualidade. Este é o primeiro estudo a estimar taxa metabólica da espécie, e indica como a complexidade estrutural afeta seu gasto energético. Os resultados nos permitiram identificar áreas e ações prioritárias para a conservação do mico-leão-preto e subsidiar diretrizes para o manejo do habitat, visando favorecer sua movimentação pela floresta e pela paisagem fragmentada. Num contexto amplo, o estudo valida metodologias para a priorização de áreas para espécies dependentes de floresta, e o uso de tecnologias de monitoramento remoto em estudos de movimento e gasto energético, fornecendo resultados relevantes à conservação de espécies animais.

PALAVRAS-CHAVE: fragmentação, modelagem, acelerômetro, área de vida, conservação de espécies

ABSTRACT

Changes in the structure of forests resulting from habitat degradation can lead to changes in the movement of animals that depend on these environments, affecting their energy balance and, ultimately, their reproduction rate and survival. Therefore, understanding movement patterns and energy expenditure of species in degraded landscapes can provide useful information for the development of guidelines for habitat management, in order to increase populations viability in these environments. We chose the black lion tamarin (*Leontopithecus chrysopygus*), endemic to the Atlantic Forest of São Paulo and threatened due to fragmentation, as a model to understand the energetic consequences of habitat fragmentation in arboreal primates. On a broad scale, a) we evaluated how processes of different scales act in the distribution of a forest dependent species; and on a local scale, b) we characterized and compared movement patterns and habitat use of black lion tamarins in different fragments, and c) evaluated how forest structure, abiotic factors and movement patterns influence their energy expenditure. Initially, we used Ecological Niche Models to predict the potential distribution of the black lion tamarin using climate and landscape variables combined. Subsequently, we worked on the issues of movement and energy expenditure of this species, using data collected remotely from GPS and accelerometer devices. We validated, through an experiment in captivity, the use of accelerometers to estimate the energy cost of movement of the black lion tamarin in its natural environment. We then monitored wild lion tamarins to characterize their movement patterns and estimate the movement-related energy expenditure. Our results show that the species is present in less than 1% of its original distribution, suggesting a profound effect of fragmentation. We also identified areas of high climatic and landscape suitability for their occurrence and determined regional priorities in terms of management strategies aimed at their conservation. From the monitoring of four individuals for 1,575 hours and obtaining more than 136 million records, we found that wild black lion tamarins spent, on average, 100.5 (± 8.4) kcal per day, while captive ones spent 84.5 (± 11.9) kcal/day. The results of field monitoring also suggested an effect of patch size on space use and sharing, and indicated that distance traveled and directionality of movement, as well as temperature, humidity, daylength, and the forest structure and composition influenced the tamarins' energy expenditure. We found a negative relationship between energy expenditure and structural (DBH, basal area and volume) and

compositional (richness) forest variables, corroborating our hypothesis that tamarins spend less energy in better quality forests. This is the first study to estimate the species' metabolic rate, and it indicates how structural complexity affects its energy expenditure. The results allowed us to identify priority areas and actions for the conservation of the black lion tamarin and provide guidelines for habitat management, aiming to favor its movement through the forest and the fragmented landscape. In a broad context, the study validates methodologies for prioritizing areas for forest-dependent species, and the use of remote monitoring technologies in movement and energy expenditure studies, providing relevant results for the conservation of animal species.

KEYWORDS: fragmentation, niche modeling, accelerometer, home range, species conservation

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1 APRESENTAÇÃO DA TESE

1.1 INTRODUÇÃO GERAL

1.1.1 MOVIMENTO E GASTO ENERGÉTICO

Alterações na estrutura das florestas, decorrentes da fragmentação e da degradação do hábitat, podem afetar, numa escala local, a disponibilidade de recursos para a fauna, ocasionando mudanças comportamentais e ecológicas nos animais, tais como nos seus padrões de movimentação e orçamento temporal de atividades (Niebuhr et al., 2015). Entre tais alterações, mudanças na estrutura tridimensional da floresta são particularmente relevantes para animais arborícolas, como os primatas neotropicais (Davies & Asner, 2014; Gouveia et al., 2014). Elas podem moldar a conectividade e a permeabilidade do hábitat arbóreo, levando a mudanças na forma com que esses animais interagem com a estrutura da vegetação, por exemplo, ao se locomover (Davies et al., 2017).

Essencialmente, comportamentos podem ser definidos a partir de padrões de movimento, tais como posturas e movimentos corporais, combinados em um determinado intervalo de tempo (Wilson et al., 2018). Os animais dividem seu tempo em estratégias comportamentais, que têm custos energéticos específicos (Wilson et al., 2006). Portanto, mudanças ambientais, que alterem a estrutura do hábitat e, por consequência, a movimentação desses animais, podem afetar o orçamento temporal de atividades e o equilíbrio energético dos indivíduos. Em última análise, o balanço temporal (e energético) entre as diferentes atividades de sua rotina definirá sua probabilidade de sobreviver e se reproduzir com sucesso, podendo afetar, portanto, a viabilidade de uma população (Jeanniard-du-Dot et al., 2017).

Outro efeito potencial da fragmentação é a limitação do movimento animal entre fragmentos de hábitat, isolando populações, cessando o fluxo gênico e, consequentemente, resultando em extinções locais (Bolger et al., 2001; Knapp, 2013). Além disso, a restrição de movimento impacta a coleta de recursos e, portanto, a sobrevivência das populações em paisagens alteradas (de Knegt et al., 2007). A resposta positiva ou negativa de um organismo a alterações na paisagem é espécie-específica, uma vez que está relacionada a sua capacidade de se mover pelo

ambiente alterado, através de uma matriz mais ou menos permeável (Jepsen et al., 2005; Taylor et al., 1993; Uezu et al., 2005).

Portanto, estudos de movimento se fazem necessários para esclarecer respostas comportamentais e consequências energéticas decorrentes de processos de alteração do hábitat, como a fragmentação e a degradação de florestas (Doherty et al., 2021; Wang et al., 2017). Com o uso de colares de GPS e *dataloggers*, é possível monitorar remotamente padrões de movimento e uso do hábitat de forma tridimensional, estimar o gasto energético, e prever reações dos indivíduos a alterações no ambiente, sejam em paisagens naturais ou antropogênicas (Tomkiewicz et al., 2010). Com isso, podemos entender se a variação no gasto de energia explica diferenças de movimento e orçamento temporal em manchas de hábitat com diferentes estruturas florestais.

1.1.2 MICO-LEÃO-PRETO

O mico-leão-preto (*Leontopithecus chrysopygus*, Primates, Callitrichidae) é um pequeno primata endêmico da Mata Atlântica, com distribuição restrita ao estado de São Paulo (Coimbra-Filho & Mittermeier, 1973). A principal ameaça a essa espécie, dependente de ambientes florestais, é a extensa redução e fragmentação do hábitat, uma vez que apenas 6,4% da cobertura florestal original de floresta estacional semidecídua ainda permanece dentro de sua área de distribuição no interior paulista. Sua ocorrência hoje está restrita a pouco mais de 20 fragmentos florestais, todos localizados na bacia hidrográfica do Rio Paranapanema (Figura 1; Garbino et al., 2016). Sua população é estimada em 1.600 indivíduos, sendo que 80% deles vive em um único remanescente de floresta, o Parque Estadual do Morro do Diabo, no Pontal do Paranapanema, região mais ocidental do Estado de São Paulo. Trata-se da única população genética e demograficamente viável. As demais populações são pequenas e isoladas, sofrendo pressões externas devido a pastagens e plantações invadindo fragmentos, à presença de rodovias e expansão urbana, sem ignorar a emergência de doenças que podem acometer primatas e os efeitos, ainda desconhecidos, das mudanças climáticas sobre essas populações. As Análises de Viabilidade Populacional e de Habitat (PHVA) mostram que as pequenas populações podem se extinguir em menos de 70 anos, caso não sejam realizadas ações para sua conservação (Forero-Sánchez, 2020). Tal cenário faz com que a espécie esteja listada

estadual, nacional e globalmente como “Em Perigo” (respectivamente, São Paulo, 2014; Brasil, 2022; Rezende et al., 2020).

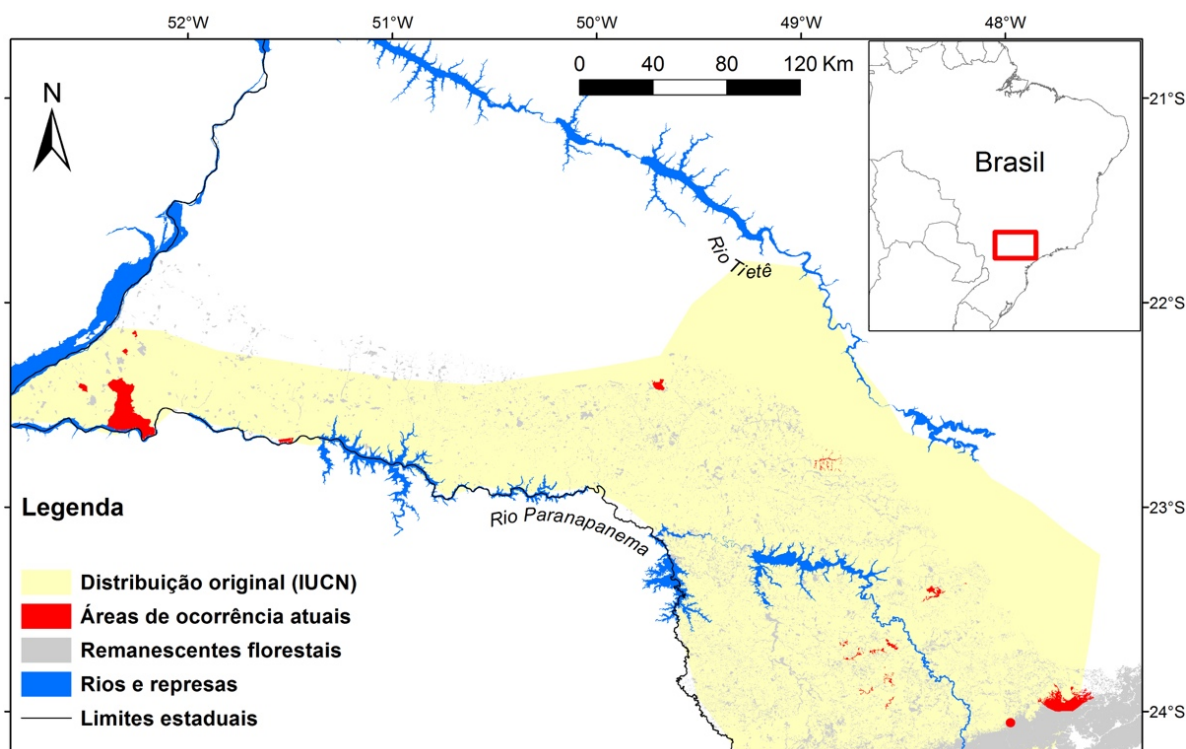


Figura 1. Mapa das áreas de ocorrência de mico-leão-preto (*Leontopithecus chrysopygus*). Fonte: elaboração própria.

Micos-leões-pretos vivem em grupos familiares, cujo tamanho pode variar de 2 a 8 indivíduos, sendo geralmente um casal reprodutor e seus descendentes (Figura 2), até que estes atinjam maturidade sexual e dispersem para a formação de novos grupos (Coimbra-Filho & Mittermeier, 1973; Medici, 2001). O grupo se locomove de forma coesa ao longo de seu período de atividade diurno, estabelecendo áreas de vida, cujo tamanho de 40 a 400 hectares pode variar de acordo com a época do ano, disponibilidade de recursos, ou tamanho do fragmento (Albernaz, 1997; Mamede-Costa, 1997; Medici, 2001; F. D. C. Passos, 1997; Valladares-Padua, 1993). Dentre os recursos requeridos pela espécie ao longo do ano estão suas fontes de alimento e seus locais de dormida. Seu nicho alimentar é frugívoro-insetívoro, com dieta composta principalmente por frutas, exsudatos vegetais, invertebrados e pequenos vertebrados, como anfíbios, lagartos, aves, e outros animais, esses últimos encontrados em micro-habitats do estrato arbóreo (Coimbra-Filho & Mittermeier, 1973;

Garbino et al., 2022; Keuroghlian & Passos, 2001). Como dormitório, utilizam principalmente ocos de árvores e ocasionalmente emaranhados de lianas, realizando uma alternância de locais ao longo dos dias, possivelmente como estratégia para proteção contra predadores durante o período noturno, quando entram em período de descanso (da Silva, 2019). Portanto, a sobrevivência de micos-leões-pretos em uma área depende da presença de árvores que ofereçam esses recursos, reforçando a dependência vital desses animais por ambientes florestais relativamente maduros. Além disso, a quantidade e qualidade desses recursos afeta a capacidade-suporte de um determinado remanescente florestal e, conseqüentemente, o número de indivíduos que podem usar/viver nessa área (Janson & Chapman, 2009).



Figura 2. Adulto carregando um filhote de mico-leão-preto. Foto: Rachel Hughes (Durrell Wildlife Conservation Trust).

Essa espécie arborícola, portanto, utiliza seu hábitat de forma tridimensional, movendo-se pelos diferentes estratos na busca de recursos, percorrendo relativamente longas distâncias – entre 1 e 3 km (Medici, 2001; Passos, 1997) e

coabrindo grandes áreas de floresta durante seu período de atividade (Valladares-Padua, 1993). Essas características nos permitem avaliar a influência da estrutura florestal de seu hábitat, atualmente degradado e alterado, em seus padrões de movimento, na escala de fragmento. Ao compreender como o mico-leão-preto usa seu hábitat e como a estrutura florestal influencia seus movimentos e gasto energético, poderemos construir modelos mais preditivos de movimentação da espécie em habitats alterados e paisagens fragmentadas. Esses modelos servirão de evidência para o desenvolvimento de diretrizes mais robustas para a restauração do hábitat e da conectividade, que contemplem as características da floresta que a espécie necessita, aumentando a viabilidade e sobrevivência das populações em paisagens alteradas.

1.2 OBJETIVOS E ESTRUTURA DA TESE

Nessa pesquisa, escolhemos o mico-leão-preto como modelo para compreender as respostas comportamentais e as consequências energéticas decorrentes da fragmentação do hábitat em primatas arborícolas. Para isso, numa escala ampla, a) testamos os efeitos de métricas de paisagem, juntamente com as variáveis climáticas, em modelos que preveem a distribuição potencial dessa espécie dependente da floresta em uma paisagem fragmentada; e numa escala local, b) caracterizamos e comparamos padrões de movimento e uso de hábitat de grupos vizinhos de micos-leões-pretos em diferentes fragmentos florestais, e c) estimamos como a estrutura florestal, os fatores abióticos e os padrões de movimento influenciam seu gasto energético. O primeiro objetivo foi tratado no primeiro capítulo através de uma modelagem de nicho ecológico, enquanto o segundo e o terceiro são abordados nos três capítulos seguintes, utilizando dados coletados a partir de acelerômetros num experimento em cativeiro e no monitoramento de micos-leões de vida livre. A seguir, descrevo resumidamente cada um dos capítulos que compõem esta tese, já redigidos em formato de manuscrito e, portanto, em inglês para posterior submissão:

CAPÍTULO 1 – “INTEGRATING CLIMATE AND LANDSCAPE MODELS TO PRIORITIZE AREAS AND CONSERVATION STRATEGIES FOR AN ENDANGERED ARBOREAL PRIMATE”

No primeiro capítulo da tese, a partir de uma abordagem de Modelagem de Nicho Ecológico (MNE), testei o efeito da incorporação de métricas de paisagem, juntamente com as variáveis climáticas, na previsão de adequabilidade do hábitat para uma espécie dependente da floresta, usando o mico-leão-preto como modelo. Construímos os modelos de clima e de paisagem, separadamente, e depois os combinamos usando a Análise *EcoLand* (Santos et al., 2020).

Nossos resultados sugerem que a fragmentação e modificação da paisagem histórica e atual tiveram efeitos profundamente adversos na distribuição dos micos-leões-pretos. Da área total considerada adequada à espécie, ela está presente atualmente em menos de 40%, o que representa menos de 1% de sua distribuição original. Com base no mapa da *EcoLand*, pudemos identificar áreas prioritárias para a conservação do mico-leão-preto e definir as principais estratégias para cada região de sua ocorrência, real ou potencial, sendo elas conservação de hábitat e manejo populacional, manejo e restauração do hábitat, e áreas relevantes em cenários de mudanças climáticas.

Essa abordagem ilustra como a combinação de modelos de nicho baseado em variáveis de clima e paisagem pode ser útil para estabelecer e direcionar medidas de conservação para espécies arborícolas e dependentes de hábitat florestal. Este capítulo foi publicado em forma de artigo na revista *American Journal of Primatology* (Rezende et al., 2020).

Palavras-chave: modelagem de nicho ecológico, método ensemble, fragmentação

CAPÍTULO 2 – “VALIDATING DYNAMIC BODY ACCELERATION METRICS AS A MEASURE OF ENERGY EXPENDITURE IN BLACK LION TAMARINS”

No segundo capítulo, o objetivo foi validar o método para estimativa do custo energético do movimento de mico-leão-preto em seu ambiente natural, através de um experimento com animais de cativeiro utilizando água duplamente marcada com isótopos de H e O ($^2\text{H}_2^{18}\text{O}$). Esse método estima a taxa metabólica a partir da diferença entre as taxas de eliminação dos isótopos marcados, medidas em dois diferentes momentos (Speakman, 1997). Os micos que receberam a água duplamente marcada foram simultaneamente monitorados com dispositivos de registro de dados biológicos (*Daily Diary loggers* – DD), que permitem a estimativa de gasto energético a partir de métricas de aceleração (aceleração dinâmica do corpo, ou *Dynamic Body Acceleration* – DBA) (Wilson et al., 2008).

A partir desse experimento, chegamos à primeira estimativa da taxa metabólica de campo (FMR – Field Metabolic Rate) para micos-leões-pretos. Os valores obtidos estão em concordância com os valores esperados da literatura para primatas de seu porte (Pontzer et al., 2014). Também encontramos, na regressão entre os valores obtidos a partir deste método e do monitoramento por acelerômetros, uma relação linear consistente e significativa, que pode ser aprimorada a partir da incorporação de informações de tempo de atividade e descanso.

Com esse experimento, validamos o método de estimativa de gasto energético através de acelerômetros, que foi então utilizado no monitoramento em campo para estimar o custo energético do movimento de mico-leão-preto em seu ambiente natural, conforme apresentado nos capítulos seguintes.

Esse capítulo, redigido em formato de manuscrito, será enviado à revista *Journal of Animal Ecology*.

Palavras-chave: experimento em cativeiro, ritmo diário, água duplamente marcada, VeDBA

CAPÍTULO 3 – “SPACE USE AND MOVEMENT PATTERNS OF BLACK LION TAMARIN NEIGHBOURING GROUPS IN FOREST PATCHES”

No terceiro capítulo, apresentamos, portanto, os resultados do monitoramento de micos-leões-pretos de vida-livre em fragmentos florestais através de dispositivos de GPS e acelerômetro. Buscamos responder a três perguntas: 1) Como os micos-leões-pretos mudam a forma que utilizam o espaço disponível e seus padrões de movimento em fragmentos florestais de diferentes tamanhos? 2) A borda do fragmento afeta o uso do espaço pelos micos? 3) Como os micos exploram sua área de vida diariamente?

Para isso, quatro grupos de micos foram capturados em dois fragmentos florestais de tamanhos distintos, no interior do estado de São Paulo, e tiveram sua movimentação diária monitorada remotamente através de dispositivos de GPS e acelerômetro, por 10 a 22 dias consecutivos. Os dados do GPS foram registrados a cada 10 minutos durante o período de atividade diurna dos micos (das 06:00 às 19:00), enquanto os dados dos acelerômetros foram coletados a uma frequência de 25 Hz (24 horas/dia). A partir desses dados, caracterizamos os padrões de movimento e estimamos a área utilizada no período por cada grupo, a sobreposição destas pelos grupos vizinhos, as áreas de atividade diária e a sobreposição destas em dias consecutivos.

Nossos resultados sugeriram um efeito do tamanho do fragmento no uso e compartilhamento do espaço. Enquanto no fragmento maior, as áreas utilizadas foram três vezes maiores e sem sobreposição com o grupo vizinho, no fragmento menor a sobreposição correspondeu a cerca de um terço da área total, incluindo também áreas núcleo. Apesar dessas diferenças, os padrões de movimento em ambos os fragmentos foram similares. Já o padrão diário de exploração de recursos mostrou-se rotativo em ambos os fragmentos, mas com diferentes janelas de tempo de retorno para um mesmo local, provavelmente em função do tamanho da área de vida e do espaço disponível.

Palavras-chave: área de vida, comprimento do passo, ângulo de virada, deslocamento diário

CAPÍTULO 4 – “MOVEMENT-RELATED ENERGY EXPENDITURE OF BLACK LION TAMARINS IN FRAGMENTED HABITATS”

O foco do quarto capítulo foi nas análises de gasto energético obtidas essencialmente a partir dos dados dos acelerômetros equipados nos mesmos indivíduos de micos-leões monitorados para o capítulo 3. Através desses dados, além das estimativas de gasto energético, também estimamos duração do período de atividade e proporção de atividade em cada fase do ritmo diário (dia vs. noite) e em cada período do dia (manhã vs. tarde). Com o objetivo de estimar e comparar o gasto energético relativo ao movimento de micos-leões-pretos que vivem em florestas com diferentes características estruturais, testamos o efeito da distância percorrida na variação do gasto energético, em três escalas temporais: diária (período de atividade), por período do dia, e por hora. Em seguida, testamos também os efeitos da estrutura e composição da floresta, da direcionalidade do movimento, seja horizontal ou vertical, e de fatores abióticos nesse gasto energético.

Nossos resultados indicaram que a distância percorrida foi o preditor mais importante de gasto energético, independentemente da escala temporal considerada em nossos modelos. Mas tanto os fatores físicos (temperatura, umidade e duração do dia) quanto os bióticos (estrutura e composição da floresta) tiveram uma influência adicional, além da direcionalidade horizontal e vertical do movimento. Encontramos uma relação negativa entre gasto energético e as variáveis estruturais (DAP, área basal e volume) e composicionais (riqueza) da floresta, corroborando a nossa hipótese de que os micos gastam menos energia em florestas de melhor qualidade.

O manuscrito relativo a esse capítulo será enviado à revista *Movement Ecology Journal*.

Palavras-chave: custo de movimento, acelerômetro, estrutura florestal, primata

Por fim, como recomendação da tese para a conservação da espécie e com base nas evidências levantadas a partir desse trabalho, propomos áreas prioritárias e diretrizes para o manejo do hábitat e da conectividade da paisagem, de modo a favorecer a ocupação de remanescentes de floresta e a movimentação do mico-leão-preto em manchas de hábitat e na paisagem. Para isso, analisamos dados de caracterização da vegetação em 11 fragmentos florestais nas regiões do Alto Paranapanema e Pontal do Paranapanema, sendo oito deles com ocorrência de mico-leão-preto, a partir da estimativa de variáveis estruturais e composicionais dessa floresta. Comparamos essas áreas, buscando identificar atributos determinantes, sejam eles estruturais ou composicionais, para o uso do hábitat pelos micos-leões, visando reduzir seu gasto energético relativo ao movimento. A partir desses atributos, trabalhamos na proposição de diretrizes para o manejo do hábitat (i.e., direcionamento de espécies para a restauração florestal) e da conectividade da paisagem (i.e., desenho para a implantação de corredores) em áreas de ocorrência real e potencial dessa espécie. Esse direcionamento para a conservação, baseado em evidências científicas, pode aumentar as chances de sucesso das ações, levando a resultados mais tangíveis.

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2 CHAPTER I: INTEGRATING CLIMATE AND LANDSCAPE MODELS TO PRIORITIZE AREAS AND CONSERVATION STRATEGIES FOR AN ENDANGERED ARBOREAL PRIMATE

(Capítulo publicado na revista *American Journal of Primatology* - Rezende et al. 2020)

2.1 RESUMO

Título: Integrando modelos climáticos e de paisagem para a priorização de áreas e estratégias de conservação para um primata arborícola ameaçado de extinção

A distribuição das espécies é influenciada tanto pelas condições climáticas quanto pela estrutura da paisagem. Aqui propomos uma análise integrada de modelos de nicho baseados em variáveis de clima e de paisagem para um primata dependente da floresta, o ameaçado mico-leão-preto (*Leontopithecus chrysopygus*). Aplicamos variáveis climáticas e de paisagem para prever a distribuição desse primata e usamos essas informações para priorizar áreas estratégicas. Nossos resultados indicam que esta abordagem pode ser benéfica para a seleção de estratégias de conservação para esta espécie ameaçada de extinção. Primeiro, construímos modelos de nicho baseados em clima e paisagem separadamente, combinando sete algoritmos, para inferir processos que atuam na distribuição da espécie em diferentes escalas. Posteriormente, combinamos os modelos de clima e de paisagem usando a análise *EcoLand*. Nossos resultados sugerem que a fragmentação e modificação da paisagem histórica e atual tiveram efeitos adversos profundos na distribuição dos micos-leões-pretos. Os modelos indicaram apenas 2.096 km² (de uma distribuição original de 92.239 km²) de áreas adequadas tanto para o clima quanto para a paisagem. Desta área adequada, a espécie está presente atualmente em menos de 40%, o que representa menos de 1% de sua distribuição original. Com base no mapa combinado, determinamos as regiões oeste e sudeste da distribuição da espécie como áreas prioritárias para sua conservação. Identificamos áreas com alta adequação climática e de paisagem, que se sobrepõem aos fragmentos florestais remanescentes em ambas as regiões, para conservação de hábitat e manejo populacional. Sugerimos que áreas com alta adequação climática, mas baixa adequação de paisagem, sejam priorizadas para o manejo e restauração do hábitat. Áreas com alta adequação de paisagem e baixa adequação climática, como a Serra

de Paranapiacaba, devem ser consideradas à luz dos cenários projetados de mudanças climáticas. Nosso estudo de caso ilustra que uma abordagem combinada de modelagem de nicho baseada em clima e paisagem pode ser útil para estabelecer medidas de conservação direcionadas que podem aumentar a probabilidade de sucesso.

PALAVRAS-CHAVE: mico-leão-preto, modelagem de nicho ecológico, método ensemble, fragmentação, *Leontopithecus chrysopygus*

2.2 ABSTRACT

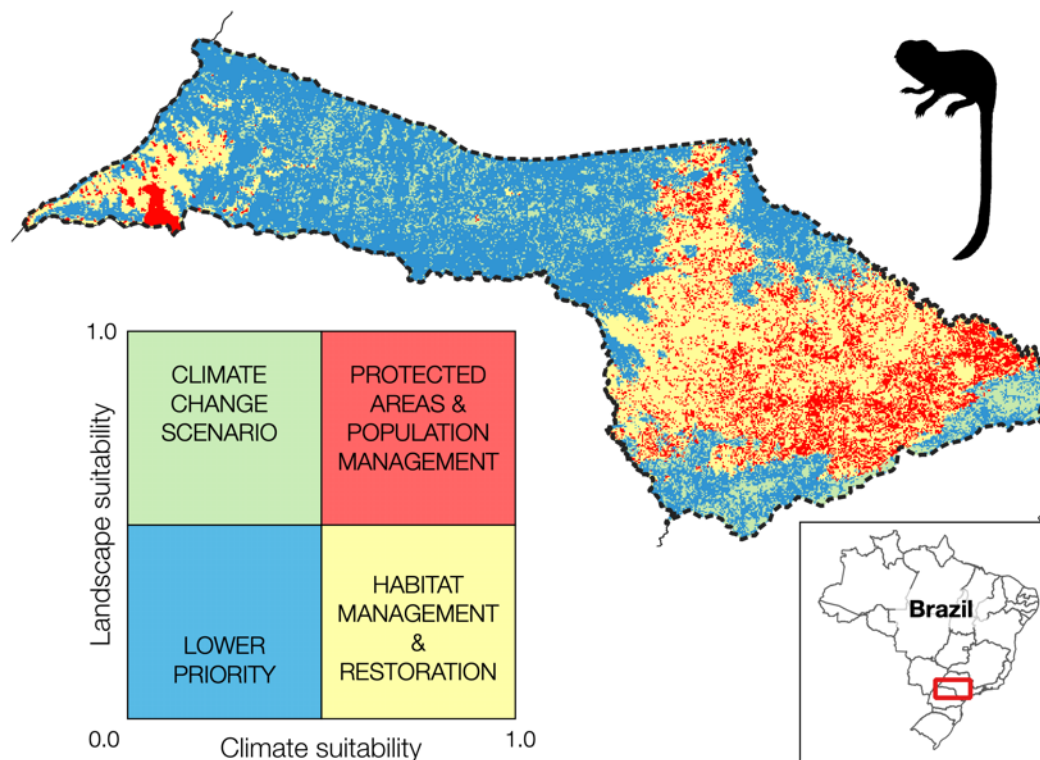
Species distributions are influenced by both climate conditions and landscape structure. Here we propose an integrated analysis of climatic and landscape niche-based models for a forest-dependent primate, the endangered black lion tamarin (*Leontopithecus chrysopygus*). We applied both climate and landscape variables to predict the distribution of this tamarin and used this information to prioritize strategic areas more accurately. We anticipated that this approach would be beneficial for the selection of pertinent conservation strategies for this flagship species. First, we built climate and landscape niche-based models separately, combining seven algorithms, to infer processes acting on the species distribution at different scales. Subsequently, we combined climate and landscape models using the *EcoLand* Analysis. Our results suggest that historic and current landscape fragmentation and modification had profoundly adverse effects on the distribution of the black lion tamarins. The models indicated just 2,096 km² (out of an original distribution of 92,239 km²) of suitable areas for both climate and landscape. Of this suitable area, the species is currently present in less than 40%, which represents less than 1% of its original distribution. Based on the combined map, we determined the western and southeast regions of the species range to be priority areas for its conservation. We identified areas with high climatic and high landscape suitability, which overlap with the remaining forest fragments in both regions, for habitat conservation and population management. We suggest that areas with high climatic but low landscape suitability should be prioritized for habitat management and restoration. Areas with high landscape suitability and low climatic suitability, such as the Paranapiacaba mountain range should be considered in light of projected climate change scenarios. Our case study illustrates that a combined approach of climatic and landscape niche-based modelling can be useful for

establishing focused conservation measures that may increase the likelihood of success.

KEYWORDS: black lion tamarin, ecological niche modeling, ensemble method, fragmentation, *Leontopithecus chrysopygus*

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2.3 GRAPHICAL ABSTRACT



Climate and landscape-based models are used to prioritize areas for the development of strategies for the black lion tamarin within its distribution range.

2.4 INTRODUCTION

Species distributions are affected by different spatio-temporal filters (Cavander-Bares et al., 2009). Climate-based processes (environmental filtering) shape species distribution at the broad scale (Kraft et al., 2015), but narrow-scale processes effects, such as biological interactions and landscape characteristics, are usually not included in species distribution inferences (Pearson and Dawson, 2003; Franklin and Miller, 2009; Guisan and Rahbeck, 2011; Peterson et al., 2011). In the Anthropocene, changes in land-use and the correlated habitat loss represent a severe threat for global biodiversity (Dirzo et al., 2011, Newbold et al., 2015). Therefore, conservation applications of species distribution modeling should employ methodologies capable of considering different-scale processes that act on species distributions (Santos et al., 2020).

The combined use of broad and narrow-scaled processes acting on species distributions is important chiefly in areas that show higher degrees of anthropogenic impact (Santos et al., 2020). On a broad scale, climate variables enable the prediction of the ecological niche of species using physiological constraints (Peterson et al., 2011). On a narrower scale, the inclusion of landscape metrics, such as patch size, functional and structural connectivity, enable modeling to incorporate the effects of landscape changes on the movement and dispersal ability of a species (a proxy of population dynamics and local extinction indexes) and the suitability of local habitat. In summary, climate variables are useful for predicting a species niche and its potential distribution, while landscape metrics predict habitat constraints based on species movement and dispersal capacity, and other population dynamics.

The black lion tamarin (*Leontopithecus chrysopygus*) is endemic to the Atlantic Forest and restricted to the Brazilian state of São Paulo (Coimbra-Filho and Mittermeier, 1973). Habitat loss and fragmentation have reduced its occurrence to a few areas within the remaining 7% of interior Atlantic forest of this state, one of the most fragmented and modified areas of this ecosystem (Ribeiro et al., 2009; Garbino et al., 2016). Such a scenario represents a threat to the black lion tamarin's persistence and accordingly it is classified as "Endangered" in the IUCN Red List (Rezende et al., 2020a). Due to a dependence on trees, species like the black lion tamarin are more likely to lose or suffer significant reductions in their ability to move across fragmented

landscapes, affecting population viability and ultimately the survival of the species (Lees and Peres, 2009).

Niche-based species distribution models that combine climatic and landscape variables can provide a realistic prediction of the habitat suitability and are pertinent for the definition of management actions tailored to the conservation of the black lion tamarin. In this regard, areas with high climatic and landscape suitability might be valuable for conservation planning, as these locations may be prioritized for the conservation of a focal species. Conversely, areas with high climatic and low landscape suitability could be beneficial for habitat restoration, as this may potentially increase the available environment for the species to occupy (Santos et al., 2020).

Here, we use both climate and landscape variables to predict, with greater precision, the potential distribution of the forest-dependent black lion tamarin, and we use this information to identify and prioritize strategic areas for the implementation of specific conservation actions for this flagship species.

2.5 METHODS

2.5.1 STUDY AREA

The potential distribution of the black lion tamarin encompasses three river basins – the Tietê, Paraná, and Paranapanema basins – which together comprise the original range of the species within the Brazilian state of Sao Paulo (Coimbra-Filho and Mittermeier, 1973; Garbino et al., 2016). To avoid biasing the model results due to a limited geographical space (Barve et al., 2011), we considered the whole area encompassed by these three river basins, ignoring political limits or putative geographic barriers for the species. Subsequently, as the landscape variables we used for the models were available only for the Atlantic Forest, we overlaid the river basin polygon with the boundaries of this ecosystem (*sensu* Muylaert et al., 2017), and used the areas common to both shapefiles as the geographical space mask for our models (see Figure 1 in Results; *Supplemental file S1* available at Rezende et al., 2020b).

In order to quantify the suitable areas for the species based on the models, we considered the limits of the black lion tamarin original distribution range, ignoring any

areas recovered as suitable by the models outside of these limits. The polygon that we used for this is an updated version of the IUCN polygon for the species (Rezende et al., 2020a), expanded to incorporate additional regions where there are confirmed occurrence records for the species but were not included in the original one (*Supplemental file S2* available at Rezende et al., 2020b).

2.5.2 CLIMATIC AND LANDSCAPE VARIABLES

We built climate and landscape niche-based models separately, to consider different scaled processes acting on black lion tamarin distribution (broad and narrow-scale ecological filters, respectively).

First, we constructed a climate-based model, to infer broad-scale processes acting on the species distribution. We used 19 bioclimatic variables, available in WorldClim database (www.worldclim.org) for the study area (see above), using a 1 km² cell-size resolution. Since climate variables are correlated with each other, we carried out a principal component analysis (PCA) to summarize the variation found in the set of climate variable and control for correlations among variables. We selected the first four axes of the climate ordinations (following DeMarco and Nóbrega, 2018) using the eigenvalues to build the models (see *Figure S1 in Supplemental files*).

We then used landscape metrics to infer narrow-scale processes acting on the species distribution. We used five landscape metrics as predictors across the study region: 1. forest cover percentage, 2. patch size, 3. edge distance, 4. slope, and 5. functional connectivity, operationalized as 180 m of matrix distance between fragments (assuming that this is the maximum distance that the black lion tamarin can travel outside a fragment, following Santos, 2016). All landscape metrics were calculated by the Spatial Ecology and Conservation Lab (LEEC/UNESP) and are similar to the ones used in Santos et al. (2020) for the entire Atlantic Forest. Together, they reflect the reliance of the species on forested areas, its dispersal capacity in fragmented landscapes, and whether the relief reflects potential geographical barriers. Following a similar procedure to that used in our climate-based models, we ran a PCA to reduce the effects of variable correlation and selected the first four axes of the landscape ordinations as variables to build the models (see *Figure S2 in Supplemental files*).

2.5.3 BLACK LION TAMARIN DATA SOURCES

In total, we used 45 presence records for black lion tamarin to build both climate and landscape models (see *Table S1 in Supplemental files*). To assemble this dataset, we initially gathered the occurrence records presented by Garbino et al. (2016), who reviewed all historical and recent black lion tamarin occurrence records. From the 40 records presented by those authors, we used 23 for building our dataset. One location (Mosquito farm) was excluded because it referred to a reintroduced population. Two additional locations (Fazenda Kitayama and Buri) were excluded because they correspond to extirpated populations occurring in fragments that are now entirely deforested and could therefore negatively influence the predictions of the landscape model. Nine records were excluded due to spatial correlation, as they were located within the same 1 km² cell-size resolution of other records. Finally, five historical records (from before 1905) were not included for three reasons: (i) available bioclimatic data is from 1960 to 1990; (ii) current landscape data does not consider past scenarios where fragmentation was less severe; (iii) the associated coordinates for those records lack sufficient accuracy on the scale of the spatial resolution used here, as they refer to broad localities registered on the label of the museum vouchers, and not to specific forest fragments such as the recent records.

After filtering, the 23 locations we used correspond to the centroid coordinates of the fragments given in Garbino et al. (2016) for records made between 1970 and 2014. As the latter authors assigned just one coordinate per fragment where the species is present, the model would interpret that large fragments have the same weight as small fragments for the occurrence of the species, where populations are even less likely to survive. To attenuate this effect, we included an additional 22 records of distinct black lion tamarin groups (to avoid spatial correlation) living in fragments that are larger than 1,000 hectares, which we gathered from the database of occurrence records of the Black Lion Tamarin Conservation Project (IPÊ).

2.5.4 GENERATING THE NICHE-BASED MODELS

We used the Ecological Niche Model (ENM) approach to test the effect of broad and narrow-scale processes on the black lion tamarin geographical distribution. Models were generated using the 'dismo', 'raster' and 'kernlab' packages in the

statistical programming software R, version 3.5.2 (Hijmans et al., 2015; Hijmans et al., 2017; Karatzoglou et al., 2019; R Core Team, 2019).

Initially, we generated two independent models. The first used only climate variables to predict the potential distribution of the species and the second used only landscape metrics. As the combined use of multiples algorithms increases the accuracy of predictions by considering different niche estimates (Araújo and New, 2007; Diniz-Filho et al., 2009), we used the seven following mathematical algorithms of presence only, presence and absence, and presence and background categorizations: i) Bioclim, ii) Gower, iii) Mahanalobis distance, iv) GAM, v) RandomForest, vi) SVM and vii) MaxEnt.

To evaluate the performance of the models, we randomly subdivided the occurrence records into a training dataset (consisting of 75% of the records) and a testing dataset (consisting of 25% of the records). We repeated this procedure 10 times, resulting in the construction of 70 climate-based models and 70 landscape-based models. For each model, we calculated the *maximum specificity and sensitivity* threshold (*Max Sens Spec*), following Liu et al. (2016), and ran the ensemble frequency method based on this same threshold value to binarize each model (0 - absence, 1 - presence), summing all models to obtain the frequency values for the species presence in each cell, with final values ranging from 0 to 1. We conducted these steps for the sets of climate and landscape-based models separately.

To predict the landscape effects on black lion tamarins' current distribution, we quantified the suitable areas according to the climate and the landscape variables, separately, within the species' original distribution area in the state of Sao Paulo. We used the approach of Peterson and colleagues (2011) that set the '10-percentile threshold' (10PT) as a decision threshold rule, which makes the distinction between suitable ($\geq 10PT$) and unsuitable ($< 10PT$) areas. Finally, we calculated the proportion of landscape suitable area within the climate suitable area to estimate the overall suitable area that was lost due to fragmentation.

To identify the strategic areas and designate appropriate management actions for each region, focused on the black lion tamarin conservation, we generated a scatterplot that combines climate and landscape suitability values, using the climate suitability values (X-axis) and the landscape suitability values (Y-axis). This plot, hereafter called EcoLand Analysis (*sensu* Silva et al., 2018; Santos et al., 2020), infers

which pixels within the study area have different combinations of either low (≤ 0.5) or high (> 0.5) climatic suitability and either low (≤ 0.5) or high (> 0.5) landscape suitability for black lion tamarin occurrence. Afterwards, the EcoLand plot was geographically mapped predicting each categorical situation to discuss the specific species management and conservation implications.

2.6 RESULTS

From the estimated original distribution range of the black lion tamarin (92,239 km²), the climate-based model suggested 14,124 km² as the most suitable areas (Table 1), distributed in the western and southeastern portions of the range (Figure 1). When compared to the climate-based model, the landscape niche-based models recovered fewer suitable areas (11,203 km²) for this forest-dependent species, and those areas coincide with regions of remaining forest (Figure 1; Table 1).

Table 1. Suitable areas (km²) for the black lion tamarin within its original distribution (92,239 km²), considering climate and landscape-based models, and their intersection. Threshold values are the 10th percentile presence threshold.

	Climate	Landscape	Intersection
Threshold value (10-percentile)	0.725	0.4125	-
Suitable area (km²)	14,124	11,203	2,096
% from total area	15%	12%	2%

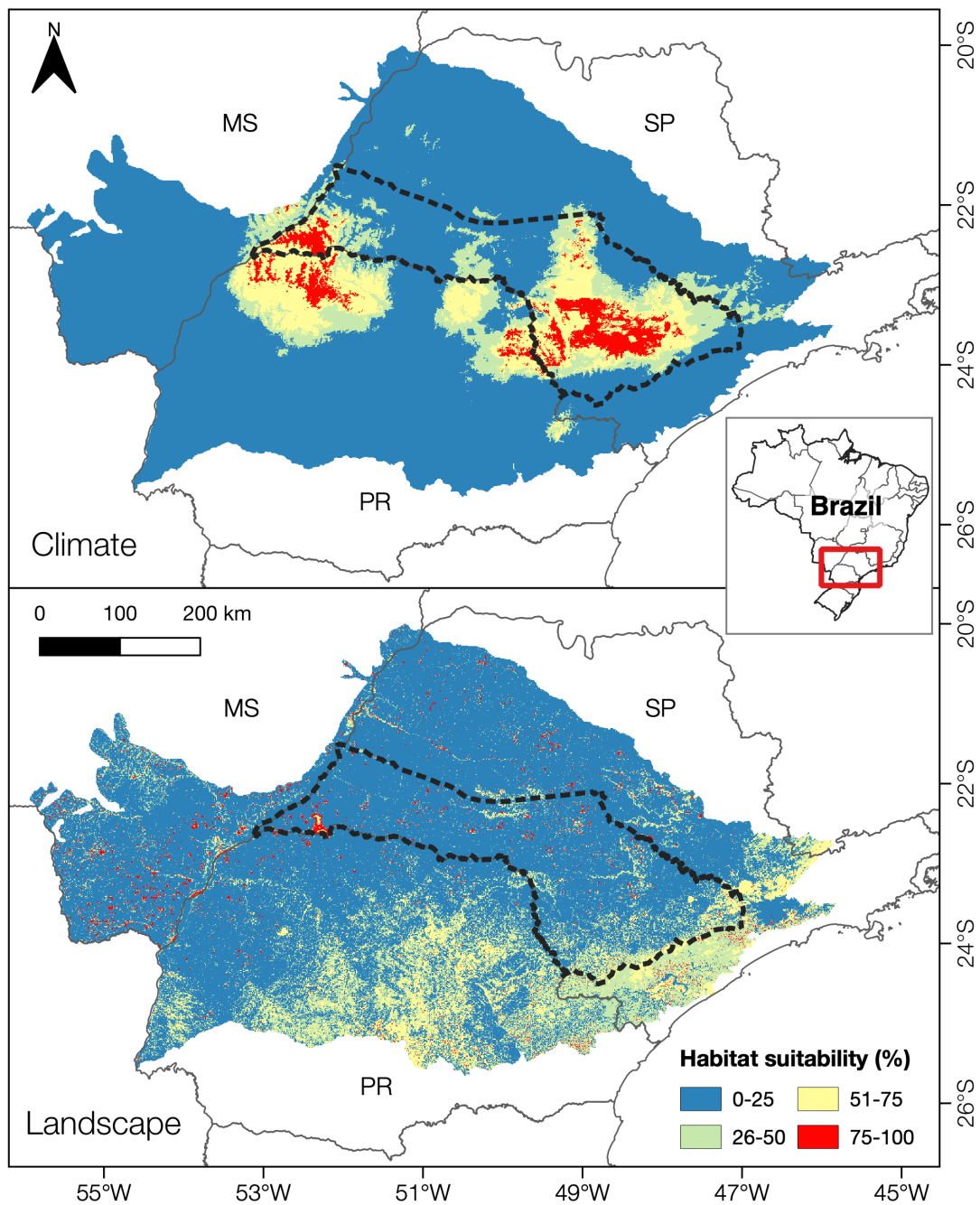


Figure 1. Ecological Niche Models based on the climate (above) and landscape (below) variables to predict the black lion tamarin distribution within the study area. The color zones indicate the variation in habitat suitability based on the variables used in each model. Dashed lines limit the original distribution of *Leontopithecus chrysopygus*.

When we compared the climate and landscape niche-based models, we found that only 2% of the total area (2,096 km²) can be considered suitable based on both climate and landscape, using the 10-percentile threshold for each model (Table 1). These results suggest that native forest loss has had a wide negative impact on the black lion tamarin distribution, corroborated by the 13% reduction of the climatically suitable area that is not currently suitable for landscape, as it has been deforested. On the other hand, there were some large fragments in the western portion of the study region, such as the Tucano farm (Garbino et al., 2016), that are recovered as highly suitable by both models, but where the species is now absent.

Our results also show that most of the areas considered as suitable by the landscape model are not indicated as such by the climate model (Figure 1). For example, the landscape-based model indicates higher suitability for the southeast region of São Paulo, in the densely forested mountain range of the Paranapiacaba Ecological Continuum (shown in yellow and green), while the same region has very low suitability according to the climate-based model (shown in blue) (Figure 1).

When we integrate the models in the EcoLand Analysis, the results indicate high climatic and landscape suitability in a few remaining forest areas in the western and south-eastern regions of the black lion tamarin's original distribution range (shown in red; Figure 2; *Supplemental file S3*). The detrimental effects of landscape modifications can be spotted as yellow pixels on the map, with an area more than twice the size of the ones in red. The EcoLand also retrieves a vast area (40,652 km²) with low climatic and landscape suitability (Figure 2).

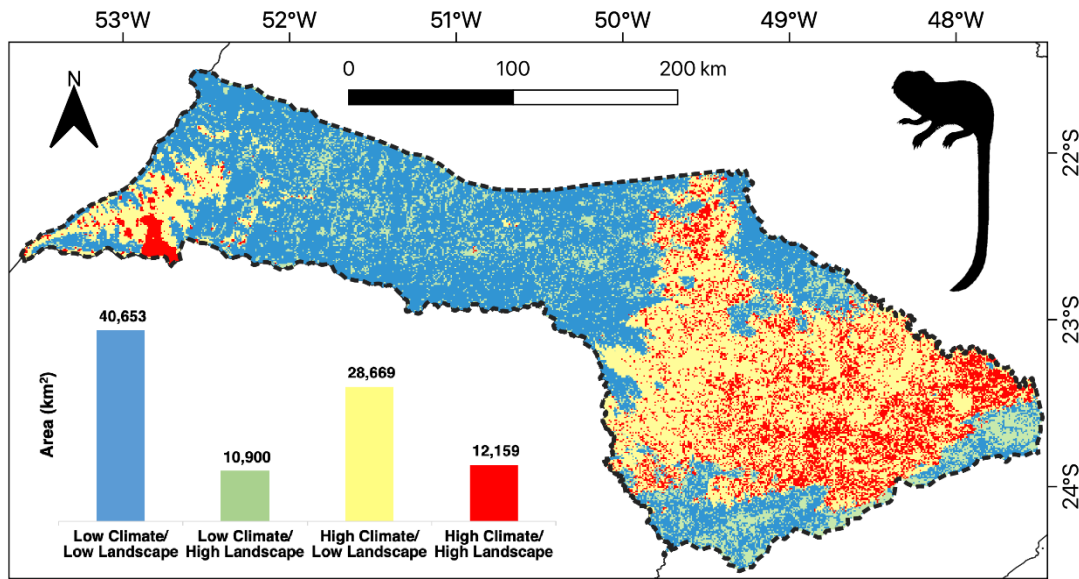


Figure 2. Habitat suitability for the occurrence of black lion tamarins within their original distribution range, predicted through the combined analysis of climatic and landscape variables (EcoLand map). Each color represents different combinations of values of climatic and landscape suitability. The graph presents the areas (in km²) for each of the four suitability zones.

2.7 DISCUSSION

Our results suggest that historic and current landscape modification has had an acutely negative impact on the distribution of the black lion tamarin. Although the models indicated just 2,096 km² of suitable areas for both climate and landscape, the species is currently present in less than 40% of this area, which represents less than 1% of its original distribution of over 90 thousand km² (G. C. Rezende, unpublished data). This finding highlights the pronounced effects of land-use change that threaten biodiversity, principally in highly human-impacted regions, such as the Atlantic Forest. We also show that when broad and narrow scaled processes are combined, a more accurate prediction of current species distributions is obtained.

Precise prediction of species distribution helps the implementation of more efficient management strategies and conservation actions. For instance, highly suitable sites predicted by both climate and landscape models should be considered as priority areas for the species conservation (e.g., those areas in red color in Figure 3), as they correspond to forest patches that have ideal climatic conditions and

dispersal accessibility for the species occurrence (Figure 3). Conservation strategies based on the EcoLand Analysis increase the likelihood that areas selected to be protected will hold black lion tamarin populations or represent the best areas to ensure their persistence in the short to medium term. The results are also pertinent for population management actions as the map may be used to select which forest fragments are more suitable for species (re) introductions, in a manner similar to that proposed for *Chelonoidis* tortoises by Sobral-Souza et al. (2017).

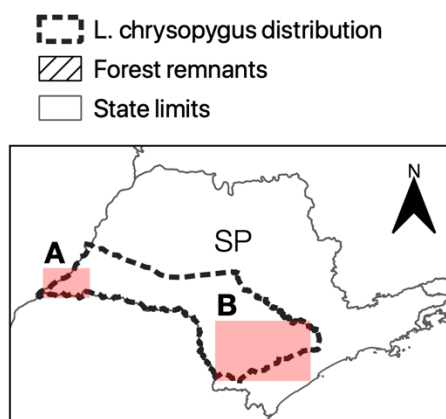
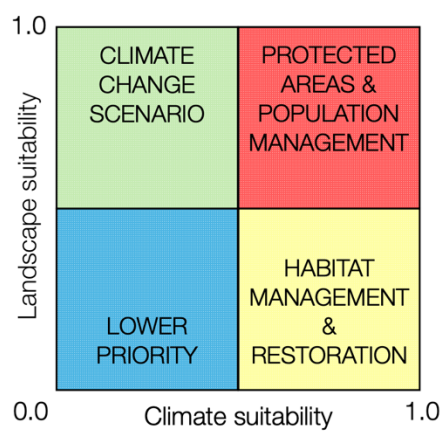
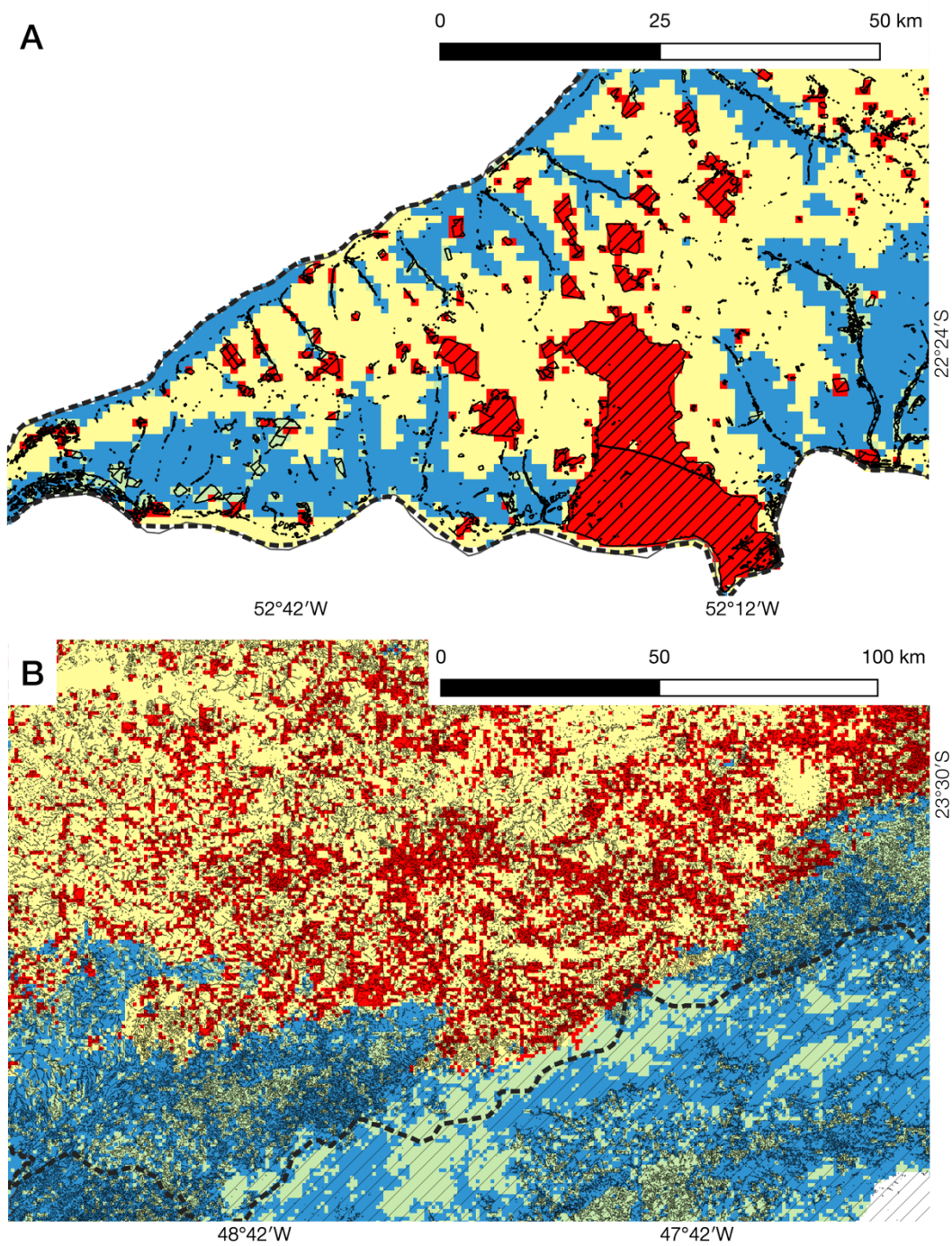


Figure 3. Priority areas and respective conservation strategies proposed for the black lion tamarin according to the results of the EcoLand map. A. The western region of São Paulo, one of the priority areas indicated by the model for the species conservation. Red pixels indicate priority areas for conservation and population management and overlap with the remaining forest fragments in the region. These areas are surrounded by yellow pixels, where habitat management and restoration are suggested. B. The southeast region of São Paulo, the other priority area for the black lion tamarin conservation. In addition to the strategies previously proposed for the areas in red and yellow, attention is called for the large forest remnants with low climatic suitability (green pixels), that should be considered in climate change scenarios.

Extensive areas with high climate suitability that show very low landscape suitability, i.e., areas with little forest cover (yellow), typically surround the areas with high climatic and landscape suitability (Figure 3). The recommended strategy for these areas is habitat restoration, particularly focusing on re-establishing the connectivity among the remaining habitat patches with the aim of increasing the available habitat for the black lion tamarin and its dispersal opportunities. This prioritization gains even greater relevance in scenarios in which ecological restoration actions necessitate a greater allocation of resources, which are often scarce for conservation (Polasky and Solow, 1999). By developing targeted species-based conservation actions, we bolster the chances of success with more cost-effective strategies. In this sense, the areas with very low climate and landscape suitability (blue) should have lower priority when devising such strategies.

Changes in the landscape (e.g., habitat restoration) and in the species occupancy due to management actions (e.g., reintroductions and translocations) can promote regional ecological changes that may require a reassessment of the models after their implementation. However, such changes may not promote macroecological impacts as intensely as those promoted by climate change. Under the climate change scenario described by Meyer et al. (2014), the black lion tamarin would lose most of the currently suitable habitat within its range as a result of the latitudinal shifts in temperature, which are projected to occur over the next 30–60 years. The most suitable area for the species within its distribution range would be in the south of the current records in the Paranapiacaba Ecological Continuum, in an area where the species is not known to currently occur. We assume that the ecological plasticity of the species will allow for some degree of adaptation, but areas with a reduced amount of

forest, such as the small fragments in the west, will seriously suffer the impacts of climate change. If such predictions materialize, then it may become imperative to carefully analyze the areas that currently show a high landscape but low climatic suitability (green), even though these are presently located outside the current distribution of the species, and consider such areas for future population management.

The management of populations through means such as reintroduction and translocation are typically considered to be short-term strategies, as the results can be seen relatively shortly after implementation. During urgent situations, population management must be given due consideration and especially if field studies indicate that the tamarins are affected by severe disturbances in their habitat due to climate or land use changes. Small primates, such as the black lion tamarin, will be particularly vulnerable to climate change, as they have limited dispersal capabilities that hamper range expansion to reach suitable climate refuges (Schloss et al., 2012).

Carvalho et al. (2019) quantified climate-related risks to changing climatic and land-use/cover conditions and suggested that Neotropical primates will be highly exposed to extreme warming events and that their habitats should thus be a major focus of conservation efforts. Constant evaluation of these changes together with predictions of shifts in the species distribution owing to climate change permits the establishment of an agenda for long-term conservation measures.

The present work provides explicit results that can be used as subsidies for planning conservation policies and actions for the black lion tamarin, increasing the chances of success of such measures.

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2.9 AUTHORS' CONTRIBUTION

CHAPTER CONTRIBUTORS: Thadeu Sobral-Souza, Laurence Culot

All authors contributed to the study's conception and design. Data preparation and analysis were performed by Gabriela C. Rezende. Thadeu Sobral-Souza ran the models. The first draft of the manuscript was written by Gabriela C. Rezende, and all authors commented on previous versions. All authors read and approved the final manuscript.

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2.11 SUPPLEMENTAL FILES

Table S1. Presence records of *Leontopithecus chrysopygus* used to build the models.

long_x	lat_y	local_ref
-52.26055556	-22.14888889	Fazenda Santa Monica_Garbino
-52.3075	-22.23833333	Fazenda Santa Maria I_Garbino
-49.68333333	-22.38333333	Estacao Ecologica dos Caetetus_Garbino_Passos
-49.691001	-22.412909	Estacao Ecologica dos Caetetus_PCMLP
-52.5018	-22.4153	Fazenda Ponte Branca_Garbino
-52.5102	-22.4259	Fazenda Ponte Branca_PCMLP
-52.46472222	-22.48611111	Fazenda Tucano_Garbino
-52.258	-22.5897	Parque Estadual do Morro do Diabo_PCMLP
-52.2044	-22.6497	Parque Estadual do Morro do Diabo_PCMLP_VP
-52.3488	-22.5077	Parque Estadual do Morro do Diabo_PCMLP_VP
-52.3215	-22.5235	Parque Estadual do Morro do Diabo_PCMLP
-52.3777	-22.5854	Parque Estadual do Morro do Diabo_PCMLP
-52.1772	-22.6203	Parque Estadual do Morro do Diabo_PCMLP
-52.332432	-22.474512	Parque Estadual do Morro do Diabo_KP
-52.384386	-22.406921	Parque Estadual do Morro do Diabo_KP
-52.356269	-22.570147	Parque Estadual do Morro do Diabo_KP
-52.324905	-22.497443	Parque Estadual do Morro do Diabo_KP
-52.290573	-22.592551	Parque Estadual do Morro do Diabo_KP
-52.342289	-22.430417	Parque Estadual do Morro do Diabo_KP
-52.313104	-22.535475	Parque Estadual do Morro do Diabo_KP
-52.33912	-22.558455	Parque Estadual do Morro do Diabo_KP
-52.210937	-22.59225	Parque Estadual do Morro do Diabo_KP
-52.407222	-22.529167	Fazenda Ribeirao Bonito_PCMLP2019
-49.0758	-22.7736	Lwarcel Borebi
-49.0219	-22.7614	Lwarcel Borebi_Garbino_Culot
-48.9	-22.78333333	Fazenda Rio Claro_Garbino_VPLC
-48.99465	-22.76116944	Fazenda Rio Claro_AS
-48.2423	-23.4169	Guarei_PCMLP_Camargo
-48.20301	-23.37508	Guarei_Garbino_Culot
-48.35	-23.4	Estacao Ecologica de Angatuba_Garbino_Medici
-48.57222222	-23.65194444	Fazenda Vale do Apiai_Garbino_Lima
-48.78388889	-23.66527778	Santa Maria_Garbino_PCMLP
-48.63805556	-23.70027778	Fazenda Floresta_Garbino_Lima
-48.65416667	-23.70916667	Riparian forest close to Buri_Garbino_Lima

long_x	lat_y	local_ref
-48.76944444	-23.74388889	Sao Jose_Garbino_PCMLP
-48.58833333	-23.78777778	Fazenda Urupes_Garbino_Lima
-48.54638889	-23.81638889	Bank of the Rio Apiai-Guacu_Garbino_
-48.57666667	-23.82111111	Riparian forest Apiai-Mirim and Apiai-Guacu_Garbino_Lima
-48.55972222	-23.83138889	Fernando Espanhol_Garbino_Lima
-48.58805556	-23.84138889	Olaria_Garbino_Lima
-48.66555556	-23.91638889	Taquarivai_Garbino_PCMLP_Culot
-48.54777778	-23.91666667	Fazenda Pezzoni_Garbino_Lima
-48.54583333	-23.92055556	Floresta Nacional Capao Bonito_Garbino_Lima
-47.6772	-23.8939	Fazenda Joao XXIII_Garbino_Rohe
-47.97472222	-24.05583333	Parque Estadual Carlos Botelho_Garbino_Rodrigues

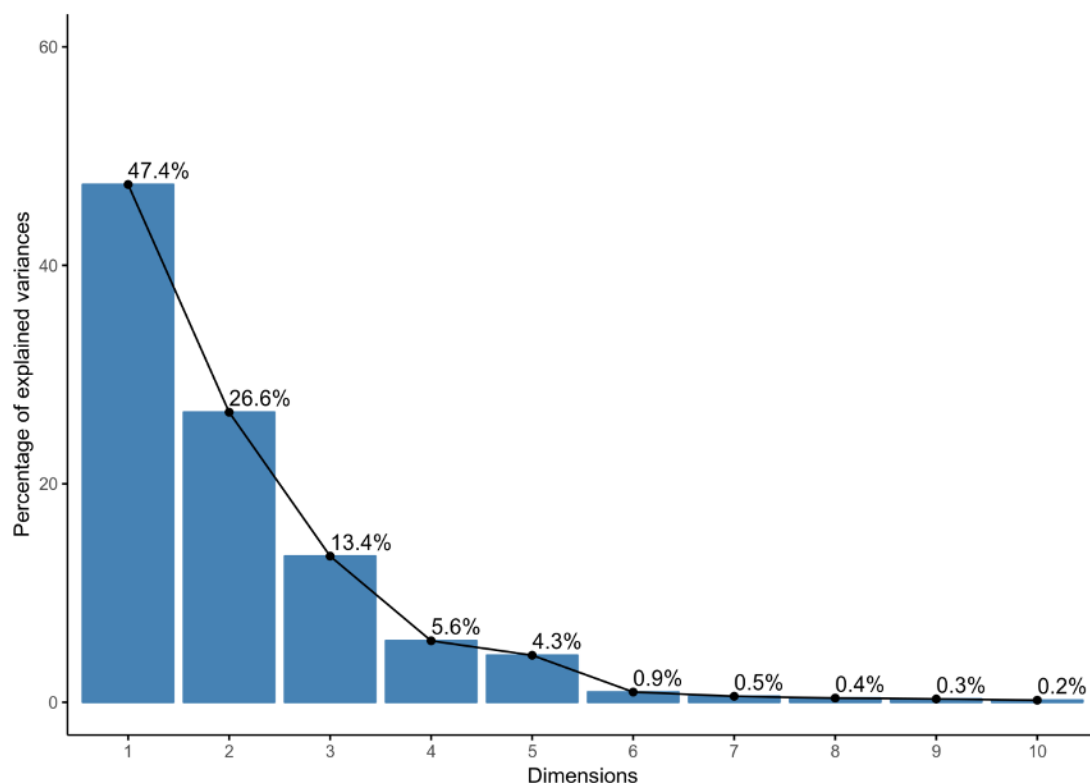


Figure S1. Climate PCA results. The first 4 axis explain approximately 95% of climate variation of the modeled area.

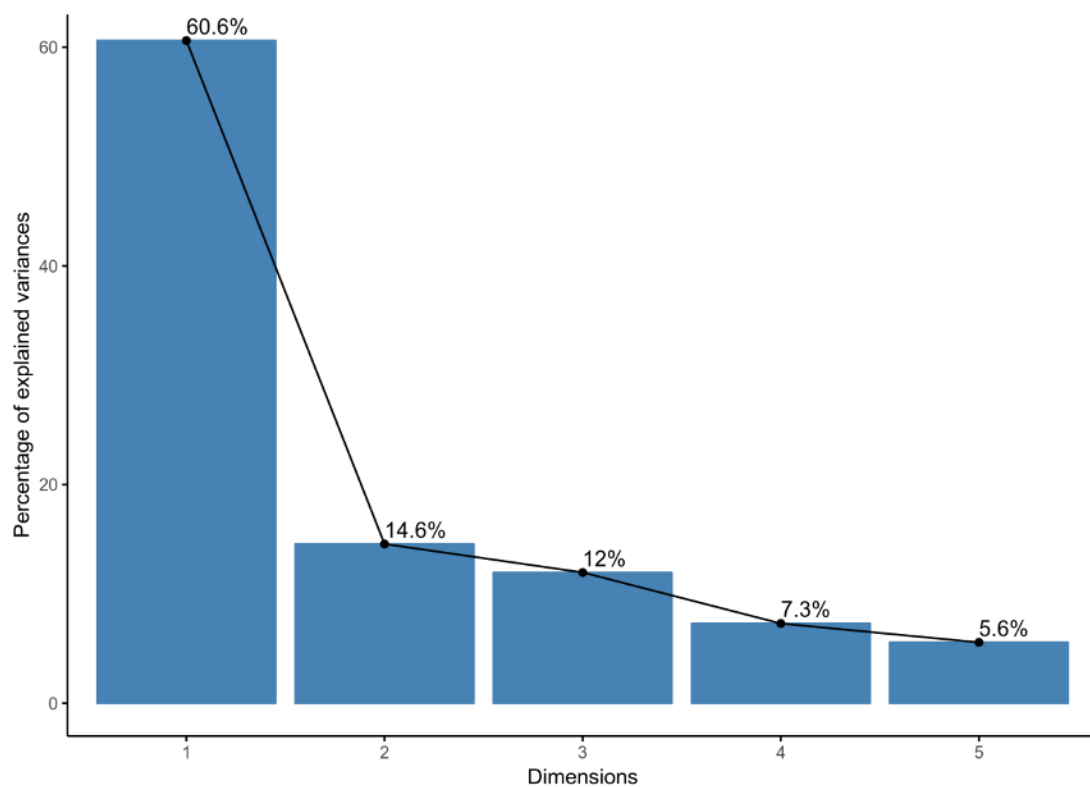


Figure S2. Landscape PCA results. The first 4 axis explain approximately 95% of landscape variation of the modeled area.

File S1. Shapefile of the mask for the modeled area, i.e., the delimitation of the geographical space used for the modeling. Available at <https://doi.org/10.17605/OSF.IO/MNV7R>

*File S2. Shapefile of the polygon of the distribution range of the black lion tamarin, *Leontopithecus chrysopygus*. Available at <https://doi.org/10.17605/OSF.IO/MNV7R>*

File S3. Raster file with the ensemble results of both climate and landscape models. Available at <https://doi.org/10.17605/OSF.IO/MNV7R>

3 CHAPTER II: VALIDATING DYNAMIC BODY ACCELERATION METRICS AS A MEASURE OF ENERGY EXPENDITURE IN BLACK LION TAMARINS

(Capítulo redigido em formato de manuscrito para submissão à revista *Journal of Animal Ecology*)

3.1 RESUMO

Título: Validando as métricas de aceleração dinâmica do corpo como medida de gasto energético em mico-leão-preto

Quantificar o gasto energético em primatas de vida livre é fundamentalmente importante, mas difícil de alcançar usando métodos padrão. Métricas baseadas em aceleração, como a Aceleração Dinâmica Corporal (DBA), obtida a partir de acelerômetros de origem animal, são um poderoso *proxy* para o gasto de energia, fornecendo medidas em escala fina sem precedentes, mas ainda não foram validadas em primatas. Aqui, validamos experimentalmente o método DBA em micos-leões-pretos (*Leontopithecus chrysopygus*) combinando o conhecido método da água duplamente marcada (DLW) com o método DBA em 10 micos-leões do Centro de Primatas do Rio de Janeiro. Em 2018, os indivíduos foram equipados durante 48 horas com uma mochila contendo um acelerômetro triaxial (peso total < 3% do peso corporal) e receberam uma injeção intraperitoneal de DLW no início do experimento, tendo uma amostra de sangue coletada no início e no final do experimento. Este último forneceu uma medida de Gasto Energético Diário médio de 326 kJ/dia (DP=66 kJ/dia), muito próximo dos valores esperados na literatura para primatas de seu porte. Os acelerômetros registraram em 40 Hz, coletando >6,9 milhões de registros por eixo para cada indivíduo. As métricas individuais de DBA foram calculadas e regredidas em relação às medidas diárias de energia vindas da DLW. A partir dessa regressão, encontramos uma relação linear consistente e significativa entre as duas métricas ($R^2 = 0,46$), que pode ser melhorada a partir da incorporação de informações de tempo de atividade e repouso ($R^2 = 0,52$). Nossos resultados fornecem as primeiras estimativas de taxa metabólica de campo para micos-leões-pretos. Também validamos o método de estimativa do gasto energético por meio de acelerômetros. Dado os níveis semelhantes de taxa metabólica de primatas em cativeiro e selvagens, este método agora pode ser usado no monitoramento de campo para estimar o custo energético do movimento do mico-leão-preto em seu ambiente natural.

PALAVRAS-CHAVE: experimento em cativeiro; ritmo diário; água duplamente marcada; *Leontopithecus chrysopygus*; VeDBA

3.2 ABSTRACT

Quantifying energetic expenditure in free-living primates is fundamentally important yet challenging to achieve using standard methods. Acceleration-based metrics such as Dynamic Body Acceleration (DBA), obtained from animal-borne accelerometers, are a powerful proxy for energy expenditure, providing unprecedentedly fine-scale measures, yet have not been validated in primates. Here, we experimentally validated the DBA method in black lion tamarins (*Leontopithecus chrysopygus*) by combining the well-known doubly labelled water (DLW) method with the DBA method on 10 tamarins housed at the Rio de Janeiro Primate Centre. In 2018, individuals were equipped over 48 hours with a backpack with a tri-axial accelerometer (total weight < 3% body weight) and received a DLW intra-peritoneal injection at the beginning of the experiment, with a blood sample taken at the beginning and end of the experiment. The latter provided a mean Daily Energy Expenditure measure of 326 kJ/day (SD=66 kJ/day), closely in agreement with expected values in the literature for primates of their size. The accelerometers recorded at 40 Hz, collecting >6.9 million records per axis for each individual. Individual DBA metrics were calculated and regressed against DLW daily energy measures. From this regression, we found a consistent and significant linear DLW/DBA relationship ($R^2 = 0.46$), which could be improved by the incorporation of activity and resting time information ($R^2 = 0.52$). Our results provide the first estimates of field metabolic rate for black lion tamarins. We also validated the method of estimating energy expenditure through accelerometers. Given the similar levels of metabolic rate of captive and wild primates, this method can now be used in field monitoring to estimate the energy cost of black lion tamarin movement in its natural environment.

KEYWORDS: captivity experiment; daily rhythm; doubly labelled water; *Leontopithecus chrysopygus*; VeDBA

3.3 INTRODUCTION

Quantifying energy expenditure in wild animals is fundamentally important in ecological research, with a range of applications in movement and behavioural ecology (e.g., Jeanniard-du-Dot et al., 2017b; Mathot et al., 2019), life history studies (e.g., Jørgensen et al., 2016), including for understanding the mechanisms underlying population dynamics (e.g., Andersen & MacMahon, 1981; Wearmouth et al., 2012) or responses to environmental change, including climate change (e.g., Fuller et al., 2016; Norin & Metcalfe, 2019). However, quantifying energy expenditure of free-living animals is a challenging task to achieve using standard methods, which rely on invasive techniques (Butler et al., 2004), or methods that are impractical in the field, such as oxygen chambers or treadmills (Pagano et al., 2018). A breakthrough was achieved by using the doubly labelled water method (DLW; Speakman, 1997), which allows to estimate average daily energy expenditure of free-living animals. Whilst the DLW method has been used on a large range of species, it provides only a measure of average daily expenditure and does not allow a decomposition into the contributing parts at shorter time scales, such as different behavioural activities (e.g., running vs. walking).

Acceleration-based metrics such as Dynamic Body Acceleration (DBA), obtained from animal-borne accelerometers, are a powerful proxy for assessing fine-scale energy expenditure of free-living animals (Wilson et al., 2020). This method was first proposed in a study with humans (Meijer et al., 1989; Montoye et al., 1983), and tested in animals two decades later, by validating the DBA-derived measures against laboratory-derived measures, such as from treadmills and oxygen chambers (Pagano et al., 2018; Wilson et al., 2006). Since then, DBA has been applied to predict costs of movement for a wide variety of species (Halsey et al., 2009; Wilson et al., 2020) – e.g., teleost fishes (Wright et al., 2014), cane toads (Halsey & White, 2010), cormorants (Laich et al., 2011; Stothart et al., 2016; Wilson et al., 2006), penguins (Hicks et al., 2020), hawks (Van Walsum et al., 2020), polar bears (Pagano & Williams, 2019), seals (Jeanniard-du-Dot et al., 2017a, 2017b), and canids (Tatler et al., 2021).

The total daily energy spent by an endothermic animal (birds and mammals) is the sum of the energy expenditure used for the maintenance of bodily functions (basal metabolic rate; Mathot & Dingemanse, 2015), for digestion (specific dynamic action;

Hawkins et al., 1997), for thermoregulation at temperatures below the lower critical limit of the thermoneutral zone (thermoregulatory thermogenesis; Scholander et al., 1950), for somatic production (such as growth and reproduction; Karasov, 1992), and for general patterns of activity, such as locomotion or movement (Christian et al., 1997). The costs of each of these components, especially those associated with basal metabolic rate, specific dynamic action and thermoregulation have been widely measured using the standard technique of indirect calorimetry, mostly by inferring heat production from measurements of gas exchange (Lighton, 2008). Although respirometry measurements have a long tradition of at least 200 years, this technique requires the confinement of the animal to a chamber or the use of oxygen masks, impractical for free-ranging animals, thus precluding energy quantification as the animals go about their daily routines.

The use of isotopes, such as DLW, circumvents some of the problems associated with respirometry (Carlson & Moreno, 1992). These techniques are based on the fact that animal bodies are in a constant flux of nutrients and resources, with substances being incorporated and eliminated at different rates. Thus, if the rate of elimination of a given substance is proportional to the metabolic rate, then this isotope technique allows for the measurement of the overall energy expenditure of free-ranging animals based on the rate of elimination of that substance (Bradshaw, 2003). Several isotopes have been used for this purpose, but the DLW technique that uses isotopes of oxygen (^{18}O) and hydrogen (^2H or ^3H) is by far the most common method used to measure overall energy expenditure of free-ranging animals (Speakman, 1997). However, this method has some limitations that may hinder its application in wild animals, for being invasive and requiring recapturing of the same individuals after a very short period (often after 24 to 48 hours), which is not always feasible in the field. Furthermore, it can only provide measures of average daily energy expenditure.

Recently, acceleration-based metrics such as Dynamic Body Acceleration (DBA), obtained from animal-borne accelerometers, have been used to measure rates of energy expenditure of free-ranging animals (reviewed in Wilson et al., 2020). The reliability of this technique to trace rates of energy expenditure has been validated against standard respirometry methods (Enstipp et al., 2011, 2016; Ladds et al., 2017; Wright et al., 2014) and against the DLW method (Dalton et al., 2014; Elliott et al., 2012; Hicks et al., 2020; Jeanniard-du-Dot et al., 2017a, 2017b; Pagano & Williams,

2019; Stothart et al., 2016; Sutton et al., 2021). Although validation against these two methods attested for the reliability of the DBA as an indirect metric to assess total rates of energy expenditure, it should be noted that when validated against DLW, the reliability tends to be lower. This is because DLW measures the total energy spent by the animal during the monitoring period, while DBA measurements reflect only the costs associated with active movements, i.e., muscular activity, such as locomotion, movement and, perhaps, the work associated with shivering thermogenesis. In this sense, the DBA method is relevant for use in animals where the dynamic part (Wilson et al., 2020), i.e., movement, is a relevant component of the total daily energy spent, and where animal-attached devices are manageable in the field.

Here we aim to validate the DBA method for estimating energetic expenditure in primates, using black lion tamarins (*Leontopithecus chrysopygus*) as our study species. Black lion tamarins are endangered small monkeys (less than 800 g), that live in small family groups of two to eight individuals, and move about in quadrupedal walking and leaps through the forest canopy as they forage for fruit and animal prey (G. C. Rezende et al., 2020). Due to their dependence on trees, they can be affected by changes in forest structure due to habitat fragmentation and degradation, such as occurring in the Brazilian Atlantic Forest, their native habitat (Ribeiro et al., 2009). Such habitat changes directly alter resource availability and distribution, which are mainly responsible for primate movement decisions (Trapanese et al., 2019). Thus, estimating movement costs can provide key information for the design of conservation actions, such as evaluating effects of forest fragmentation and planning forest corridors based on a forest structure that benefits tamarins' movements.

Given that energy expenditure measured on free-living primates remains comparable with primates in captivity (Pontzer et al., 2014), we could do a more controlled and less invasive experiment with captive tamarins. We used the standard procedure of combining the DLW method (Speakman & Racey, 1988; Speakman & Hambly, 2016) with the DBA method (reviewed in Wilson et al., 2006) simultaneously on the same individuals, and regressing DBA estimates against the DLW ones. Once validated, we used the fine-scale information from the accelerometer data to determine the daily rhythm (day and night phases) and the fine-scale activity and resting patterns within each phase. Then, we used the latter to decompose the observed daily energy expenditure rates (based on dynamic acceleration) into the contributions of day/night

phases and activity/resting behaviours in black lion tamarins to assess individual variability and improve the DLW/DBA energy rates relationship.

3.4 OBJECTIVES

- I. Validate the DBA method for estimating the fine-scale, behaviour-based energetic expenditure of black lion tamarin movements.
- II. Determine the daily rhythm and the fine-scale activity and resting patterns within each daily phase.
- III. Quantify the contribution of activity and resting behaviours to the daily energy spent by black lion tamarins and assess inter-individual variability.

3.5 METHODS

3.5.1 *EX SITU* EXPERIMENT WITH ACCELEROMETERS AND DLW

To validate the use of animal-attached sensor activity metrics to estimate energy expenditure in black lion tamarins in its natural environment, we conducted a study on captive animals at the Rio de Janeiro Primate Centre (Guapimirim, RJ, Brazil). Working in controlled environments with confined animals allows for more precise data collection and reduces the impact of multiple captures on wild animals.

In March 2018, ten healthy, adult black lion tamarins (eight males and two nonpregnant, nonlactating females, age 1.5 to 16 years old, weight 520-690 g; Table A1 in Appendix), were equipped for over 48 hours with “Daily Diaries” (DD) biologging units (Williams et al., 2020; R. Wilson et al., 2008). These units contain tri-axial accelerometer (providing information on posture and movement, and DBA measures) and magnetometer (providing orientation to magnetic north) sensors, and environmental temperature and pressure sensors (the latter providing information on altitudinal movements), recording at a range (40 – 4 Hz) of sub-second frequencies (Table 1). In particular, the accelerometer data provided the individual DBA metrics used as proxy for energy expenditure (Wilson et al., 2020).

Table 1. A list of variables the Daily Diary (DD) collected with corresponding recording frequency, units' measurement, and range.

Channel	Recording frequency (Hz)	Measurement
Accelerometer X axis Sway (Side – Side)	40	0 to 6 g
Accelerometer Y axis Surge (Forward – Backward)	40	0 to 6 g
Accelerometer Z axis Heave (Upward – Downward)	40	0 to 6 g
Magnetometer axis 1	16	Max. of earth's magnetic field
Magnetometer axis 2	16	Max. of earth's magnetic field
Magnetometer axis 3	16	Max. of earth's magnetic field
Barometric pressure	4	100 to 2000 mbar
External Temperature	4	-20 to 60°C

The device was attached to the animal using a backpack-style harness made of nylon cord holding a plastic housing (Figure 1) containing the DD circuit board powered by a 3.7V 123 mAh rechargeable lithium battery. The shape and size of the devices used were developed specifically for lion tamarins, considering its weight, ergonomics, and anatomy restrictions (Figure 1), and based on models currently in use by field projects with similar species (Savage et al., 1993). Each tag was colour-coded externally to allow visual individual identification during the experiment (Figure 1). The total weight of the backpack was 18 g, making up 2.6-3.5% of the animals' body mass (500-700 g) staying within the '5% rule' ethical guidelines for mammals (Sikes & Gannon, 2011; Wilson et al., 1996).



Figure 1. Daily Diaries used on the black lion tamarins at Rio de Janeiro Primate Centre (CPRJ) (left). Two black lion tamarins with the daily diaries on their backs, at CPRJ, Guapimirim, RJ, Brazil (right).

Immediately before attaching the DD, each individual was weighted (Pesola® 1000 g, d = 10 g) and subsequently injected intra-peritoneally with 0.4 to 0.53 ml (depending on body mass) of a water solution enriched with 65% of ^{18}O and 35% of ^2H . Based on the enrichment level of the amount of water injected and the body mass (Speakman 1997), a 2-3-hour period was allowed for the injected solution to equilibrate with the body water pool. After this period, a blood sample was taken from the femoral vein into capillary tubes, which were flame sealed and stored at 2-4°C before being sent to analysis. Soon after this initial blood sampling, individuals were returned to their respective enclosures (3.0 x 6.0 x 2.5 m), where they were free to move and develop their usual behaviours. Two days later, individuals were removed from their outdoor cages, had their body mass measured again, and a second blood sample was taken and processed in a similar way as the first bleeding procedure.

The blood samples were analysed by the DLW Resource Centre, at the Zoology Department in the University of Aberdeen (Scotland) following Westerterp (2017) to estimate the elimination rates of ^{18}O (ko) and ^2H (kd). The isotopic dilution space was estimated from ^{18}O , and is equivalent to the total body water pool, expressed as a percentage of the body mass prior to injection. Using these data, the amount of CO_2 produced (VCO_2) was calculated and averaged on a daily basis (mlCO_2/day). Since the initial blood sampling was taken right after the equilibrium period, the Plateau method was used to calculate VCO_2 , following equation 7.17 of Speakman (1997; see also Speakman & Król, 2005). We also tested the Intercept method and used three

different equations for each method to get daily energy expenditure (DEE) values (Estimate 1 = equation 35 *sensu* Lifson & McClintock, 1966; Estimate 9 = equation 7.17 *sensu* Speakman, 1997; and Estimate 4 = equation A6 *sensu* Schoeller et al., 1986, modified by Schoeller, 1988; Table A1 in Appendix), which provided very similar and highly correlated estimates (Figure A1 in Appendix). Thus, for further analysis we used the results obtained from Estimate 9 Plateau, which is considered the most appropriate estimate for small mammals. Finally, a respiratory quotient of 0.8 was used to calculate the total DEE (in kJ/day) from VCO_2 (Speakman 1997). This value of DEE was then later compared with the data from the DD to validate the use of DBA as a measurement of energy expenditure.

3.5.2 ACCELEROMETER DATA PROCESSING AND DBA ESTIMATION

Data management, visualisation, and analysis of the Daily Diary biologging data was done using the specialised software Daily Diary Multiple Trace Graphing Tool (DDMT; Wildbyte Technologies Ltd., Swansea, UK). The programme produces interpolated time-based plots to show how acceleration and other channels change over time at high resolution (Figure 2) and allows to quickly subset the data, calculate DBA and other derived metrics, and identify different behavioural phases using the Boolean time-based decision-tree template method (Wilson et al., 2018).

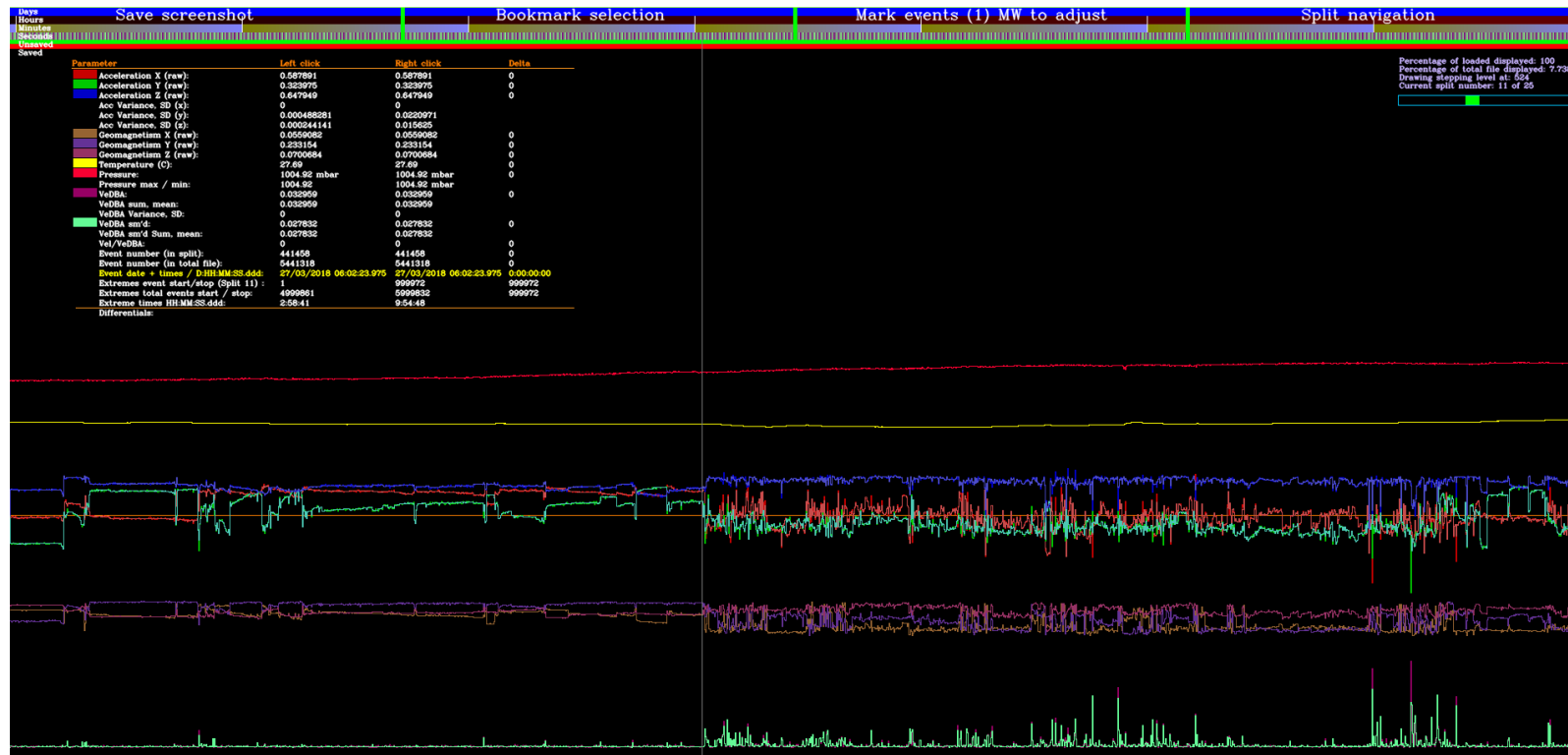


Figure 2. Screenshot of the Daily Diary Multiple Trace Graphing Tool (DDMT) software, used to manage, visualise, inspect and subset the data, and obtain the DBA metrics. On this screen, seven hours (from 3am to 10am) of data collected by each of the eight channels from individual BLT05 is shown, from top to bottom: pressure (red line), temperature (yellow line), tri-axial accelerometer (blue, red, and green lines), tri-axial magnetometer (purple, pink, and orange lines). The bottom line (cyan) is the smoothed Vectorial Dynamic Body Acceleration (sVeDBA) derived from the accelerometer data. The table (top left) show values of selected records for each channel. The vertical white line in the centre shows the exact time when the individual changed from inactivity to activity periods.

For the analyses, we considered the data collected whenever the animal was free to move on its own in the enclosure, but not including the time when the animal was being hold or manipulated, as this would otherwise directly influence the accelerometer records. This interval coincided with the same time interval between the two blood samples taken for the DLW estimate, assuring full comparability. From the acceleration data, an activity metric called Vectoral Dynamic Body Acceleration (VeDBA) was calculated using DDMT via the following equation:

$$VeDBA = \sqrt{(DBAX)^2 + (DBAY)^2 + (DBAZ)^2} \quad (Eq.1)$$

where DBA is the dynamic body acceleration in three dimensions: X or sway (side to side), Y or surge (back and forth) and Z or heave (up and down). Dynamic acceleration is calculated for each record by subtracting the static from the raw acceleration, to obtain a measure that reflects only active movements, using a 2 second moving average window (i.e., 80 records at 40 Hz), centred on each record, to estimate the static acceleration signal (Wilson et al., 2020).

To reduce the noise in the metric, we applied a running mean across 200 data points (5 seconds) to produce smoothed VeDBA (sVeDBA). Other DBA metrics derived from the acceleration data, such as Overall Dynamic Body Acceleration (ODBA) and smoothed ODBA, were also used (Wilson et al., 2020) but, since these metrics were highly correlated (see Figure A1 in Appendix), we focused our analyses on sVeDBA.

3.5.3 DAILY RHYTHM PHASES: THE DISTINCTION BETWEEN DAY AND NIGHT PHASES AND ACTIVE AND INACTIVE BEHAVIOURS

Further analysis on the accelerometer data was carried out to identify active or inactive phases (Figure 3). As the sensor is very sensitive to even small movements of the animal, reflected in higher values of g , differences in the signal between inactivity and activity are generally very clear (E. Shepard et al., 2008), being at very low g values during inactivity and markedly larger and usually more variable when the animal is active (Figure 3).

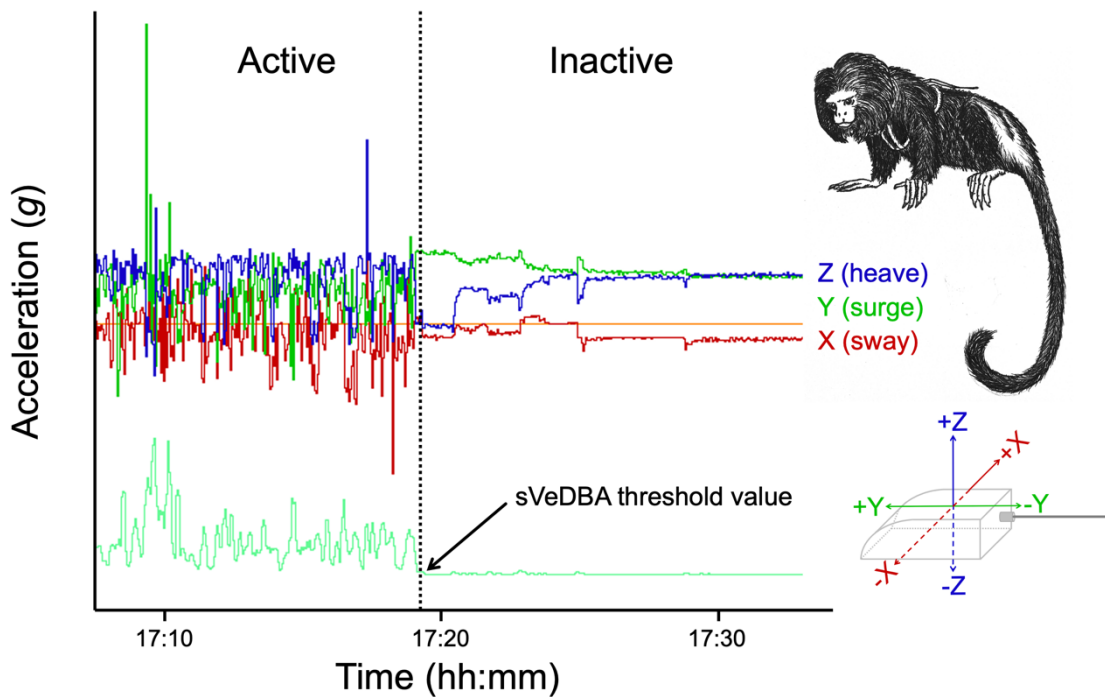


Figure 3. Patterns observed on the accelerometer vectors (red, green, and blue lines) and smoothed Vectorial Dynamic Body Acceleration (sVeDBA; cyan line) when the black lion tamarins (top-right) are active or inactive. The vertical dotted line indicates the exact time where the transition to the inactivity (night) phase happened, which coincides with sVeDBA values below the threshold chosen here to identify resting behaviour (indicated by the arrow). The orange line corresponds to acceleration = 0. The three axes shown on the device (bottom-right) indicate the respective vectors when the tamarin is in this horizontal position. Tamarin illustrator: Gustavo Libardi.

To determine the daily rhythm of each individual and identify activity (day) and inactivity (night) cycles, we visually inspected the data to find start and end of activity hours based on a threshold value of sVeDBA. To define this threshold value that would represent a change between activity and inactivity (Figure 3), initially we exported the sVeDBA values for each record over the monitoring period and subdivided this data into day and night phases based on the civil twilight times for that day in Guapimirim, RJ (05h36 to 18h19). Then we run descriptive statistics (mean, median, and quartiles) for each dataset corresponding to the night phase for the ten black lion tamarins. Based on the third quartile values of sVeDBA, we defined the threshold value that would correspond to the highest value to describe inactivity ($\text{sVeDBA} < 0.04$).

Using DDMT, we marked the data points based on this threshold value, with all data points with a sVeDBA value lower than the threshold considered as 'inactive', and higher as 'active'. From the length of these bouts, we could clearly identify the transition

times between active and inactive phases as whenever the activity records were longer than the inactivity ones (Figure 4). The opposite criterion was used for the start of the inactive phase. Based on these times, we subdivided the data into these two phases of the daily rhythm, which here were named as “DAY” and “NIGHT” phases, respectively. This way we could estimate the length of each phase of the daily rhythm for each individual, and the proportion of time that they spent on each day/night phase.

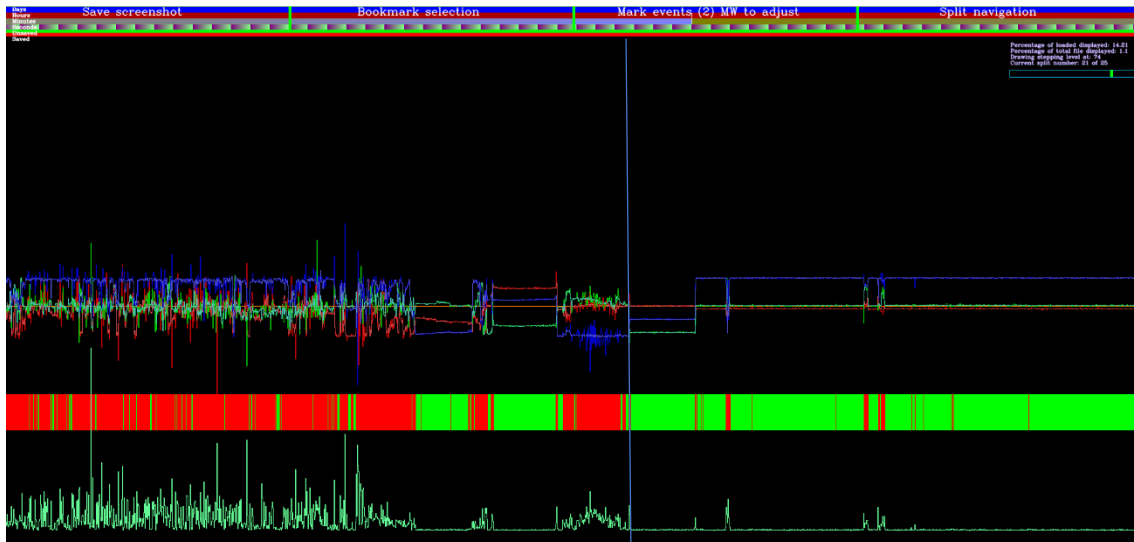


Figure 4. Screenshot of the Daily Diary Multiple Trace Graphing Tool (DDMT) software showing tri-axial accelerometer data (blue, green, and red lines) and derived smoothed Vectorial Dynamic Body Acceleration (sVeDBA) whose values were used to mark behaviour based on a threshold value for inactivity ($sVeDBA < 0.04$). Behaviours marked in red show activity, while the ones marked in green show inactivity. The transition between day and night phases was identified whenever there was a consistent change of activity pattern, i.e., when the length of green bars was longer than the red ones, indicated by the vertical white line.

In addition to the simple rule to separate the active daytime and the inactive nighttime, we defined two supplementary rules to identify fine-scale changes between active and inactive behaviours within each of the day and night time phases (e.g., short bouts of posture change during sleep, or resting bouts during the day), using time-based behaviour identification rules (Wilson et al., 2018). To clearly decipher between inactive resting periods (rather than pauses) during the DAY, the animal had to be defined as inactive by the sVeDBA threshold (<0.04) for a minimum interval of a minute (2400 records) – listed as Rule 1, or daytime resting behaviour. This was then repeated to ensure the species was active during the NIGHT, also avoiding flinching and other instantaneous active behaviours, using the same threshold value to define activity

(sVeDBA > 0.04 for over a minute) – named Rule 2, or nighttime activity behaviour. On DDMT, we marked all records following these rules, applying Rule 1 for the DAY phase (1-marked records are resting, 0-marked are active) and Rule 2 for the NIGHT phase (0-marked records are resting, 1-marked are active).

After marking the behaviours, we could create six subsets of data that would include all (T), resting (R), and activity (A) events, in each phase of the daily rhythm (DAY vs. NIGHT): T_{DAY}, R_{DAY}, A_{DAY}, T_{NIGHT}, R_{NIGHT}, and A_{NIGHT}, respectively.

3.5.4 ENERGY EXPENDITURE ESTIMATES

To calculate DBA-based daily energy estimates, we summed the sVeDBA values for each record during the length of the experiment (~48 h), generating a total sVeDBA, and estimated the daily sVeDBA proportionally to a 24-hour period. This is the same approach hence, over the same time period, as used to obtain the Daily Energy Expenditure estimates from the DLW data. These daily sVeDBA values for each tamarin were regressed against the DLW daily energy measures (DEE) to validate the former (“stats” package, R Core Team, 2022). Standard residual diagnostic checks were applied and fit was evaluated using R^2 metrics (Elliott et al., 2012; Stothart et al., 2016). Since we used sVeDBA values to run all the previous analyses, and this metric is highly correlated to the other DBA metrics, i.e., VeDBA, ODBA and sODBA (Wilson et al., 2020) (see Figure A1 in Appendix), we chose to use sVeDBA (*sensu* Stothart et al., 2016) for validating the DD energy expenditure estimates against the DLW ones.

We also checked the impact that collecting accelerometer data at a different frequency would have on the regression using 20Hz datasets (as lower frequency – 25Hz was used for the wild animals, see next chapters). For this, we subsampled the dataset collected at 40Hz, taking only the even or odd lines to simulate a dataset collected at 20Hz and, again, regressed these DBA values against the DLW daily energy measures.

Subsequently, to improve the relationship between DBA and DLW estimates, we quantified the contribution of activity and resting behaviours to the daily energy spent by the black lion tamarins. For this, we estimated total and daily sVeDBA, and associated time lengths, for each day/night phase and active/inactive behaviour. We

summed the sVeDBA values of the records within each subset and adjusted it proportionally to the time length of each. Based on these sVeDBA values partitioned in different behaviours and their respective time length, we used an approach similar to described by Jeanniard-du-Dot et al. (2017a) to estimate behaviour-specific energy expenditure. For this, we fit the following model for all our tamarins to obtain the parameter estimates for each behaviour (a, b, c and d):

$$EE = a \times T_{A_day} + b \times T_{R_day} + c \times T_{R_night} + d \times T_{A_night} \quad (Eq.2)$$

where:

EE = total energy spent during the experiment

a, b, c, d = rate of energy expenditure for each behaviour

T_i = Time spent in each behaviour

All analyses were done using the software DDMT, R 4.0.2 (R Core Team, 2020) and R Studio 1.3.1073 (RStudio Team, 2020).

3.6 RESULTS

3.6.1 VALIDATION OF DBA METRICS

The results from the DLW blood samples analysis provided a mean Daily Energy Expenditure measure of 353.5 kJ/day (SD=73.8 kJ/day, or 84.5 ± 17.6 kcal/day), with the lowest values obtained from the two females (

Table 2). We did not observe a direct association between body mass and variation in energy expenditure ($R^2 = 0.27$, $p > 0.05$). The analysis of the Daily Diaries data provided a mean daily sVeDBA of 279,706.2 g (SD=58,747.4 g), with no differences associated to the sex or weight of the individuals (

Table 2). We found a consistent and significant linear relationship between sVeDBA and DEE values ($F_{1,8} = 6.739$, $R^2 = 0.46$, $p = 0.03$; Figure 5). DEE values (in kJ/day) increased by 0.00085 kJ for each g of DBA, according to the following equation:

$$DEE = ((115.8 \pm 93.4) + (0.00085 \pm 0.000327) * sVeDBA) \quad (Eq.3)$$

Table 2. Daily energy expenditure (DEE) in kJ and kcal per day and Daily smoothed Vectorial Dynamic Body Acceleration (sVeDBA) in acceleration units (g) for each black lion tamarin (ID). The values of mean body mass (BM) in kilograms (kg), consider the tamarins' weights at the beginning and at the end of the experiment. The mean and standard deviation (SD) values for each variable, considering all animals of the experiment (All), the females (F) and the males (M), are presented on the last three rows, respectively.

ID	Sex	Mean BM (kg)	DEE (kJ/day)	DEE (kcal/day)	Daily sVeDBA (g)
BLT01	M	0.5225	375.7	89.8	324,023.50
BLT02	F	0.5125	194.3	46.4	200,697.50
BLT03	M	0.6725	352.3	84.2	248,294.60
BLT04	M	0.6075	396.6	94.8	357,749.60
BLT05	M	0.6525	367.6	87.9	200,531.50
BLT06	F	0.5325	275.3	65.8	270,877.30
BLT07	M	0.5950	408.9	97.7	291,076.10
BLT08	M	0.6000	417.4	99.8	361,334.90
BLT09	M	0.5975	313.6	75.0	237,620.60
BLT10	M	0.6000	432.9	103.5	309,007.80
MEAN ±SD	All	0.5893 ±0.0529	353.5 ±73.8	84.5 ±17.6	280,121.3 ±58,737.7
	F	0.5225 ±0.0141	234.8 ±57.3	56.1 ±13.7	235,787.4 ±49,624.6
	M	0.6059 ±0.0444	383.1 ±38.9	91.6 ±9.3	291,204.8 ±58,155.8

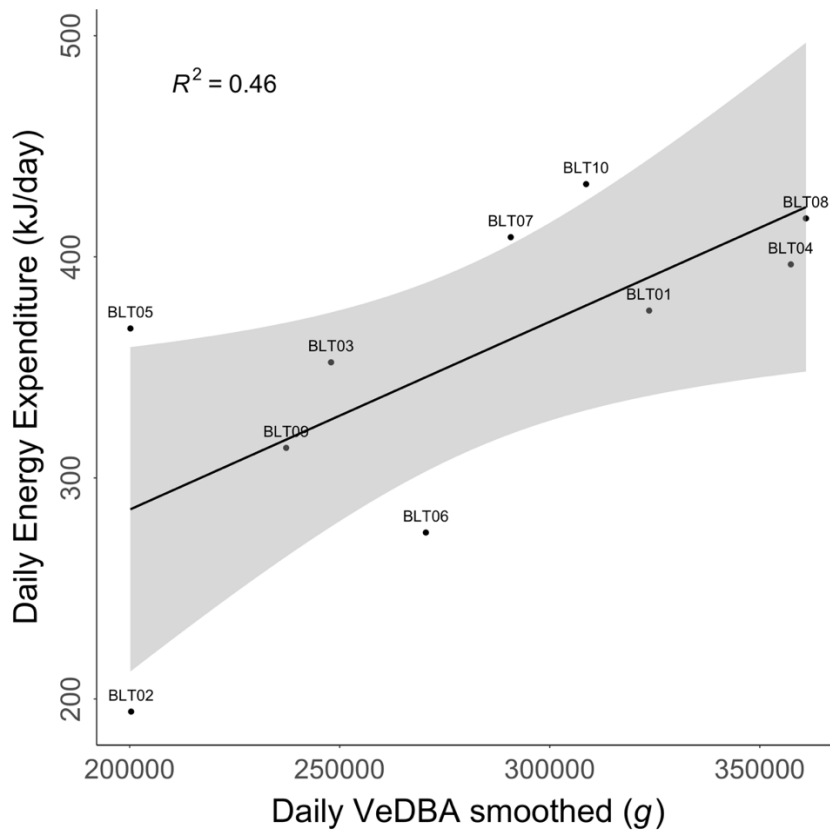


Figure 5. Linear regression between daily energy expenditure (DEE), in kJ per day, and smoothed Vectorial Dynamic Body Acceleration (sVeDBA), in g (acceleration unit) per day. The ID of each individual is shown next to each point on the graph. The grey area indicates the 95% C.I.

When we rerun the regression using 20-Hz subsampled datasets, the results showed a similar relationship, with the same intercept value (115.8) but a proportional change on the slope, where DEE values increase by 0.0017 kJ for each g of DBA. We got the same results for either odd or even datasets.

3.6.2 BEHAVIOUR-SPECIFIC ENERGY EXPENDITURE

The black lion tamarins were monitored for a mean period of 47h10m12s ($\pm 26m07s$) (Table 3). During this time, they spent, on average, 48.2% ($\pm 2.8\%$) on the DAY phase of the daily rhythm and 51.8% ($\pm 2.8\%$) on the NIGHT phase (Table 3). The animal that spent the longest time on the NIGHT phase (BLT02) was a 15-year-old female that was most affected by the anaesthetic process and was kept in a controlled environment for recovery until the next morning.

Table 3. Length of the activity (DAY) and inactivity (NIGHT) phases, proportion of time spent in each phase, and total monitoring period (time of the device on the animal) over the two days of the experiment. The colours on the rows indicate the animals that were kept in the same enclosures. The mean ($\pm SD$) length and proportions are presented on the last row. The shortest and longest lengths and monitoring periods are highlighted (bold).

ID	Length of NIGHT phase (hh:mm:ss)	Length of DAY phase (hh:mm:ss)	% Time on NIGHT phase	% Time on DAY phase	Total monitoring period
BLT01	24:55:29	22:43:36	52.3%	47.7%	47:39:05
BLT02	27:49:20	19:11:38	59.2%	40.8%	47:00:58
BLT03	23:21:00	23:37:44	49.7%	50.3%	46:58:44
BLT04	23:29:15	23:20:15	50.2%	49.8%	46:49:30
BLT05	24:37:55	22:03:10	52.8%	47.2%	46:41:05
BLT06	24:04:08	23:44:09	50.3%	49.7%	47:48:17
BLT07	23:52:21	23:55:09	50.0%	50.0%	47:47:30
BLT08	23:34:55	23:43:54	49.8%	50.2%	47:18:49
BLT09	24:12:38	22:36:49	51.7%	48.3%	46:49:27
BLT10	24:15:39	22:32:54	51.8%	48.2%	46:48:33
MEAN ($\pm SD$)	24:25:16 $\pm 01:17:41$	22:44:56 $\pm 01:23:56$	51.8% ± 2.8	48.2% ± 2.8	47:10:12 $\pm 00:26:07$

Despite the similar time spent in each phase of the daily rhythm, the mean sVeDBA for the DAY was four times higher ($T_{DAY} = 78.7\% \pm 4.7$; $T_{NIGHT} = 21.3\% \pm 4.7$), with most of this sVeDBA corresponding to active behaviour ($76.0\% \pm 5.5$). We also

observed that there is activity during the NIGHT, although very infrequent both in time ($0.7\% \pm 0.5$) and in contribution to total sVeDBA ($1.5\% \pm 1.6$), while resting during the DAY accounted for $8.1\% (\pm 4)$ of the time and $2.6\% (\pm 1.6)$ of the sVeDBA (Figure 6). The same female previously mentioned (BLT02) presented the lowest sVeDBA values for A_{DAY} (see Table A2 and A3 in Appendix).

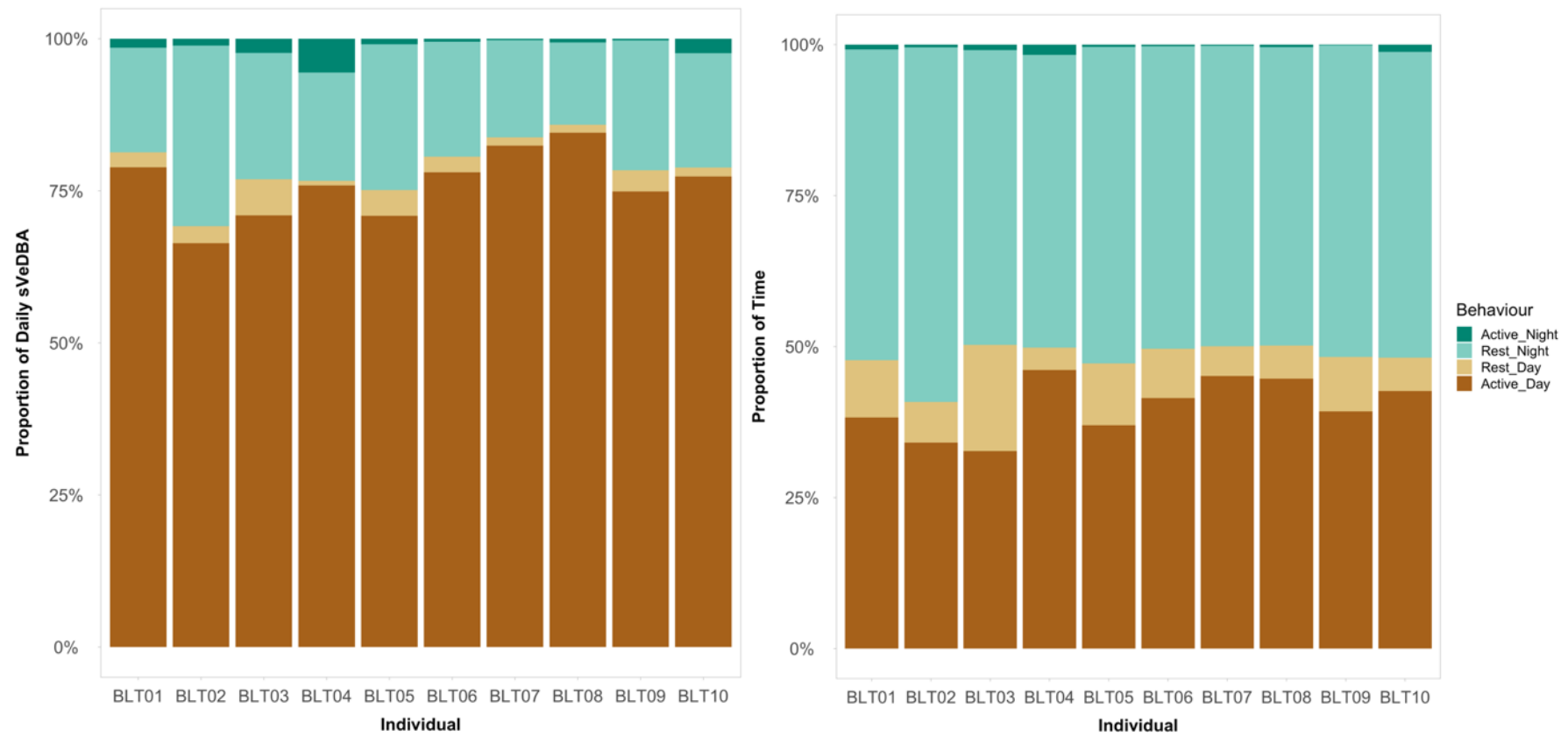


Figure 6. Proportion of each behaviour (active or resting, during the day or night) on the sVeDBA (left) and time (right) within 24 hours for each black lion tamarin.

We fit the model for Equation 2 using Energy Expenditure values based on DLW metrics for the total monitoring period. We found a negative parameter estimate for the resting behaviour at night, but the confidence interval included zero (Table 4). As the p-value associated with this behaviour and phase of the daily rhythm were higher than 0.05, we ran alternative models including as covariate the different combinations of the proportion of time spent in each behaviour and the phases of the daily rhythm (Table 4). We found that activity and the day phase, alone or combined, were the main factors that influenced energy expenditure rates in black lion tamarins ($p \leq 0.01$). The model that included only the total proportion of time in activity, independent of the phase (m5), was the best predictor of EE (Table 4). This model did not have a better fit than the one from Equation 2 (m1; F-test $p > 0.3$) but presented a much lower AIC value ($\Delta AIC = 14.3$; Table 4).

Table 4. Parameter estimates of the models on the relationship between energy expenditure (in kJ) and the costs of activity and resting behaviours, during day and night, for black lion tamarins.

Model	Dependent variable	Parameter (in days)	Estimate (in kJ/day)	SE	p	R ²	AICc
m0	TEE (DLW)	totTime	353.13	52.55	<0.001	0.958	132.69
m1	TEE (DLW)	timeActDay	1289.3	866.01	0.011	0.977	142.20
		timeRestDay	868.83	1291.37	0.151		
		timeRestNight	-500.23	775.7	0.166		
		timeActNight	3206.96	9020.86	0.418		
m2	TEE (DLW)	timeActDay	814.65	178.56	<0.001	0.973	131.38
		timeActNight	4052.55	8981.41	0.329		
m3	TEE (DLW)	totTimeDay	1302.35	785.08	0.005	0.976	130.16
		totTimeNight	-532.05	732.3	0.132		
m4	TEE (DLW)	totTimeAct	917.15	585.57	0.007	0.971	132.14
		totTimeRest	-36.03	405.37	0.843		
m5	TEE (DLW)	totTimeAct	866.00	44.51	<0.001	0.974	127.90

Legend: EE = total Energy Expenditure on the monitoring period; SE = Standard Error; p = significance level; R² = adjusted R²; AICc = Akaike Information Criterion; totTime = total monitoring time; timeRestDay/Night = time spent resting during the respective phase; timeActDay/Night = time spent in activity during the respective phase; totTimeDay/Night = total time spent on the respective phase; totTimeRest/Act = total time spent on the respective behaviour.

According to the selected model (m5), we calculated the energy spent in activity (in kJ) by multiplying the respective parameter estimate from the model (in kJ/day) by the respective time spent on it (in days) for each black lion tamarin (i.e., $EE_{ACT} \text{ (kJ)} = 866 * \text{totTimeAct}$). Then, we regressed this value against the sVeDBA value for this behaviour ($A_{DAY} + A_{NIGHT}$; Table S2 in Appendix) and found that this regression greatly improved our VeDBA/EE relationship ($R^2 = 0.69$, $p = 0.003$; Figure 7), when compared to the original one ($R^2 = 0.46$, $p = 0.03$; see Figure 5).

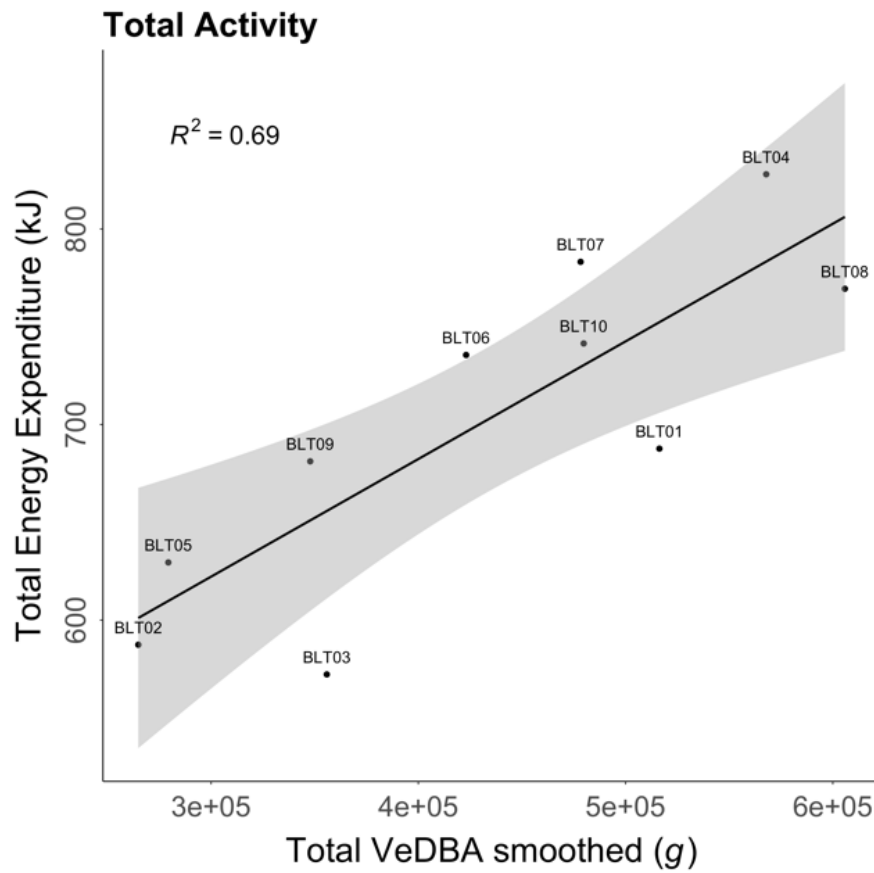


Figure 7. Linear regression between energy expenditure (EE), in kJ, and smoothed Vectorial Dynamic Body Acceleration (sVeDBA), in g, including only activity records. The ID of each individual is shown next to each point on the graph. The grey area indicates the 95% C.I.

Finally, from this relationship, we derived equation 4 to predict total energy expended by the animals based on the sVeDBA values from activity, and equation 5 to predict daily energy values:

$$TEE = ((441.8 \pm 64.1) + (0.000602 \pm 0.000144) * \text{totVeDBA}_{Act}) \quad (Eq.4)$$

$$DEE = ((226.9 \pm 31.2) + (0.000581 \pm 0.000143) * \text{dailyVeDBA}_{Act}) \quad (Eq.5)$$

When we compared the predicted values from equations 4 and 5, with the measure ones using the DLW method, we found that the relationship improved from the original one ($R^2 \geq 0.5$, $p = 0.02$; Figure 8).

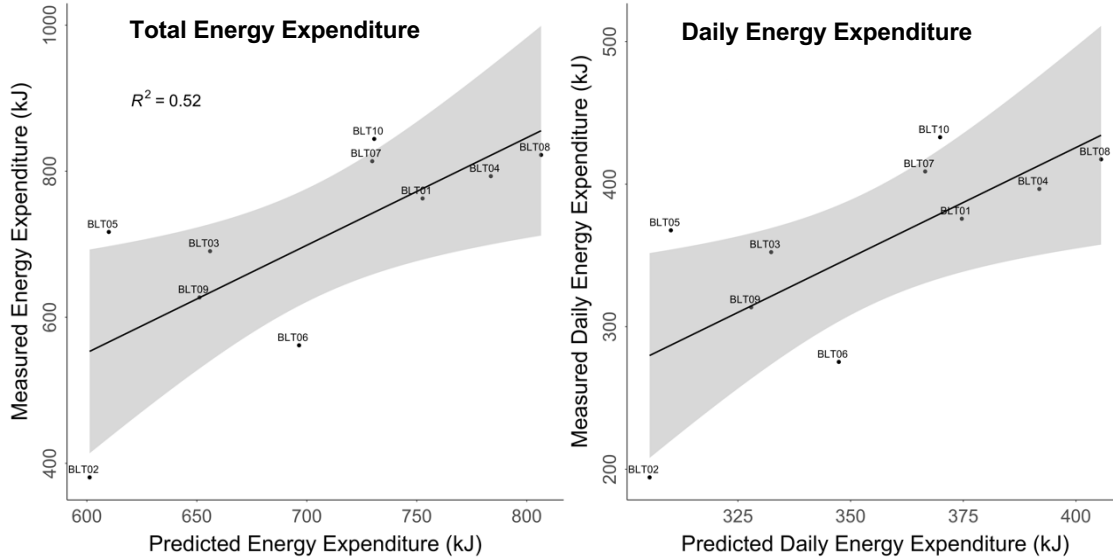


Figure 8. Comparison between measured energy expenditure by black lion tamarins, using the DLW method (in kJ) and the predicted values (in kJ) estimated from Equation 3 (left) and 4 (right). ($R^2 > 0.5$, $p = 0.02$)

3.7 DISCUSSION

We provide the first estimates of field metabolic rate for captive black lion tamarins. Values obtained from DLW are in close agreement with expected values from the literature ($84.6 \text{ kcal} \pm 5.2$, range: $50.2 \text{ kcal} \pm 3.2 - 142.6 \text{ kcal} \pm 8.6$; Table A4 in Appendix; Pontzer et al., 2014), including known parameters from marmosets. They are also similar to the values estimated for wild golden lion tamarins, using the same method ($87.9 \text{ kcal} \pm 10.8$; A. P. da Cruz-Neto, unpublished data). When we regressed the DLW results against the DBA values, we found a consistent linear and significant relationship between the two measures. The accuracy we found is within the range of values reported in the literature for DLW/DBA relations, with lower R^2 compared to other studies in penguins (0.72 in Hicks et al., 2020), cormorants (0.81 in Stothart et al., 2016) and polar bears (0.70 in Pagano & Williams, 2019), but higher R^2 when compared to wild fur seals (0.36 in Jeanniard-du-Dot et al., 2017b), and similar to those observed for semi-captive sea lions (0.47 in Fahlman et al., 2008). This is the first time

this technique has been validated for primates (along with A. P. da Cruz-Neto, unpublished data, for wild golden lion tamarins).

When we sliced our sVeDBA values into activity and resting, we saw that nearly 80% of it is associated to active states, corroborating the fact that black lion tamarin's movement is a relevant component of the total daily energy spent. Particularly, energy expenditure (expressed in DBA metrics) related to activity during the night accounted for 1.5% of total sVeDBA. Very low activity rate during night is expected for the species as callitrichids are known to reach states of torpor during sleep, probably as an energy-saving mechanism (Thompson et al., 1994). It is worth noting that we were not able to accurately estimate resting metabolic rates (RMR) from our methods. Thompson et al. (1994) reported, for captive golden lion tamarins, resting-phase RMR equivalent to $2.46 \text{ kcal.h}^{-1}.\text{kg}^{-1}$ ($43.4 \pm 7.4 \text{ kcal.day}^{-1}$, mean weight: $0.733 \text{ kg} \pm 0.099$). Considering physiological similarities between these species, if we apply this same rate to black lion tamarins, we find an average RMR of $34.8 \text{ kcal.day}^{-1}$ (± 3.1). This is nearly 40% of the total DEE for males and over 54% for females. The latter agrees to another study with wild female golden lion tamarins that presented RMR estimations that were more than half of their DEE rates (Miller et al., 2006). More precise estimations of RMR can be achieved in function of the ambient temperature (*sensu* Thompson et al., 1994). Thus, further analysis may elucidate on the contribution of the RMR related to each phase of the daily rhythm to the DEE in tamarins.

Both females of our study presented the lowest DEE values, a common fact in primates, when it comes to non-lactating females (Key & Ross, 1999). The restriction of space for locomotion during the time the female BLT02 was kept may have also affected her dynamic activity (measured by DBA metrics), resulting in the lowest values presented. Despite this, her energy expenditure was consistent with the movement performed. Differences in DEE rates between males and females are more prominent in primates with sexual dimorphism, especially due to body size differences, but still present in similar-sized different-sex individuals, which is the case for black lion tamarins. However, our low sample size does not allow us to state that this difference was significant.

The results of our models reinforced that activity was the best predictor of energy expenditure, while resting energy expenditure rates were neither accurate nor significant, presenting negative estimates and high standard errors. This reflects that

the DBA method is often not appropriate for estimating energy expenditure rates of behaviours that account for subtle or insignificant movement, even collecting data at a very fine scale (Gleiss et al., 2011; Green et al., 2009; Jeanniard-du-Dot et al., 2017). Following the approach taken by Jeanniard-du-Dot and collaborators (2017a), we could increase the accuracy of our relation by using only the VeDBA values related to activity, excluding resting, and pairing with the time each animal spent active within the monitoring period. Accelerometer data allow to infer fine scale behaviour of tagged animals to a resolution that goes well beyond the difference between moving *versus* resting used here, by defining algorithms derived from acceleration-sensor metrics representative of these behaviours (Wilson et al., 2018). It was already demonstrated that slopes of VeDBA/EE relationships can vary by activity type (Hicks et al., 2020; Jeanniard-du-Dot et al., 2017a). Therefore, additional analyses of the accelerometer data could break the black lion tamarins' activity in more specific behaviours, especially the more costly ones, such as walking and travelling, but also grooming, jumping, feeding, etc., to define more specific activity budgets and further refine the use of DBA metrics for estimating energy expenditure in wild tamarins.

The validation of this methodology for estimating the energy expenditure of black lion tamarins based on DBA-metrics sets a precedent for the use of accelerometers in studies of this nature in small primates in different contexts, whether in captivity or in the wild. The fine-scale decomposition of daily energy expenditure into contributions of day/night and active/resting bouts highlights the unique potential to use the DBA-metrics to compare energy expenditure of populations living in forests with different degrees of fragmentation and forest structure, which is vital to provide a more quantitative evidence base for conservation and mitigation measures. It will be particularly interesting to assess if DEE of individuals of different populations changes in a linear or non-linear measure (e.g., if there are sudden breakpoints) with forest fragmentation, and if this is further affected by seasonal changes, effects of group size, etc. Furthermore, the accelerometer data can be used to further identify key behaviours, such as displacement types and foraging, applying the same rule approach (Wilson et al. 2018) used here to identify activity and resting bouts (Figure 4; Table 5). The latter can then be used to understand if differences in daily energy expenditure of populations, living in contrasting forest fragments, are due to differences in movement costs, or investment in foraging effort, etc., further improving the evidence

base for more efficient management and conservation measures for black lion tamarins in human-dominated landscapes.

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3.9 AUTHORS' CONTRIBUTION

CHAPTER CONTRIBUTORS: Ariovaldo P. Cruz-Neto, Luca Börger, James Redcliffe, Catherine Hambly, John Speakman, Guilherme S. T. Garbino, Alcides Pissinatti, Silvia Bahadian, Rory Wilson, Laurence Culot

Gabriela C. Rezende, Ariovaldo P. Cruz-Neto, Luca Börger, Rory Wilson and Laurence Culot contributed to the study's conception and design. Data collection was performed by Ariovaldo P. Cruz-Neto, Luca Börger, Guilherme S. T. Garbino, Alcides Pissinatti and Silvia Bahadian. Gabriela C. Rezende, Ariovaldo P. Cruz-Neto, Luca Börger, James Redcliffe, Catherine Hambly and John Speakman developed the data analysis. The first draft of the manuscript was written by Gabriela C. Rezende, and all authors commented on previous versions. All authors read and approved the final manuscript.

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3.11 APPENDIX

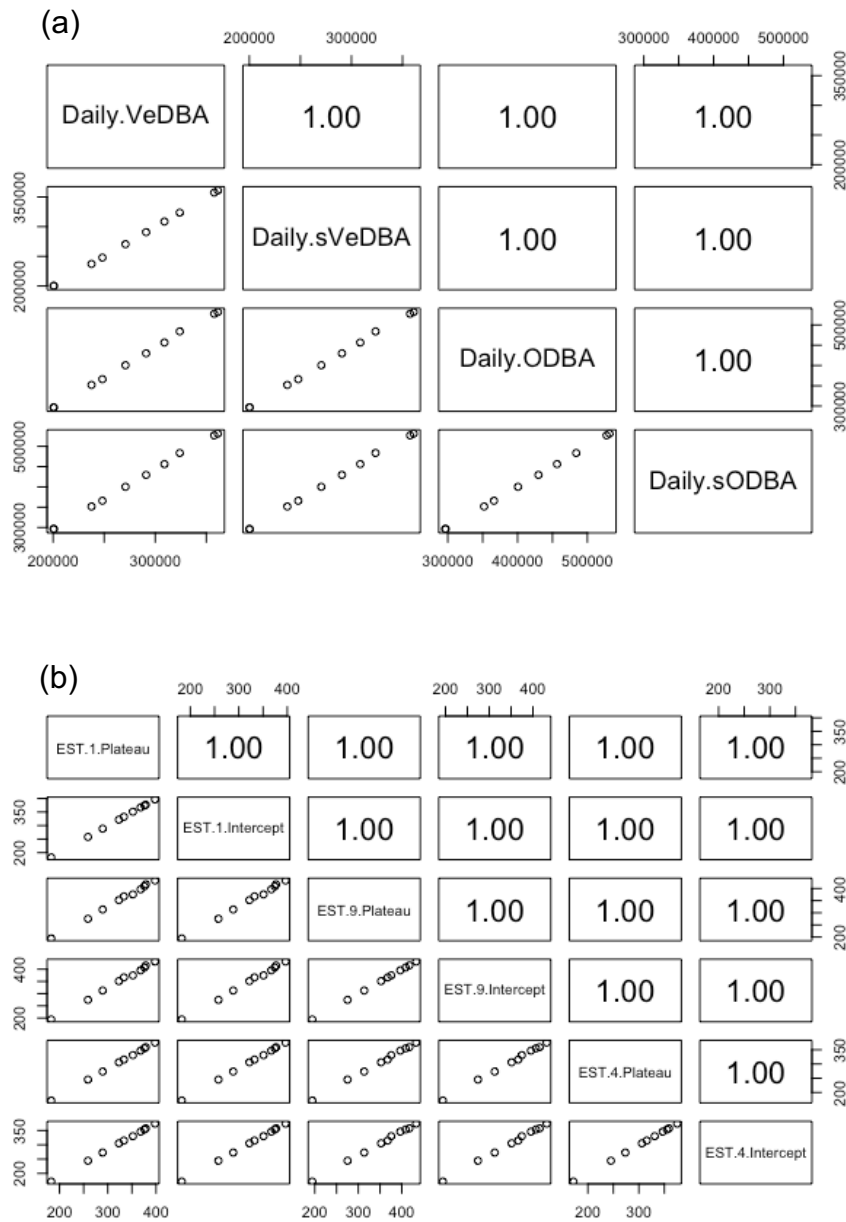


Figure A1. Correlation between the four daily Dynamic Body Acceleration (DBA) metrics (a) and the six Daily Energy Expenditure (DEE) estimates based on different calculation models (sensu Speakman, 1997 and Speakman & Król, 2005) for the doubly labelled water (DLW) (b).

Table A1. Results from the estimate of Daily Energy Expenditure (DEE) in kJ/day, based on six different calculation models, for each black lion tamarin (ID). The sex, age, enclosure, group size, and values of body mass in grams (g), at the beginning and at the end of the experiment, as well as the mean, are also presented for each individual. The mean and standard deviation (SD) values for each variable, considering all animals of the experiment are presented on the last row.

ID	Sex	Age	Enclosure	Group size	BODY MASS (g)			DEE (KJ/DAY)					
					Initial	Final	Mean	EST 1* Plateau	EST 1* Intercept	EST 9** Plateau	EST 9** Intercept	EST 4*** Plateau	EST 4*** Intercept
BLT01	M	6y5m	A	2	520	545	522.5	352.0	351.0	375.7	374.6	331.1	330.2
BLT02	F	15y1m	A	2	570	620	512.5	182.8	182.4	194.3	194.0	171.7	171.5
BLT03	M	16y5m	B	2	570	625	672.5	323.0	321.9	352.3	351.2	306.0	305.2
BLT04	M	6y5m	B	2	580	620	607.5	368.1	367.1	396.6	395.5	346.9	346.0
BLT05	M	9y5m	C	1	580	620	652.5	333.4	332.3	367.6	366.4	315.6	314.7
BLT06	F	8y2m	D	6	510	515	532.5	258.9	258.0	275.3	274.3	245.2	244.4
BLT07	M	2y2m	D	6	510	535	595	376.0	374.3	408.9	407.0	355.1	353.7
BLT08	M	1y4m	D	6	690	525	600	378.7	376.8	417.4	415.3	359.1	357.4
BLT09	M	11y6m	D	6	660	685	597.5	289.4	288.5	313.6	312.6	273.5	272.8
BLT10	M	2y2m	D	6	640	665	600	397.8	396.4	432.9	431.4	375.2	374.0
MEAN	-	-	-	-	583.0	595.5	589.3	326.0	324.9	353.5	352.2	307.9	307.0
±SD	-	-	-	-	±62.9	±60.7	±52.9	±66.1	±65.7	±73.8	±73.4	±62.5	±62.2

* Estimate 1 = Lifson and McClintock 1966, equation 35

** Estimate 9 = Speakman 1997, equation 7.17

*** Estimate 4 = Schoeller et al 1986, equation A6, modified by Schoeller 1988

Obs.: in enclosure D there was an infant in the group that was not considered for the experiment.

Table A2. Total smoothed Vectorial Dynamic Body Acceleration (sVeDBA) values estimated for each of the six subsets created, considering all records (T), the ones of resting (R) behaviour, and the ones of activity (A) behaviour, in each phase of the Daily Rhythm (DAY vs. NIGHT): T_{DAY} , R_{DAY} , A_{DAY} , T_{NIGHT} , R_{NIGHT} , and A_{NIGHT} , respectively. Time is indicated in number of records collected at 40 Hz, which corresponds to approximately 40 records for each second. Proportions (%) of values in the R and A datasets (shaded cells) were calculated in relation to the T datasets, while the proportions in the T datasets were calculated in relation to the values for 2-day period.

ID	2-day period		Daytime (over 2 days)						Nighttime (over 2 days)					
	Total sVeDBA	Total time – N records	Total sVeDBA – T_{DAY}	Total time – N records	Total sVeDBA – R_{DAY}	Time resting – N records	Total sVeDBA – A_{DAY}	Time active – N records	Total sVeDBA – T_{NIGHT}	Total time – N records	Total sVeDBA – R_{NIGHT}	Time resting – N records	Total sVeDBA – A_{NIGHT}	Time active – N records
BLT01	642,481.3	7,021,765	522,476.5 (81.3%)	3,352,405 (47.7%)	15,692.2 (3.0%)	665,335 (19.9%)	506,784.3 (97.0%)	2,687,070 (80.3%)	120,004.8 (18.7%)	3,669,360 (52.3%)	110,468.7 (92.1%)	3,613,708 (98.5%)	9,536.1 (7.9%)	55,652 (1.5%)
BLT02	392,337.8	6,778,635	271,535.1 (69.2%)	2,767,144 (40.8%)	11,117.6 (4.1%)	456,241 (16.5%)	260,417.5 (95.9%)	2,310,903 (83.6%)	120,802.7 (30.7%)	4,011,491 (59.2%)	116,344.9 (96.3%)	3,980,882 (99.2%)	4,457.8 (3.7%)	30,609 (0.8%)
BLT03	485,207.9	6,779,208	373,169.1 (76.9%)	3,409,324 (50.3%)	28,749.8 (7.7%)	1,190,935 (34.9%)	344,419.3 (92.3%)	2,218,389 (65.1%)	112,038.8 (23.1%)	3,369,884 (49.7%)	100,623.9 (89.9%)	3,307,335 (98.2%)	11,414.9 (10.2%)	62,549 (1.9%)
BLT04	697,282.7	6,910,047	534,511.5 (76.7%)	3,444,032 (49.8%)	5,486.8 (1.0%)	256,069 (7.4%)	529,024.7 (99.0%)	3,187,963 (92.6%)	162,771.2 (23.3%)	3,466,015 (50.2%)	123,927.9 (76.1%)	3,348,232 (96.5%)	38,843.3 (23.9%)	117,783 (3.4%)
BLT05	389,274.2	6,729,825	292,431.7 (75.1%)	3,178,602 (47.2%)	16,525.6 (5.7%)	690,882 (21.7%)	275,906.0 (94.3%)	2,487,720 (78.3%)	96,842.5 (24.8%)	3,551,223 (52.8%)	93,393.6 (96.4%)	3,525,155 (99.2%)	3,448.9 (3.6%)	26,068 (0.7%)
BLT06	538,697.2	7,039,659	434,255.4 (80.6%)	3,495,456 (49.7%)	13,902.1 (3.2%)	576,115 (16.5%)	420,353.3 (96.8%)	2,919,341 (83.4%)	104,441.8 (19.4%)	3,544,203 (50.3%)	101,743.6 (97.4%)	3,525,196 (99.6%)	2,698.2 (2.6%)	19,007 (0.5%)
BLT07	578,808.6	6,878,080	484,862.0 (83.8%)	3,443,098 (50.1%)	7,819.5 (1.6%)	337,425 (9.8%)	477,042.4 (98.4%)	3,105,673 (90.3%)	93,946.6 (16.2%)	3,434,982 (49.9%)	92,684.5 (98.7%)	3,421,631 (99.5%)	1,262.1 (1.3%)	13,351 (0.4%)
BLT08	711,514.7	6,805,117	610,807.5 (85.8%)	3,413,393 (50.2%)	9,266.4 (1.5%)	371,141 (10.9%)	601,541.0 (98.5%)	3,042,252 (89.1%)	100,707.2 (14.2%)	3,391,724 (49.8%)	96,441.5 (95.8%)	3,363,461 (99.2%)	4,265.7 (4.2%)	28,263 (0.8%)
BLT09	462,739.6	6,904,782	362,757.8 (78.4%)	3,334,733 (48.3%)	16,104.7 (4.4%)	621,778 (18.6%)	346,653.1 (95.6%)	2,712,955 (81.3%)	99,981.8 (21.6%)	3,570,049 (51.7%)	98,795.4 (98.8%)	3,561,217 (99.8%)	1,186.4 (1.2%)	8,832 (0.2%)
BLT10	601,877.9	6,747,681	474,554.6 (78.8%)	3,250,270 (48.2%)	9,000.4 (1.9%)	372,925 (11.5%)	465,554.3 (98.1%)	2,877,345 (88.5%)	127,323.3 (21.2%)	3,497,411 (51.8%)	113,081.9 (88.8%)	3,417,178 (97.8%)	14,241.4 (11.2%)	80,233 (2.3%)

Table A3. Daily smoothed Vectorial Dynamic Body Acceleration (sVeDBA) values estimated for each of the six subsets created, considering all records (T), and the resting (R) and active (A) behaviours in each phase of the daily cycle (DAY vs. NIGHT): T_{DAY} , R_{DAY} , A_{DAY} , T_{NIGHT} , R_{NIGHT} , and A_{NIGHT} , respectively. Time is indicated in number of records collected at 40 Hz, which corresponds to approximately 40 records for each second. Proportions (%) adjusted for time to calculate values for a 24-hour period.

ID	24-hour period		Daytime (over 24 h)						Nighttime (over 24 h)					
	Daily sVeDBA	Total time – N records	Daily sVeDBA – T_{DAY}	Total time – N records	Daily sVeDBA – R_{DAY}	Time resting – N records	Daily sVeDBA – A_{DAY}	Time active – N records	Daily sVeDBA – T_{NIGHT}	Total time – N records	Daily sVeDBA – R_{NIGHT}	Time resting – N records	Daily sVeDBA – A_{NIGHT}	Time active – N records
BLT01	324,023.5	3,456,000	263,150.9 81.3%	1,650,000 47.7%	7,903.50 2.44%	327,467 9.48%	255,247.40 78.88%	1,322,533 38.27%	60,441.1 18.7%	1,806,000 52.3%	55,638.20 17.19%	1,778,609 51.46%	4,802.90 1.48%	27,391 0.79%
BLT02	200,697.5	3,456,000	138,606.8 69.2%	1,410,793 40.8%	5,675.10 2.83%	232,609 6.73%	132,931.70 66.38%	1,178,184 34.09%	61,666.0 30.7%	2,045,207 59.2%	59,390.40 29.65%	2,029,601 58.73%	2,275.60 1.14%	15,606 0.45%
BLT03	248,294.6	3,456,000	190,640.3 76.9%	1,738,053 50.3%	14,687.40 5.93%	607,132 17.57%	175,952.90 70.98%	1,130,921 32.72%	57,236.9 23.1%	1,717,947 49.7%	51,405.40 20.74%	1,686,060 48.79%	5,831.50 2.35%	31,887 0.92%
BLT04	357,749.6	3,456,000	273,961.5 76.7%	1,722,503 49.8%	2,812.30 0.79%	128,071 3.71%	271,149.20 75.87%	1,594,432 46.14%	83,428.0 23.3%	1,733,497 50.2%	63,519.00 17.77%	1,674,589 48.45%	19,909.10 5.57%	58,908 1.70%
BLT05	200,531.5	3,456,000	150,335.9 75.1%	1,632,323 47.2%	8,495.60 4.25%	354,792 10.27%	141,840.20 70.88%	1,277,531 36.97%	49,785.3 24.8%	1,823,677 52.8%	48,012.30 23.99%	1,810,290 52.38%	1,773.00 0.89%	13,387 0.39%
BLT06	270,877.3	3,456,000	218,017.1 80.6%	1,716,034 49.7%	6,979.50 2.58%	282,834 8.18%	211,037.60 78.03%	1,433,200 41.47%	52,433.6 19.4%	1,739,966 50.3%	51,079.10 18.89%	1,730,635 50.08%	1,354.60 0.50%	9,331 0.27%
BLT07	291,076.1	3,456,000	243,489.5 83.8%	1,730,039 50.1%	3,926.80 1.35%	169,545 4.91%	239,562.70 82.42%	1,560,494 45.15%	47,177.8 16.2%	1,725,961 49.9%	46,544.00 16.01%	1,719,253 49.75%	633.8 0.22%	6,708 0.19%
BLT08	361,334.9	3,456,000	309,832.9 85.8%	1,733,502 50.2%	4,700.40 1.30%	188,485 5.45%	305,132.50 84.54%	1,545,017 44.71%	51,084.3 14.2%	1,722,498 49.8%	48,920.50 13.55%	1,708,145 49.43%	2,163.80 0.60%	14,353 0.42%
BLT09	237,620.6	3,456,000	185,933.0 78.4%	1,669,110 48.3%	8,254.50 3.48%	311,214 9.01%	177,678.40 74.91%	1,357,896 39.29%	51,246.4 21.6%	1,786,890 51.7%	50,638.30 21.35%	1,782,469 51.58%	608.1 0.26%	4,421 0.13%
BLT10	309,007.8	3,456,000	243,313.5 78.8%	1,664,710 48.2%	4,614.70 1.50%	191,003 5.53%	238,698.90 77.35%	1,473,707 42.64%	65,281.3 21.2%	1,791,290 51.8%	57,979.40 18.79%	1,750,197 50.64%	7,301.90 2.37%	41,093 1.19%
MEAN (±SD)			221,728.1 ±55,190.2	1,666,706.7 ±97,793.6	6,805.0 ±3,383.9	279,315.1 ±137,301	214,923.2 ±56,845	1,387,391.6 ±161,216.1	57,978.1 ±10,690.6	1,789,293.3 ±97,793.6	53,312.7 ±5,550.5	1,766,984.7 ±102,006.1	4,665.4 ±5,818.7	22,308.6 ±17,415
MEAN% (±SD)%			78.66% ±4.68	48.23% ±2.84	2.64% ±1.58	8.08% ±3.97	76.02% ±5.51	40.14% ±4.66	21.32% ±4.65	51.77% ±2.84	19.79% ±4.52	51.13% ±2.95	1.54% ±1.62	0.65% ±0.50

Table A4. Obtained values of Daily Energy Expenditure (DEE), in kcal, from this study and the expected ones, including prediction interval, based on the equation provided by Pontzer et al. (2014) for primates. $(\log_{10}(\text{DEE}) = 0.69 \pm 0.03 * (\log_{10}(\text{weight})) + 2.09 \pm 0.03)$

ID	DEE obtained values (kcal/day)	DEE expected values (kcal/day)	Lower prediction interval (kcal/day)	Upper prediction interval (kcal/day)
BLT01	89.8	77.9	46.2	131.7
BLT02	46.4	76.9	45.5	130.0
BLT03	84.2	92.8	55.1	156.0
BLT04	94.8	86.5	51.3	145.7
BLT05	87.9	90.8	54.0	152.9
BLT06	65.8	79.0	46.8	133.3
BLT07	97.7	85.3	50.6	143.7
BLT08	99.8	85.7	50.9	144.5
BLT09	75	85.5	50.7	144.1
BLT10	103.5	85.7	50.9	144.5
Mean $\pm$ SD	84.5 $\pm$ 17.7	84.6 $\pm$ 5.2	50.2 $\pm$ 3.2	142.6 $\pm$ 8.6

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4 CHAPTER III: SPACE USE AND MOVEMENT PATTERNS OF BLACK LION TAMARIN NEIGHBOURING GROUPS IN FOREST PATCHES

4.1 RESUMO

Título: Uso do espaço e padrões de movimento de grupos vizinhos de mico-leão-preto em fragmentos de floresta

A forma como uma espécie usa o habitat disponível ao longo do tempo define se suas necessidades estão sendo atendidas e, em última análise, se esse habitat será capaz de manter uma população viável no longo prazo. Portanto, entender como uma espécie muda seus padrões de movimento em diferentes locais e escalas temporais pode auxiliar no desenvolvimento de estratégias de conservação. Aqui, procuramos responder a três perguntas sobre os padrões de movimento e uso do espaço de um primata ameaçado de extinção: (1) Como os micos-leões-pretos mudam seu uso do espaço e padrões de movimento, incluindo sobreposição de áreas de vida entre grupos vizinhos, em manchas florestais de diferentes tamanhos? (2) A borda do fragmento afeta o uso do espaço pelo mico? (3) Como os micos exploram sua área de vida diariamente? Para isso, quatro grupos de micos-leões-pretos tiveram seus movimentos diários monitorados remotamente por meio de dispositivos de GPS e acelerômetros, por 10 a 22 dias consecutivos, em dois fragmentos florestais de tamanhos diferentes, onde ocorrem naturalmente. Os dados do GPS foram registrados a cada 10 minutos durante o período de atividade dos micos (das 6h às 19h), enquanto os dados do acelerômetro foram coletados a 25 Hz (24 horas/dia). A partir desses dados, caracterizamos os padrões de movimento e estimamos a área de vida de cada grupo, a sobreposição de área de vida entre grupos vizinhos, as áreas de atividade diária e a sobreposição destas entre dias consecutivos em diferentes janelas temporais. Também estimamos as distâncias de suas localizações da borda da floresta. Nossos resultados sugeriram um efeito do tamanho do fragmento no uso e compartilhamento do espaço. Enquanto no fragmento maior as áreas de vida eram três vezes maiores e sem sobreposição entre grupos vizinhos, no fragmento menor a sobreposição correspondia a cerca de um terço da área de vida total, incluindo também as áreas núcleo. Apesar dessas diferenças, os padrões de movimento em ambos os fragmentos foram semelhantes. Por outro lado, os grupos apresentaram um padrão diário alternado de exploração de recursos em ambos os fragmentos, mas com

diferentes janelas de tempo de retorno, provavelmente em função do tamanho da área de vida e do espaço disponível. Concluimos que os micos-leões-pretos são flexíveis em termos de ajuste do tamanho da área de vida em diferentes manchas de habitat, mas ainda mantendo uma área defensável, e que seus padrões gerais e diários de uso do espaço também podem ser afetados pelo tamanho do fragmento e pela distância da borda da floresta, mas os padrões de movimento permaneceram semelhantes entre as áreas, provavelmente associados a características intrínsecas à espécie.

PALAVRAS-CHAVE: área de vida, *comprimento do passo*, *ângulo de virada*, deslocamento diário, primatas, *Leontopithecus chrysopygus*, Mata Atlântica

4.2 ABSTRACT

The way a species uses the available habitat over time defines whether its needs are being met and, ultimately, whether this habitat will be able to maintain a population viable in the long term. Therefore, understanding how a species changes its movement patterns in different locations and time scales can assist the development of conservation strategies. Here, we sought to answer three questions on the movement and ranging patterns of the endangered black lion tamarin: (1) How do black lion tamarins change their space use and movement patterns, including home range overlap between neighbouring groups, in forest patches of different sizes? (2) Does the edge of the fragment affect tamarin space use? (3) How do tamarins explore their home range on a daily basis? For this, four black lion tamarin groups had their daily movement monitored remotely through GPS and accelerometer devices, for 10 to 22 consecutive days, in two forest fragments of different sizes where they naturally occur. GPS data were recorded every 10 minutes during the tamarins' activity period (from 6:00 am to 7:00 pm), while accelerometer data were collected at 25 Hz (24 hours/day). From these data, we characterized the movement patterns and estimated the home range of each group, the home range overlap between neighbouring groups, the daily activity ranges, and the overlap of these between consecutive days over different time windows. We also estimated the distances of their locations from the forest edge and compared to random locations. Our results suggested an effect of patch size on space use and sharing. While in the larger fragment, the home ranges were three times larger and without overlapping between neighbouring groups, in the smaller fragment the

overlap corresponded to about one third of the total home range, also including core areas. Despite these differences, the movement patterns in both fragments were similar. On the other hand, they presented an alternating daily pattern of resource exploitation in both fragments, but with different return time windows, probably as a consequence of the home range size and the available space. We concluded that black lion tamarins are flexible in terms of adjusting home range size in different habitat patches though keeping a defensible area, and that their general and daily patterns of space use may also be affected by patch size and the distance to the forest edge, but movement patterns remained similar among areas, probably associated to characteristics intrinsic to the species.

KEYWORDS: home range, step length, turning angle, daily path length, primates, *Leontopithecus chrysopygus*, Atlantic Forest

4.3 INTRODUCTION

Animals often restrict their movements to delimited areas that can provide them with the conditions and resources to grow, reproduce and raise their offspring, and survive. This area is called the home range (Burt, 1943). A species' home range can change in size and location over an organism's life, across different temporal scales, reflecting individual requirements and the way each individual uses and shares the available space (Campos et al., 2014; Pearce et al., 2013). Key ecological questions about animal home ranges concern the drivers of these temporal changes, since the way a species uses the available habitat defines whether its needs are being met and, ultimately, whether this habitat will be able to maintain a population viable in the long term (Fieberg & Börger, 2012; Larson et al., 2004; Luck, 2002).

Given the intrinsic relationship between habitat use and movement, changes in the former can directly affect the patterns of the latter and, therefore, individuals' behaviours, population dynamics and survival, that ultimately affect a population viability (Kays et al., 2015; Morales et al., 2010). Therefore, understanding how a species changes its movement patterns in different locations and time scales can assist the development of conservation strategies that address issues such as the plasticity of a given species and its resilience to changes in the available habitat (Allen & Singh, 2016; Bro-Jørgensen et al., 2019).

For forest-dependent species, such as Neotropical primates, forest fragmentation has been the most significant factor causing changes in their habitat, whether in quantity or quality, and consequently their major threat (Estrada et al., 2018). Among these species, is the black lion tamarin (*Leontopithecus chrysopygus*), an endangered small primate, whose main threat is habitat loss and fragmentation (Rezende et al., 2020a). Their populations are currently present in nearly 20 forest patches of Atlantic Forest remnants across their distribution range in the state of São Paulo, in southeast Brazil, which correspond to less than 1% of their original distribution (Garbino et al., 2016; Rezende et al., 2020b). They live in family groups, containing 2 to 8 individuals, that establish and defend territories, from which they obtain the resources they need for survival (Coimbra-Filho & Mittermeier, 1973). Their group home range size can vary significantly within the same fragment or among different areas, from 40 ha to almost 400 ha (Albernaz, 1997; Alcolea, 2016; Bufalo,

2020; da Silva, 2019; Keuroghlian & Passos, 2001; Mamede-Costa, 1997; Medici, 2001; Messaoudi, 2015; Passos, 1997; Valladares-Padua, 1993). This broad variation may be due to several factors, including methodological and biological ones, such as the use of different methods for home range estimation, but also seasonal variation of resources within the same forest patch, or differences in resources availability and distribution among different areas, in this case, influenced by other factors, such as anthropogenic ones, including the history of forest exploitation and landscape configuration (Campos et al., 2014; Kay et al., 2017).

Despite the information available regarding black lion tamarin home ranges in different fragments, a single study comparing home ranges of groups living in different fragments has never been carried out. An exception is the pre and post-translocation monitoring of two groups, carried out by Medici, 2001. Similarly, no study has addressed the understanding of how neighbouring black lion tamarin groups use and share space.

Given the importance of understanding species movement patterns and space use for effective conservation planning and designing of management strategies, both in terms of populations, habitat, and landscape, three questions on the movement and ranging patterns of this endangered primate emerged to be explored: (1) How do black lion tamarins change their space use and movement patterns, including home range overlap between neighbouring groups, in forest patches of different sizes? (2) Does the edge of the fragment affect tamarin space use? (3) How do tamarins explore their home range on a daily basis?

Here, these questions were examined based on the data remotely collected using dataloggers (GPS and accelerometer devices) on four black lion tamarin neighbouring groups living in two forest patches of different sizes. Answering these questions can shed light on the important drivers determining home range size and patterns of space use, which will ultimately enable better estimates of a fragment's carrying capacity to subsidize population management actions.

4.4 METHODS

4.4.1 STUDY SITE AND IN SITU MONITORING

Black lion tamarin groups were monitored *in situ* in two forest patches of different sizes (Ponte Branca – 1,303 ha and Guareí – 105 ha), in the state of São Paulo, southeast Brazil (Figure 1). All fragments are remnants of tropical seasonal semideciduous forests, within the Atlantic Forest Domain (IBGE, 2012; Veloso et al., 1991). The climate is characterized by a dry and cold season (winter) alternating with a warm and humid period (summer), with rains concentrated between September and April (Rolim et al., 2007).

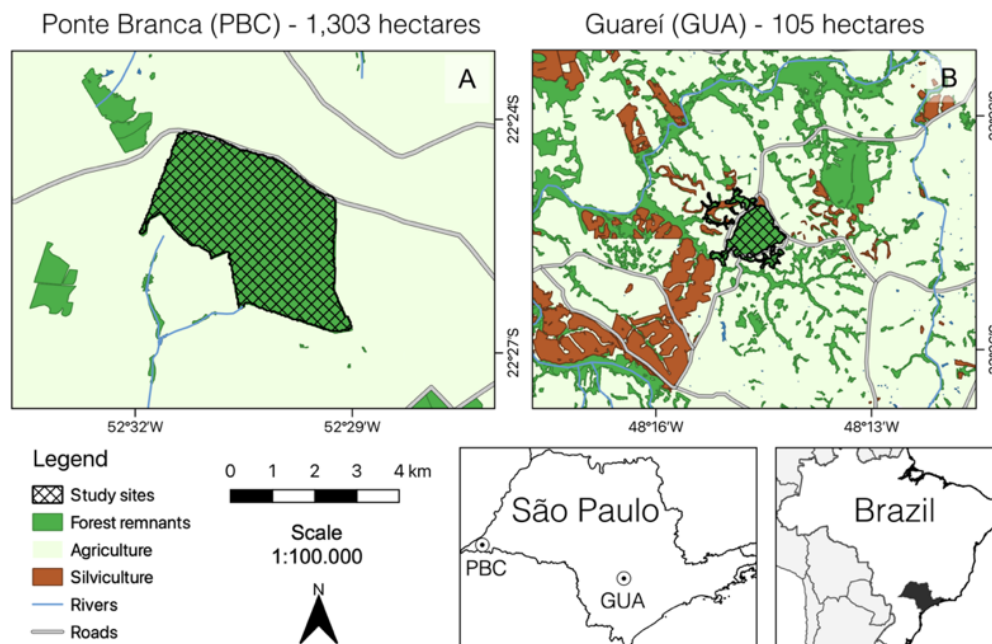


Figure 1. Study sites (cross-hatched areas): A. Ponte Branca (PBC), in Pontal do Paranapanema; B. Guareí (GUA), in Alto Paranapanema, both in the Brazilian state of São Paulo.

Movement data was collected from four groups, two per area. One black lion tamarin from each group was equipped with a 14-g backpack-style harness with a small housing for GPS and triaxial accelerometers (Axy Trek, TechnoSmart, Italy). One individual of each group was also equipped with a VHF collar (RI-2D, Holohil, Canada), to allow us to find the group for subsequent equipment retrieving. The GPS devices were programmed to map the daily movement of the lion tamarins for a month, recording locations every 10 minutes, 13 hours a day - estimated activity period from sunrise to sunset, from 09:00 UTC to 21:59 UTC, or, in local time, from 06:00 BRT to

18:59 BRT, totalling 78 records per day. Accelerometers recorded at 25 Hz, 24 hours a day, for a set of 2.16 million records per day.

In September 2019, we captured two neighbouring groups in the fragment in Guareí (GUA01 – $n = 7$, and GUA02 – $n = 5$). In January and March 2020, the groups were respectively recaptured to retrieve the device with the data. In September 2020, we captured one group in Ponte Branca (PBC01 – $n = 4$), which was recaptured a month later, in October 2020, for device recovering. In February 2021, a second group in Ponte Branca (PBC02 – $n = 1$), living in an area adjacent to the first group, was found and captured. This individual was found dead after a month, in March 2021.

All captures were carried out with the support of the Black Lion Tamarin Conservation Program team, from IPÊ – Instituto de Pesquisas Ecológicas, and the presence of a veterinarian. Only clinically healthy adult males were selected for deployment of the backpacks. The weight of the individuals ranged from 600 to 630 grams ($620 \text{ g} \pm 12.25$, $n = 4$). The GPS backpacks were attached in a parallel position relative to the body of the animal, on the tamarins' back, using a flexible polyester chord (shoelace) sewn around the animal's thoracic region (*sensu* Savage et al., 1993), to ensure comfort and stability and prevent that a change in the device position would interfere in accelerometer data acquisition (Figure 2). The animals were anaesthetised during the whole procedure to reduce stress and handled in accordance with protocols described in “Capture Protocols for Wild Lion Tamarins (*Leontopithecus* spp.)” (ICMBio, in prep.). During this research, two anaesthetic protocols were used for the chemical immobilization of the animals. In 2019, the animals in Guareí were anesthetized with a combination of ketamine 12 mg/kg (Dopalen; Ceva Saúde Animal Ltda., SP, Brazil) and midazolam 0.5 mg/kg (União Química Farmacêutica Nacional S.A, MG, Brazil) intramuscularly. Alternatively, the groups captured in the following years in Ponte Branca were subjected to inhalation anesthetic induction with isoflurane. Heart rate, respiratory rate, and rectal temperature were measured every 10 minutes during the immobilization period. Licenses for capturing, handling, and monitoring animals were duly provided by the responsible agencies (SISBio 41375 and 62116; COTEC nº 167/2015) and the project is approved by the Ethics Committee for Animal Use of the senior author's University (CEUA Decision IB-UNESP-CRC nº 12/2018).



Figure 2. Anesthetised black lion tamarins equipped with GPS + accelerometer device (Axy Trek, TechnoSmart, Italy) in dorsal (left) and ventral (right) views.

4.4.2 DATA ANALYSES

The results on the amount and quality of the data collected during the monitoring period of each group and how the GPS data was processed for further analyses is described in Supplementary Material 9.1.

4.4.2.1 HOME RANGE, SPACE USE AND MOVEMENT PATTERNS

To characterize space use and movement patterns of black lion tamarins, we used the GPS locations to estimate step length, turning angles and home range size

at a 10-day time scale, the minimum number of days that we were able to collect data from the groups, using the “adeHabitatHR” R package (Calenge, 2015; Calenge, 2006). Furthermore, using home range accumulation curves by day, calculated using the Autocorrelated Kernel Density Estimate (AKDE) method (Fleming et al., 2015) from the “amt” R package (Signer et al., 2019, 2022), we observed that home range size estimates asymptote at or before day 10 (Figure A1, Appendix), further validating the 10-day time scale. In addition, we also estimated a 22-day time scale home range for the two groups monitored for longer time. Due to the autocorrelated nature of our data, we used the Biased Random Bridge (BRB)¹ method (Benhamou, 2011). It considers serial autocorrelation of the relocations, similar to the Brownian bridge approach, but allowing for the inclusion of parameters such as proportion of activity within each step (supplied here by the accelerometers – see Methods in Chapter 4) and a smoothing parameter that accounts for the grid resolution, the step length distribution and the standard deviation of the GPS inaccuracy. To run the analyses, we used a standardized 4000x4000-m grid of 5-m pixels (640,000 pixels) for each fragment, centred on the centroid of the recorded locations in each area. We considered the total home range and the core areas as the regions with 95% and 50% probability of use, respectively. We also checked whether the 50% Utilization Distribution really represent the core area for these animals by comparing the observed space-use pattern with that expected from a uniform pattern of use (Samuel et al., 1985). As we studied neighbouring groups at both sites, we also estimated the area shared by the two groups, considering both the total home range and the core areas in each fragment.

For step length and turning angle estimations, we calculated the distance and the angle, respectively, between two subsequent locations recorded in a trajectory, which is a sequence of steps that connect successive locations of the monitored animal (Turchin, 1998), using the “adehabitatLT” R package (Calenge, 2019; Calenge, 2006). We tested for differences in mean step length and turning angle between groups and between the steps present within and outside of the core areas (BRB 70%). Additionally, for the GUA01 and GUA02 groups, where we observed an overlap in the total home ranges (as well as in the core areas), we tested whether the mean step

¹ In Supplementary Material 9.2, we made available a material where we explored other methods of home range estimation using this data, based on Fixed Kernel Utilization Distribution, and justify the choice for the Biased Random Bridge method for the development of the further analyses in this chapter.

length and turning angle differ between the overlapping and non-overlapping areas of the two groups. Differences in step length were tested using permutation tests to compare means. For turning angles, we used the Rayleigh test of uniformity and Watson-Wheeler test for differences between samples, using the “circular” R package (Ulric et al., 2022). For comparisons among average angles, we used the absolute values as the *adehabitatLT* package returns relative angles from -180° to $+180^{\circ}$, and we were interested in an estimate of how much tamarins turn at each step in relation to the previous one without regard to the right or left directions.

4.4.2.2 EFFECT OF THE FRAGMENT EDGE

To assess whether the edge of the fragment affects tamarin space use, we analysed their movements in relation to the distance from the edge. For this, we used the NNjoin plugin in QGIS software to calculate the distance between each GPS location in relation to the nearest fragment edge. To understand whether the distance of the animals' locations from the edges differed from a random pattern, we generated random locations (same number as the actual locations) within the home ranges of the four studied groups and calculated the distance of random locations from the edges of the fragment. The density of these random distances for each group was compared to the density of the distances from the real locations graphically and statistically, using Kruskal Wallis tests. We also compared the real distances among groups using Dunn's Test.

4.4.2.3 DAILY PATTERNS OF USE

To understand the daily patterns of use of their home range, we estimated each group's daily activity range, i.e., the extrapolated area covered by the activities within 24 hours. For this, we used the Autocorrelated Kernel Density Estimate (AKDE) method (Fleming et al., 2015), from the “amt” R package (Signer et al., 2019, 2022), as this method also accounts for autocorrelated data but performs better than BRB in smaller datasets. Then, to understand whether the same areas are explored in short time windows, we calculated the overlap between two consecutive days (e.g., days 1 and 2), every 2 days (e.g., days 1 and 3) and every 3 days (e.g., days 1 and 4), for total home range (AKDE 95%) and for core areas (AKDE 70% and 50%). To explore what proportion of the total home range is used in a single day, we estimated the

overlap between each day over the total home range, i.e., the fraction of the total home range that is intersected by each daily activity range.

To estimate the mean daily path length, i.e., the distance covered by each group per day, we calculated the total distance covered by each trajectory by summing all 10-minute scale steps of each 13-hour trajectory (i.e. within the daytime activity period). We calculated the movement trajectories for each study group using the “adehabitatLT” R package (Calenge, 2019; Calenge, 2006). With these values, we examined the relationship between daily path length and daily activity range by fitting a Generalized Additive Model (GAM), including the groups as random effect, using the “mgcv” R package (Wood, 2006, 2022). Standard residual diagnostic checks were applied (Figure A2 in Appendix) and fit was evaluated using R^2 metrics.

For all estimations, except when specified, we considered the full dataset collected for each group, using permutation tests, or including group as a random factor to account for repeated data collected on individuals and differences in dataset length. All data visualization, management and analyses were run in R 4.1.3 (R Core Team, 2022), R Studio 2022.2.3.492 (RStudio Team, 2022) and QGIS 3.18 Zürich (Quantum GIS Development Team, 2022).

4.5 RESULTS

4.5.1 HOME RANGE, SPACE USE AND MOVEMENT PATTERNS

We found an up to 3-fold difference in home range and core areas sizes (10-day time scale) among the groups (Table 1; Figure 3). We observed a high overlap either when considering total home range or core areas between GUA01 and GUA02 (Table 1; Figure 3). However, for the groups in PBC no overlap was found. Also, the home ranges in PBC reflected a more concentrated use pattern, with “non-use” gaps in certain regions of both groups’ home range, while GUA showed a more continuous space use pattern.

Table 1. Black lion tamarin total home range (95% Utilization Distribution) and core areas (70% and 50%UD), in hectares, for each group in the Guareí (GUA) and Ponte Branca (PBC) fragments, as well as the respective proportion (%) of area shared with the neighbouring group in GUA. Estimates are based on Biased Random Bridge method.

Group	95%UD	Shared	70%UD	Shared	50%UD	Shared
GUA 01	37.5	29.1%	16.8	25.0%	9.3	19.4%
GUA 02	39.5	27.6%	21.8	19.3%	12.9	14.0%
PBC 01	92.9	-	43.5	-	24.3	-
PBC 02	101.4	-	47.2	-	26.4	-

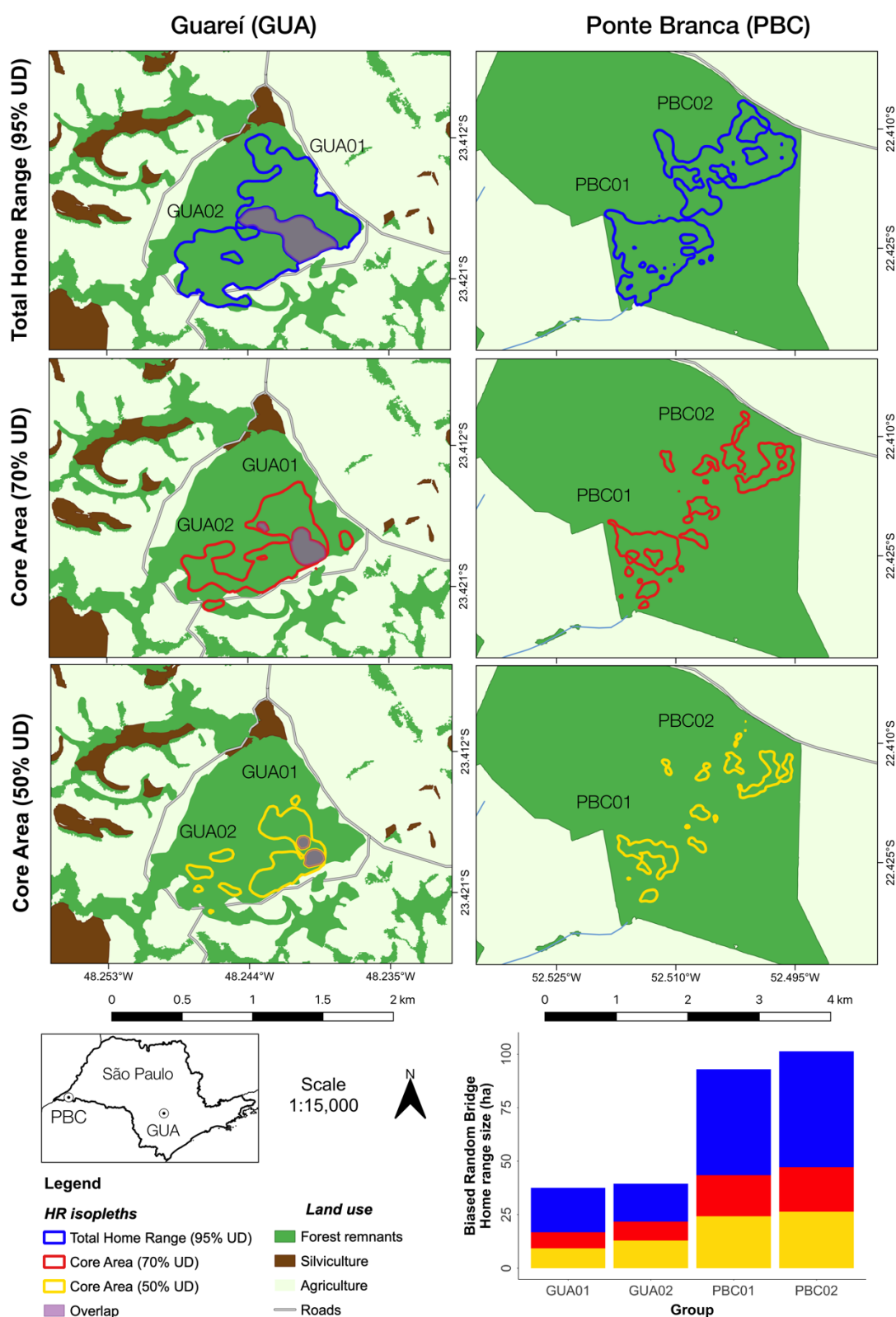


Figure 3. Total home range (BRB 95%UD) and core areas (BRB 70% and 50%UD) of the black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments. Overlapping areas of the groups in GUA are highlighted.

Average step length only differed between the two groups in PBC ($P = 0.03$), with PBC02 showing the smallest averages among the four, even having shown the largest home range size (Table 2). When analysing the turning angles, we found that all groups, except GUA01, showed a non-uniform distribution (GUA02: $P < 0.05$, PBC01 and PBC02: $P < 0.001$), i.e., they have a directionality, while for GUA01 the distribution does not differ from a uniform one (Figure 4). GUA01 also presented the highest average angle among the groups, and it was the only group that differed from the other three (Table 2; GUA01 vs. GUA02: $P < 0.05$; vs. PBC01; vs. PBC02: $P < 0.001$).

Table 2. Mean, minimum and maximum step length, in metres, and mean turning angle, in degrees, and the respective number of steps used on the estimates for each black lion tamarin group in the Guareí (GUA) and Ponte Branca (PBC) fragments. Groups that differed from the others are indicated ().*

Group	N steps	Mean Step Length ($\pm$ SD) - m	Min-Max Step Length - m	Mean Turning Angle ($\pm$ SD) - °
GUA 01	1468	36.7 $\pm$ 31.3	0.0-308.4	92.9° $\pm$ 60.6 *
GUA 02	633	38.3 $\pm$ 33.9	0.0-237.6	84.6° $\pm$ 58.3
PBC 01	1567	38.0 $\pm$ 30.1	0.0-306.7	81.3° $\pm$ 59.3
PBC 02	690	35.5 $\pm$ 31.5 *	0.1-308.6	76.0° $\pm$ 57.9

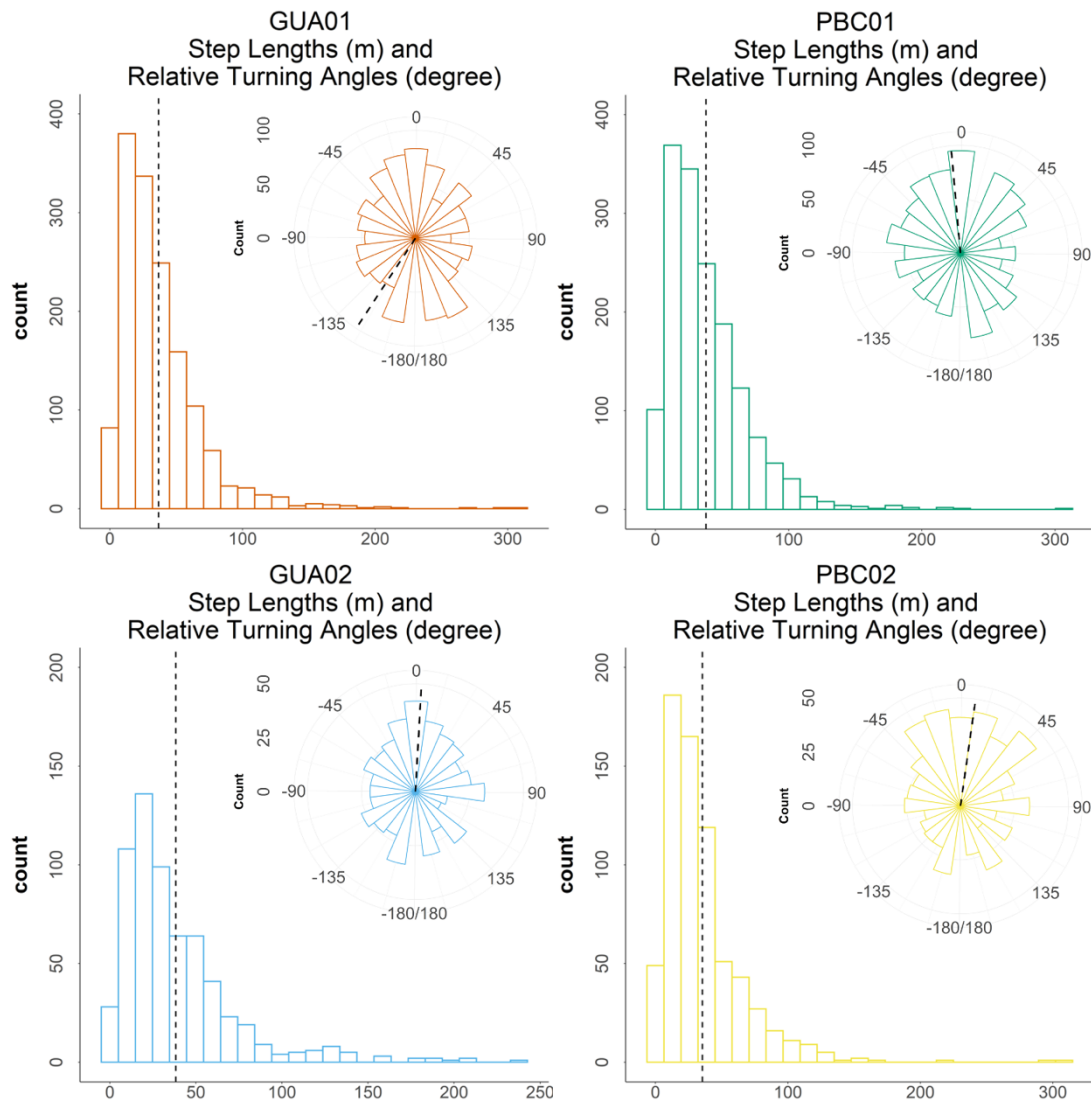


Figure 4. Histogram of step lengths (y axis in metres) and relative turning angles (circular histogram, y axis in degrees) of the four studied black lion tamarin groups. Dashed lines show the average step length and turning angle (estimated based on the non-modular values) for each group.

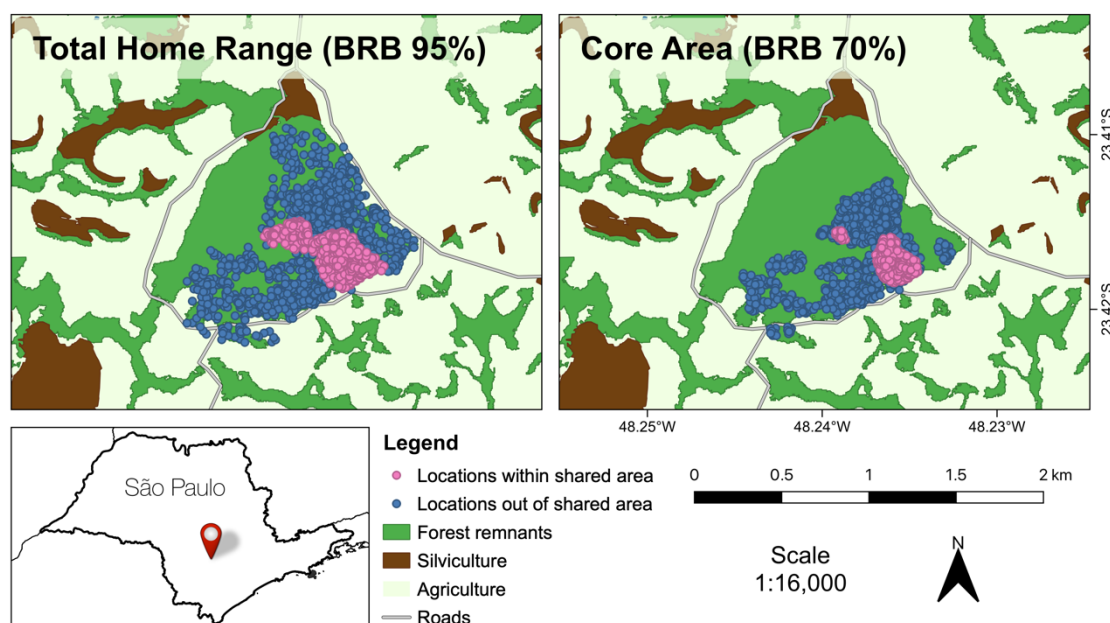
When we tested for differences between step lengths within and out of core areas (BRB 70% vs. 95%), all groups differed, with shorter distances moved within the core area (Table 3). On the other hand, for turning angles (Table 3), only PBC02 differed ($P = 0.01$), presenting a higher value inside. But again, GUA01 showed a non-uniform orientation for both within and outside the core area, as well as GUA02 for the angles outside of the core area.

Table 3. Mean step lengths (in metres) and relative turning angles (in degrees) of locations present within and outside the core areas (BRB70%) of the four studied black lion tamarin groups. Mean turning angles were calculated based on the modules of the angles. Standard deviations are presented.

Group	Mean Step Length ($\pm$ SD) - m			Mean Turning Angle ($\pm$ SD) - degrees		
	Inside HR70%	Outside HR70%	P-value	Inside HR70%	Outside HR70%	P-value
GUA 01	35.6 $\pm$ 29.8	40.1 $\pm$ 35.1	0.03*	92.8° $\pm$ 59.2	93.2° $\pm$ 64.5	0.89
GUA 02	35.6 $\pm$ 31.7	51.1 $\pm$ 41.2	< 0.001***	84.6° $\pm$ 57.7	84.7° $\pm$ 60.7	0.47
PBC 01	35.4 $\pm$ 28.3	47.8 $\pm$ 34.7	< 0.001***	83.3° $\pm$ 59.3	73.7° $\pm$ 58.9	0.09
PBC 02	30.4 $\pm$ 26.7	60.6 $\pm$ 41.1	< 0.001***	79.8° $\pm$ 59.2	60.2° $\pm$ 48.3	0.01**

Legend: $P \leq 0.001$ ***; ≤ 0.01 **, ≤ 0.05 *

Finally, considering the locations present within the overlapping areas of the total home range (BRB 95%) and core areas (BRB 70%) of the two groups in Guareí, we found that in both cases step lengths are shorter in the overlapping areas ($P < 0.05$) (Figure 5). Despite having a uniform distribution for both the angles inside and outside the overlap area, we observed smaller mean turning angles outside the overlapping areas of both total home range (mean $\pm$ SD: inside = 95.3° $\pm$ 59.0; outside = 87.3° $\pm$ 60.4; $P = 0.02$) and core areas (mean $\pm$ SD: inside = 91.0° $\pm$ 59.0; outside = 89.8° $\pm$ 58.8; $P = 0.96$), but that only differed for total home range ($P = 0.02$).



Area	N steps	Mean ($\pm$ SD) Step length (m)	Min. Step length (m)	Max. Step length (m)	p-value
Non-shared BRB 95%	1314	38.9 $\pm$ 33.3	0.0	308.4	
Shared BRB 95%	780	34.4 $\pm$ 29.9	0.0	237.6	0.002**
Non-shared BRB 70%	1224	36.5 $\pm$ 30.8	2.3	293.9	
Shared BRB 70%	382	32.8 $\pm$ 29.0	0.0	237.6	0.04*

Legend: $P \leq 0.001$ ***, ≤ 0.01 **, ≤ 0.05 *

Figure 5. Sets of points contained within (pink) and out (blue) of the overlapping areas of total home ranges (BRB 95%, left) and core areas (BRB 70%, right) (pink) of the two groups monitored in Guareí, and their respective values of average, minimum and maximum step length recorded in these areas. P-values refer to comparison using Permutation test.

4.5.2 EFFECT OF THE FRAGMENT EDGE

The mean distances to the forest edge were significantly different ($P < 0.0001$) among the four groups (mean $\pm$ SD: GUA01 = 195.0 m $\pm$ 111.2; GUA02 = 131.2 m $\pm$ 96.7; PBC01 = 531.7 m $\pm$ 312.5; PBC02 = 692.7 m $\pm$ 367.2) (Figure 6). These observed distances from the forest edge also differed from random distances in the smaller patch (GUA), being longer than expected for GUA01 ($P < 0.001$) and shorter for GUA02 ($P < 0.001$) but did not differ in the large patch (PBC) for both groups ($P > 0.05$) (Figure 7).

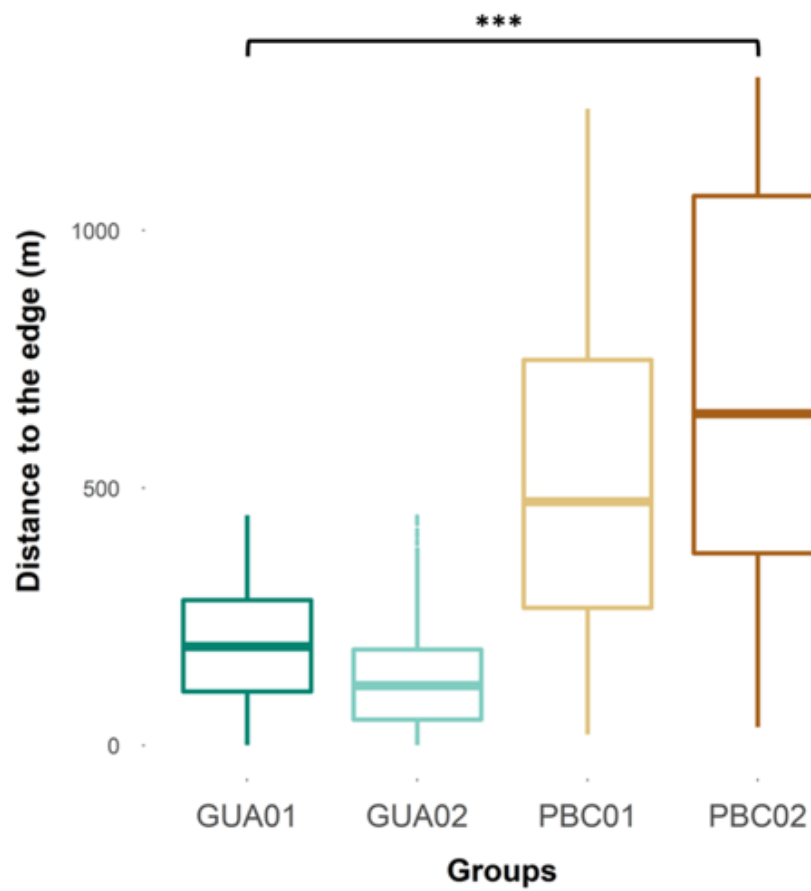


Figure 6. Box plot of the distance to the fragment's edge from each location recorded for the individuals of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments. The asterisks (***) indicate highly significant difference ($P < 0.0001$) among groups.

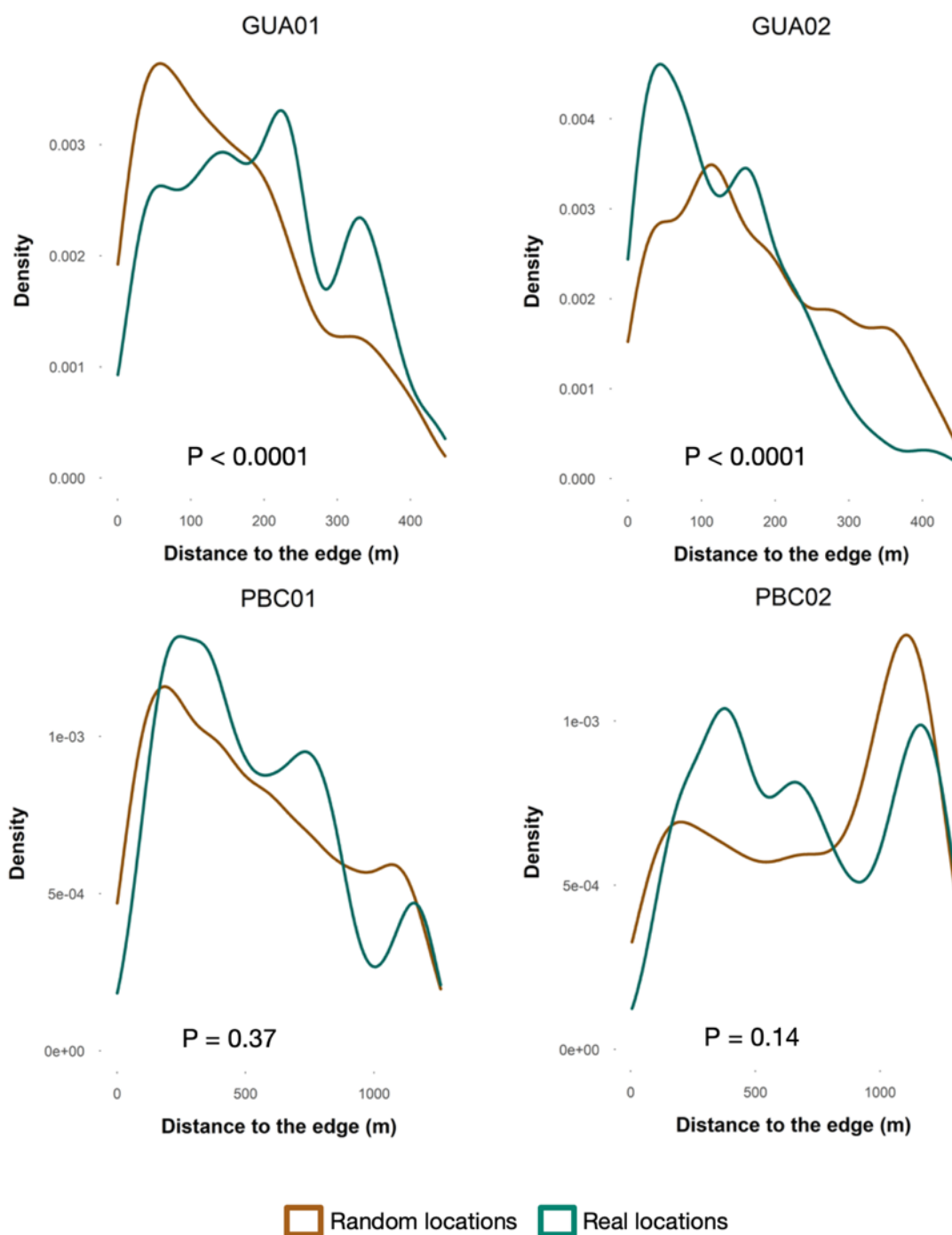


Figure 7. Density of GPS locations (real) and the locations randomly generated within the estimated home range (random), according to the distance to the forest edge of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments.

4.5.3 DAILY PATTERNS OF USE

Considering the daily activity range, the magnitude of differences was less pronounced than for longer time scales home ranges, being up to twice as larger between the groups (Table 4). The proportion of the home range that is used daily corresponds to one-third to one-fifth of the total. Only GUA01 differed from PBC01 ($P = 0.004$) and PBC02 ($P < 0.01$), showing ranges that were half the size of the PBC groups. GUA01 also showed a smaller variation of the area size used along the days, while PBC01 had larger variations (Table 4; Figure A3 in Appendix).

Table 4. Black lion tamarin average daily activity range and core areas based on Autocorrelated Kernel Density Estimate (AKDE) with 95, 70 and 50% Utilization Distribution, respectively, and proportion of the total home range (95%) and core areas (70 and 50%) estimated for each group in the Guareí (GUA) and Ponte Branca (PBC) fragments. Values are in hectares (ha) and percentage. Standard deviations are presented.

Group (N of days)	AKDE 95%		AKDE 70%		AKDE 50%	
	Estimate (ha)	% Total	Estimate (ha)	% Total	Estimate (ha)	% Total
GUA 01 (N=22)	15.5± 6.4	33±11	7.5±3.2	29±10	4.5±1.9	24±11
GUA 02 (N=10)	23.0±12.0	39±18	7.3±2.5	26±10	6.4±3.6	18±13
PBC 01 (N=22)	31.1±18.9	24±13	14.1±9.6	16±10	7.9±5.7	11±9
PBC 02 (N=10)	33.6±28.3	18±14	15.5±14.6	14±13	9.0±8.9	11±10

We found a low proportion of overlap of daily activity ranges between consecutive days, especially of core areas (Figure 8). When we compared the groups in each fragment, we observed a contrasting pattern for the overlap of core areas over the different time windows (1 to 3 days), with the groups in GUA increasing the overlap as the time window increases, while in PBC there is a clear decrease of overlap with longer time windows (Figure 8), with PBC02 reaching a mean overlap of 1.2% (± 2.2) after 3 days. Specifically, for PBC01 we observed ten consecutive days (days 4 to 14)

with no overlap of core areas (AKDE50%), while for the other groups the maximum number of consecutive days without overlapping was two. At the same time, PBC01 presented the highest proportion of core area overlap, between days 15 and 16 (82.3% for AKDE70% and 84.8% for AKDE50%). This pattern is kept when we analysed different time intervals (every 2 days and every 3 days), with PBC01 still presenting the highest proportion as well as the longer periods with no overlap (see Tables A1 to A4 in Appendix for daily values and proportions).

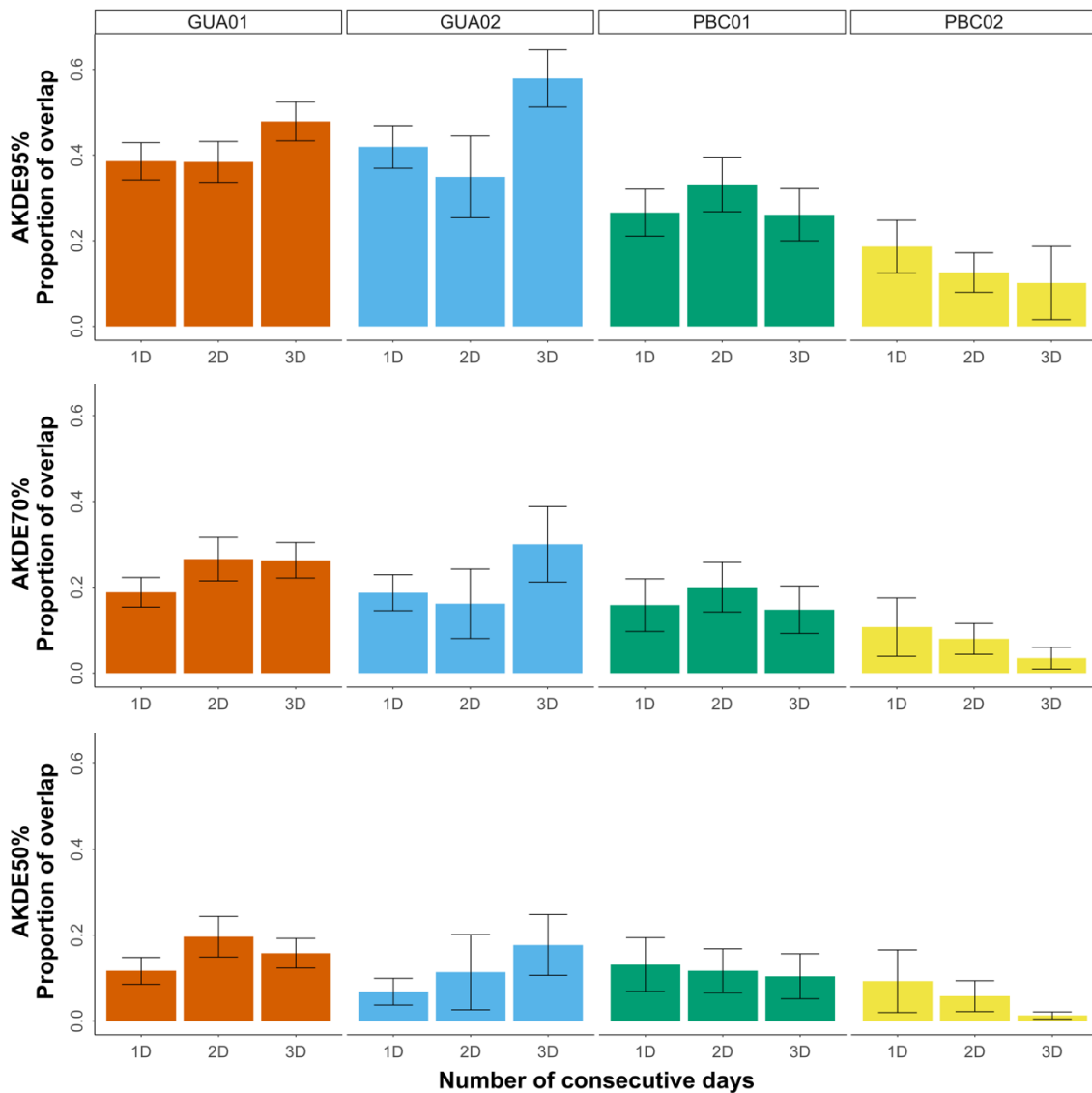


Figure 8. Average proportion of overlap of daily activity range between two consecutive days, every 2 days, and every 3 days, based on Autocorrelated Kernel Density Estimate (AKDE) 95, 70 and 50% Utilization Distribution, estimated for each group in the Guareí (GUA) and Ponte Branca (PBC) fragments. Standard errors are presented.

Despite differences in home range size and daily activity range, mean daily path lengths were similar between the groups (GUA01: 2446.7 m $\pm$ 401.4; GUA02: 2417.6 m $\pm$ 367.8; PBC01: 2701.9 m $\pm$ 415.7; PBC02: 2444.7 m $\pm$ 515.3; $P > 0.05$). We found a significant positive relationship between daily path length and daily activity range, especially when considering the effect of the group. This model explained 59.9% of the overall deviance (adjusted $R^2 = 0.544$, $P < 0.0001$, AIC = 917.1) (Figure 9; model residuals check on Figure A4 in Appendix).

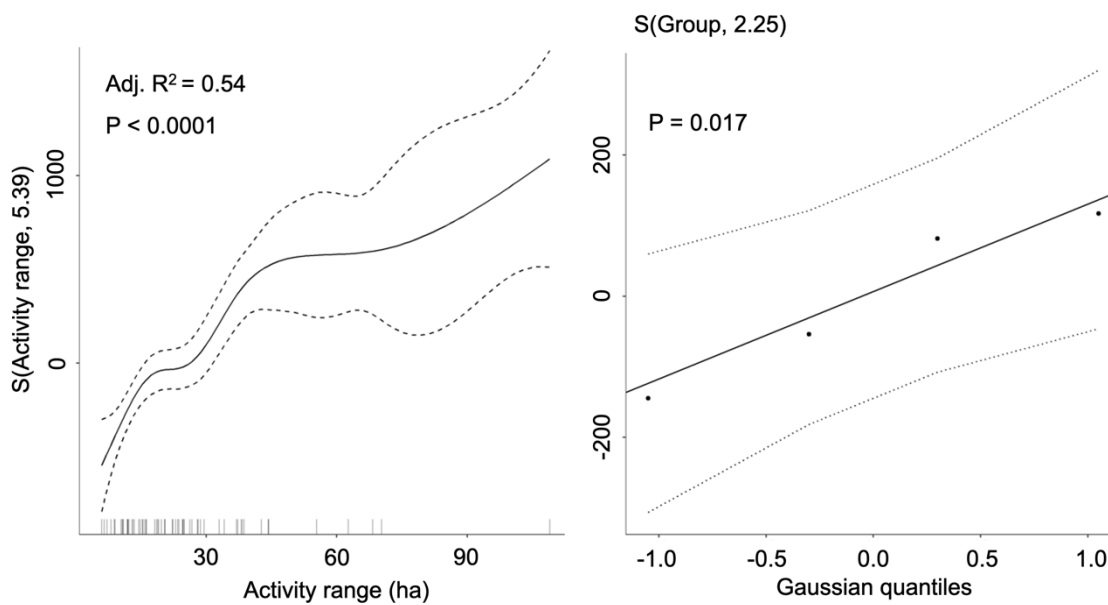


Figure 9. Output from the generalized additive model (GAM) for the relationship between daily path length (m) and daily activity range (ha) (left), and the effect of the groups, included as random factor (right). Solid line is the predicted output, while the dashed lines are the upper and lower 95% confidence intervals.

4.6 DISCUSSION

Our study reports data from the second deployment of GPS datalogger devices attached to a free-ranging wild Neotropical primate, with considerable improvement on the performance (36.6% acquisition rate in Sánchez-Giraldo & Daza, 2019, against the 93% we obtained, or 99.5% if we consider locations expected within the activity period) and accuracy (73.8% of highly accurate positions on this same study, against 82.7% in ours, based on the same criteria; see Supplementary Material 9.1). Our analyses

show that these devices are effective to be used in studies on the space use and movement patterns of small arboreal primates, with the advantage of not requiring field in-person monitoring, excluding the observer effects in spatial data collection. Data obtained here for home ranges is congruent with the expected based on traditional methods (see Table 6 for references). With the joint use of the accelerometers, we obtained a gain in quality in the data collection (e.g., by identifying gaps of data and inactivity periods), bringing more robustness to the analysis of movement data, such as with the inclusion of the activity rate as a parameter on the home range analysis using autocorrelated data (Benhamou, 2011). This combination of GPS and accelerometers can provide more data to explain how movement patterns influence home range establishment and dynamics over time.

4.6.1 HOW DO BLACK LION TAMARINS CHANGE THEIR SPACE USE AND MOVEMENT PATTERNS, INCLUDING HOME RANGE OVERLAP BETWEEN NEIGHBOURING GROUPS, IN FOREST PATCHES OF DIFFERENT SIZES?

The estimated home ranges for the groups in the small fragment are among the smallest ever recorded for the species (Table 5). A wide variation in home range size in different locations is also observed in other species of the genus *Leontopithecus* (Table 5), showing that lion tamarins have some behavioural plasticity in space use patterns. However, little is known about the mechanisms that regulate home range size in these primates. Koprowski (2005) found a positive correlation between home range size and fragment size for three species of arboreal squirrels, which, like lion tamarins, are forest-dependent species. This suggests a process of home range compaction due to fragmentation. This same correlation was found for home range data for lion tamarin species ($\rho = 0.71$, $P = 0.0001$; Table 5), suggesting a strong effect of patch size. Although the groups are coexisting and surviving in smaller fragments, there are several deterministic and stochastic events that can lead, alone or synergistically, to medium-long-term drastic consequences in reduced-size populations (Link et al., 2010), such as decrease of food availability (Arroyo-Rodriguez & Dias, 2010), higher exposure to diseases (Chapman et al., 2006), and genetic inbreeding (Knapp, 2013), resulting in loss of population viability and local extinctions.

Table 5. Estimated home ranges for the four lion tamarin species (*Leontopithecus* spp.) in different locations.

Species	Home range size (min-max; in ha)	Location	Fragment area (ha)*	Reference
<i>Leontopithecus chrysopygus</i>	37-40	Guareí (Fazenda Santo Antônio)	105	This study
	40	Fazenda Rio Claro	165	Mamede-Costa, 1997
	81-83	Fazenda Santa Maria	515	Alcolea, 2016; Messaoudi, 2015
	93-207	Ponte Branca (ESEC MLP)	1.303	This study
	53-112	Fazenda Mosquito	1.344	Medici, 2001
	54-118	Estação Ecológica Caetetus	2.254	Keuroghlian & Passos, 2001; Passos, 1992
	106-199	Parque Estadual Morro do Diabo	32.641*	Albernaz, 1997; Valladares-Padua, 1993
<i>L. caissara</i>	277-558	Ariri	7.426*	Nascimento et al., 2011
	70-321	Ilha do Superagui	11.459*	Ludwig, 2011; Prado, 1999; Schmidlin, 2004
<i>L. chrysomelas</i>	22-84	Mosaicos de floresta e cabruca	NA	Oliveira et al., 2011
	36	Lemos Maia	466	Rylands, 1989
	93-197	Reserva Biológica de Una	7.059	Oliveira et al., 2011; Raboy & Dietz, 2004
<i>L. rosalia</i>	22-48	fragmentos isolados na APA da Bacia do Rio São João	30-200	Lucas et al., 2019
	21-149	Reserva Biológica de Poço das Antas	2.360*	Dietz et al., 1997; Lucas et al., 2019
	65-229	Reserva Biológica União	2.400*	Kierulff, 2000; Lapenta et al., 2007

* Estimated area of available forest habitat for the species in the fragment.

At the same time, home ranges remain large in proportion to the body size of these primates (Ferrari, 1993), which may have resulted in the overlap observed in the present study for the GUA groups, as a compensation to maintain the home range size required by the demand for resources, against the available forest area. Home range overlap has already been observed in other callitrichid species (Alba-Mejia et al., 2013; Pontes & Monteiro da Cruz, 1995; Raboy et al., 2008), including some in the same genus (Lapenta et al., 2007b; Nascimento et al., 2011; Raboy & Dietz, 2004). However, among the lion tamarins, only in *L. caissara* the overlap was of a similar magnitude (above 30%) and with an overlap also of the core areas. Nascimento et al. (2011) recorded 32-54% overlap of two neighbouring *L. caissara* groups, in home ranges 5-

10 times larger than in Guareí (present study). In a study involving 3 groups of *L. chrysomelas*, Raboy and Dietz (2004) found 10-12% overlap and home ranges 2-3 times larger than those observed in Guareí, a result similar to that observed in *L. rosalia* by Lapenta et al. (2007; 15-20% overlap and home ranges 1.3-2.2 times larger). Important to highlight that the absence of overlapping areas between the PBC groups may be due to the different monitoring periods (PBC01 in October and PBC02 in February), but also due to the lower density of individuals in this fragment (0.035 ind/ha), estimated at a quarter of the value found in GUA (Forero-Sánchez, 2020). Further analysis on the dynamic interaction between the two groups in GUA and using dynamic interaction indices (Long et al., 2014), considering the days that data was simultaneously collected for both groups and testing whether these groups influence each other's movement behaviour (*sensu* Alba-Mejia et al., 2013), could clarify if they stay in close proximity to one another or avoid themselves in these areas.

We also observed that for the groups in GUA, this overlap included core areas and the movement patterns within these overlapping areas differed, with shorter step lengths (SL) and larger turning angles (TA). Opposed to the overlap of core areas that we observed here, there is a predominant pattern of under-use of overlapping areas of primates' ranges (Chapman, 1990; Herbinger et al., 2001; Wrangham et al., 2007). The over-use of overlapping areas suggests these should be areas of high resource density, in other words, places where the animals would spend more time exploring these available resources. This is corroborated by the significantly shorter SL that we found within the overlapping zones of both the home ranges and the core areas, indicating that the tamarins move slower and spend more time in this overlap area. Despite the uniform distribution observed for the TA of both groups in GUA, showing that they turn randomly to any direction being either inside or outside the overlap areas, the higher angles found within the overlap areas may suggest more exploratory movements (with more turns), or foraging, in such areas.

Intergroup encounters of black lion tamarins are more frequent in smaller fragments (Bury, 2020), but usually offering low risk of injury between individuals, as physical aggressions are not commonly observed, despite other behavioural expressions of territoriality, such as vigilance, vocalizations and displays, as recorded for other callitrichids (Garber, 1988; Pontes & Monteiro da Cruz, 1995). This fact gives support to the 'risk hypothesis' proposed by Wrangham et al. (2007), where overlap

zones are larger or more used in species that are subject to a lower risk of lethal aggression in intergroup encounters. Therefore, overlapping core areas may be an effect of home range compression due to lower habitat availability, which requires areas with high availability of resources to be shared between groups in smaller forest patches. But concentrating their foraging effort in such areas of high energy benefit has been shown to be advantageous, despite the chance of group encounters involved.

Even with considerable differences in home range sizes, average step lengths were similar, except for one group that contrastingly features the largest home range but the smallest movement steps. When we compared the areas used more and less intensively within the home range, the shorter SL within core areas were expected, since the animals spend more time exploring the resources in these areas, thus, traveling shorter distances and slower. However, this exploratory pattern was not supported by the TAs for three of the groups, as only PBC02 showed difference between the areas, with values that indeed suggest a more directed movement outside the core areas. Movement tortuosity is usually associated to the foraging intensity of an animal, with more tortuous moves reflecting a fine-scale searching for food sources (Benhamou, 2004; Calenge et al., 2009). The assessment of movement directionality may present different results according to the temporal scale used, both in the data collection or in the analysis. On the other hand, if movement parameters are properly defined, movement behavioural states can be derived from different frequency tracking data (Bennison et al., 2018; Teimouri et al., 2018). Further analysis of movement directionality and tortuosity, considering smaller temporal windows and associated with the accelerometer data, can contribute to the identification of foraging patches, which are not necessarily being distinguished by the core area analyses (Petroelje et al., 2020).

4.6.2 DOES THE EDGE OF THE FRAGMENT AFFECT TAMARIN SPACE USE?

Our results indicate that the GUA01 group tends to avoid areas closer to the edge of the fragment. This result may have been because GUA02 uses a forest corridor contiguous to the fragment, to the south, while GUA01 uses areas only inside the main fragment, despite having access to a corridor to the north of the fragment. There is evidence of a third group occupying this fragment, in its north-western portion,

and records of them using this corridor. The presence of this third group should limit the use of this corridor by GUA01. In Ponte Branca, the groups explore larger areas and farther away from the edge than Guareí due to the fragment size, but we could also see a certain preference for areas closer to the edge, with most locations within 500 m from it. Lenz et al. (2014) found a positive effect of the fragment edge on the population density of *Saguinus* and *Sapajus* (i.e., higher densities in edge habitats), possibly explained by the diet of these primate species. These two genera, as well as the lion tamarins (Kierulff et al., 2002), consume significant amounts of animal prey (e.g., invertebrates and frogs), generally more abundant and less concealed at the forest edge (De Carvalho Guimarães et al., 2014). An assessment of the availability of resources (i.e., fruit trees, insects, and roosts) in these edge areas, along with differences in movement patterns (e.g., step lengths and turning angles) in these areas, and detailed behaviour identification from biologging sensors such as accelerometers (Williams et al., 2020), might further elucidate these issues.

4.6.3 HOW DO TAMARINS EXPLORE THEIR HOME RANGE ON A DAILY BASIS?

The low overlap of daily activity ranges between consecutive days, especially for core areas, suggests an alternating pattern of resource exploitation. This pattern agrees with the alternation of sleeping sites observed in black lion tamarins (da Silva, 2019), probably as a predator avoidance strategy. Following the classification of Chapman et al. (1989), black lion tamarins may be considered Multiple Central Place Foragers (MCPF). This strategy of alternating sleeping sites is an efficient way of lowering travel costs for the animals, as the new sleeping sites are close to the feeding areas of the respective day (Chapman et al., 1989). Additionally, it allows them to efficiently use and explore a relatively large home range, while it ensures time for the renewal of resources in the exploited area (i.e., ripening of new fruits, reoccupation of microhabitats by other insects, etc.) until they return to this area after a few days. From our analysis, we could not find a pattern regarding the period of return within 3 days, but the decreasing overlap observed day after day in PBC may be a result of the larger home range, as they have a greater area to exploit resources. In accordance with this alternating pattern is the observation that the core area encompasses a large part of the total home range (70%), suggesting that tamarins intensively explore a significant part of their home range. Further analyses testing the MCPF strategy and exploring

the daily patterns of space use over longer times, associated with the choice of sleeping sites, may elucidate on the choices of paths and daily areas within the home range.

In addition to the need for energy intake throughout the day as determinant of the daily ranges (Hanya & Bernard, 2016; Santhosh et al., 2015), the need for territorial defence is another pressure that befalls them (Peres, 1989, 1992). Despite the direct relationship between territoriality and the competition for resources, the 'economic defendability' of these resources must be taken into account, i.e., the cost to patrol the territory boundaries should be minimal relative to the effort for acquisition of food (J. L. Brown, 1964). In this sense, Mitani and Rodman (1979) proposed the 'index of defendability', where territoriality is related to the DPL being longer than the home range diameter, as the cost to return to the territory boundaries would be minimal. Our data showed that even for the higher values of home range size, the average daily path lengths remained similar among the groups and were always longer than the home range diameters, actually being at least twice its size, supporting that tamarins establish defensible home ranges (Bury, 2020) and would not have to add extra cost to their movement to defend the borders of their home range that limit with other groups.

4.7 CONCLUSION

The suggested effect of patch size on tamarin space use and how they share the available space, associated with the higher population density found in the smallest area, indicate a process of home range compaction due to fragmentation. In other words, the available habitat may be crowding and may suffer medium-long-term effects as a result of reduced population size and greater population density. Despite the flexibility in terms of home range size, the studied black lion tamarin groups presented similar movement patterns in the areas, which can be, therefore, associated with characteristics intrinsic to the species. The daily path lengths always longer than the home range diameters indicate that even with more space available, the species maintains a defensible area. But the daily pattern of resources exploitation within the home range, despite having been shown to be alternating in both fragments, had different return time windows, probably as an effect of the total home range size and

available space. The time scale and sampling size with which we worked does not allow us to reach conclusive inferences at the population level, but even so, we were able to obtain promising results, which validate the use of biologgers for studying the movement and space use of black lion tamarins, and help to clarify our questions, raising issues relevant to the conservation of the species. Therefore, in conclusion, it is important to consider the patch size as a key factor for the long-term maintenance of black lion tamarins in fragmented habitats.

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4.9 AUTHORS' CONTRIBUTION

CHAPTER CONTRIBUTORS: Luca Börger, Eduardo Miguel Zanette, Daniel Felippi, Vinicius Alves, Milene Alves-Eigenheer, Laurence Culot

Gabriela C. Rezende, Luca Börger and Laurence Culot contributed to the study's conception and design. Data collection was performed by Gabriela C. Rezende, Daniel Felippi and Vinicius Alves. Gabriela C. Rezende, Luca Börger, Eduardo Miguel Zanette and Milene Alves-Eigenheer designed and developed the data analysis. The first draft of the manuscript was written by Gabriela C. Rezende, and all authors commented on previous versions. All authors read and approved the final manuscript.

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4.11 APPENDIX

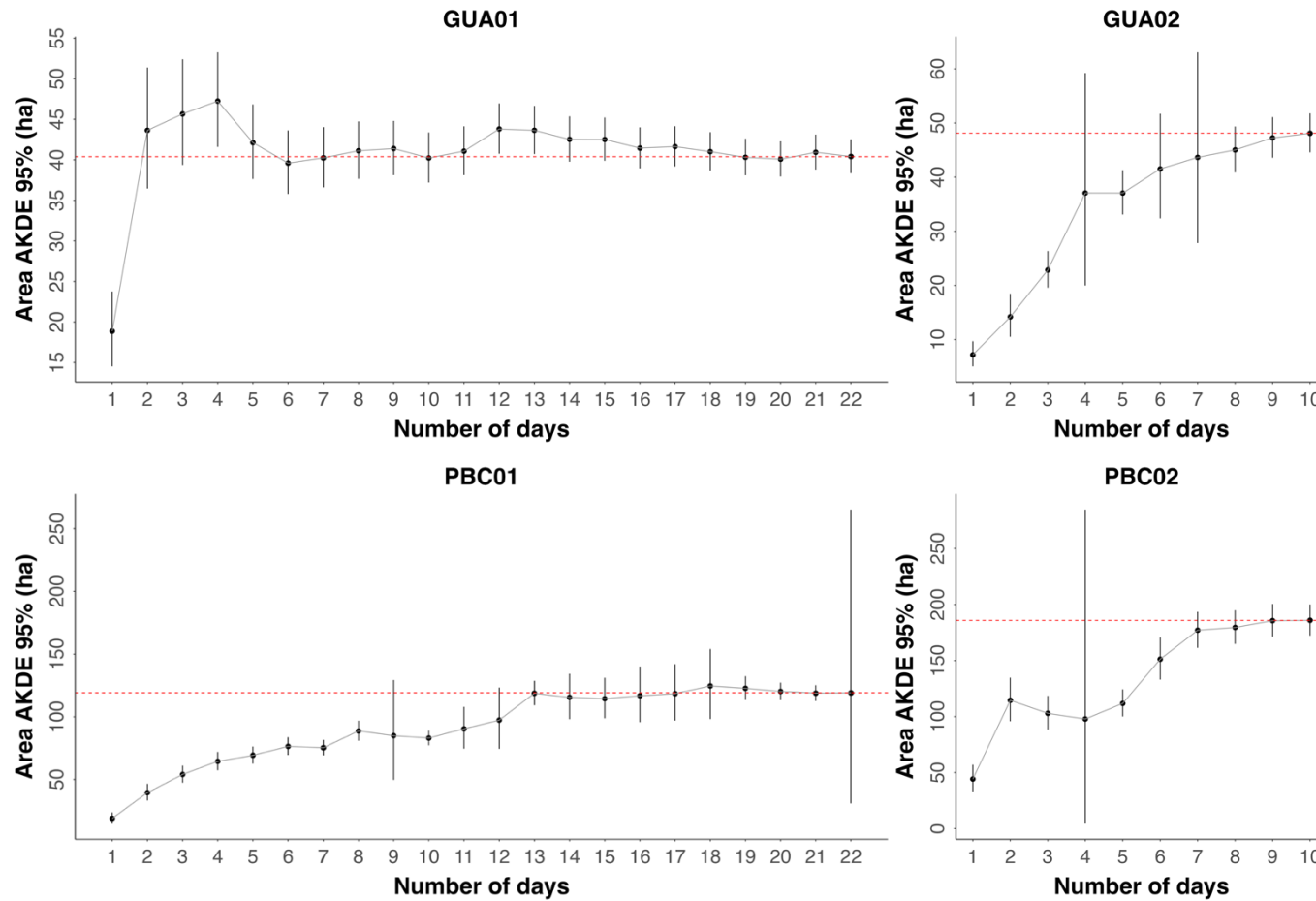


Figure A1. Cumulative home range (in ha) over the days, based on Autocorrelated Kernel Density Estimate (AKDE) 95% Utilization Distribution, estimated for each group in the Guareí (GUA) and Ponte Branca (PBC) fragments. The red dashed line indicates the total home range considering the full dataset. Lower and upper confidence intervals (95%) are presented for each day.

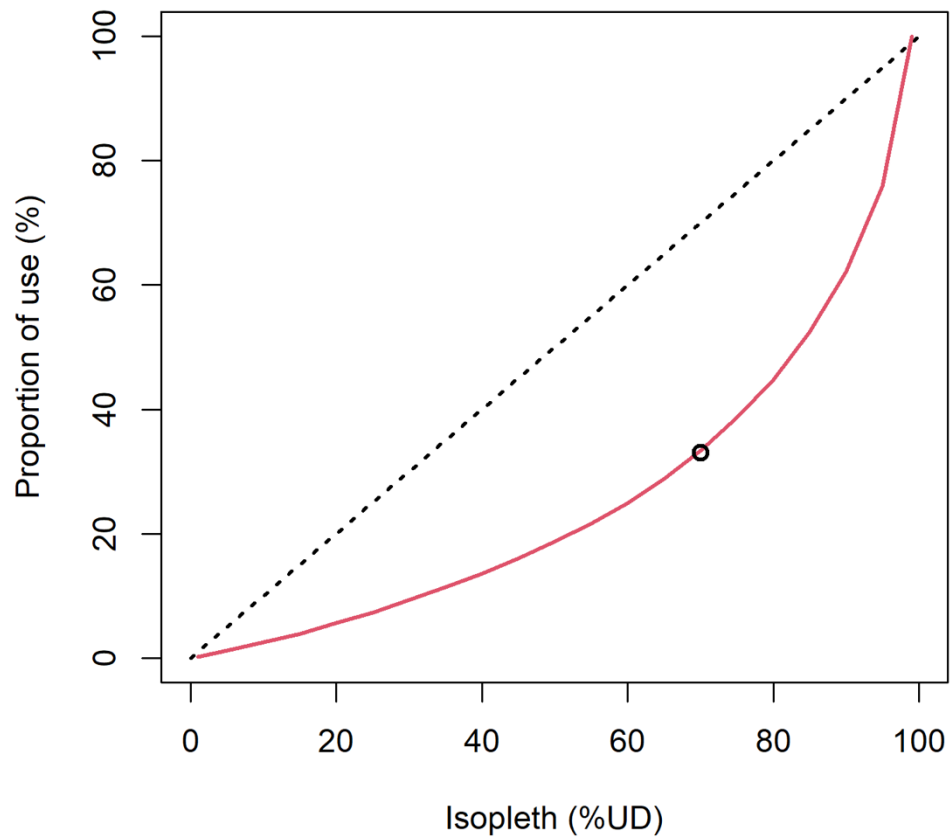


Figure A2. The red line shows the space-use pattern, based on FKUD estimates, for the black lion tamarin groups, while the dashed line indicates a uniform pattern of use. The black point indicates the point of maximum deviation from the equality line, showing that the 70% isopleth represents the core area for the black lion tamarin.

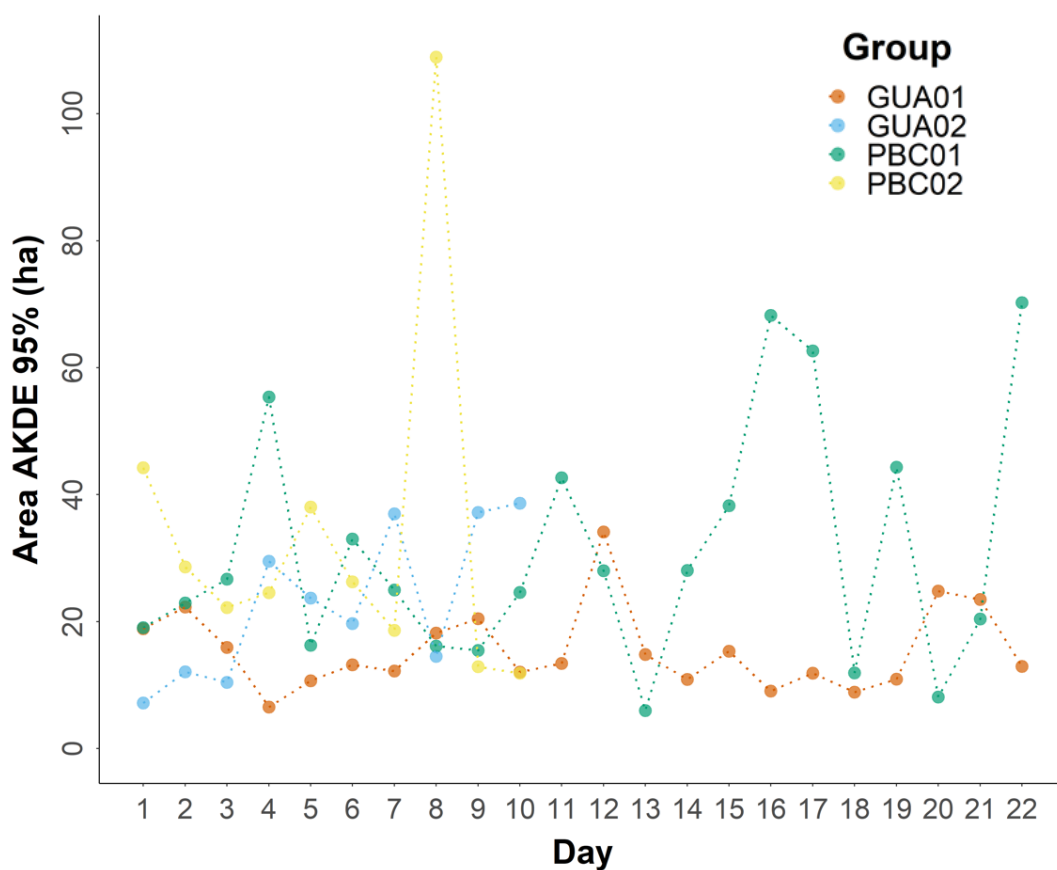


Figure A3. Black lion tamarin daily activity range based on Autocorrelated Kernel Density Estimate (AKDE) 95% Utilization Distribution estimated for each group in the Guareí (GUA) and Ponte Branca (PBC) fragments.

Table A1. Area (in ha) of the daily activity range for each group, based on Autocorrelated Kernel Density Estimate (AKDE), considering the 95%, 70% and 50% probability of use. Lowest and highest values are highlighted.

Days	AKDE95% (ha)				AKDE70% (ha)				AKDE50% (ha)			
	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02
1	18.87	7.17	19.03	44.25	9.95	9.95	6.75	16.68	6.22	1.98	3.53	8.24
2	22.31	12.07	22.94	28.61	9.82	9.82	8.98	9.95	5.60	2.79	4.99	5.00
3	15.93	10.43	26.69	22.22	8.10	8.10	11.70	10.79	5.14	2.78	6.22	6.38
4	6.54	29.51	55.37	24.55	3.23	3.23	28.16	12.31	1.97	7.84	17.26	7.81
5	10.66	23.72	16.27	38.05	5.28	5.28	7.15	19.25	3.29	5.43	4.06	11.39
6	13.18	19.68	33.02	26.25	6.67	6.67	13.59	12.28	4.30	6.11	7.17	6.98
7	12.21	37.00	24.98	18.61	5.38	5.38	9.75	7.54	3.02	11.68	5.39	4.25
8	18.20	14.54	16.14	108.95	9.29	9.29	7.43	55.08	5.87	4.02	4.44	33.40
9	20.47	37.20	15.46	12.90	10.28	10.28	5.13	5.05	6.05	10.08	2.66	2.55
10	12.03	38.66	24.59	11.87	5.38	5.38	12.37	6.25	2.97	10.85	7.57	3.93
11	13.41	na	42.65	na	6.18	na	19.57	na	3.49	na	9.81	na
12	34.13	na	28.00	na	16.56	na	12.02	na	9.82	na	6.64	na
13	14.83	na	5.98	na	7.52	na	2.79	na	4.61	na	1.68	na
14	10.87	na	28.05	na	5.48	na	11.77	na	3.48	na	6.19	na
15	15.32	na	38.27	na	7.60	na	19.09	na	4.63	na	11.36	na
16	9.05	na	68.26	na	4.47	na	33.61	na	2.74	na	18.94	na
17	11.87	na	62.65	na	5.43	na	30.88	na	3.10	na	17.35	na
18	8.88	na	11.91	na	3.93	na	5.92	na	2.16	na	3.55	na
19	10.93	na	44.34	na	5.20	na	17.37	na	3.17	na	9.46	na
20	24.81	na	8.12	na	12.02	na	3.30	na	7.06	na	1.59	na
21	23.48	na	20.43	na	11.64	na	8.86	na	7.32	na	4.34	na
22	12.96	na	70.25	na	6.05	na	33.90	na	3.48	na	20.46	na
Mean	15.50	23.00	31.06	33.63	7.52	7.34	14.10	15.52	4.52	6.36	7.94	8.99
SD	6.44	12.00	18.93	28.34	3.20	2.48	9.63	14.58	1.94	3.58	5.69	8.94
min	6.54	7.17	5.98	11.87	3.23	3.23	2.79	5.05	1.97	1.98	1.59	2.55
max	34.13	38.66	70.25	108.95	16.56	10.28	33.90	55.08	9.82	11.68	20.46	33.40

Table A2. Proportion of overlap between two consecutive days of the daily activity range for each group, based on Autocorrelated Kernel Density Estimate (AKDE), considering the 95%, 70% and 50% probability of use. Highest values for each isopleth and longest period with zero overlap are highlighted.

Days	AKDE95%				AKDE70%				AKDE50%			
	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02
1-2	21.6%	57.5%	42.3%	9.5%	10.4%	10.4%	0.6%	0.0%	0.0%	2.0%	0.0%	0.0%
2-3	29.9%	19.1%	49.9%	0.0%	6.6%	6.6%	45.2%	0.0%	0.0%	0.0%	24.7%	0.0%
3-4	8.5%	36.4%	53.7%	49.0%	1.8%	1.8%	15.9%	20.9%	0.1%	0.8%	0.3%	11.6%
4-5	24.9%	28.4%	9.5%	19.3%	10.6%	10.6%	0.0%	0.7%	7.2%	0.0%	0.0%	0.0%
5-6	75.8%	54.8%	4.0%	19.6%	59.8%	59.8%	0.0%	12.7%	49.7%	21.9%	0.0%	5.2%
6-7	26.7%	42.7%	5.0%	0.7%	0.0%	0.0%	0.0%	0.0%	0.0%	4.2%	0.0%	0.0%
7-8	32.5%	31.5%	0.0%	48.7%	4.5%	4.5%	0.0%	61.2%	0.0%	9.9%	0.0%	66.6%
8-9	29.0%	65.1%	22.1%	7.5%	28.5%	28.5%	0.0%	0.9%	35.0%	22.7%	0.0%	0.0%
9-10	22.5%	41.8%	4.6%	13.1%	12.7%	12.7%	0.0%	0.0%	2.7%	0.0%	0.0%	0.0%
10-11	53.3%	64.1%	14.0%	6.4%	19.4%	19.4%	3.0%	7.0%	6.1%	59.8%	0.0%	7.1%
11-12	33.2%	na	7.2%	na	26.5%	na	0.0%	na	23.6%	na	0.0%	na
12-13	22.1%	na	1.5%	na	10.1%	na	0.0%	na	0.7%	na	0.0%	na
13-14	44.3%	na	21.6%	na	26.2%	na	0.0%	na	8.8%	na	0.0%	na
14-15	64.7%	na	74.1%	na	35.2%	na	73.6%	na	26.9%	na	81.6%	na
15-16	23.0%	na	77.6%	na	14.6%	na	82.3%	na	11.7%	na	84.8%	na
16-17	67.5%	na	28.4%	na	30.0%	na	11.0%	na	17.6%	na	0.0%	na
17-18	33.3%	na	15.6%	na	4.6%	na	10.2%	na	0.0%	na	2.9%	na
18-19	30.5%	na	26.5%	na	0.3%	na	0.0%	na	0.0%	na	0.0%	na
19-20	75.5%	na	13.8%	na	41.1%	na	11.9%	na	31.1%	na	7.4%	na
20-21	64.3%	na	13.6%	na	39.3%	na	0.0%	na	20.0%	na	0.0%	na
21-22	26.6%	na	72.4%	na	12.7%	na	78.7%	na	4.1%	na	74.7%	na
Mean	38.6%	44.1%	26.5%	17.4%	18.8%	15.4%	15.8%	10.3%	11.7%	12.1%	13.2%	9.1%
SD	19.9%	15.8%	25.1%	17.8%	15.9%	17.7%	28.1%	19.2%	14.3%	18.9%	28.7%	20.6%
min	8.5%	19.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
max	75.8%	65.1%	77.6%	49.0%	59.8%	59.8%	82.3%	61.2%	49.7%	59.8%	84.8%	66.6%

Table A3. Proportion of overlap between every two days of the daily activity range for each group, based on Autocorrelated Kernel Density Estimate (AKDE), considering the 95%, 70% and 50% probability of use. Highest values for each isopleth and longest period with zero overlap are highlighted.

Days	AKDE95%				AKDE70%				AKDE50%			
	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02
1-3	20.0%	20.9%	23.5%	20.9%	12.3%	0.0%	3.0%	28.5%	12.2%	0.0%	0.0%	30.0%
2-4	6.9%	28.2%	53.4%	22.9%	0.8%	0.0%	13.4%	14.8%	0.0%	0.0%	0.0%	5.6%
3-5	43.7%	47.3%	14.7%	35.6%	34.6%	21.6%	0.4%	11.5%	26.3%	6.3%	0.0%	5.1%
4-6	30.2%	1.3%	47.3%	0.0%	13.6%	0.0%	38.1%	0.0%	0.0%	0.0%	35.0%	0.0%
5-7	28.6%	72.9%	40.9%	0.0%	0.8%	66.6%	27.3%	0.0%	0.0%	72.2%	10.3%	0.0%
6-8	43.1%	0.0%	2.3%	10.5%	25.4%	0.0%	0.0%	0.5%	16.3%	0.0%	0.0%	0.0%
7-9	3.1%	45.6%	38.9%	0.0%	0.0%	21.9%	36.9%	0.0%	0.0%	6.2%	25.3%	0.0%
8-10	44.1%	63.1%	0.1%	10.6%	21.4%	19.0%	0.0%	8.6%	11.4%	6.2%	0.0%	5.6%
9-11	14.0%	na	77.1%	na	12.6%	na	52.3%	na	15.1%	na	20.9%	na
10-12	64.9%	na	27.2%	na	70.5%	na	5.7%	na	58.6%	na	0.0%	na
11-13	56.0%	na	0.0%	na	47.4%	na	0.0%	na	14.7%	na	0.0%	na
12-14	23.6%	na	67.3%	na	21.0%	na	29.3%	na	18.5%	na	7.5%	na
13-15	53.1%	na	0.0%	na	44.0%	na	0.0%	na	34.8%	na	0.0%	na
14-16	56.6%	na	83.0%	na	43.2%	na	99.5%	na	38.3%	na	91.4%	na
15-17	19.2%	na	62.6%	na	3.4%	na	25.2%	na	0.0%	na	0.0%	na
16-18	31.1%	na	0.2%	na	19.5%	na	0.0%	na	3.5%	na	0.0%	na
17-19	64.9%	na	38.6%	na	54.5%	na	14.6%	na	42.7%	na	0.0%	na
18-20	86.4%	na	0.0%	na	75.5%	na	0.0%	na	76.7%	na	0.0%	na
19-21	43.0%	na	18.7%	na	20.0%	na	3.4%	na	19.3%	na	0.0%	na
20-22	35.6%	na	67.2%	na	10.5%	na	51.2%	na	4.4%	na	43.4%	na
Mean	38.4%	34.9%	33.2%	12.6%	26.6%	16.1%	20.0%	8.0%	19.6%	11.4%	11.7%	5.8%
SD	21.3%	27.0%	28.5%	13.0%	22.6%	22.9%	25.9%	10.2%	21.2%	24.8%	22.9%	10.1%
min	3.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
max	86.4%	72.9%	83.0%	35.6%	75.5%	66.6%	99.5%	28.5%	76.7%	72.2%	91.4%	30.0%

Table A4. Proportion of overlap between every three days of the daily activity range for each group, based on Autocorrelated Kernel Density Estimate (AKDE), considering the 95%, 70% and 50% probability of use. Highest values for each isopleth and longest period with zero overlap are highlighted.

Days	AKDE95%				AKDE70%				AKDE50%			
	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02	GUA01	GUA02	PBC01	PBC02
1-4	24.8%	61.9%	97.7%	10.2%	22.1%	0.0%	95.6%	7.0%	19.1%	0.0%	93.8%	4.4%
2-5	26.5%	72.6%	37.6%	0.0%	14.4%	47.1%	31.6%	0.0%	0.7%	27.6%	20.3%	0.0%
3-6	29.8%	45.3%	9.0%	0.0%	19.6%	30.1%	0.0%	0.0%	16.6%	14.9%	0.0%	0.0%
4-7	43.8%	78.5%	14.1%	0.0%	10.8%	60.2%	0.0%	0.0%	4.4%	41.9%	0.0%	0.0%
5-8	37.3%	26.6%	32.6%	60.7%	8.6%	11.3%	3.3%	17.4%	0.6%	0.0%	0.0%	4.6%
6-9	55.0%	54.7%	2.5%	0.0%	42.8%	10.8%	0.0%	0.0%	28.1%	0.0%	0.0%	0.0%
7-10	48.3%	65.7%	13.0%	0.0%	9.4%	50.5%	0.0%	0.0%	0.0%	39.5%	0.0%	0.0%
8-11	51.7%	na	9.7%	na	48.7%	na	0.0%	na	40.0%	na	0.0%	na
9-12	86.1%	na	7.3%	na	46.9%	na	0.0%	na	18.2%	na	0.0%	na
10-13	66.0%	na	0.0%	na	36.3%	na	0.0%	na	22.5%	na	0.0%	na
11-14	33.1%	na	9.4%	na	12.7%	na	2.0%	na	9.3%	na	0.0%	na
12-15	14.3%	na	55.7%	na	7.5%	na	19.8%	na	3.3%	na	3.4%	na
13-16	35.5%	na	5.4%	na	20.2%	na	0.0%	na	8.2%	na	0.0%	na
14-17	47.9%	na	56.7%	na	17.8%	na	19.5%	na	8.2%	na	0.0%	na
15-18	37.6%	na	0.0%	na	28.2%	na	0.0%	na	10.5%	na	0.0%	na
16-19	73.3%	na	35.3%	na	55.5%	na	29.8%	na	41.4%	na	20.8%	na
17-20	63.8%	na	10.1%	na	24.6%	na	4.7%	na	18.2%	na	0.0%	na
18-21	51.4%	na	39.1%	na	6.6%	na	33.4%	na	0.0%	na	29.2%	na
19-22	83.1%	na	60.0%	na	66.8%	na	40.6%	na	50.5%	na	30.4%	na
Mean	47.9%	57.9%	26.1%	10.1%	26.3%	30.0%	14.8%	3.5%	15.8%	17.7%	10.4%	1.3%
SD	19.8%	17.7%	26.5%	22.6%	18.1%	23.3%	24.1%	6.7%	15.1%	18.7%	22.8%	2.2%
min	14.3%	17.7%	0.0%	0.0%	6.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
max	86.1%	78.5%	97.7%	60.7%	66.8%	60.2%	95.6%	17.4%	50.5%	41.9%	93.8%	4.6%

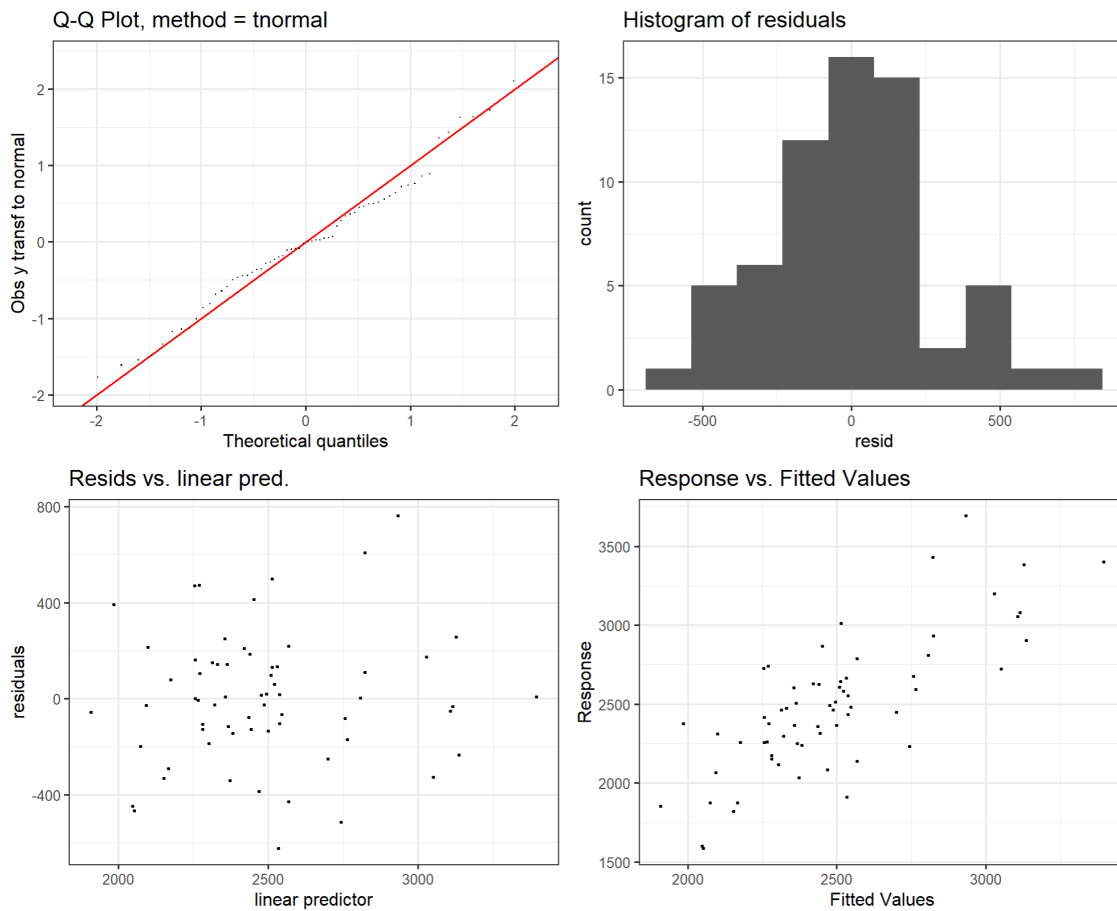


Figure A4. Plots of the residuals relative to the results of the GAM model for model fit checking: Q-Q plot (top-left); Histogram of residuals (top-right); Plot of residual values (bottom-left); and Plot of response against fitted values (bottom-right).

4.12 SUPPLEMENTARY MATERIAL

4.12.1 DATA PROCESSING AND CRITERIA FOR DATA EXCLUSION/INCLUSION

In this material, we present all the steps followed for processing the data that was used for all further analyses on chapters 3 and 4. Here, we provide the assessment of the performance of GPS and accelerometer biologgers deployed in a free-ranging wild Neotropical primate. Our analyses showed that these devices are effective to be used in movement studies of small arboreal primates and demonstrate the advantages of using GPS and accelerometer combined.

4.12.1.1 METHODS

We excluded GPS data from the first day of each group, to mitigate biases caused by the capture stress, and from the last day, whenever the GPS battery ran out before the end of the activity period for that day, as it would affect the daily path analysis (Criterion 1). Second, on the remaining days, we identified the start and end times of the activity period for each group based on a visual inspection of the accelerometer data. Black lion tamarins spend their inactivity period (night) in selected sleeping sites that are usually tree cavities or vine tangles (Rylands & Mittermeier, 2013). The lack of a clear sky view could affect GPS data collection and results in false positives or no recordings within the 13 hours of the fixed monitoring period. So, using accelerometer data to identify the exact time that the tamarins started and ended the activity period allowed us to exclude the GPS data from the inactivity period for further analyses (Criterion 2).

As the GPS were programmed to collect data every ten minutes during their activity period, we could identify missing data during the activity period (day) and check if the animal was resting at that time. If the animal was indeed immobile, we assumed that the reason for the missing location(s) was due to lack of a sky view because the individual was inside a sleeping site for a resting. Whenever we identified this situation, to allow for a better estimation of the utilization distribution method for the home range analyses (cf. Supplementary material 9.2 for details), we duplicated the location recorded immediately before or after the respective daytime rest (whichever was closer to its start or end time) (Criterion 3). In practice, it would correspond to the same situation of recording locations at the same place while the animal is not moving.

To identify if there was any interval longer than one hour with missing data, we established a point aggregation criterion (burst), in which a trajectory would correspond to the set of points with less than an hour interval between them, since they were collected every 10 minutes. A new trajectory was created in every instance that the GPS signal was lost for more than one hour (Criterion 4). However, based on this criterion, there were only unique trajectories within the same 24-hour period (i.e., no intervals of over 1 hour without GPS locations), so we did not exclude any locations but could use these bursts to estimate the daily path distances.

Lastly, we carefully analysed the accuracy of locations recorded using their horizontal dilution of precision (HDOP), a parameter provided by the GPS unit that describes the error caused by the relative position of the GPS satellites when the location was recorded. In other words, a low HDOP value represents a better positional precision due to the wider angular separation between the satellites used to calculate the position. We assessed the accuracy dividing the HDOP values in three categories, being highly accurate the locations with $\text{HDOP} \leq 4$, acceptably accurate between 4 and 15, and lowly accurate the ones with $\text{HDOP} > 15$. Then, we thoroughly analysed these latter, as the error associated to these locations could be inaccurate by more than 90 metres, and decided whether they should be considered for the analysis (Criterion 5). Spatial data visualisation and analyses were made in the QGIS software (Quantum GIS Development Team, 2022).

4.12.1.2 RESULTS

All four groups combined, the GPS recorded 4,801 locations in 1,575.5 hours, from the 5,167 expected by the schedule for this period, which corresponds to a 93% average efficiency (Table S1). When we applied Criterion 1, we excluded 129 locations corresponding to the first days of each group (GUA01 = 36; GUA02 = 17; PBC01 = 47; PBC02 = 29), and 16 locations corresponding to the last day of group GUA01, as the GPS battery for this device ran out at 11:30 am (Table S1). For GUA02, PBC01 and PBC02, we kept the locations of the last days.

When we applied Criterion 2, we excluded from the database another 327 locations that were recorded out of the activity period, remaining only 24 missing data during the activity period (Table S1). When we applied Criterion 3, we could add to the dataset 13 repeated locations for when the animal was not moving (resting). Finally,

based on Criterion 5, 28 locations (0.6%) presented low accuracy (being 4 with HDOP > 20). These were carefully analysed and as they did not explicitly show a discrepant spatial pattern, we opt to not exclude them, ending up with a database of 4,358 locations to be used for further analyses, with 88.8% of highly accurate ones (HDOP ≤ 4) and 93.6% acquired with ≥ 4 satellites. This corresponds to an average of $1,090 \pm 496$ locations per group, over 10 to 22 monitoring days (68 ± 3 locations per day), achieving a 99.5% average efficiency of the GPS in collecting data during the activity period (Table S1).

Table S1. Summary of the GPS parameters during the monitoring period of the four black lion tamarins belonging to four different groups in the wild.

Group	First location – date and time	Last location – date and time	Battery length (hhh:mm)	N of expected locations	N of non-marked locations	Efficiency for the scheduled monitoring	N of non-marked locations during activity period	Efficiency during activity period (N of expected locations)	Mean # of satellites
GUA01	24/Sep/2019 13:42	17/Oct/2019 11:30	549:48	1776	91	94.8%	8	99.5% (N=1472)	3.3
GUA02	18/Sep/2019 17:40	28/Sep/2019 21:50	244:10	805	67	91.7%	5	99.3% (N=634)	3.3
PBC01	24/Sep/2020 12:23	16/Oct/2020 21:50	537:27	1772	125	92.9%	8	99.5% (N=1570)	3.2
PBC02	01/Feb/2021 16:21	11/Feb/2021 20:20	243:59	814	83	89.8%	3	99.6% (N=693)	3.3
TOTAL	-	-	1575:24	5167	366	93% (mean)	24	99.5% (mean)	3.3 (mean)

Legend:

N of expected locations = number of expected locations based on the monitoring schedule of locations every 10 minutes from 6:00 to 19:00 BRT;

N of non-marked locations = number of locations missed by the GPS based on the monitoring schedule;

Efficiency for the scheduled monitoring = proportion of marked locations over the scheduled ones based on the monitoring schedule;

N of non-marked locations during activity period = number of locations missed by the GPS when only the true activity period of the monitored animal was considered;

Efficiency during activity period (N of expected locations) = proportion of marked locations over the scheduled ones based on the true activity period of the monitored animal.

4.12.2 HOME RANGE ESTIMATION BASED ON THREE METHODS

This material was prepared with the objective of presenting the methods used to calculate the home range of the black lion tamarins in this study, and justify the choice for the Biased Random Bridge method for the development of the further analyses in this chapter.

4.12.2.1 METHODS

To estimate black lion tamarins' home range, following the recommendation to use multiple methods and compare the sensitivity of the results to the influence of the method (Fieberg & Börger, 2012), we used three methods: the Fixed Kernel Utilization Distribution (FKUD) with two values for the bandwidth (smoothing parameter, h), one based on the reference method (Href; Worton, 1989) and the other as the minimum value below which the home range polygon breaks up (minH; Fieberg & Börger, 2012), and the Biased Random Bridge (BRB) (Benhamou, 2011). The latter considers serial autocorrelation of the relocations, similar to the Brownian bridge approach, but allowing for the inclusion of parameters such as proportion of activity within each step (supplied here by the accelerometers – see Methods in Chapter 4) and a fixed smoothing parameter (h) that accounts for the grid resolution, the step length distribution and the standard deviation of the GPS inaccuracy (Table S1). For all estimations, we used a standardized 4000x4000-m grid of 5-m pixels (640,000 pixels), centred on the centroid of the recorded locations on each fragment. We could not use the boundary argument to delimit the estimations based on the fragment edge (considering that the tamarins would not use non-forest areas), as implemented in the `adehabitatHR` R package (Calenge, 2015), due to the complexity of the fragment shape. Therefore, we clipped the total home range areas *a posteriori* to exclude non-forest areas and compared the proportion of clipped areas among the different methods.

Table S1. Estimated smoothing parameters used on each of the home range estimation methods, based on the dataset for each group. A standardized value was defined for Hmin on BRB as the parameters analysed for its estimation were very similar among the groups' datasets.

Group	Href - FKUD	minH - FKUD	Hmin - BRB	minH - BRB
GUA 01	49.2	29.5	30	29
GUA 02	70.2	52.7	30	48
PBC 01	89.3	49.1	30	61
PBC 02	131.8	98.9	30	93

Legend: Href = smoothing parameter based on the reference method; minH = the minimum value below which the home range polygon breaks up (here we present the values used for the Fixed Kernel Utilization Distribution - FKUD estimates, and the values that would work for Biased Random Bridge - BRB); Hmin is the smoothing parameter for BRB defined by considering the grid resolution (5 m), the distribution of step lengths (as a random component inherent to the animal behaviour) and the standard deviation of the locations' inaccuracy (HDOP 2.5 ~ 15 m).

We considered the total home range and the core areas as the regions with 95% and 50% probability of use, respectively. We also checked whether the 50% Utilization Distribution really represent the core area for these animals by comparing the observed space-use pattern with that expected from a uniform pattern of use (Samuel et al., 1985).

4.12.2.2 RESULTS

Depending on the method used, we found 3- to 5-fold differences in home range size among the groups (Figure S1; Table S2). Lower differences were shown on the estimates using BRB. This method was also responsible for smaller proportions of areas clipped by the fragment shape, along with FKUD minH for GUA01 (Table S3). Similarly, the core area sizes show differences of more than 5 times among the groups (Figure S1; Table S4). Importantly though the relative differences between groups remained broadly consistent, which is the important biological signal (*sensu* Börger et al., 2006) – see below for further discussion of the observed differences. We also found that a 70% Utilization Distribution is the observed core area for the black lion tamarins when compared to an expected uniform pattern of use (Figure S2). For this reason, all further analysis considered the 70% isopleth as the core area for the tamarins, although we also present the values for 50%.

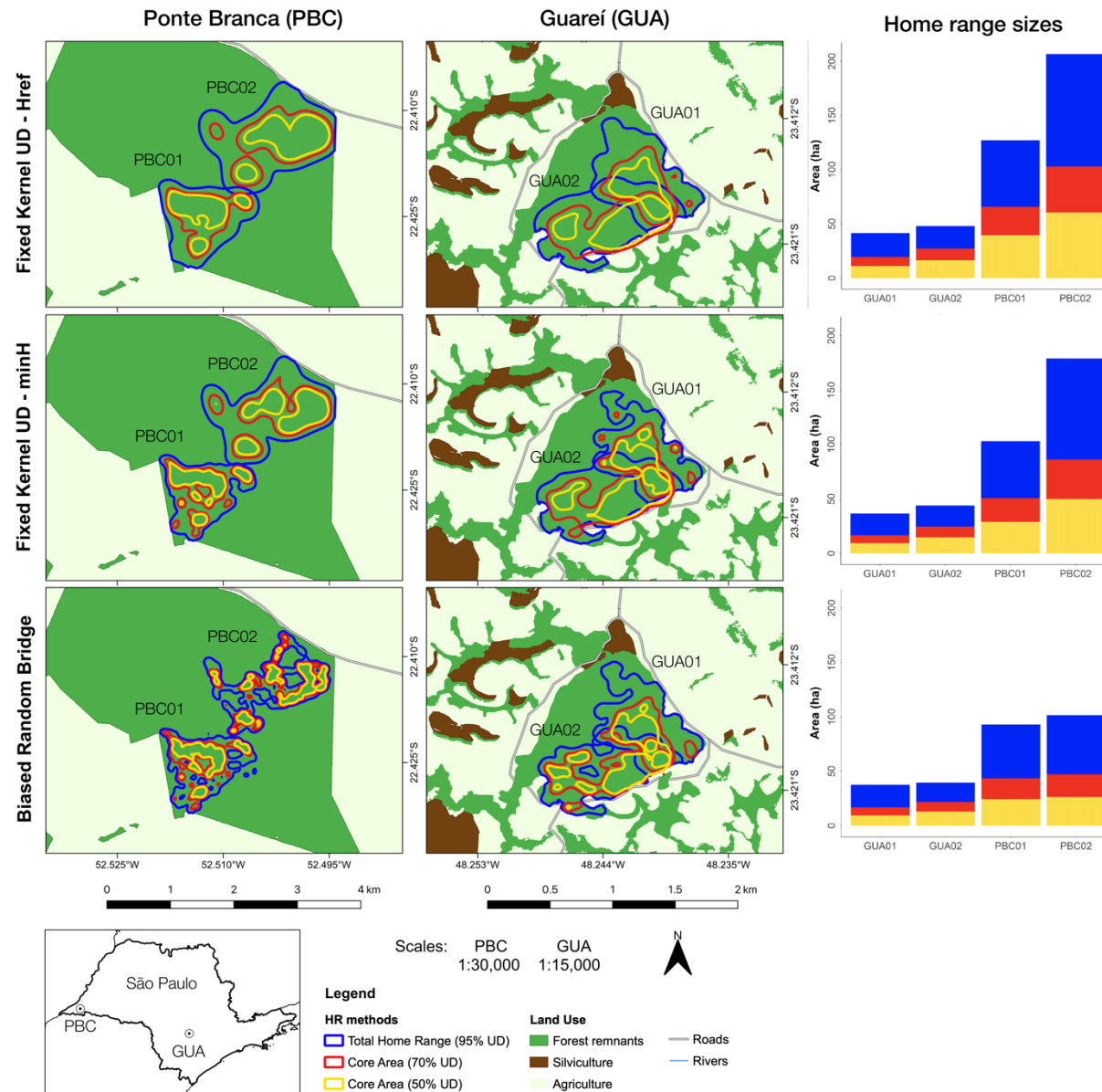


Figure S1. Home range (95%UD - blue) and core areas (70%UD - red; and 50%UD - yellow) for each black lion tamarin group in the Ponte Branca (left) and Guareí (right) fragments, based on three methods: Fixed Kernel Utilization Distribution (FKUD) with the smoothing parameter based on the reference method (Href; top), FKUD with the smoothing parameter as the minimum value below which the home range polygon breaks up (minH, center) and the Biased Random Bridge (BRB; bottom). Bar charts show the area (in ha) for each estimate of the respective method.

Table S2. Black lion tamarin total home range (95% Utilization Distribution) areas based on Fixed Kernel Utilization Distribution (FKUD) and Biased Random Bridge (BRB), for GUA01 and PBC01, considering the full dataset (22 days) and the 13 subsets of 10 consecutive days, derived from the full dataset. Letters indicate when less subsets were included due to limitation of the method to generate an estimate. All values are in hectares (ha).

Group	22 days			10 days (Mean $\pm$ SD; min-max)		
	FKUD Href	FKUD minH	BRB	FKUD Href	FKUD minH	BRB
GUA 01	44.6	37.8	39.0	43.2 $\pm$ 5.3; 31.7-49.2	37.8 $\pm$ 6.9; 33.1-47.1 ^a	35.3 $\pm$ 4.2; 26.3-39.4 ^b
PBC 01	128.1	103.1	92.9	126.2 $\pm$ 16.5; 97.9-147.1	114.8 $\pm$ 23.1; 74.0-147.1 ^c	75.6 $\pm$ 9.3; 57.1-87.2

Legend: ^a N=10; ^b N=11; ^c N=12.

Table S3. Black lion tamarin total home range (95% Utilization Distribution) based on Fixed Kernel Utilization Distribution (FKUD) and Biased Random Bridge (BRB), for each group in the Guareí (GUA) and Ponte Branca (PBC) fragments. For values clipped by the fragment boundaries, the percentage of reduced area is presented.

Group	FKUD Href (ha)		FKUD minH (ha)		BRB (ha)	
	Estimated	Clipped (%)	Estimated	Clipped (%)	Estimated	Clipped (%)
GUA 01	44.6	41.5 (-7.0%)	37.8	36.5 (-3.4%)	39.0	37.5 (-3.8%)
GUA 02	57.6	47.9 (-16.8%)	50.6	44.0 (-13.0%)	42.6	39.5 (-7.3%)
PBC 01	128.1	127.2 (-0.7%)	103.1	103.1 (0%)	92.9	92.9 (0%)
PBC 02	209.6	206.7 (-1.4%)	179.1	179.1 (0%)	101.4	101.4 (0%)

Legend: Href = smoothing parameter based on the reference method; minH = the minimum value below which the home range polygon breaks.

Table S4. Black lion tamarin core areas (50% and 70% Utilization Distribution) based on Fixed Kernel Utilization Distribution (FKUD) and Biased Random Bridge (BRB), for each group in the Guareí (GUA) and Ponte Branca (PBC) fragments. All values are in hectares (ha).

Group	FKUD Href (ha)		FKUD minH (ha)		BRB (ha)	
	50%UD	70%UD	50%UD	70%UD	50%UD	70%UD
GUA 01	11.0	19.6	9.4	16.6	9.3	16.8
GUA 02	17.7	29.4	15.5	25.9	12.9	21.8
PBC 01	39.6	65.7	28.9	50.8	24.3	43.5
PBC 02	60.6	102.9	50.0	86.1	26.4	47.2

Legend: Href = smoothing parameter based on the reference method; minH = the minimum value below which the home range polygon breaks.

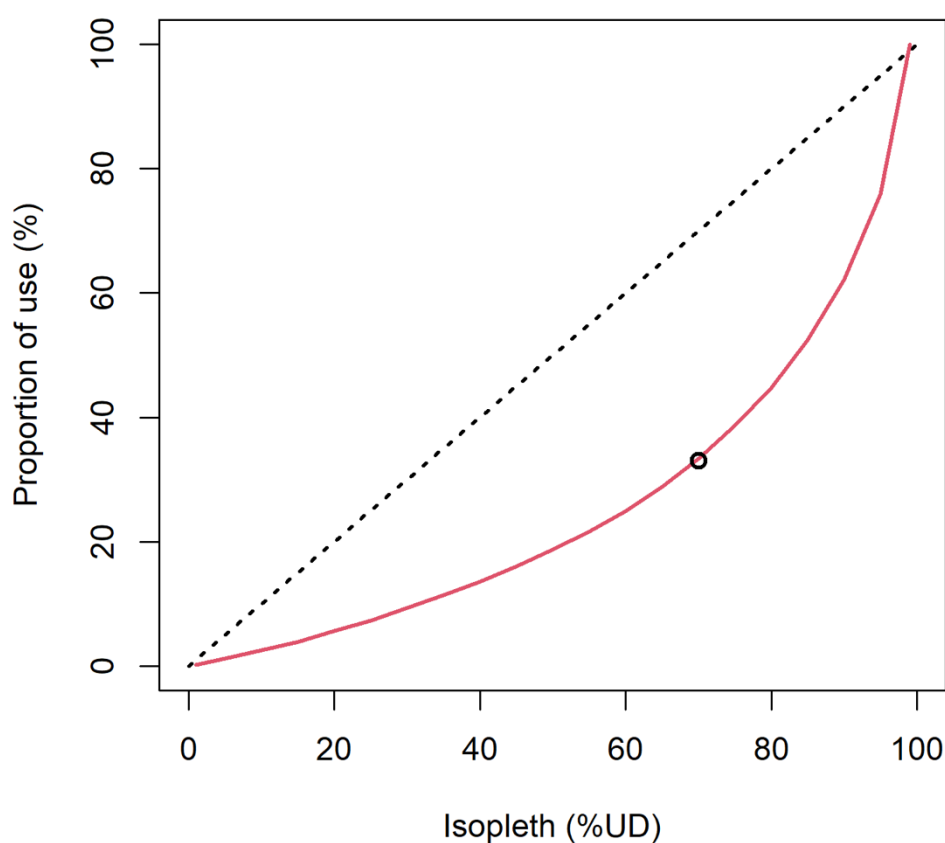


Figure S2. The red line shows the space-use pattern, based on FKUD estimates, for the black lion tamarin groups, while the dashed line indicates a uniform pattern of use. The black point indicates the point of maximum deviation from the equality line, showing that the 70% isopleth represents the core area for the black lion tamarin.

4.12.2.3 DISCUSSION

Our home range estimations showed larger variation among methods for the PBC groups. This variation was directly related to the differences on the smoothing parameters (h) used for each method (Table S1). Because on BRB we used a fixed value for all groups, as the parameters analysed for its estimation (i.e., the grid resolution, the distribution of step lengths, and the standard deviation of the locations' inaccuracy) were very similar among the groups' datasets, the estimates for this method were more discrepant for the PBC01 and PBC02 groups where the differences of the h value (in relation to the ones used for the other methods) were more pronounced. However, this choice of h was enough to yield a contiguous 95% isopleth for at least one group (GUA01) and avoided oversmoothing the data, which would reflect in the inclusion of a high proportion of non-used areas. At the same time, the proportion of area clipped by the fragment boundary was smaller for BRB, as it better reflected the real use of the space by the tamarins, with less extrapolation to areas not actually used. In fact, the higher proportion of clipped area were related to higher differences between the h used in the different methods compared. However, we emphasize that we worked with datasets related to short periods of time (10 and 22 days) and these results might change by including more days or if the animals are monitored in different seasons, since resource availability and distribution, as important drivers of ranging patterns, varies across different temporal scales (Börger et al., 2006; Campos et al., 2014; Souza-Alves et al., 2021). Therefore, we highlight the importance of selecting both the appropriate method and the smoothing parameter according to the research questions and the time scale considered.

In conclusion, for this study, we chose the BRB method for our home range estimations, with a fixed smoothing parameter ($h = 30$) among the different groups, as this method allows for the incorporation of the accelerometer data as the proportion of activity within each step, and a smoothing parameter that accounted for intrinsic factors to our data (such as the GPS inaccuracy) and to the species (such as the distribution of step lengths). Given that we are working in fragmented habitat and with small time scales, we considered that oversmoothing the data would produce results that would mask the real patterns of space use, hindering our interpretation.

5 CHAPTER IV: MOVEMENT-RELATED ENERGY EXPENDITURE OF BLACK LION TAMARINS IN FRAGMENTED HABITATS

(Capítulo redigido em formato de manuscrito para submissão à revista *Movement Ecology Journal*)

5.1 RESUMO

Título: Gasto energético relacionado ao movimento de micos-leões-pretos em habitats fragmentados

O gasto de energia relacionado ao movimento indica como os animais se comportam em habitats alterados. O mico-leão-preto (*Leontopithecus chrysopygus*), um primata arborícola, endêmico da Mata Atlântica brasileira e ameaçado de extinção, pode ser afetado por mudanças na estrutura da floresta devido à fragmentação e degradação do habitat. Avaliar seu gasto energético em diferentes fragmentos permitiria, assim, compreender como as características da floresta afetam o custo de movimentação. Monitoramos quatro grupos (um mico/grupo) usando dispositivos de GPS e acelerômetro triaxial acoplados nos animais – dois grupos em um fragmento grande (1.303 ha) e dois em um pequeno (105 ha). Caracterizamos a estrutura da vegetação com base em medições de árvores e também obtivemos valores de temperatura, umidade e duração do dia de cada área. Os movimentos dos micos foram monitorados ao longo de um mês, com localizações de GPS registradas a cada 10 minutos durante seu período de atividade (~8h/dia), que foram usadas para estimar o deslocamento diário médio (DPL). Os dados do acelerômetro foram registrados 24 horas/dia a uma frequência de 25 Hz, fornecendo estimativas de duração do período de atividade diário, proporção de atividade e gasto energético diário (DEE), usando VeDBA total (Vetor da Aceleração Dinâmica do Corpo) como *proxy* para gasto energético, em cada fase do ritmo diário (dia x noite), período do dia (manhã x tarde) e cada hora. Através de modelos lineares de efeitos mistos (LMM) e modelos mistos aditivos generalizados (GAM), testamos o efeito da estrutura da vegetação, padrões de movimento (DPL e direcionalidade) e condições ambientais físicas (temperatura, umidade e fotoperíodo) no DEE entre os grupos. O DPL médio não diferiu entre as áreas ou grupos ($P > 0,05$), enquanto o DEE médio foi maior no fragmento maior ($P < 0,0001$). Nossos resultados indicaram que a distância percorrida foi o preditor mais importante do gasto energético, independentemente da escala temporal considerada em nossos modelos.

Tanto os fatores físicos quanto os bióticos (estrutura e composição da floresta) também influenciaram o DEE, além da direcionalidade do movimento. Encontramos uma relação negativa entre o gasto energético e as variáveis estruturais e composicionais da floresta, corroborando nossa hipótese de que os micos gastam menos energia em florestas de melhor qualidade. Os resultados nos permitiram fornecer recomendações para o manejo do hábitat, visando diminuir o custo energético do movimento em manchas florestais para esta espécie ameaçada de extinção.

PALAVRAS-CHAVE: custo de movimentação, acelerômetro, estrutura florestal, primata, *Leontopithecus chrysopygus*, Mata Atlântica

5.2 ABSTRACT

Movement-related energy expenditure indicates how animals fare in altered habitats. The endangered black lion tamarin (*Leontopithecus chrysopygus*), an arboreal primate endemic to the Brazilian Atlantic Forest, can be affected by changes in forest structure due to habitat fragmentation and degradation. Assessing its energy expenditure in different fragments would allow thus to understand the underlying drivers of how forest characteristics affect movement cost. We monitored four groups (one tamarin/group) using animal-attached GPS and tri-axial accelerometer devices - two groups from a large fragment (1,303 ha) and two from a small one (105 ha). We characterized the vegetation structure based on *in situ* tree measurements, and obtained values of temperature, humidity and daylength from each area. Tamarin movements were monitored over a month with GPS locations recorded every 10 minutes during their activity period (~8h/day), which were used to estimate mean daily path length (DPL). Accelerometer data was recorded for 24 hours/day at a 25-Hz frequency, providing daily length of activity period, proportion of activity and daily energy expenditure (DEE) estimates, using total VeDBA (Vectorial Dynamic Body Acceleration) as a proxy for energy expenditure, in each phase of the daily rhythm (day x night), period of the day (morning vs. afternoon) and each daytime hour. We ran linear mixed-effects models and generalised additive mixed models to test the effect of vegetation structure, movement patterns (DPL and directionality), and physical environmental conditions (temperature, humidity and daylength) on DEE among groups. Mean DPL did not differ between the areas or groups ($P > 0.05$), while mean DEE was higher in the larger

fragment ($P < 0.0001$). Our results indicated that the distance travelled was the most important predictor of energy expenditure, regardless of the time scale considered in our models. Both physical factors and biotic factors (forest structure and composition) also influenced DEE, in addition to the directionality of movement. We found a negative relationship between energy expenditure and the structural and compositional variables of the forest, corroborating our hypothesis that tamarins spend less energy in better quality forests. Results allowed us to provide recommendations for habitat management, aiming at lowering the energetic cost of movement in forest patches for this endangered species.

KEYWORDS: movement cost, accelerometer, forest structure, primate, *Leontopithecus chrysopygus*, Atlantic Forest

5.3 INTRODUCTION

Movement accounts for most of the energy that is expended by animals above the basal metabolic rate (Karasov, 1992; Levine, 2004). The movement capacity of an animal determines its efficiency in resource gathering and thus its survival under changes in the environmental conditions (de Knegt et al., 2007). Especially because there is a trade-off between energy spent in moving and energy invested in other vital functions (Jasienska, 2003; Sparrow & Newell, 1998), this might become critical for individuals and populations dealing with altered habitats (e.g. searching for food, escaping predators, etc.).

An interesting case concerns movement patterns of arboreal animals, such as Neotropical primates. These species predominantly travel and feed in the forest canopy and hence are expected to be strongly affected by changes in the forest structure (McLean et al., 2016). Thus, they are a good study system for understanding the relation between the structural configuration of the forest and movement-related energy expenditure. In particular, quantifying the movement costs of these animals in fragmented habitats can shed light on a key threat affecting the survival of many forest species (Hinam & Clair, 2008; Shepard et al., 2013) and inform more efficient conservation strategies (Allen & Singh, 2016; Doherty & Driscoll, 2018). In this context, animal-attached biologgers, including GPS, accelerometers, magnetometers, thermometers or atmospheric pressure sensors enable to remotely monitor fine scale movement patterns, habitat use and conditions, and estimate energy expenditure and predict individual reactions to natural and anthropogenic environmental changes (D. D. Brown et al., 2013; Tomkiewicz et al., 2010; Williams et al., 2020; R. P. Wilson et al., 2020).

The black lion tamarin, *Leontopithecus chrysopygus*, the study species for this work, is an endangered primate (G. C. Rezende et al., 2020), endemic to the Atlantic Forest and restricted to the Brazilian state of São Paulo, one of the most fragmented and modified areas of the Atlantic Forest (Coimbra-Filho & Mittermeier, 1973; Ribeiro et al., 2009). Whilst forest fragmentation is one of the key drivers of extinction in this species (G. C. Rezende et al., 2020), we do not know at which level forest fragmentation, and subsequent change in forest structure, starts to negatively impact the movements of black lion tamarins. In other words, when forest degradation affects

the energetic costs of movement. This lack of knowledge clearly impacts the ability to devise efficient conservation strategies, including the protection of forest fragments and the design of corridors connecting existing ones.

Having that in mind, here, we estimated and compared the movement-related energy expenditure of black lion tamarins living in forests with different structural characteristics. We aimed at understanding the effects of movement patterns, physical and biotic habitat conditions on the energy spent by these primates. With this information, we sought to identify determinant forest attributes, whether structural or compositional, that influence movement-related energy expenditure of black lion tamarins.

Given that black lion tamarins are arboreal primates, we expect to find greater movement-related energy expenditure in more altered forests, where the frequency of changes in movement directionality increases as a consequence of the greater variability in forest structure, when compared to more preserved ones (e.g., more frequent leaps, or leaps further away from one tree to another, or changes of locomotion type). If true, this will corroborate our hypothesis of the negative correlation between energy expenditure and variation in forest structure, such as tree height and density. The results will provide valuable insights into how the structural configuration of the habitat affects the movements of arboreal primates and their energy expenditure and will provide new evidence base for developing sound guidelines for managing the habitat for black lion tamarins.

5.4 OBJECTIVES

5.4.1 GENERAL

Estimate and compare the movement-related energy expenditure of black lion tamarins living in forests with different structural characteristics.

5.4.2 SPECIFIC

- I. Assess the effects of movement patterns on the energy spent by black lion tamarins;

- II. Assess the effects of physical and biotic habitat conditions on the energy spent by this species;
- III. Identify determinant forest attributes, whether structural or compositional, for the habitat use by black lion tamarins, aiming to reduce energy expenditure related to movement.

5.5 METHODS

5.5.1 STUDY SITE AND FIELD DATA COLLECTION

Field data was collected in two Atlantic Forest patches in São Paulo state, southeast Brazil. The first area is a 105-ha forest remnant within a private farm located in the municipality of Guareí (GUA: 23°24'59.7"S, 48°14'35.7"W), in the southeast portion of the state. The second is a 1,303-ha forest fragment called Ponte Branca (PBC: 22°25'08.9"S, 52°30'23.3"W) that belongs to the Black Lion Tamarin Ecological Station (ICMBio), a protected area in the municipality of Euclides da Cunha Paulista, in the westernmost tip of the state (Figure 1). All fragments are remnants of tropical seasonal semideciduous forests (IBGE, 2012; Veloso et al., 1991).

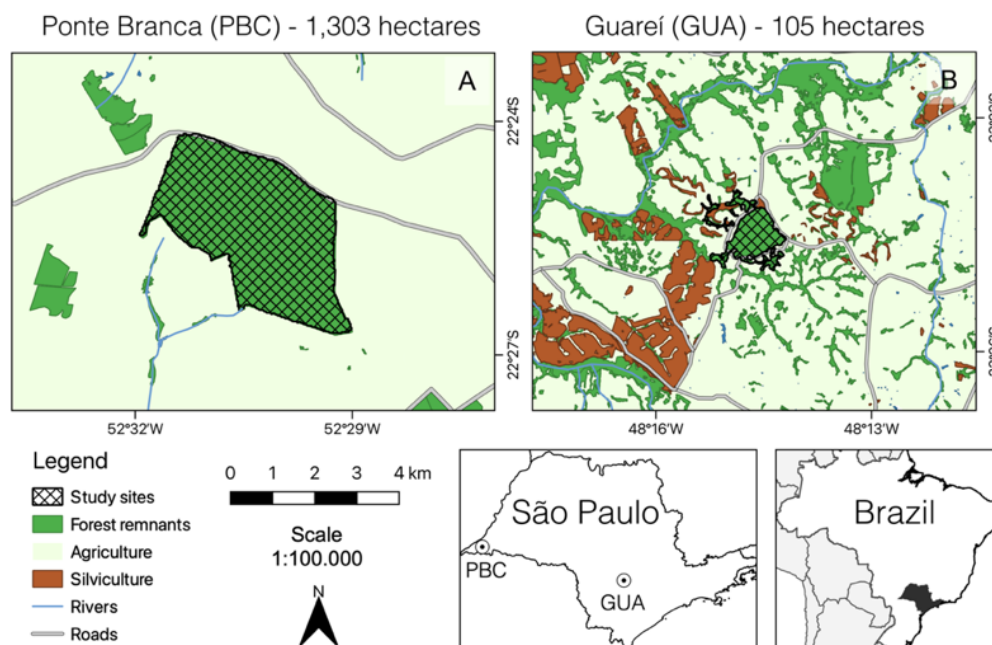


Figure 1. Study sites (cross-hatched areas): A. Ponte Branca, in Pontal do Paranapanema; B. Guareí, in Alto Paranapanema, both in the Brazilian state of São Paulo.

Movement data was collected through *in situ* monitoring of four black lion tamarin groups, two per area. One adult male black lion tamarin (mean weight: 620g $\pm$ 12.25) from each group was equipped with a 14-g backpack-style harness with a small housing for GPS and triaxial accelerometers (Axy Trek, TechnoSmart, Italy). One individual of each group was also equipped with a VHF collar (RI-2D, Holohil, Canada), to allow finding the group for subsequent equipment retrieving. The GPS devices were programmed to map the daily movement of the lion tamarins for a month, recording locations every 10 minutes, 13 hours a day (estimated activity period, from 09:00 UTC to 21:59 UTC, or 06:00 BRT to 18:59 BRT - local time), totalling 78 records per day. Accelerometers recorded at 25 Hz, 24 hours a day, for a set of 2.16 million records per day for each of the three axes (Figure 2). GPS data were managed and processed as described in Supplementary Material 9.1 presented in chapter 3.

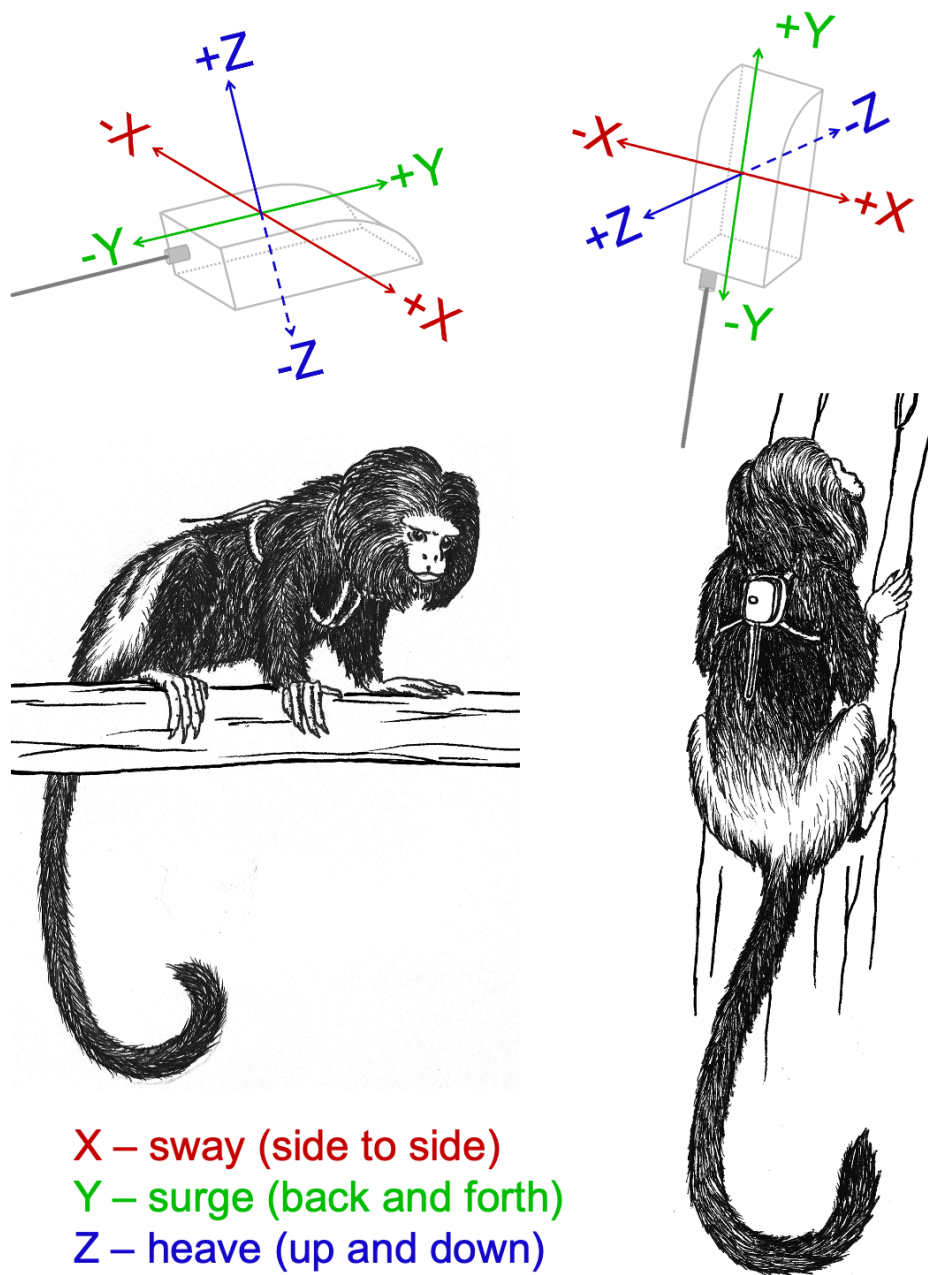


Figure 2. Black lion tamarin equipped with a GPS + accelerometer device (Axy Trek, TechnoSmart, Italy) in horizontal/sitting (left) and vertical/clinging (right) positions, indicating the three accelerometer axes (X-axis in red, Y-axis in green, Z-axis in blue) and their respective movement directions. Tamarin illustrator: Gustavo Libardi.

The groups in GUA were monitored in September and October/2019, while the groups in PBC were monitored in September and October/2020 and February/2021, respectively. Monitoring lasted for 10 to 22 days, according to the battery life of each device. We excluded the data from the first day of each group, to mitigate biases

caused by the capture stress, and from the last day, whenever the battery ran out before the end of the activity period for that day, as it would affect the daily path length analysis (Table 1). Both groups in each fragment had adjacent home ranges (see Chapter 3 of this dissertation).

Table 1. Monitoring period and data collected from the four black lion tamarin groups in the wild.

Group	Group size	N days	Period	GPS	Acc
GUA 01	7	22	25/Sep to 16/Oct/2019	1647	47.5 mi
GUA 02	5	10	19/Sep to 28/Sep/2019	731	21,4 mi
PBC 01	4	22	25/Sep to 16/Oct/2020	1685	45.5 mi
PBC 02	1	10	02/Feb to 11/Feb/2021	738	21,6 mi
Total	17	64	1575h24m	4801	136 mi

Legend: GPS = number of GPS locations recorded; Acc = number of records of the tri-axial accelerometer. Total Period is provided in hours of monitoring.

The GPS backpacks were attached in a longitudinal position relative to the body of the animal, on the dorsum of the tamarins, using a flexible polyester cord (shoelace) sewn around the animal's thoracic region, to ensure comfort and stability and prevent that a change in the device position would interfere in data collection (Figure 2). All captures were carried out with the support of the Black Lion Tamarin Conservation Program team, from IPÊ – Instituto de Pesquisas Ecológicas, and the presence of a veterinarian. The animals were anaesthetised during the whole procedure to reduce stress (GUA: intramuscular ketamine 12 mg/kg and midazolam 0.5 mg/kg; PBC: inhalation anaesthetic induction with isoflurane) and handled in accordance with protocols described in “Capture Protocols for Wild Lion Tamarins (*Leontopithecus* spp.)” (ICMBio, in prep.). Licenses for capturing, handling, and monitoring animals were duly provided by the responsible agencies (SISBio 41375 and 62116; COTEC nº 167/2015) and the project was approved by the Ethics Committee for Animal Use of the senior author's University (CEUA Decision IB-UNESP-CRC nº 12/2018).

5.5.2 HABITAT CHARACTERIZATION: PHYSICAL AND BIOTIC FACTORS

We characterized the forest structure and vegetation diversity in the two fragments where the groups were monitored by sampling all trees and palms with Diameter at Breast Height (DBH) ≥ 4.5 cm, contained in 21 plots of 10 x 10 m, systematically distributed in an area that includes the estimated home range for the groups monitored in each fragment (Caiafa & Martins, 2007; Ganzhorn et al., 2011). We estimated eleven variables from the field measurements (Table 2; Soares et al., 2006), which were used to verify whether there are significant differences in the structural characteristics or diversity among the areas. To compare the areas in terms of tree species composition, we estimated species richness, Shannon and Simpson diversity indexes, using interpolated (rarefaction) and extrapolated (prediction) accumulation curves corrected by Hill numbers ($q = 0, 1$ and 2 , respectively) (Chao et al., 2014). This sample-size-based method for comparing communities allows the comparison of uneven sample sizes, as it considers the inventory completeness (or sample coverage) (Chao et al., 2014). Analyses were developed using the “iNEXT” package (Hsieh et al., 2016) in software R 4.1.3 (R Core Team, 2022) and R Studio 2022.2.3.492 (RStudio Team, 2022).

Table 2. Estimated variables for the characterization of forest structure in each study site.

Measured variable	Estimated variable
Number of trees per plot (with DBH ≥ 4.5 cm)	Mean (SD) density of trees (trees/m ²)
Species of trees and palms	Species Richness Shannon and Simpson Diversity index Gamma diversity
Perimeter at Breast Height (PBH) of the trees (cm)	Mean (SD) DBH (cm) Mean (SD) basal area (m ²) Cumulative basal area per hectare (m ² /ha)
Height of trees (m)	Mean (SD) height (m) Mean (SD) volume (m ³) Cumulative volume per hectare (m ³ /ha)

We compared the habitat in the study sites based on the forest structure and composition. Habitat structure estimated variables (Table 2) were compared using pairwise Kruskal-Wallis tests. The comparison of rarefaction and extrapolation curves of habitat composition variables was based on the overlap of the 95% confidence

interval estimates (Chao & Chiu, 2016). Using these same variables, we also assessed differences in vegetation structure and composition among the areas used by each group, considering only the data collected in the plots located within their respective estimated home range (FKUD 95%) (cf. Chapter 3). All variables referring to the groups home range were incorporated as covariates on the linear models that tested for the effect of vegetation structure and composition on the daytime energy expenditure of the tamarins (cf. item 3.4).

The climate in the study sites is marked by a dry and cold season (from April to September, or “winter”), alternating with a warm and humid period (from October to March, or “summer”) (Rolim et al., 2007). Daylength also varies between seasons, presenting the shortest days during winter (GUA: 10h42min; PBC: 10h45min), and longest during summer (GUA: 13h35min; PBC: 13h31min). As the daily light–dark cycle (day vs. night), the temperature rhythm and/or the humidity cycle are important triggers of phase-setting mechanisms in primates (Erkert, 2011), we considered these physical environmental variables to assess their added effects on the tamarins’ movements and energy expenditure. We obtained temperature (in °C) and specific humidity (in g/kg) data for each of the study areas, considering the central coordinate of each fragment (GUA: 23°24’59.7”S, 48°14’35.7”W; PBC: 22°25’08.9”S, 52°30’23.3”W), using the “microclima” R package (Maclean et al., 2019). Hourly data was obtained for the same monitoring period of the groups in the field. These variables were incorporated as covariates in generalised additive models (GAM) that tested for non-linear effects of physical environmental factors on the hourly energy expenditure of the tamarins (cf. item 3.4). We also obtained daylength (in seconds), i.e., the length between sunrise and sunset hours for each monitoring day, based on the times provided for each fragment’s municipality from the ‘Time and Date’ website (<https://www.timeanddate.com>). Daylength was incorporated as covariate in the linear mixed models per day and per period. We divided each day in two periods: the first period (morning) was from sunrise until 11:59:59 BRT, and the second (afternoon) was from 12:00:00 BRT until sunset (cf. item 5.4.3).

5.5.3 MOVEMENT PATTERNS AND ENERGY EXPENDITURE

GPS locations were used to estimate mean step length (SL) and mean turning angle (TA). For SL and TA estimations, we calculated the distance and the angle,

respectively, between two subsequent locations recorded in a trajectory, which is a sequence of steps connecting successive relocations of the monitored animal in a certain period of time (Turchin, 1998). These metrics were calculated for each study group using the “adehabitatLT” package in R (Calenge, 2019; Calenge, 2006). From the SL values, we estimated displacement within different time scales: (i) daily path length (DPL), i.e., the distance covered by each animal within the activity phase of a day (daytime), (ii) distance covered within each period of the day, defined as morning (DIST_M) from the time they started their activities until 11:59 BRT, and afternoon (DIST_A) from 12:00 BRT until the time they ended their activities of the respective day, and (iii) distance covered within an hour (DIST_H). To get the displacement values, we summed the values for each step (SL) part of the respective trajectory (DPL or DIST), within the respective time scales. Similarly, we estimated the cumulative turning angle by summing the modular angles within these same time scales.

Accelerometer data provided proxies for energy expenditure (EE, *sensu* Wilson et al., 2020), daily length of activity period and proportion of activity in each phase of the daily rhythm (daytime vs. nighttime). Proxies for EE estimates were provided by Dynamic Body Acceleration (DBA) metrics (Wilson et al., 2020). These estimates were validated for black lion tamarins as detailed in Chapter 2 of this study. Specifically, we used the smoothed Vectorial DBA (sVeDBA) metric. VeDBA was calculated via the following equation:

$$VeDBA = \sqrt{(DBAX)^2 + (DBAY)^2 + (DBAZ)^2} ,$$

where DBA is obtained in three dimensions: X or sway (side to side), Y or surge (back and forth) and Z or heave (up and down). Dynamic acceleration is calculated by subtracting the static from the raw acceleration signal, to eliminate the effects of gravitational force (Wilson et al., 2020). Then, as was done in Chapter 2, we applied a running mean across 120 records (5 seconds) to produce sVeDBA. In addition to the Daily sVeDBA, where we summed the sVeDBA values of all records for each 24-h period, we estimated values for each hour, day period (morning vs. afternoon) and the daytime (activity phase), also summing the sVeDBA values of all records within the respective period.

Accelerometer data were visualized and managed using DDMT software (Daily Diary Multiple Trace Graphing Tool, Wildbyte Technologies Ltd., Swansea), a

specialised software to manage and display large sets of complex multi-sensor biologging data. DDMT produces multiple visualisations, including interpolated time-based plots to show how acceleration changes over time at high resolution (in this case, 25 Hz), and calculates multiple metrics from the raw tri-axial accelerometer records, such as Overall DBA (ODBA), VeDBA, and pitch and roll angles (i.e., the rotational angles around the X- and Y-axis, respectively, thus measuring left-right and up-down movements of the body of the tamarins). The latter were used to estimate cumulative pitch and cumulative roll, by adding the modular angles within the same time scales as previous metrics.

To define start and end of activity period, we visually inspected the accelerometer data and the sVeDBA signal on DDMT. Considering that, during inactivity, the signals have very low, near zero, values, and that these values are considerably larger when the animal is active (Shepard et al., 2008), we identified the sudden transition from inactivity (night) to activity (day) phases. This was identified in every 24-hour period by detecting the exact time of this change on the accelerometer and sVeDBA channels (cf. Figure 3 in Chapter 2). This way we could estimate the daily length of activity period for each monitored animal. This information was also used to exclude the GPS data collected during the inactivity period, as the lack of a clear sky view inside the tamarins sleeping site (typically tree holes) could affect GPS data collection and results in strongly inaccurate positions or missing locations within the 13 hours of the fixed monitoring period.

To estimate the proportion of activity and define the behaviours in each phase of the daily rhythm, a threshold value of sVeDBA to describe inactivity was estimated, applying the methods described in Chapter 2 to the data collected in the field. In this case, $sVeDBA < 0.05$ was defined as the highest value (“breakpoint”) to identify inactivity and was used to identify the active and inactive behaviours within each of the day and nighttime phases. As the data scale is very fine, instantaneous behaviours are easily recorded (e.g., short bouts of posture change during sleep, or resting bouts during day). Therefore, to avoid momentary disruptions on the active or inactive behaviours, we also included time-based rules to mark the records based on this threshold value. In this case, we merged same behaviour bouts that were interrupted by a different behaviour that lasted for less than 20 seconds (500 records) and then only considered those unique behaviours that lasted for a minimum interval of a minute

(1500 records). We marked all records following these rules, using the ‘Behaviour Builder’ extension on DDMT, and estimated proportion of activity during the day and nighttime, for each hour and each day period (morning vs. afternoon). Then, the daily sVeDBA values related to activity (dailyVeDBA_{Act}) were converted into energetic metrics (in kcal) based on the equation generated in Chapter 2, with slope values adapted to the frequency of field data collection, i.e., 25Hz:

$$EE = \left(226.9 + \left(0.0009296 * \text{dailyVeDBA}_{\text{Act}} \right) \right) * 0.239$$

We also used the information on the proportion of activity during the day to estimate average speed (in m/s) for each step and displacement within each time scale (DIST and DPL), as it is a way of accounting for the time that the animal was stationary during the respective time length. Then, we used linear models to check for a relationship between speed and the movement directionality metrics (i.e., cumulative angles).

We tested for differences in movement metrics between morning versus afternoon within the same group, and comparing the same period among the four groups using non-parametric tests and ANOVA.

5.5.4 MODELS ON THE EFFECT OF HABITAT CHARACTERISTICS AND MOVEMENT PATTERNS ON BLACK LION TAMARIN ENERGY EXPENDITURE

We ran Linear Mixed-Effects Models (LMM) and Generalised Additive Mixed Models (GAMM) to test the effect of displacement length on the energy spent within each specified scale (i.e., daytime, morning and afternoon, or hourly), either between fragments or among groups, using sVeDBA as proxy for EE. In all equations, group was included as a random intercept, to account for the repeated sampling.

Then, we tested the effect of a set of hypothesised covariates on the energy spent during different time scales among the groups (Table 3). We tested different combinations of the explanatory variables, avoiding including in the same models strongly correlated covariates (defined as $R > 0.6$; see Figure A2 in Appendix for correlation plots); and compared these models against a null model. All continuous variables were standardised by subtracting the mean and dividing by the standard deviation. We used the Akaike Information Criterion (AIC) for model selection,

considering models with $\Delta\text{AIC} < 2$ as equally plausible (Burnham & Anderson, 2004). Models and model selection were run and assessed using the R packages 'lme4' (Bates et al., 2015), 'mgcv' (Wood, 2006, 2022), 'AICcmodavg' (Mazerolle, 2020) and 'sjPlot' (Lüdecke et al., 2021). All analyses were run in R (R Core Team, 2022) and R Studio (RStudio Team, 2022).

Table 3. Linear Mixed-Effects Models (LMM) and Generalised Additive Models (GAM) used to test the effect of displacement (in metres) on the energy spent (using Vectorial Dynamic Body Acceleration as proxy) by the black lion tamarins within a specified time scale (daytime, period – morning and afternoon, or hour), and the covariates included in the respective models. Group was included as a random factor (RE) and hour as a cyclic variable (CC).

Model + random factor	Added Covariates (fixed factors)
Per day (LMM):	Daylength (sec)
Daily VeDBA ~ DPL + group (RE)	Mean and SD density of trees (trees/m ²)
	Mean and SD DBH (cm)
	Mean and SD basal area (m ²)
	Cumulative basal area per hectare (m ² /ha)
	Mean and SD height (m)
	Mean and SD volume (m ³)
	Cumulative volume per hectare (m ³ /ha)
	Species Richness
	Shannon and Simpson Diversity index
	Gamma diversity
Per period (LMM):	Period (morning vs. afternoon)
Total VeDBA _(M/T) ~ DIST _(M/T) + group (RE)	Period length (sec)
	Cumulative Pitch (°)
	Cumulative Roll (°)
	Cumulative Turning Angle (°)
	Mean and SD Turning Angle (°)
Per hour (GAM):	Hour (CC)
Total VeDBA _H ~ DIST _H + group (RE)	Temperature (°C)
	Humidity (g/kg)

5.6 RESULTS

5.6.1 HABITAT CHARACTERIZATION: PHYSICAL AND BIOTIC FACTORS

All variables for habitat structure, except mean tree density, differed between the areas ($P > 0.001$), presenting higher values in GUA than in PBC (Table 4). The species richness and diversity (Shannon and Simpson indexes) corrected by Hill numbers also differed between the areas, showing no overlap of the 95% confidence interval estimates (Figure 3a; Table 5). On the comparison of the forest structure variables among groups, PBC01 differed from GUA01 on DBH ($P = 0.006$), basal area ($P = 0.006$), height ($P = 0.02$), cumulative basal area ($P = 0.007$) and total volume ($P = 0.02$); PBC02 differed from GUA02 on height ($P = 0.03$), cumulative basal area ($P = 0.0001$) and total volume ($P = 0.002$), and from GUA01 only on height ($P = 0.003$). On the other hand, regarding forest composition, the four groups did not differ in species richness, showing a high overlap of the 95% confidence interval estimates, but differed in species diversity only between groups of different fragments (Figure 3b; Table 5).

The variables that derived from direct measurements of trees (PBH and height, see Table 2) presented a high correlation between them ($\rho > 0.6$; Figure A1 in Appendix) and were not included as covariate on the same models.

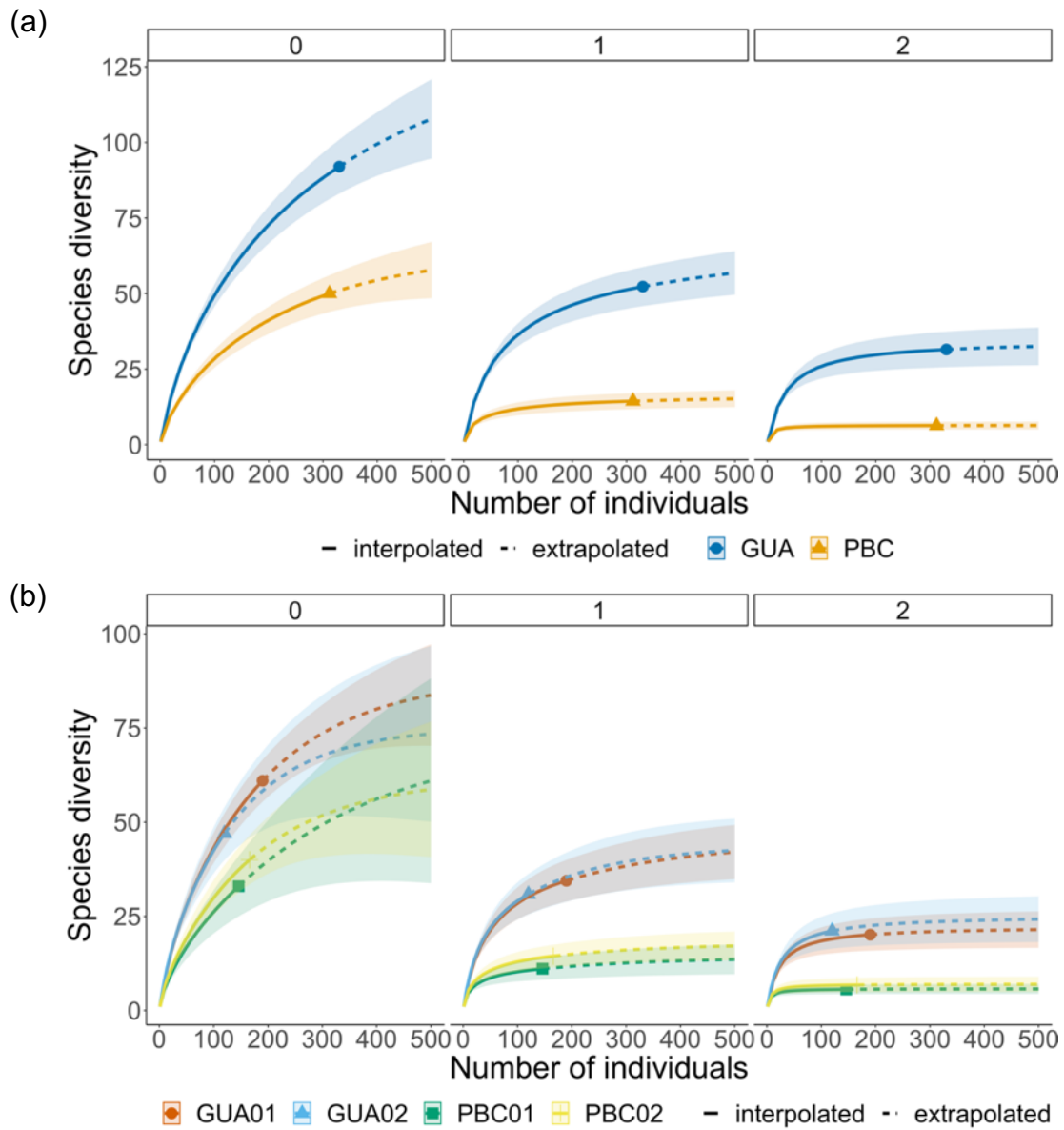


Figure 3. Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines) of tree species richness (left), Shannon (middle) and Simpson (right) diversity indexes, based on the Hill numbers ($q = 0, 1, 2$, respectively) for Guareí (blue) and Ponte Branca (orange) fragments (a) and for each studied group in Guareí (red and blue) and Ponte Branca (green and yellow) (b). The 95% confidence intervals are shown by the respective shaded regions and reference samples are denoted by the solid symbols.

Table 4. Habitat variables for forest structure and diversity, estimated from a sampled area of 2,100m² (21 plots of 10x10 m) in each of the study sites. Values for mean tree density, mean basal area, and mean volume are multiplied by 100.

Study site	N Trees	Mean (±SD) density (trees/m ²) *100	Mean (±SD) DBH (cm)	Mean (±SD) basal area (m ²) *100	Mean (±SD) tree height (m)	Mean (±SD) volume (m ³) *100	Cumulative basal area per hectare (m ² /ha)	Total volume per hectare (m ³ /ha)	Observed/ Estimated Species richness (±SE)	Observed/ Estimated Shannon diversity index (±SE)	Observed/ Estimated Simpson diversity index (±SE)
GUA	330	15.7 ± 3.7	14.3 ± 11.6	2.7 ± 5.4	8.8 ± 5.3	28.5 ± 80.5	41.6	448.5	92.0/ 131.9 ± 16.9	52.3/ 65.4 ± 4.5	31.5/ 34.7 ± 3.3
PBC	312	14.9 ± 4.2	10.6 ± 8.0	1.4 ± 2.9	6.6 ± 2.4	10.1 ± 32.6	20.5	150.6	50.0/ 63.8 ± 8.3	14.4/ 16.2 ± 1.4	6.3/ 6.4 ± 0.7

Table 5. Habitat variables for forest structure and diversity, considering the plots present within the home range of each group. Values for mean density, mean basal area and mean volume are multiplied by 100.

Group	N trees	N plots (100 m ²)	Mean (±SD) density (trees/m ²) *100	Mean (±SD) DBH (cm)	Mean (±SD) basal area (m ²) *100	Mean (±SD) tree height (m)	Mean (±SD) volume (m ³) *100	Cumulative basal area per hectare (m ² /ha)	Total volume per hectare (m ³ /ha)	Observed/ Estimated Species richness (±SE)	Observed/ Estimated Shannon diversity index (±SE)	Observed/ Estimated Simpson diversity index (±SE)
GUA01	190	11	17.3 ± 3.6	14.6 ± 12.2	2.9 ± 6.2	8.9 ± 5.3	31.1 ± 95.2	49.2	536.4	61.0/ 88.9 ± 13.7	34.4/ 44.8 ± 4.1	20.1/ 22.4 ± 2.9
GUA02	120	8	15.0 ± 2.5	12.8 ± 8.8	1.8 ± 2.8	8.5 ± 4.6	17.5 ± 33.0	28.2	262.5	47.0/ 75.2 ± 15.1	30.9/ 43.7 ± 4.7	21.1/ 25.4 ± 3.5
PBC01	146	9	16.2 ± 4.9	10.8 ± 8.9	1.5 ± 3.4	6.7 ± 2.3	11.4 ± 36.7	24.8	184.4	33.0/ 72.7 ± 25.9	11.1/ 14.2 ± 2.5	5.6/ 5.8 ± 0.8
PBC02	166	12	13.8 ± 3.6	10.5 ± 7.1	1.3 ± 2.4	6.5 ± 2.5	9.0 ± 28.6	17.3	125.0	40.0/ 61.9 ± 12.7	14.4/ 17.8 ± 2.4	6.8/ 7.0 ± 1.1

The physical environmental variables also differed among monitoring periods of each group ($P > 0.001$) (Table 6; Figure 4). These variables were not highly correlated ($\rho = 0.29$) and could, thus, be included in the same models.

Table 6. Abiotic variables (temperature in °C and specific humidity in g/kg) obtained for the monitoring periods of each group. The metrics are calculated from original data obtained per hour.

Group	Monitoring Period	Mean ($\pm$ SD) Temperature (°C)	Min-Max Temperature (°C)	Mean ($\pm$ SD) Specific Humidity (g/kg)	Min-Max Specific Humidity (g/kg)
GUA01	19/Sep/2019 0h00 to 28/Sep/2019 23h00	21.8 $\pm$ 5.9	10.9 – 37.2	12.9 $\pm$ 2.2	8.5 – 19.1
GUA02	25/Sep/2019 0h00 to 16/Oct/2019 23h00	19.1 $\pm$ 5.4	9.7 – 34.5	11.4 $\pm$ 1.7	7.9 – 15.5
PBC01	25/Sep/2020 0h00 to 16/Oct/2020 23h00	28.3 $\pm$ 6.6	16.7 – 44.6	14.1 $\pm$ 2.9	9.1 – 21.6
PBC02	02/Feb/2021 0h00 to 11/Feb/2021 23h00	23.3 $\pm$ 3.7	17.1 – 33.2	17.4 $\pm$ 2.4	13.4 – 24.0

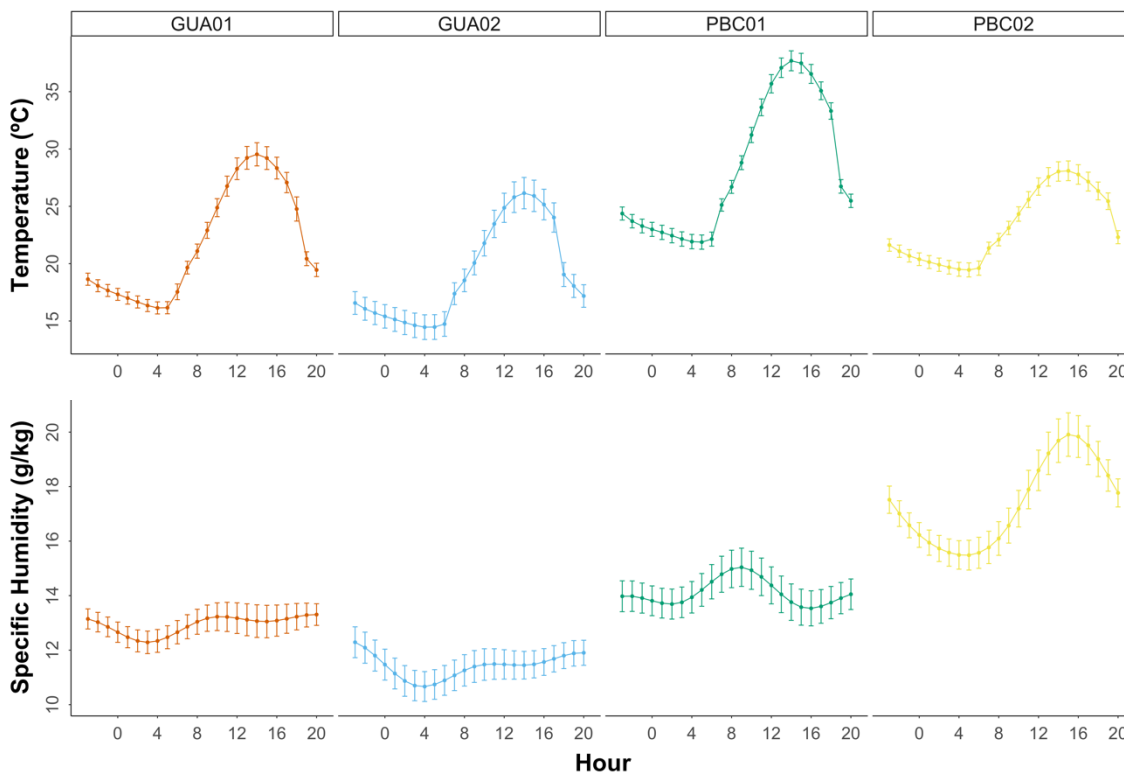


Figure 4. Mean temperature (in °C) and specific humidity (in g/kg) per hour for the monitoring periods of each group. Standard errors are presented.

5.6.2 MOVEMENT PATTERNS AND ENERGY EXPENDITURE

We found similar values of mean step length (SL) and turning angle (TA) between the day periods for the groups, differing only for PBC01 (Table 7). When we compared the same period among the groups, no difference was found for SL, but for morning TA, GUA01 differed from the other three groups (P-value: GUA02 = 0.02, PBC01 < 0.0001, PBC02 = 0.002), showing a less directional movement pattern; for afternoon TA, PBC02 differed from the other three (P-value: GUA01 < 0.001, GUA02 = 0.03, PBC01 = 0.002), showing a more directional movement (Figure 5).

Table 7. Estimated mean step length (in metres) and mean modular turning angle (in degrees) per period of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments. Significance (P-value) of the comparison between periods for each group is presented.

Group	Mean Step Length ($\pm$ SD) - m			Mean Turning Angle ($\pm$ SD) - degrees		
	Morning	Afternoon	P-value	Morning	Afternoon	P-value
GUA 01	36.9 $\pm$ 29.7	36.8 $\pm$ 33.1	0.21	90.1° $\pm$ 59.2	95.7° $\pm$ 61.8	0.16
GUA 02	40.5 $\pm$ 35.5	35.6 $\pm$ 32.1	0.07	77.8° $\pm$ 58.4	91.6° $\pm$ 57.3	0.05
PBC 01	40.4 $\pm$ 29.9	35.5 $\pm$ 29.7	< 0.001***	68.5° $\pm$ 55.7	93.8° $\pm$ 59.9	< 0.001***
PBC 02	35.7 $\pm$ 29.2	34.9 $\pm$ 33.6	0.38	75.4° $\pm$ 55.5	76.6° $\pm$ 60.1	0.92

Similarly, only PBC01 differed between periods for the directionality values ($P < 0.0001$; Figure 6). Despite the highly significant relationship we found between the cumulative angles (TA, pitch and roll) and speed, these three movement variables could poorly explain, alone, the average speed per period, although a stronger relation was observed in the afternoon ($R^2 \leq 0.23$; Figure 7).

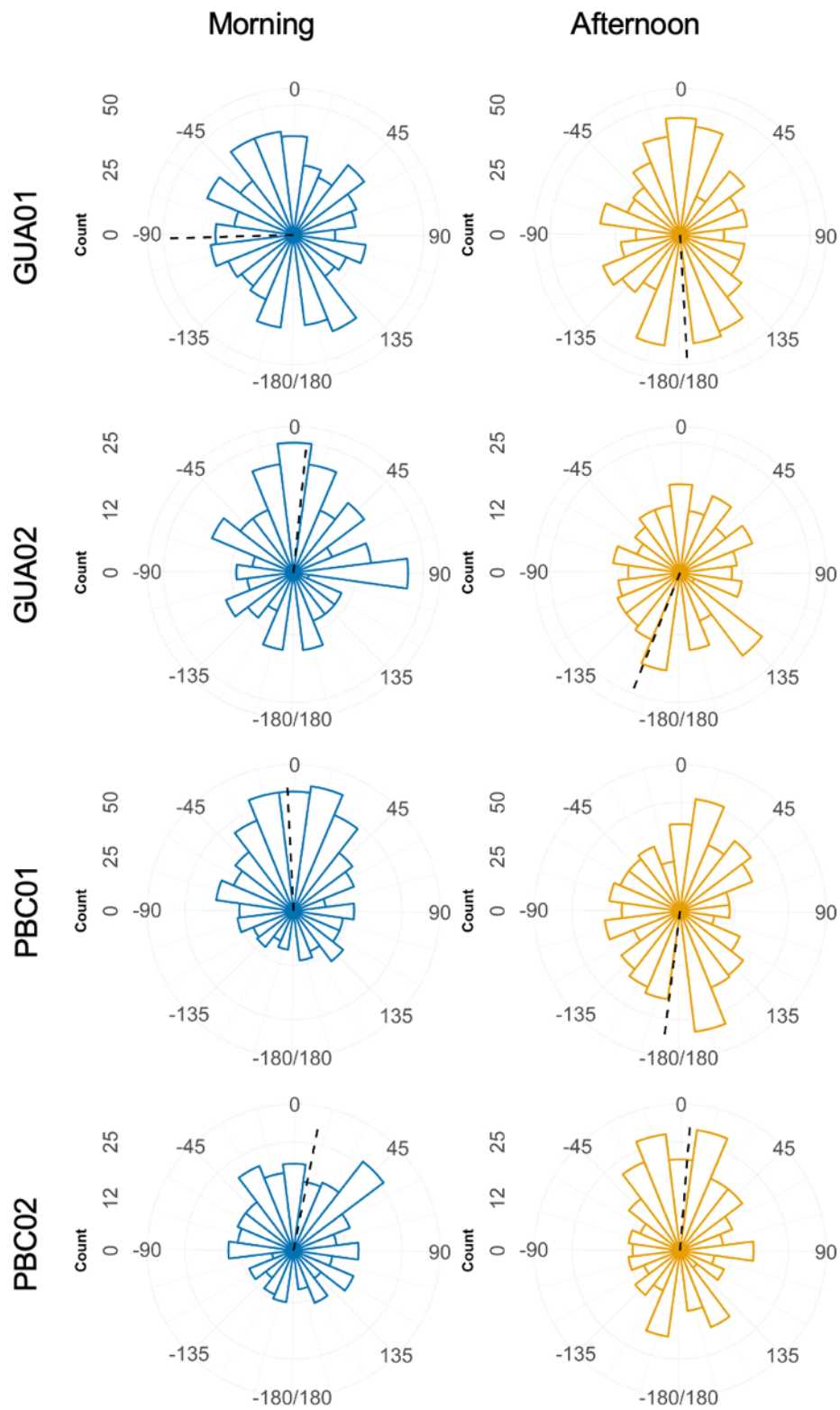
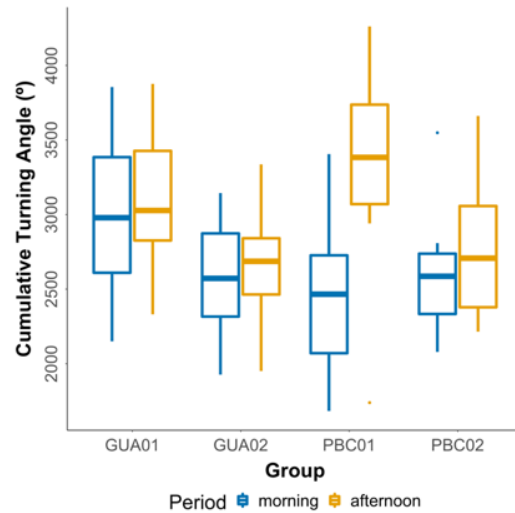
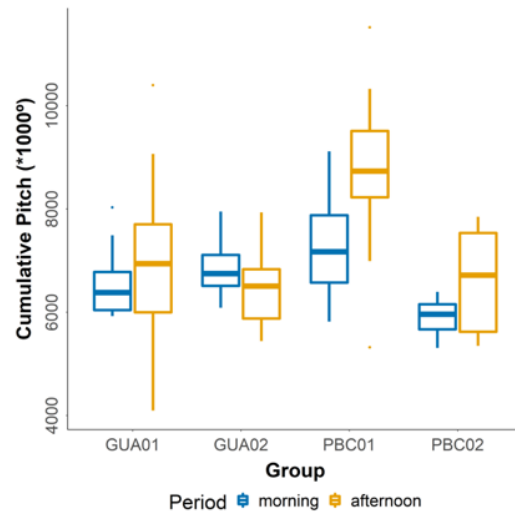


Figure 5. Circular histogram of relative turning angles (y axis in degrees) for each period of the four studied black lion tamarin groups. Dashed lines show the average turning angle (estimated based on the non-modular values) for each group.



Cumulative Turning Angle – pairwise comparison between periods and groups

	GUA01 M	GUA01 A	GUA02 M	GUA02 A	PBC01 M	PBC01 A	PBC02 M
GUA01 A	0.55						
GUA02 M	0.02						
GUA02 A		0.04	0.57				
PBC01 M	0.0003		0.48				
PBC01 A		0.02		0.0001	0.00		
PBC02 M	0.04		0.89		0.39		
PBC02 A		0.12		0.65		0.001	0.38



Cumulative Pitch – pairwise comparison between periods and groups

	GUA01 M	GUA01 A	GUA02 M	GUA02 A	PBC01 M	PBC01 A	PBC02 M
GUA01 A	0.21						
GUA02 M	0.40						
GUA02 A		0.26	0.40				
PBC01 M	0.02		0.30				
PBC01 A		0.00		0.00	0.00		
PBC02 M	0.12		0.04		0.001		
PBC02 A		0.44		0.76		0.00	0.13

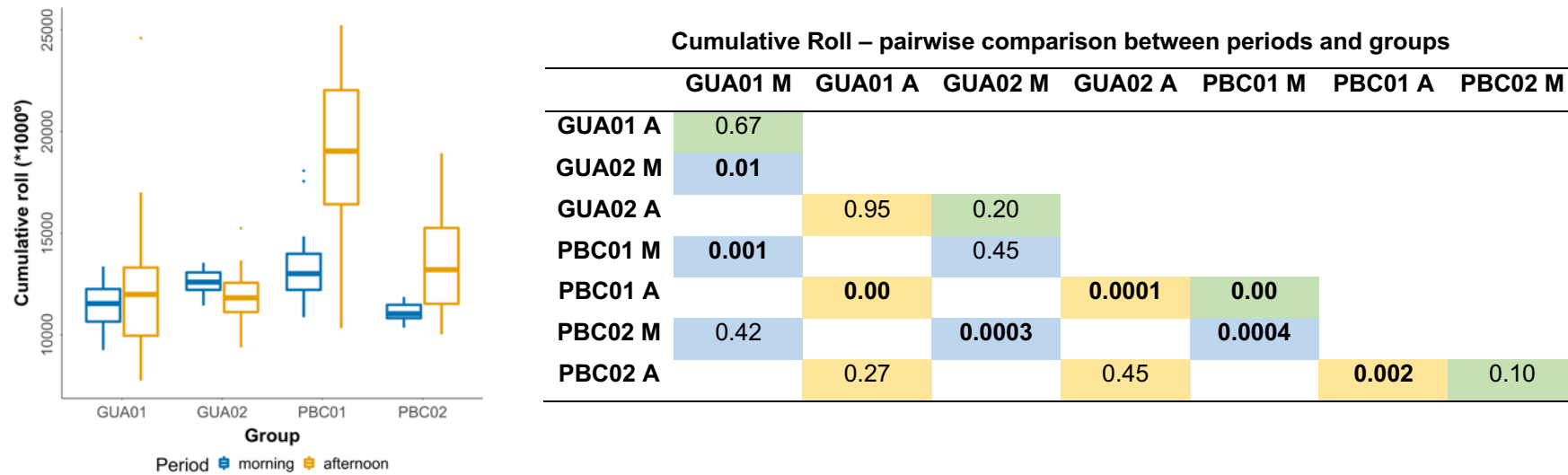


Figure 6. Cumulative turning angle (top), cumulative pitch (centre) and cumulative roll (bottom), in degrees, per period (M = morning, in blue on the plot and table; A = afternoon, in yellow on the plot and table) of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments, and the significance (P-value) of the pairwise parametric tests, indicating in bold when the measures differed. Green cells show comparisons between different periods (MxA) of the same group, while blue and yellow cells show comparison within the same period (M and A, respectively) between different groups.

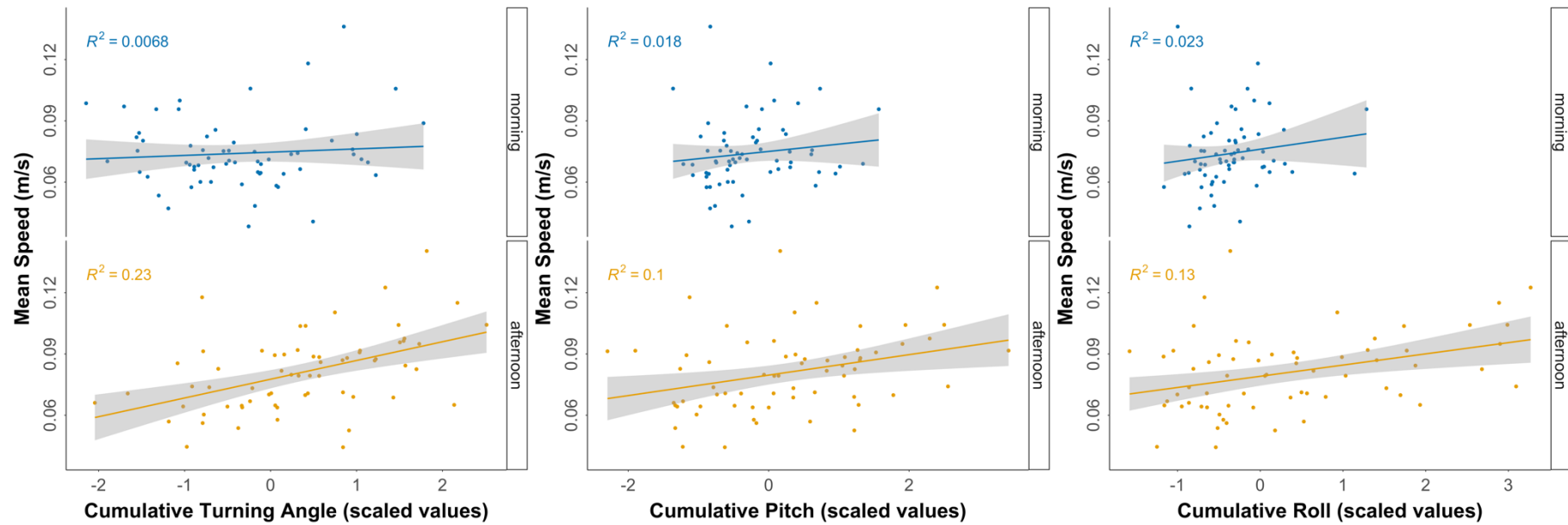


Figure 7. Relationship between average speed (m/s) and the movement directionality metrics (cumulative angles) on values per period. All relations were highly significant ($P < 0.001$). R^2 values are presented. Values of the independent variables were standardised by subtracting the mean and dividing by the standard deviation (scaled values).

Wild black lion tamarins spent, on average, 100.5 (± 8.4) kcal per day, with 80.6% (± 2.2) of this spent during daytime (Figure 8a; Table 8). Only the GUA01 group differed from the others ($P < 0.01$), with significantly lower values of energy expenditure (Figure 9a; Table 8). Despite the higher proportion of energy spent during daytime, this phase lasted on average, slightly less ($47.8\% \pm 2.2$) than the nighttime for the groups (Figure 8). The daily length of the activity period was on average 48min23sec longer for the groups in the larger fragment ($P < 0.0001$; Table 8), but we found a very small yet significant relationship between length of activity period and the daylength (hours of sunlight) (Adj. $R^2 = 0.08$, $P = 0.01$) (Figure 9b and 9c). GUA02 had the shortest activity periods, differing by 5 to 13% from the other three groups (p-values: GUA01 = 0.03; PBC01 < 0.0001 ; PBC02 = 0.003), while PBC01 had the longest activity periods and differed from GUA01 and GUA02 ($P < 0.0001$). GUA01 and PBC02 had similar activity period lengths (Figure 9b; Table 8). Interestingly, GUA02 individuals rested almost 0% of the time during the day (0.0004%), while the other three groups spent, on average, about 10% of the time resting ($10.6\% \pm 3.4$, or 2h33min ± 49 min) (Figure 8b).

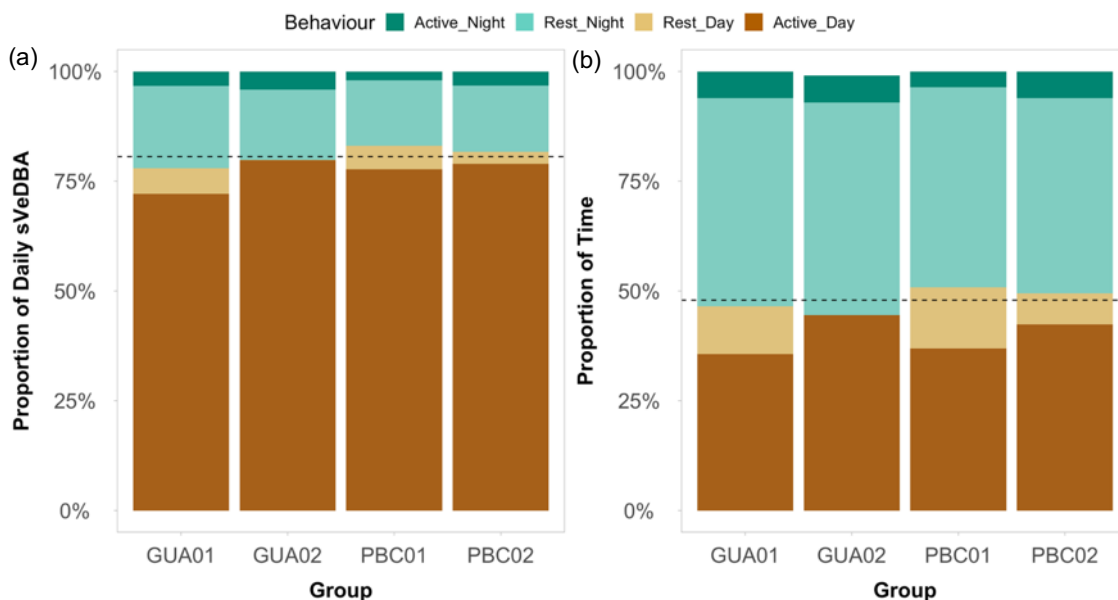


Figure 8. (a) Proportion of energy and (b) proportion of time spent on each behaviour class (resting or active) within each phase of the daily rhythm of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments. The dashed line indicates the average proportion of energy and time spent between day and night.

Table 8. Daily energy expenditure and length of activity period of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments. Values are shown per group and per study area.

Group	Mean length of daily activity period ($\pm$ SD) – hh:mm:ss $\pm$ mm:ss	Mean daily energy expenditure ($\pm$ SD) – kcal
GUA01	10:54:40 $\pm$ 36:06	GUA 93.5 $\pm$ 5.4
GUA02	10:21:06 $\pm$ 29:26	101.8 $\pm$ 5.4 96.1 $\pm$ 6.6
PBC01	11:39:15 $\pm$ 43:19	PBC 104.3 $\pm$ 7.8
PBC02	11:17:46 $\pm$ 34:34	106.5 $\pm$ 7.5 105.0 $\pm$ 7.7

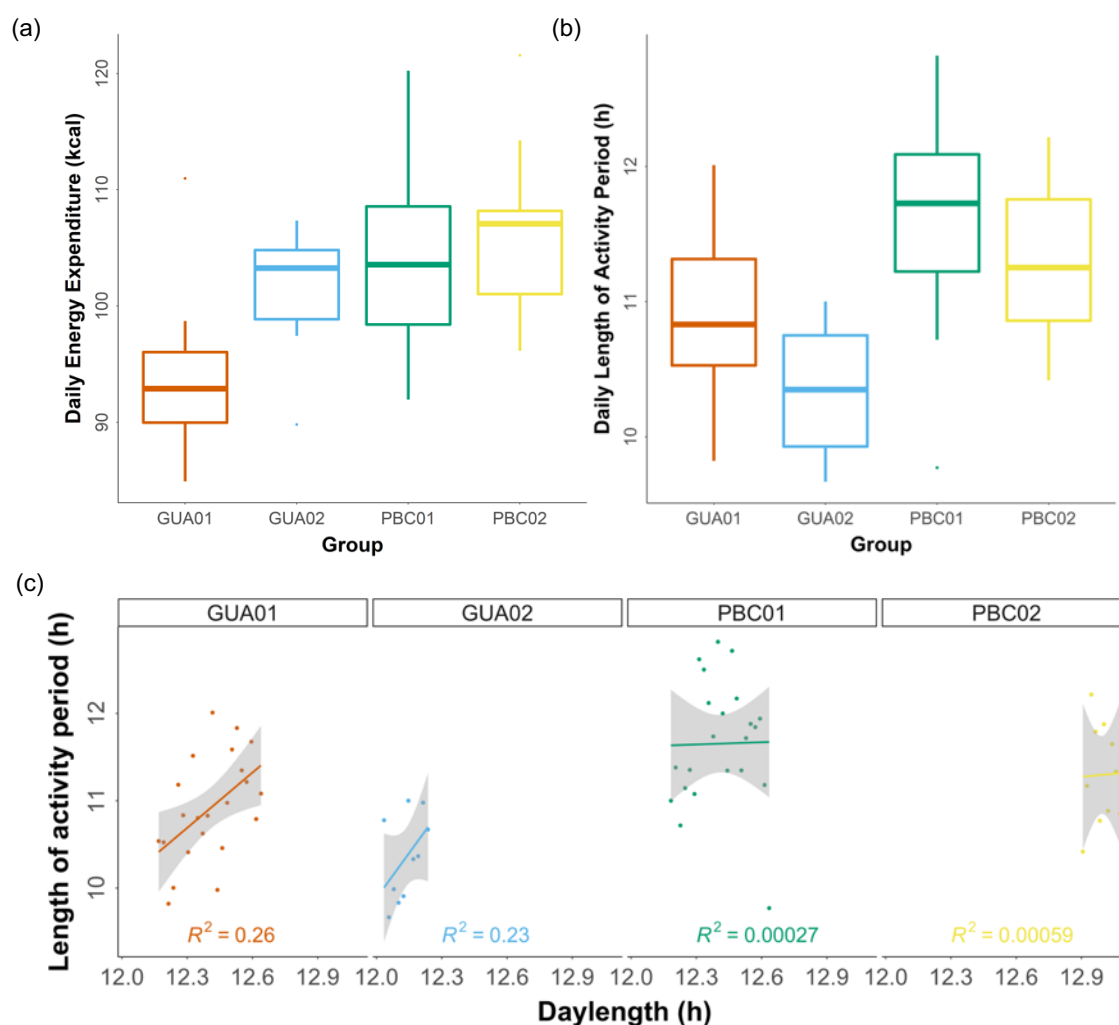


Figure 9. (a) Daily energy expenditure (in kcal), (b) length of activity period (in hours) and (c) the relation between the latter and the daylength (in hours) of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments.

The four groups presented similar mean daily path length (DPL), but the mean daytime energy expenditure (EE) was significantly larger for the groups in PBC ($P <$

0.0001) (Table 9; Figure 10). However, in the pairwise comparison, only GUA01 differed from the other three groups ($P < 0.01$ from GUA02 and $P < 0.0001$ from PBC01 and PBC02), presenting lower EE values.

Table 9. Estimated mean daily path length (in metres) and mean daytime energy expenditure (in kcal) of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments. Values are shown per group and per study area.

Group	N days	Mean daily path length ($\pm$ SD) – m		Mean daytime energy expenditure ($\pm$ SD) – kcal	
GUA01	22	2413.9 $\pm$ 401.4	GUA	84.9 $\pm$ 7.5	GUA
GUA02	10	2370.1 $\pm$ 388.5	2400.2 $\pm$ 391.6	94.8 $\pm$ 7.1	88.0 $\pm$ 8.6
PBC01	22	2654.9 $\pm$ 422.3	PBC	101.3 $\pm$ 10.7	PBC
PBC02	10	2395.7 $\pm$ 485.4	2573.9 $\pm$ 451.8	101.9 $\pm$ 9.4	101.5 $\pm$ 10.1

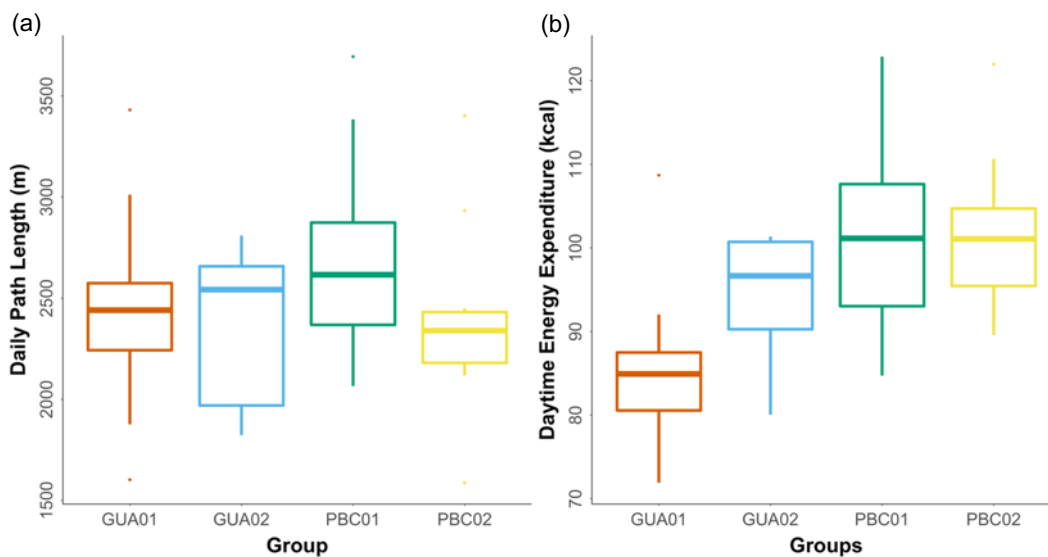


Figure 10. (a) Daily path length and (b) daytime energy expenditure of the four black lion tamarin groups monitored in the Guareí (GUA) and Ponte Branca (PBC) fragments.

Black lion tamarin's total distance moved (DIST) did not differ between the two daytime periods (morning vs. afternoon) for each group (Figure 11a). Conversely, black lion tamarins spent significantly more energy (EE) in the morning than in the afternoon, except for PBC02 (P-value: GUA01 < 0.02 , GUA02 = 0.004, PBC01 = 0.0005) (Figure 11b). Regarding the post-hoc comparisons among groups, only GUA01 differed from the others for total EE in the morning (p-value: GUA02 = 0.003, PBC01 < 0.0001 , PBC02 = 0.0002) and afternoon periods (P-value: PBC01 = 0.0001,

PBC02 = 0.0003), showing lower EE values in all cases. For DIST, only GUA02 differed from PBC01 in the afternoon ($P = 0.04$; Figure 11a), with GUA02 showing the lowest DIST and PBC01 the largest.

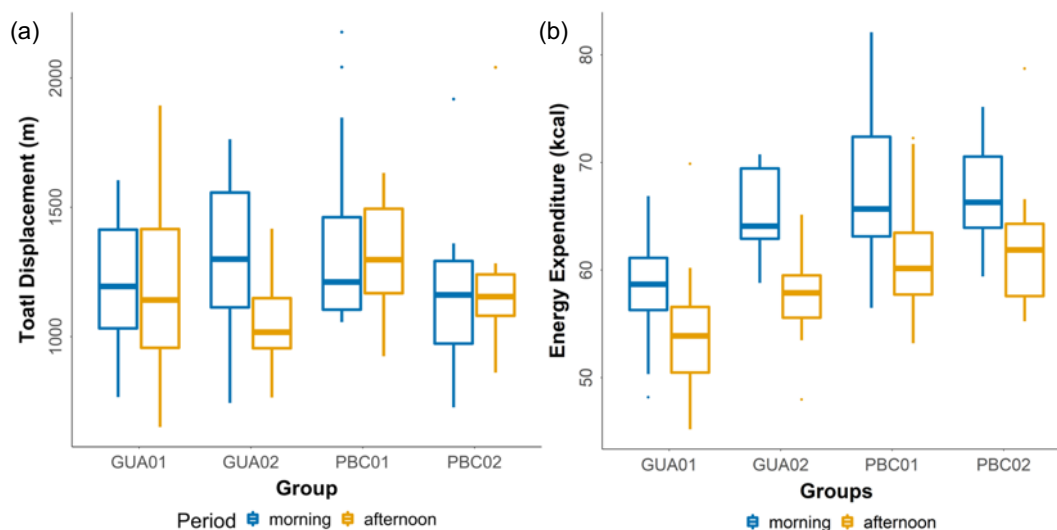


Figure 11. (a) Total morning and afternoon displacements, in metres, and (b) corresponding total estimated energy expenditure, in kcal, for the four black lion tamarin groups monitored in the Guareí (GUA) and Ponte Branca (PBC) fragments.

At smaller time scales, all groups showed consistent daily patterns in movement metrics and energy expenditure; specifically, average step length (SL; hourly average of 10-minute scale step length, hence equivalent to 10-minute scale movement speed), hourly total distance moved (DIST) and hourly total energy expenditure (EE) (Figure 12). Whilst all groups showed two peaks of EE in correspondence with the morning start and afternoon ends of the activity period and a midday decline, this was not matched by the daily patterns in both movement metrics. Interestingly, the step length showed a consistent steep increase at the end of the activity period, even when both EE and DIST were already declining, whereas for the rest of the day SL and DIST were more closely related, and with a consistent midday decline for both movement and the energy expenditure metrics. It is important to mention that the first and last hours of the day have fewer GPS and accelerometer records, as data collection starts at the exact beginning of the activity period, and may not complete the 60 minutes of recording as for the other hours in between.

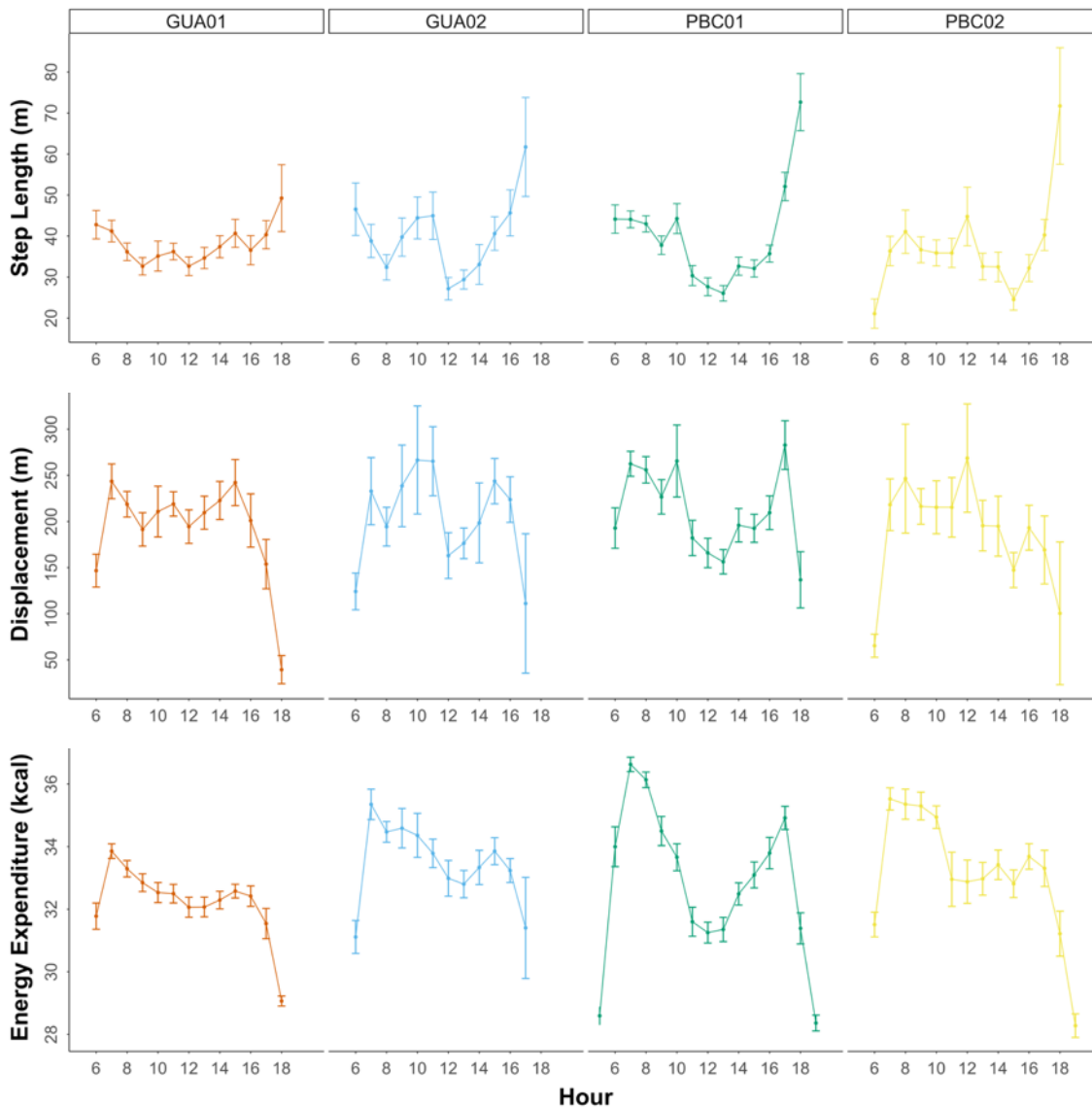


Figure 12. Hourly mean of 10-min scale step length (in metres; top), mean hourly total displacement (in metres; centre), and mean hourly total energy spent (in kcal; bottom) by the black lion tamarins during every hour of the activity period in each of the four groups monitored in Guareí (GUA) and Ponta Branca (PBC) fragments. Standard error bars are shown for each hour.

5.5.3 MODELS ON THE EFFECTS OF HABITAT CHARACTERISTICS AND MOVEMENT PATTERNS ON THE BLACK LION TAMARINS' ENERGY EXPENDITURE

In the comparison among groups, daytime EE (here expressed as the daily sVeDBA) increased with daily path length (Marginal $R^2 = 0.233$, Conditional $R^2 = 0.555$, Intraclass Correlation Coefficient (ICC) = 0.42, $P < 0.0001$) (Figure 13). When adding the forest structure and composition variables and daylength to the mixed models,

seven models were considered plausible ($\Delta AIC < 2$), all explaining over 60% of the variance (Table 10). In all of them the covariate(s) explained nearly all the variance of the random effect, thus this latter had null effect on the selected models ($ICC = 0$, i.e., the variance explained by the random effect) (Table A1 in Appendix). In all cases, daytime EE increased with decreasing values of the vegetation variables ($P < 0.0001$; Figures A2 and A3 in Appendix). In three of the models, daylength positively affected daytime EE, but the effect was only significant for this variable in one of them ($P = 0.04$ in M3; Appendix). When compared to the simple model (daytime sVeDBA $\sim$ DPL), all of them differed significantly ($P < 0.001$).

Table 10. Model selection results for the effect of the vegetation structure on Daily Energy Expenditure (estimated as the daily smoothed Vectorial Dynamic Body Acceleration values - sVeDBA) of black lion tamarins. In all models, sVeDBA was regressed against daily path length (M0), with group as random factor. The alternative models use the habitat structure values relative to each group as covariates.

Models	Added variables	# Est. par.	AICc	$\Delta AICc$	Model Lik	AICc weight	Marginal R^2
M1	M0 + M.BA	5	130.2	0	1	0.15	0.621
M2	M0 + M.Vol	5	130.4	0.18	0.91	0.14	0.620
M3	M0 + SD.Vol+DayL	6	131.4	1.15	0.56	0.08	0.628
M4	M0 + SD.DBH	5	131.6	1.36	0.51	0.08	0.612
M5	M0 + M.BA+DayL	6	131.7	1.45	0.49	0.07	0.627
M6	M0 + M.Vol+DayL	6	131.8	1.60	0.45	0.07	0.626
M7	M0 + Sp.Rich	5	131.9	1.68	0.43	0.07	0.611
M0	DPL	4	141.4	11.2	0.004	0.0006	0.233

Legend: SD = Standard deviation, M = Mean, SD = Standard Deviation, BA = Basal Area, Vol = Volume, DayL = Daylength, DBH = Diameter at Breast Height, Sp.Rich = Species Richness, # Est.par. = number of Estimated Parameters.

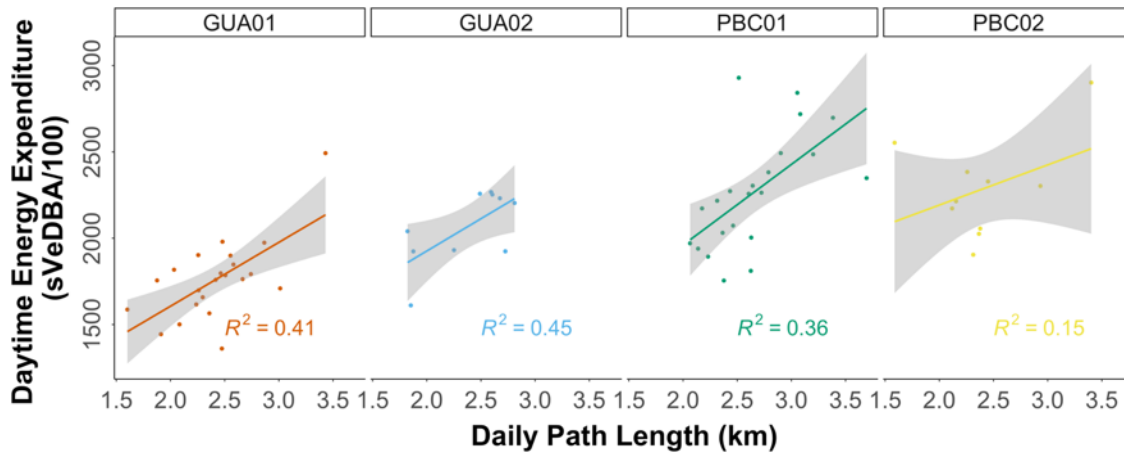


Figure 13. Relation between daily path length (in km) and the daytime energy expenditure (here expressed as the daytime sVeDBA, in g) of the four black lion tamarin groups monitored in Guareí (GUA) and Ponte Branca (PBC) fragments. R^2 values are presented for each group.

Total distance moved, the degree of turning (left-right), and up and down movements of the body, markedly contributed to the total energy expenditure, explaining a total of 66.6% of the variance (Marginal R^2 : 0.491; Table 11; Table A2 and Figures A4, A5 and A6 in Appendix). Specifically, energy expenditure significantly increased with distance moved (positive effect of Displacement), whereas unexpectedly a higher degree of turning (negative effect of cumulative TA) was associated with lower energy expenditure. More up and down movements of the body axis instead were associated with a higher energy expenditure (positive effect of cumulative pitch, where the latter records body orientation changes such as from horizontal to vertical position) (Table 11).

Table 11. Results of the linear mixed model testing the effects of movement metrics on the energy spent by the black lion tamarins per daytime period.

Predictors	Estimates	CI	p
Intercept [morning]	323.85	311.70 – 335.99	<0.001
Displacement	11.26	8.37 – 14.16	<0.001
Period [Afternoon]	-18.47	-24.58 – -12.36	<0.001
Cumulative TA	-8.59	-12.00 – -5.18	<0.001
Cumulative Pitch	8.69	4.92 – 12.47	<0.001
Random Effects			
σ^2	248.07		
T00_group	130.85		
ICC	0.35		
N_group	4		
Observations	128		
Marginal R ²	0.491		
Conditional R ²	0.666		

Legend: σ^2 : average random effect variance of the model, or within-subject variance; T00_group: random intercept variance, or between-subject variance; ICC: Intraclass Correlation Coefficients, or the variance explained by the random effect; N_group: number of levels of the variable “group”.

The drivers of hourly total energy expenditure (EE) were total hourly distance moved, time of day, temperature, and humidity, explaining 59.9% of the variance (GAM models with group as random effect smooth), with markedly non-linear effects (Figure 14; Table A3 and Figure A7 in Appendix). Specifically, hourly total energy expenditure strongly increases with distance moved, until a plateau around 500 m (Figure 14a), with also the largest effect size. Instead, energy expenditure remains high and constant between 10 °C and +28 °C, after which it strongly declines linearly up to +40 °C (Figure 14b), whilst time of day shows the same pattern as for total morning and afternoon EE, with two peaks at morning and evening (at around 7 to 8 am and 4 to 5 pm, respectively) and a minimum around midday (Figure 14d). Humidity has an additional, weakly positive effect, with a consistent, mostly linear increase of EE with humidity (Figure 14c).

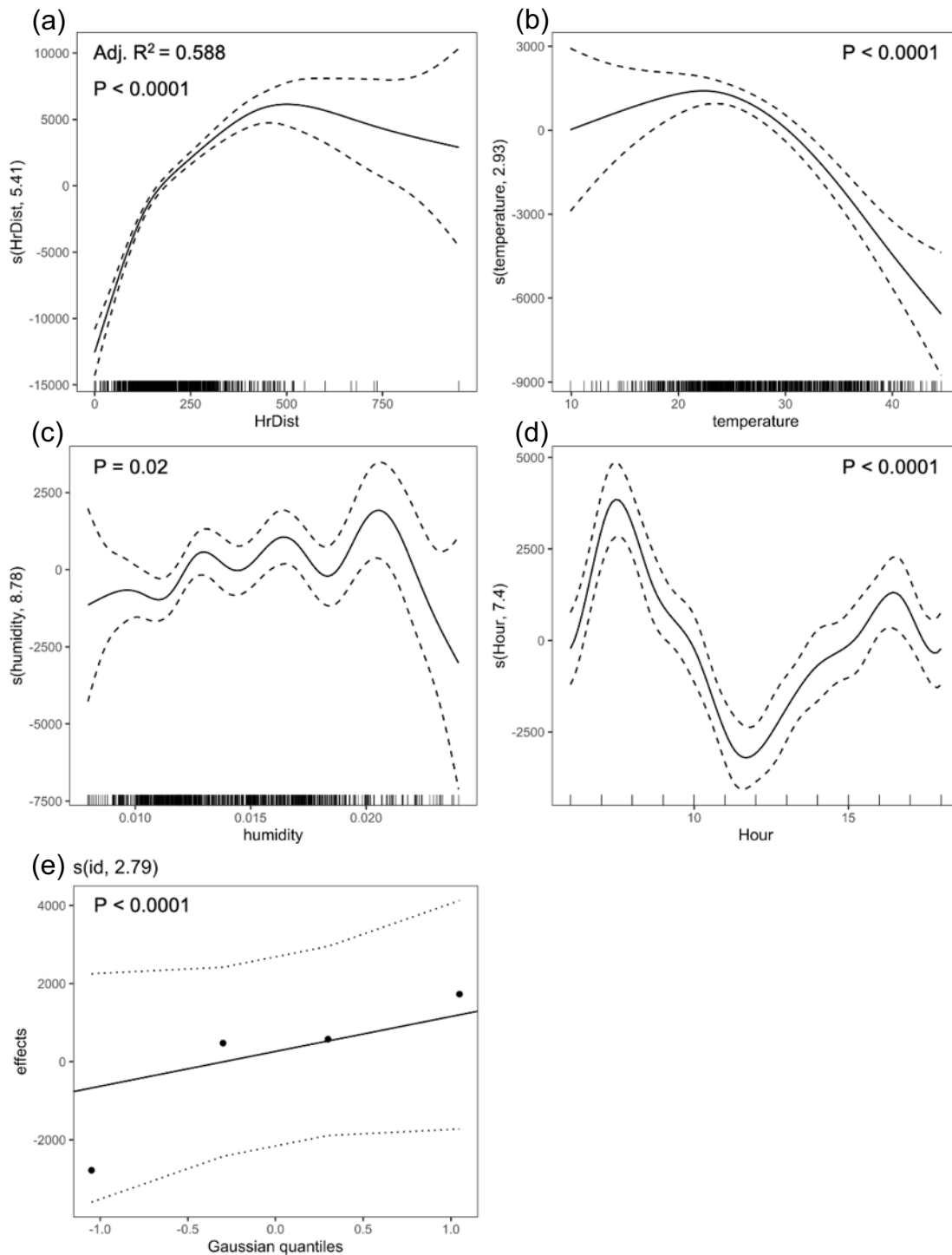


Figure 14. Output from the generalized additive model (GAM) for the effects of physical environmental conditions (temperature, in b and humidity, in c) and total hourly displacement (HrDist, in a) on the energy spent per hour (in d) by black lion tamarin groups (id, in e) in Guareí and Ponte Branca fragments. Solid line is the predicted output, while the dashed lines are the upper and lower 95% confidence intervals.

5.6 DISCUSSION

We provide the first estimates of daily energy expenditure (DEE) for a callitrichid species in the wild, based on direct sensor measurements, with the only previous study based on estimates of the energy content of food intake (fruits and frogs; Miller et al. 2006), providing also the first decomposition of energy expenditure at sub-daily time scales and a quantification of the effects of movement metrics and abiotic conditions. Wild black lion tamarins showed higher energy expenditure than captive ones (respectively, $100.8 \text{ kcal/day} \pm 5.9$ and $84.5 \text{ kcal/day} \pm 11.9$; see results from chapter 2), despite showing similar proportions on the active and resting behaviours during the different phases of the daily rhythm. This pattern is probably explained by differences in intensity of physical activity, as captive animals presented, proportionally, 68% of the total VeDBA of the wild ones (see chapter 2), with obviously very markedly lower space available to move in captivity. Nonetheless, the values in this study are still in accordance with the expected ones for primates of this size ($87.7 \text{ kcal} \pm 1.4$, expected prediction interval: $52.1 \text{ kcal} \pm 0.8 - 147.7 \text{ kcal} \pm 2.3$; Table A4 in Appendix; Pontzer et al., 2014).

Displacement was consistently the most important predictor of energy expenditure, independently of the time scale considered in our models, but both physical and biotic factors had an additional influence. Along the days of our study, temperatures reached their highest values and started to decrease around 14:00 BRT, while energy expenditure rates go on the opposite direction, starting to rise after midday and reaching a maximum value for the afternoon just before the end of the activity period, around 16:00-17:00 BRT. A midday reduced activity pattern is commonly observed in diurnal primates (Braza et al., 1981; Koizumi et al., 2021; Rea et al., 2014), as a response of high ambient temperature (Campos & Fedigan, 2009; Hill, 2006). This also corroborates our results that showed that black lion tamarins spent less energy during the afternoon. Additionally, daylength emerged as an important factor in some models, indicating that hours of light might also influence energy expenditure, although we found a weak relationship between this factor and the tamarins' length of the activity period.

Several biotic variables, as well as the directionality of movement (cumulative turning angle) and vertical direction (cumulative pitch – up and down movements of

the body) also contributed to the energy expenditure of tamarins in the wild. A greater intensity in the change of vertical direction resulted in greater energy expenditure. We would expect that, for this reason, the variation in tree height would reflect this variation, reflecting a more frequent vertical ascending and descending in the tree trunks, but we did not find such a relationship. On the other hand, the more directional horizontal movement resulted in higher energy expenditure. Again, forest structure variables, such as smaller tree density that could require larger leaps or trajectory changes, thus influencing the cumulative turning angle, did not prove to be relevant. A possible explanation would be that, in more directional movements, the speed would be higher, resulting in greater energy expenditure. However, the relationship found was inverse, with a higher average speed in periods with a greater cumulative turning angle. Further analyses exploring how fine-scale movement patterns are directly affected by forest structure, such as the way they move from one tree (or food source) to the other (Ramos-Fernández et al., 2004), the residence time on food sources (Plante et al., 2014), and how the food sources are spatially distributed within the home range (Trapanese et al., 2019) could shed light on this higher expenditure of more directional movements.

On the other hand, metrics that derive from DBH measures, such as volume, basal area and the DBH itself, suggested an effect of forest structure on the energy expended by the black lion tamarins during their activity period. The isolated presence of these three variables in the selected models may be due to the high correlation between them. DBH measures are considered a good estimator of fruit abundance (Chapman et al., 1992). The home range of GUA01 presented the higher values of both DBH, basal area and volume, suggesting that it is the area with the highest fruit availability. This suggests that less energy is spent if they spend more time on the same tree and make shorter moves between one food source and the other. This pattern can be suggested based on the constant hourly values of step length (SL) observed for the GUA01 group along the day, in contrast to a pattern with greater hour-to-hour variation in SL for the other groups. Still, GUA01 area also presented the highest standard deviations for these structural variables, indicating a more heterogeneous forest structure. Finally, tree species richness was also an important feature to be considered in terms of energy expenditure, and the smaller forest patch

(GUA) showed significantly higher values of species richness and lower energy expenditure.

The negative correlation between energy expenditure and the variables of habitat characterization suggests that both forest structure and composition are equally important determinants of movement-related energy expenditure in black lion tamarins. Our results also indirectly point to the fact that patch size is not necessarily a good indicator of energy expenditure rates, as smaller patches can present higher habitat quality in the forest. By quality here we mean ideal structural and compositional conditions that supply enough resources required by the species. On the other hand, small habitat patches limit population size for these frugivorous primates which, proportionally to their body sizes, uses large home ranges; and small population sizes can lead to local extinction in medium to long term (Estrada & Coates-Estrada, 1996; Knapp, 2013; Link et al., 2010). As feeding resources availability and distribution are key drivers of primates' trajectories (Albert et al., 2013; Janson, 2016; Reyna-Hurtado et al., 2018), and resource availability is related to forest structural features, habitat quality assessment for black lion tamarins must consider not only composition but forest structure and heterogeneity within the fragment. Habitat management actions may include planting to enrich existing forest fragments, as well as establishing connectivity with the implementation of new areas of planted forest. The choice of species should be based on tree species that offer the resources required and consumed by the tamarins (i.e., fruiting trees and sleeping sites) and that may also provide the necessary forest structure to reduce its energy expenditure for movements. We particularly emphasize the use of species with the highest DBH values observed in the studied areas – suggesting a value for older forest patches and the need to avoid clear cuts and re-planting. After all, the reduction of movement-related energy expenditure can increase the viability of a population of this arboreal endangered primate and guarantee its survival, even in reduced-size forest patches.

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5.8 AUTHORS' CONTRIBUTION

CHAPTER CONTRIBUTORS: Luca Börger, Ariovaldo Pereira da Cruz Neto, Daniel Felippi, Vinicius Alves, Catarina Cibim, Gabriel Pavan Sabino, Felipe Bufalo, Rodrigo Amaral, Rory Wilson, Laurence Culot

Gabriela C. Rezende, Luca Börger and Laurence Culot contributed to the study's conception and design. Data collection was performed by Gabriela C. Rezende, Daniel Felippi, Vinicius Alves, Catarina Cibim, Gabriel Pavan Sabino, Felipe Bufalo and Rodrigo Amaral. Gabriela C. Rezende and Luca Börger developed the data analysis. The first draft of the manuscript was written by Gabriela C. Rezende, and all authors commented on previous versions. All authors read and approved the final manuscript.

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5.10 APPENDICES

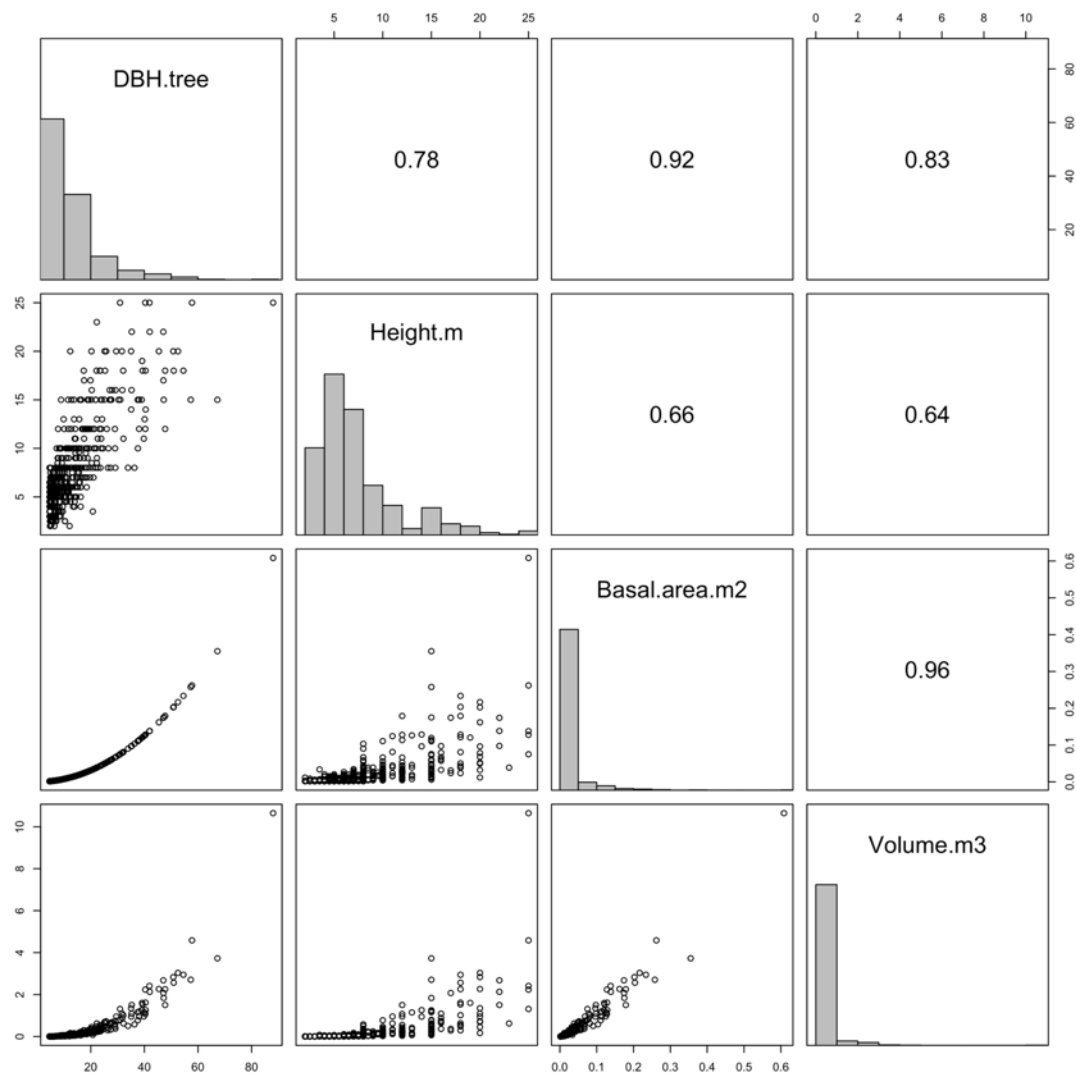


Figure A1. Correlation plot and respective Pearson's coefficient between the variables of vegetation structure characterization.

Table A1. Model selection results, based on delta AIC ranking, for the effect of the vegetation structure on daytime Energy Expenditure (estimated as the daytime smoothed Vectorial Dynamic Body Acceleration values - sVeDBA) of black lion tamarins. Group was considered as random factor in all models.

Model	Added variables	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
m8	DPL+Mean.BA	5	130.23	0.00	1.00	0.15	-59.60	0.15
m6	DPL+Mean.Vol	5	130.42	0.18	0.91	0.14	-59.69	0.29
m7.1	DPL+SD.Vol+Daylenght	6	131.38	1.15	0.56	0.08	-58.95	0.37
m11	DPL+SD.DBH	5	131.59	1.36	0.51	0.08	-60.28	0.45
m8.1	DPL+Mean.BA+Daylenght	6	131.68	1.45	0.49	0.07	-59.10	0.52
m6.1	DPL+Mean.Vol+Daylenght	6	131.83	1.60	0.45	0.07	-59.18	0.59
m23	DPL+Sp.Richness	5	131.91	1.68	0.43	0.06	-60.44	0.65
m22	DPL+SD.Height+SD.Density	6	132.51	2.28	0.32	0.05	-59.52	0.70
m10	DPL+Mean.DBH	5	132.81	2.57	0.28	0.04	-60.89	0.74
m7	DPL+SD.Vol	5	133.31	3.08	0.21	0.03	-61.14	0.77
m9.1	DPL+SD.BA+Daylenght	6	133.64	3.41	0.18	0.03	-60.08	0.80
m11.1	DPL+SD.DBH+Daylenght	6	133.67	3.44	0.18	0.03	-60.10	0.83
m21	DPL+Mean.Height+SD.Density	6	134.04	3.80	0.15	0.02	-60.28	0.85
m9	DPL+SD.BA	5	134.09	3.86	0.15	0.02	-61.53	0.87
m28	DPL+Mean.Height+SD.Density+Shannon	7	134.79	4.55	0.10	0.02	-59.39	0.89
m29	DPL+Mean.Height+SD.Density+Simpson	7	134.79	4.55	0.10	0.02	-59.39	0.90
m26	DPL+Mean.Height+SD.Density+Gama.Div	7	134.79	4.55	0.10	0.02	-59.39	0.92
m27	DPL+Mean.Height+SD.Density+Sp.Richness	7	134.79	4.55	0.10	0.02	-59.39	0.93
m10.1	DPL+Mean.DBH+Daylenght	6	134.89	4.65	0.10	0.01	-60.71	0.95

Model	Added variables	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
m22.1	DPL+SD.Height+SD.Density+Daylenght	7	134.99	4.76	0.09	0.01	-59.49	0.96
m23.1	DPL+Mean.Height+SD.Density+Gama.Div+Daylenght	8	135.35	5.11	0.08	0.01	-58.36	0.97
m21.1	DPL+Mean.Height+SD.Density+Daylenght	7	136.34	6.11	0.05	0.01	-60.17	0.98
m13	DPL+SD.Height	5	137.80	7.57	0.02	0.00	-63.38	0.98
m12	DPL+Mean.Height	5	137.93	7.70	0.02	0.00	-63.45	0.99
m16	DPL+Gama.Div	5	138.94	8.70	0.01	0.00	-63.95	0.99
m14	DPL+Mean.Density	5	139.10	8.87	0.01	0.00	-64.03	0.99
m13.1	DPL+SD.Height+Daylenght	6	139.43	9.20	0.01	0.00	-62.98	0.99
m24	DPL+Shannon	5	139.84	9.61	0.01	0.00	-64.40	0.99
m12.1	DPL+Mean.Height+Daylenght	6	139.93	9.69	0.01	0.00	-63.23	1.00
m16.1	DPL+Gama.Div+Daylenght	6	140.40	10.17	0.01	0.00	-63.46	1.00
m14.1	DPL+Mean.Density+Daylenght	6	140.48	10.25	0.01	0.00	-63.50	1.00
m2	DPL+Daylenght	5	140.76	10.53	0.01	0.00	-64.86	1.00
m25	DPL+Simpson	5	140.97	10.73	0.00	0.00	-64.97	1.00
m1	DPL	4	141.41	11.18	0.00	0.00	-66.37	1.00
m15.1	DPL+SD.Density+Daylenght	6	143.17	12.94	0.00	0.00	-64.85	1.00
m15	DPL+SD.Density	5	143.62	13.39	0.00	0.00	-66.29	1.00
m23.2	Daylenght+Mean.Height+SD.Density+Gama.Div	7	154.85	24.61	0.00	0.00	-69.42	1.00
m6.2	Daylenght+Mean.Vol	5	155.00	24.76	0.00	0.00	-71.98	1.00
m8.2	Daylenght+Mean.BA	5	155.19	24.95	0.00	0.00	-72.08	1.00
m10.2	Daylenght+Mean.DBH	5	155.93	25.69	0.00	0.00	-72.45	1.00
m7.2	Daylenght+SD.Vol	5	156.65	26.42	0.00	0.00	-72.81	1.00
m18	SD.Height	4	157.13	26.89	0.00	0.00	-74.23	1.00

Model	Added variables	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
m17	Mean.Height	4	158.01	27.78	0.00	0.00	-74.67	1.00
m22.2	Daylenght+SD.Height + SD.Density	6	158.79	28.55	0.00	0.00	-72.66	1.00
m5.1	SD.BA+Daylenght	5	158.89	28.66	0.00	0.00	-73.93	1.00
m9.2	Daylenght+SD.BA	5	158.89	28.66	0.00	0.00	-73.93	1.00
m18.1	SD.Height+Daylenght	5	159.07	28.83	0.00	0.00	-74.02	1.00
m13.2	Daylenght+SD.Height	5	159.07	28.83	0.00	0.00	-74.02	1.00
m11.2	Daylenght+SD.DBH	5	159.74	29.50	0.00	0.00	-74.35	1.00
m5	SD.BA	4	160.07	29.83	0.00	0.00	-75.69	1.00
m17.1	Mean.Height+Daylenght	5	160.33	30.10	0.00	0.00	-74.65	1.00
m12.2	Daylenght+Mean.Height	5	160.33	30.10	0.00	0.00	-74.65	1.00
m16.2	Daylenght+Gama.Div	5	160.58	30.34	0.00	0.00	-74.77	1.00
m3	Daylenght	4	160.58	30.35	0.00	0.00	-75.95	1.00
m21.2	Daylenght+Mean.Height+SD.Density	6	160.58	30.35	0.00	0.00	-73.56	1.00
m19.1	MeanDensity+Daylenght	5	162.35	32.12	0.00	0.00	-75.66	1.00
m14.2	Daylenght+Mean.Density	5	162.35	32.12	0.00	0.00	-75.66	1.00
m20.1	SD.Density+Daylenght	5	162.79	32.55	0.00	0.00	-75.88	1.00
m15.2	Daylenght+SD.Density	5	162.79	32.55	0.00	0.00	-75.88	1.00
m19	Mean.Density	4	163.55	33.32	0.00	0.00	-77.44	1.00
m0	null	3	163.96	33.73	0.00	0.00	-78.78	1.00
m20	SD.Density	4	165.68	35.44	0.00	0.00	-78.50	1.00

Legend: SD = Standard Deviation, BA = Basal Area, Vol = Volume, DBH = Diameter at Breast Hight, Sp.Rich = Species Richness, Gama.Div = Gama Diversity

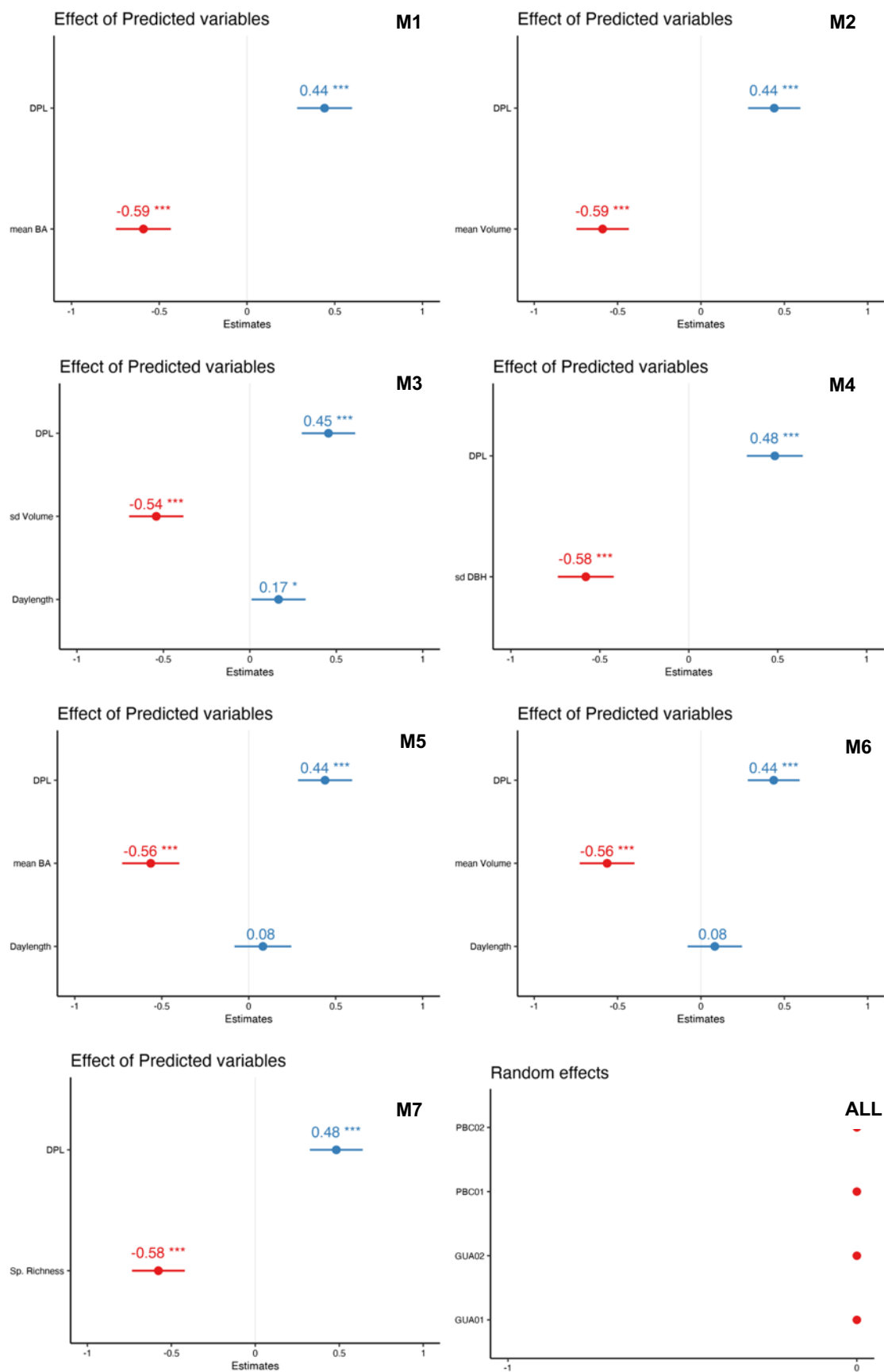


Figure A2. Effect of predicted variables of each model and the random effect on the daytime energy expenditure of each of the seven selected models.

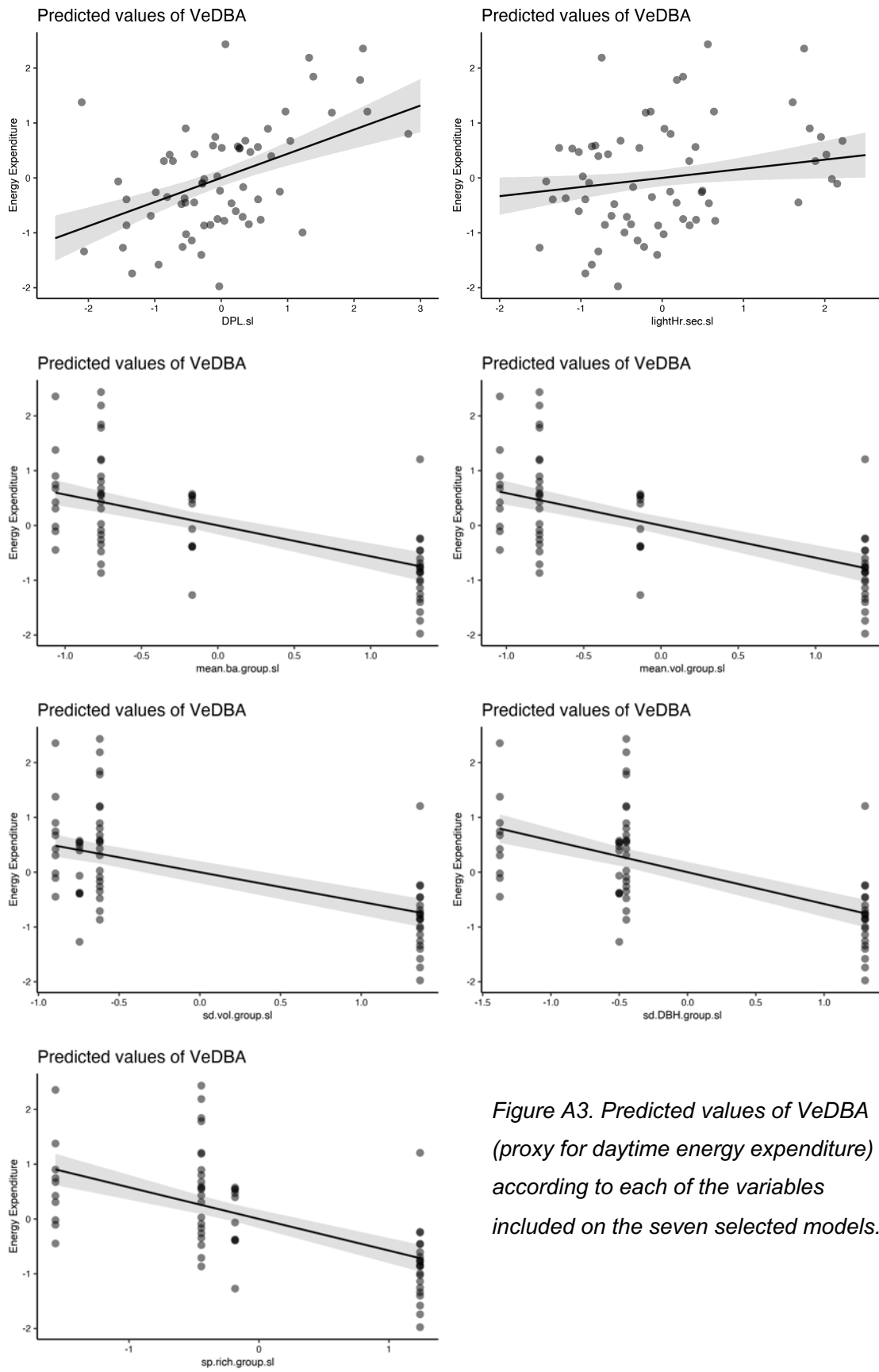


Figure A3. Predicted values of VeDBA (proxy for daytime energy expenditure) according to each of the variables included on the seven selected models.

Table A2. Model selection results, based on delta AIC ranking, for the effect of the movement patterns on Energy Expenditure per period (estimated as the sum of the smoothed Vectorial Dynamic Body Acceleration values – sVeDBA for each period of the day) of black lion tamarins. Group was considered as random factor (RE) in all models, except the ones where the effect of fragment or period were tested instead (m6, m5 and m3).

Model	Added variables	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
m17	DIST+Period+Cum.TA+Cum.Pitch	7	380.65	0.00	1.00	0.73	-182.86	0.73
m17.1	DIST+Period+Cum.TA+Cum.Pitch+PeriodLength	8	382.69	2.03	0.36	0.27	-182.74	1.00
m16	DIST+Period+Cum.TA	6	397.97	17.31	0.00	0.00	-192.64	1.00
m12	DIST+Period+Cum.Pitch	6	399.83	19.17	0.00	0.00	-193.57	1.00
m16.1	DIST+Period+Cum.TA+PeriodLength	7	399.83	19.18	0.00	0.00	-192.45	1.00
m12.1	DIST+Period+Cum.Pitch+PeriodLength	7	402.00	21.35	0.00	0.00	-193.53	1.00
m4	DIST+Period	5	404.43	23.77	0.00	0.00	-196.97	1.00
m15	DIST+Period+SD.TA	6	405.27	24.62	0.00	0.00	-196.29	1.00
m14	DIST+Period+Mean.TA	6	406.18	25.53	0.00	0.00	-196.75	1.00
m13	DIST+Period+Cum.Roll	6	406.24	25.59	0.00	0.00	-196.77	1.00
m15.1	DIST+Period+SD.TA+PeriodLength	7	407.16	26.51	0.00	0.00	-196.11	1.00
m14.1	DIST+Period+Mean.TA+PeriodLength	7	408.26	27.60	0.00	0.00	-196.66	1.00
m13.1	DIST+Period+Cum.Roll+PeriodLength	7	408.37	27.72	0.00	0.00	-196.72	1.00
m2	DIST+Period	5	410.09	29.44	0.00	0.00	-199.80	1.00
m6	DIST+Period+fragment(RE)	5	420.18	39.52	0.00	0.00	-204.84	1.00
m7	Period+Cum.Pitch	5	437.54	56.89	0.00	0.00	-213.53	1.00
m1	DIST	4	437.81	57.16	0.00	0.00	-214.74	1.00
m7.1	Period+Cum.Pitch+PeriodLength	6	439.55	58.90	0.00	0.00	-213.43	1.00
m11	Period+Cum.TA	5	445.02	64.37	0.00	0.00	-217.27	1.00
m8	Period+Cum.Roll	5	446.13	65.48	0.00	0.00	-217.82	1.00
m11.1	Period+Cum.TA+PeriodLength	6	446.65	66.00	0.00	0.00	-216.98	1.00

Model	Added variables	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
m10	Period+SD.TA	5	447.12	66.47	0.00	0.00	-218.31	1.00
m8.1	Period+Cum.Roll+PeriodLength	6	448.14	67.49	0.00	0.00	-217.72	1.00
m9	Period+Mean.TA	5	448.48	67.82	0.00	0.00	-218.99	1.00
m10.1	Period+SD.TA+PeriodLength	6	448.66	68.01	0.00	0.00	-217.98	1.00
m5	DIST+fragment(RE)	4	449.21	68.56	0.00	0.00	-220.44	1.00
m9.1	Period+Mean.TA+PeriodLength	6	450.29	69.64	0.00	0.00	-218.80	1.00
m3	DIST+Period(RE)	4	458.65	78.00	0.00	0.00	-225.16	1.00
m0	null	3	476.94	96.29	0.00	0.00	-235.38	1.00

Legend: DIST = total displacement within the period, SD = Standard Deviation, TA = Turning Angle, Cum = Cumulative

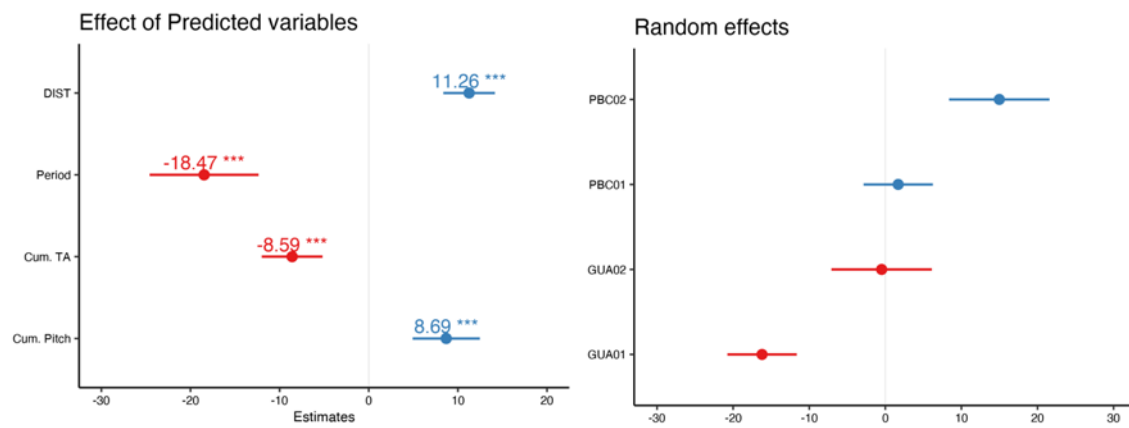


Figure A4. Effect of predicted variables and the random effect on the energy expenditure per period of the selected model.

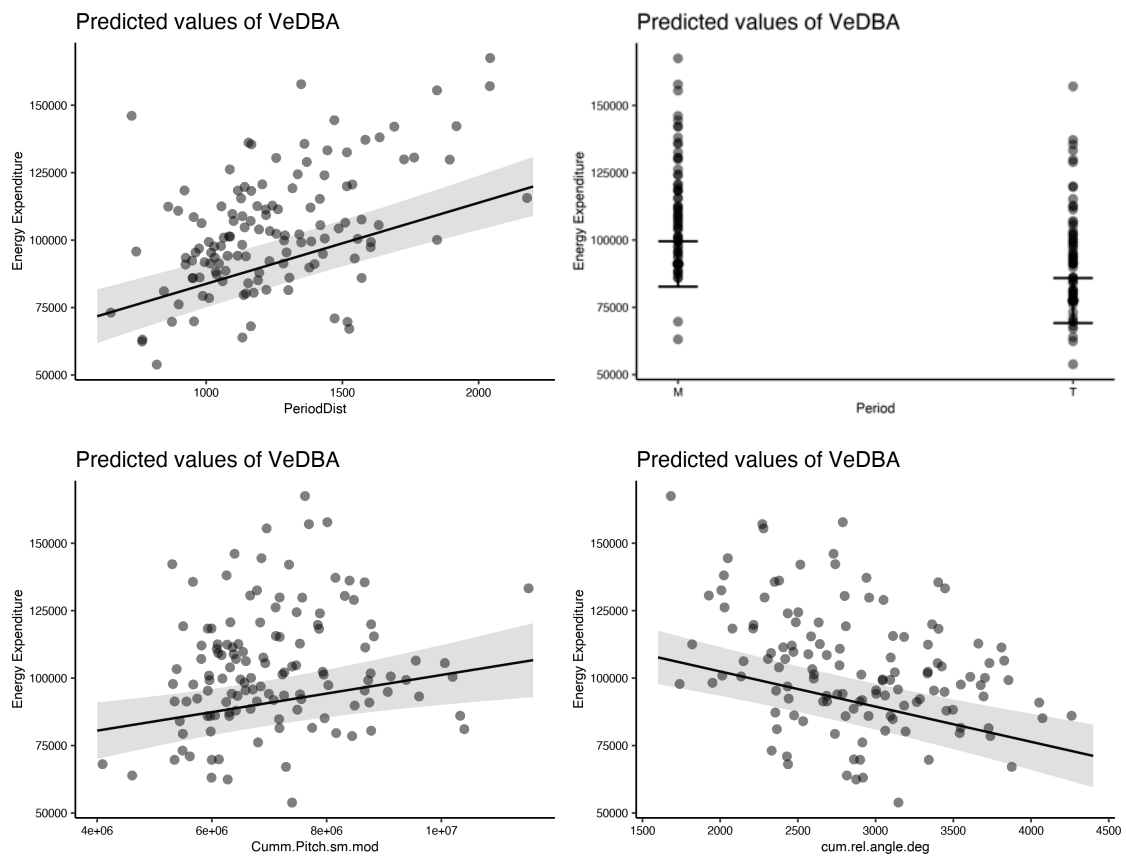


Figure A5. Predicted values of VeDBA (proxy for energy expenditure per period) according to each of the variables included on the selected model.

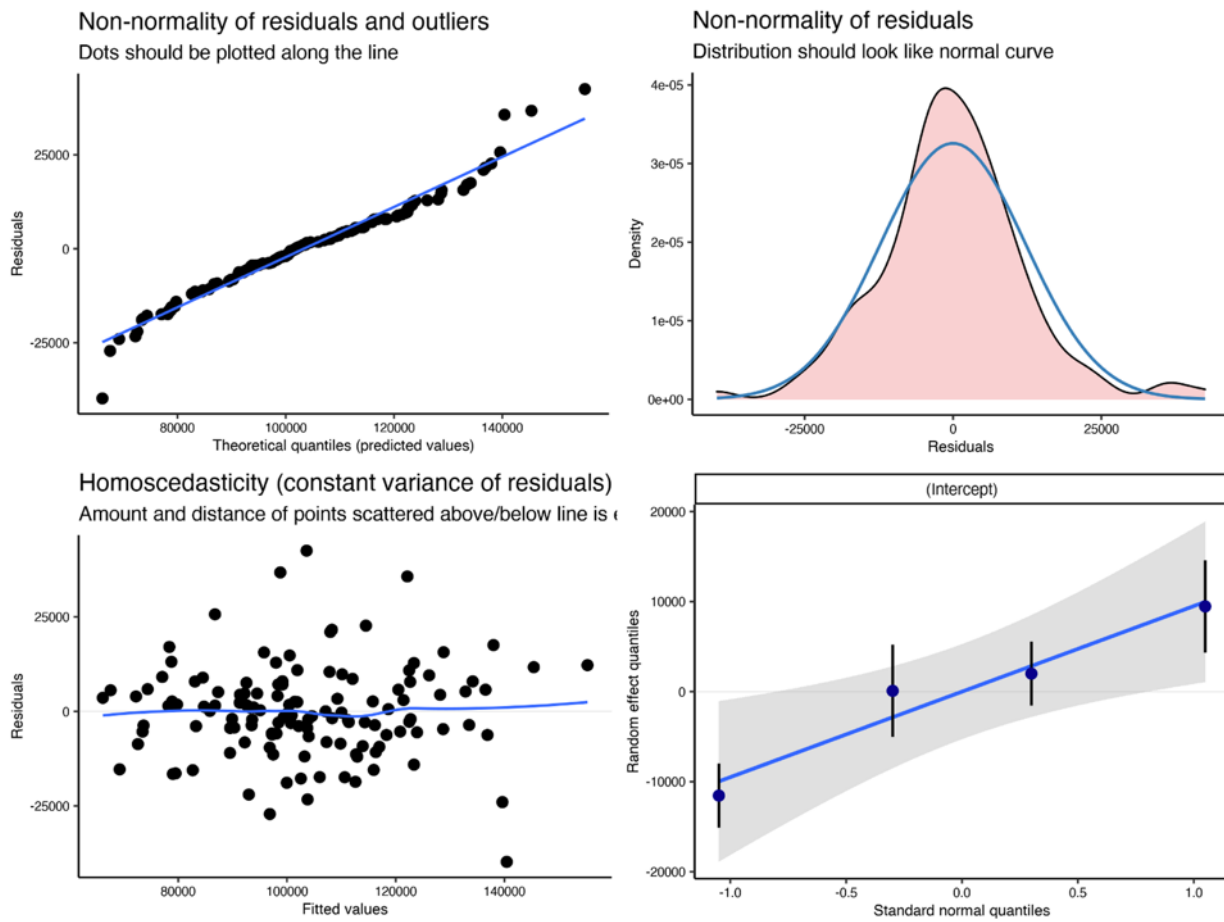


Figure A6. Plots of the residuals relative to the results of the LMM model for model fit checking: Q-Q plot (top-left); Density plot of residuals (top-right); Plot of residual values (bottom-left); and Plot of random effect (bottom-right).

Table A3. Model selection results, based on delta AIC ranking, for the effect of the physical environmental variables on hourly Energy Expenditure (estimated as the hourly smoothed Vectorial Dynamic Body Acceleration values - sVeDBA) of black lion tamarins. Group was included as random factor and Hour as a cyclic variable in all models where they are indicated as covariate. HrDist = total displacement within an hour.

Model	Variables added	df	AIC	Delta-AICc	Deviance explained (%)	Adj. R ²
GAM20	HrDist+group+hour+temperature+humidity	29.3	15235.19	0	60.2	0.588
GAM18	HrDist+group+hour+temperature	20.8	15243.63	8.44	58.9	0.579
GAM19	HrDist+group+hour+humidity	27.9	15297.44	62.25	56.8	0.553
GAM11	HrDist+group+hour	18.6	15339.45	104.26	53.3	0.522
GAM14	HrDist+group+temperature+humidity	15.0	15340.11	104.92	52.8	0.520
GAM12	HrDist+group+temperature	13.2	15347.84	112.65	52.1	0.514
GAM13	HrDist+group+humidity	11.7	15489.63	254.44	42.3	0.416
GAM10	HrDist+group	11.3	15510.92	275.73	40.6	0.339
GAM9	HrDist	8.2	15585.06	349.87	34.2	0.336
GAM5	Hour+group+temperature+humidity	17.9	15983.63	748.44	41.5	0.403
GAM3	Hour+group+temperature	16.0	15986.6	751.41	41.0	0.400
GAM4	Hour+group+humidity	14.9	16044.69	809.50	36.4	0.354
GAM2	Hour+group	12.7	16048.58	813.39	35.7	0.349
GAM8	Hour+temperature+humidity	20.6	16064.5	829.31	35.7	0.342
GAM6	Hour+temperature	13.4	16075.73	840.54	33.6	0.327
GAM7	Hour+humidity	17.6	16091.87	856.68	33.0	0.316
GAM1	Hour	9.9	16110.3	875.11	30.1	0.294
GAM17	temperature+humidity	9.3	16328.43	1093.24	7.96	0.071
GAM15	temperature	5.6	16334.4	1099.21	6.41	0.060
GAM16	humidity	4.4	16374.27	1139.08	1.32	0.010
GAM0	null	2.0	16380.01	1144.82	0	0

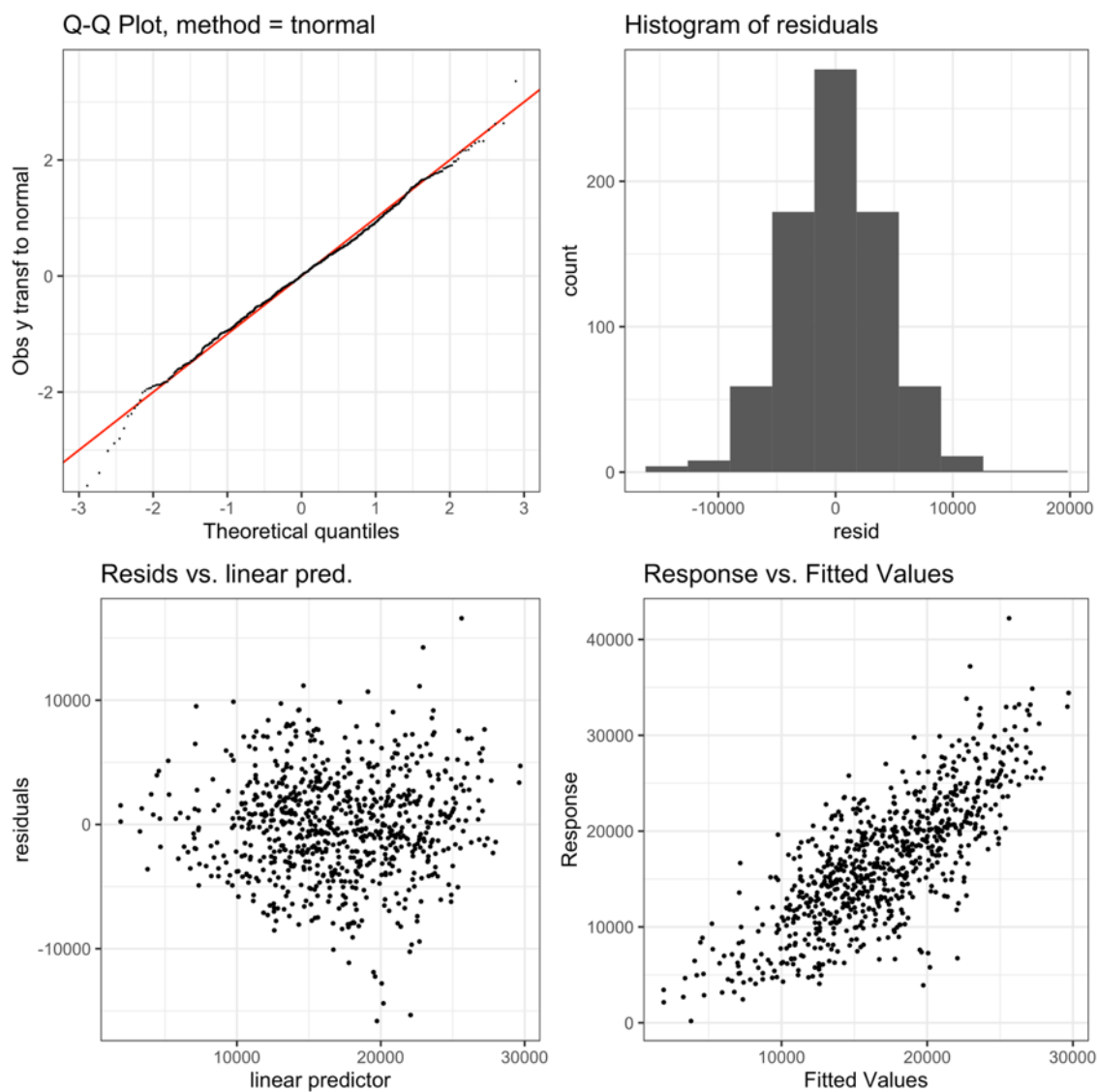


Figure A7. Plots of the residuals relative to the results of the GAM model for model fit checking: Q-Q plot (top-left); Histogram of residuals (top-right); Plot of residual values (bottom-left); and Plot of response against fitted values (bottom-right).

Table A4. Obtained values of Daily Energy Expenditure (DEE) from this study, based on the DBA metrics converted to DEE, and the expected ones, including prediction interval, based on the equation provided by Pontzer et al. (2014) for primates ($\log_{10}[\text{DEE}] = 0.69 \pm 0.03 * (\log_{10}[\text{weight}]) + 2.09 \pm 0.03$).

ID	DEE obtained values (kcal/day)	DEE expected values (kcal/day)	Lower prediction interval (kcal/day)	Upper prediction interval (kcal/day)
GUA01	92.1	85.7	50.9	144.5
GUA02	103.1	88.7	52.7	149.3
PBC01	102.6	88.7	52.7	149.3
PBC02	105.4	87.7	52.1	147.7
Mean	100.8	87.7	52.1	147.7
±SD	±5.9	±1.4	±0.8	±2.3

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6 CONSIDERAÇÕES FINAIS

Devido a sua dependência por ambientes florestais, primatas arborícolas como o mico-leão-preto são mais propensos a terem sua capacidade de movimentação afetada por processos de fragmentação e degradação do hábitat, afetando a viabilidade de suas populações e a sobrevivência da espécie como um todo (Lees & Peres, 2009). Nesse sentido, buscamos compreender como a espécie é afetada, em diferentes escalas, por tais processos, a fim de oferecer evidências científicas que possam subsidiar estratégias para sua conservação.

Nossos modelos de nicho ecológico indicaram que a modificação da paisagem histórica e atual teve um impacto extremamente negativo na distribuição do mico-leão-preto, mostrando que a espécie está presente em menos de 1% de sua área de ocorrência original. Também identificamos duas regiões prioritárias para o desenvolvimento de estratégias de conservação focadas no manejo de populações e do hábitat: a região do Alto Paranapanema, no sudeste de São Paulo, e a região do Pontal do Paranapanema, no extremo oeste do estado.

Partindo para uma escala menor, obtivemos a primeira estimativa da taxa metabólica de campo para micos-leões-pretos e validamos a utilização de acelerômetros para estudos dessa finalidade com esse primata. Ao monitorar os animais em campo com dispositivos de GPS e acelerômetro, também validamos o uso desses equipamentos de monitoramento remoto para estudos de movimento, uso de espaço e gasto energético de primatas de pequeno porte.

Nossos resultados sugeriram um efeito do tamanho do fragmento no uso, exploração diária de recursos e compartilhamento do espaço, e ressaltaram que alguns padrões de movimento podem estar associados a características intrínsecas à espécie, não apresentando variação de uma área para a outra. Ao mesmo tempo, o tamanho do fragmento não se mostrou como um bom indicador de taxas de gasto energético. Nesse sentido, os fatores físicos (temperatura, umidade e duração do dia) e bióticos (estrutura e composição da floresta), bem como a direcionalidade do movimento tiveram influência nas estimativas de gasto energético dos micos. Encontramos uma relação negativa entre gasto energético e as variáveis estruturais (DAP, área basal e volume) e composicionais (riqueza de espécies) da floresta,

corroborando a nossa hipótese de que os micos gastam menos energia em florestas de melhor qualidade.

Concluímos, então, com esse trabalho que, para conservar o mico-leão-preto em habitats fragmentados, é necessário trabalhar para melhorar a qualidade da floresta, tanto em termos estruturais quanto composicionais, mas também considerar o tamanho dos fragmentos como fator chave para a manutenção de populações no longo prazo.

7 RECOMENDAÇÕES PARA O MANEJO DO HÁBITAT E CONSERVAÇÃO DO MICO-LEÃO-PRETO

Os resultados desta pesquisa já têm direcionado o planejamento de estratégias de conservação para o mico-leão-preto. Com base no mapa de áreas e estratégias prioritárias resultante do primeiro capítulo desta tese (Rezende et al., 2020), o Programa de Conservação do Mico-leão-preto/IPÊ desenvolveu uma proposta de corredores florestais para a região do Alto Paranapanema a partir do passivo ambiental de Áreas de Preservação Permanente (APP) e Reservas Legais das propriedades rurais (Figura 3). Esse plano de corredores complementa e oferece diretrizes mais específicas à proposta já existente (em implementação) relativa à região do Pontal do Paranapanema (Cullen Jr. et al., 2017). Com o objetivo de estabelecer duas populações viáveis da espécie a partir da conexão das subpopulações de micos em cada região, a proposta original contempla a restauração de 3.000 ha de corredores para estabelecer uma floresta contínua de 45.000 ha no Pontal do Paranapanema, enquanto a nova proposta adiciona a essa meta mais 12.000 ha de corredores florestais, visando o estabelecimento de 73.000 ha de floresta contínua para o Alto Paranapanema. Essa proposta tem potencial de dobrar o tamanho populacional da espécie a partir do aumento da capacidade-suporte disponível.

Proposta de corredores florestais para conectar populações de mico-leão-preto

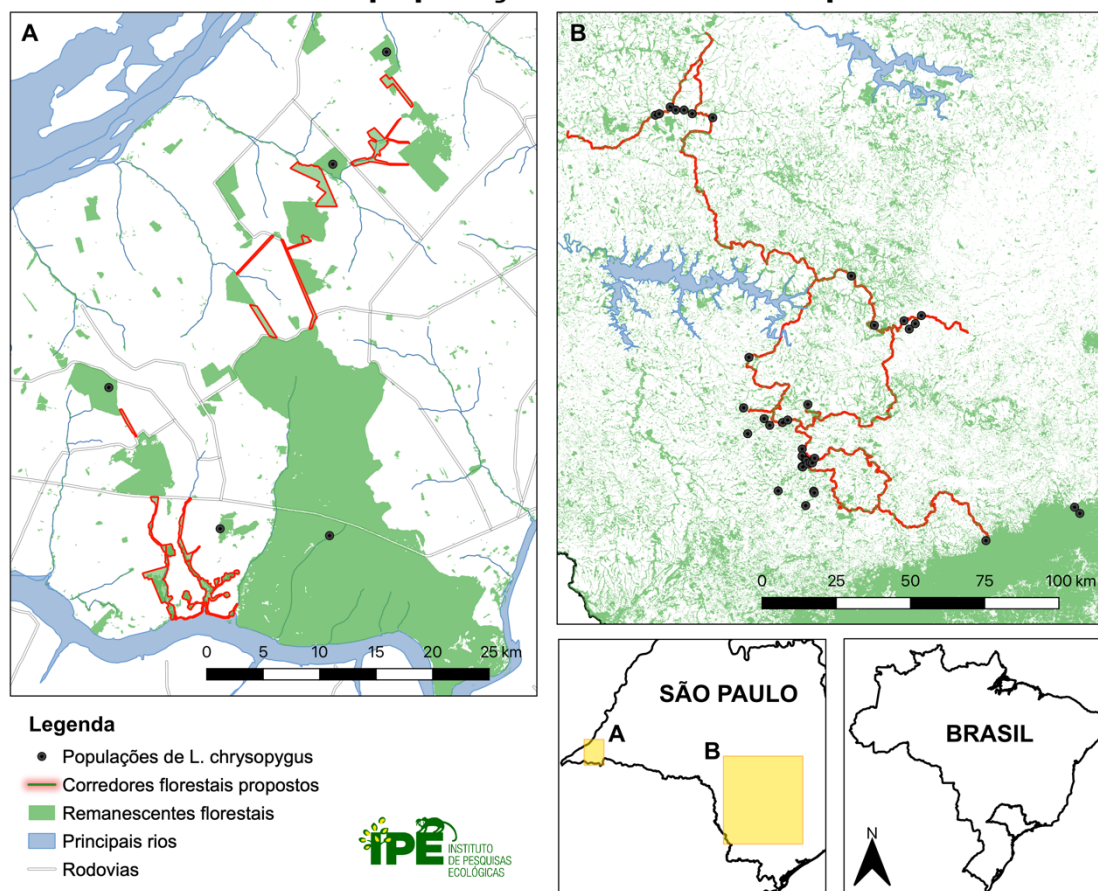


Figura 3. Proposta de corredores florestais visando conectar as populações de mico-leão-preto nas regiões do Pontal do Paranapanema (A) e Alto Paranapanema (B). Fonte: Programa de conservação do Mico-leão-preto/IPÊ.

Diante dessa possibilidade, a seguir, traçamos recomendações no sentido de direcionar o processo de restauração desses corredores e o enriquecimento dos habitats disponíveis para a espécie, a partir das evidências científicas apresentadas neste estudo. Para isso, também avaliamos a estrutura e composição da vegetação de 11 fragmentos florestais nas regiões do Alto Paranapanema e Pontal do Paranapanema, sendo oito deles com ocorrência de mico-leão-preto (Anexo 1 desta tese). Comparamos essas áreas, buscando identificar atributos determinantes da vegetação, sejam eles estruturais ou composicionais, para o uso do habitat pelos micos-leões, visando otimizar o gasto energético relativo ao movimento. A partir desses atributos, propomos, então, diretrizes para o manejo desse habitat em áreas

de ocorrência real e potencial dessa espécie, de modo a favorecer o uso e ocupação dessas áreas e sua movimentação pela paisagem através de corredores restaurados.

Inicialmente, para avaliar e fazer comparações entre os fragmentos, consideramos o Parque Estadual Morro do Diabo (PMD) o referencial de mata mais preservada adequada para a espécie, já que este é o maior remanescente e que abriga a única população viável e autossustentável de micos. Observamos que, no que diz respeito à riqueza e diversidade, o PMD teve os melhores índices da região do Pontal do Paranapanema, diferindo dos demais fragmentos dessa região (Figura 4). Mas quando comparado aos fragmentos do Alto Paranapanema, teve riqueza similar a todos eles, e diversidade próxima a Guareí (GUA), fragmento com tamanho equivalente a 0,3% da área do PMD. Entretanto, a diversidade do PMD foi inferior à Fazenda Rio Claro (FRC) e superior à Estação Ecológica de Angatuba (ANG) e Fazenda Garibaldi (GRB) (Figura 4). No que diz respeito à estrutura da floresta, o PMD também diferiu em diâmetro à altura do peito (DAP) e área basal dos demais fragmentos da mesma região, exceto do corredor florestal restaurado (COR), com valores mais elevados, mas similares aos encontrados para essas métricas nos fragmentos do Alto Paranapanema (Tabela 1). Já no que diz respeito à altura, o PMD apresentou diferenças com relação ao observado no Alto Paranapanema, com valores mais baixos e similares aos fragmentos do Pontal, com exceção do Água Sumida (AGS), fragmento pertencente à Estação Ecológica Mico-leão-preto (ESEC MLP) (Tabela 1).

Com base nessa avaliação e nos parâmetros que afetam o gasto energético relativo ao movimento dos micos-leões identificados no quarto capítulo desta tese, podemos sugerir que a estrutura e composição das florestas encontradas na região do Alto Paranapanema são mais favoráveis aos micos. Neste sentido, os fragmentos favorecem que indivíduos da espécie otimizem seu gasto energético e possam obter um maior saldo a ser investido em crescimento somático e reprodução. Também, diante do observado no corredor florestal restaurado, em que as condições estruturais e composicionais se apresentam similares ao PMD, identificamos o potencial da restauração no reestabelecimento das condições favoráveis aos micos e recomendamos que ações de manejo do hábitat visando a suplementação das áreas de floresta existentes sejam realizadas nos fragmentos da região do Pontal. Nesse sentido, a escolha das espécies a serem utilizadas em processos de restauração da

floresta e enriquecimento do hábitat para o mico-leão-preto deve contemplar espécies arbóreas que ofereçam os recursos necessários aos micos (ou seja, árvores frutíferas e para locais de dormir). As espécies escolhidas para o reflorestamento também devem ser selecionadas no sentido de estabelecer uma floresta com estrutura suficiente para reduzir o gasto energético relativo ao movimento dos indivíduos dessa espécie. Por isso, destacamos o uso de espécies utilizadas como recurso pelos micos, que estejam presentes em ambas as regiões, com maiores valores de DAP e volume, como indicativos de espécies que tem contribuído para a estruturação dessa floresta (Tabela 1). Ressaltamos, portanto, as espécies *Tapirira guianensis*, *Psidium guajava*, *Syagrus romanzoffiana*, *Inga vera* e *Trichilia catigua*, utilizadas como alimentação, *Aspidosperma polyneuron*, *Cariniana estrellensis* e *Lonchocarpus cultratus*, utilizadas como dormitório, e *Campomanesia xanthocarpa* e *Plinia rivularis*, utilizadas tanto para alimentação quanto para descanso em ambas as regiões. Especificamente para a região do Pontal do Paranapanema, identificamos também *Jacaratia spinosa* e *Cabralea canjerana*, e para a região do Alto Paranapanema, *Trichilia claussoni*, *Chrysophyllum gonocarpum* e *Inga striata*, como espécies florestais de grande relevância para o processo de restauração.

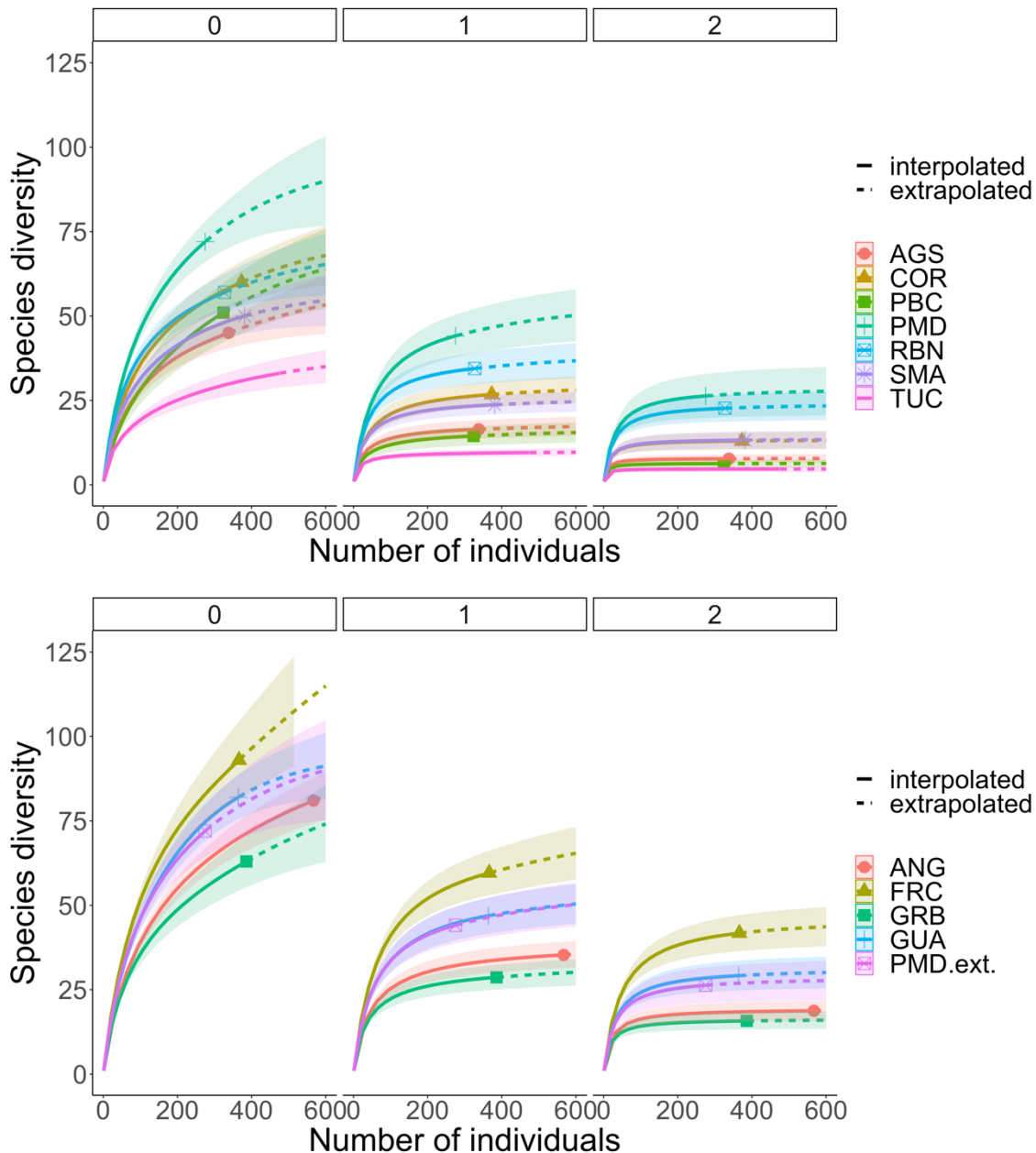


Figura 4. Índices de riqueza de espécies de árvores (esquerda), diversidade de Shannon (meio) e diversidade de Simpson (direita), com base nos números de Hill ($q = 0, 1, 2$, respectivamente) para os fragmentos avaliados nas regiões do Pontal do Paranapanema (a) e Alto Paranapanema (b). A rarefação (linhas sólidas) e extrapolação (linhas tracejadas) dos valores foi feita com base no tamanho das amostras (símbolos). Os intervalos de confiança de 95% são mostrados pelas respectivas regiões sombreadas. AGS = Água Sumida (ESEC MLP), COR = corredor florestal restaurado, PBC = Ponte Branca (ESEC MLP), PMD = Parque Estadual Morro do Diabo, RBN = Fazenda Ribeirão Bonito, SMA = Fazenda Santa Maria, TUC = Tucano (ESEC MLP); ANG = ESEC Angatuba, FRC = Fazenda Rio Claro, GRB = Fazenda Garibaldi, GUA = Guareí. ext. = grupo externo.

Tabela 1. Características estruturais da vegetação em fragmentos com presença e ausência de mico-leão-preto nas regiões do Alto Paranapanema e Pontal do Paranapanema, com destaque para o Parque Estadual do Morro do Diabo (PMD - em cinza), utilizado como área de referência. Valores de desvio padrão são apresentados junto às médias e diferenças na comparação com o PMD indicadas junto aos valores (*** = $P \leq 0.001$; ** = $0.001 < P \leq 0.01$; * = $0.01 < P \leq 0.05$).

	Áreas com mico-leão-preto								Áreas sem mico-leão-preto		
	Alto Paranapanema				Pontal do Paranapanema				Pontal do Paranapanema		
	ANG	FRC	GRB	GUA	PMD	PBC	RBN	SMA	AGS	COR	TUC
Área do fragmento (ha)	1,394	1,800	100	105	33,700	1,306	418	515	1,199	1,340	2,115
DAP médio (cm)	12.48 ±7.51	13.36 ±12.86	13.85 ±10.74	14.29 ±11.72	13.27 ±10.35	10.83 ±7.94*	10.02 ±5.98**	9.56 ±5.25***	10.81 ±8.34**	12.49 ±8.03	9.80 ±6.42***
Altura média (m)	7.80 ±2.35***	10.21 ±6.92***	7.21 ±2.27***	8.84 ±5.35***	6.96 ±3.69	6.64 ±2.40	6.17 ±1.88	5.85 ±2.04*	7.50 ±3.24***	5.73 ±1.68	6.21 ±1.66
Área Basal média (m ² *100)	1.67 ±2.17	2.69 ±8.88	2.41 ±5.46	2.68 ±5.47	2.22 ±4.31	1.41 ±2.93*	1.07 ±1.54**	0.93 ±1.28***	1.46 ±3.87**	1.73 ±2.29	1.08 ±2.09***
Área basal acumulada (m ² /ha)	36.55	40.28	33.98	41.80	28.41	20.78	12.98	14.71	20.33	16.94	19.97
Volume médio (m ³)	11.03 ±16.84*	35.51 ±158.95*	16.68 ±49.40*	29.27 ±82.45	18.49 ±56.17	10.27 ±32.34	5.81 ±11.31	5.18 ±12.58**	13.58 ±67.53	7.76 ±10.84	6.10 ±17.91*
Volume total (m ³ /ha)	242.03	530.91	235.13	456.57	236.63	150.94	70.53	81.57	188.81	76.00	113.17
Densidade média (ind./ha)	0.22 ±0.10***	0.15 ±0.05	0.14 ±0.06	0.16 ±0.04*	0.13 ±0.03	0.15 ±0.05	0.12 ±0.04	0.16 ±0.06	0.14 ±0.05	0.08 ±0.06**	0.19 ±0.06**

Tabela 2. Características estruturais das espécies vegetais utilizadas para alimentação (A), dormitório (D) ou ambos (AD) pelo mico-leão-preto nas regiões do Alto Paranapanema e Pontal do Paranapanema. Valores de desvio padrão são apresentados junto às médias quando houve mais de um indivíduo avaliado. Estão destacadas as espécies encontradas em ambas as regiões avaliadas (na coluna Espécie), as que contribuíram com maiores valores de DAP médio (cm), maior volume total (m³/ha) e maior relação de volume total por indivíduo (nas respectivas colunas). No caso de a espécie ocorrer exclusivamente em uma das regiões, a região encontra-se em destaque na respectiva coluna.

Tipo de recurso	Região	Espécie	N	DAP médio (cm)	Altura média (m)	Área Basal média (m ²)	Área Basal acumulada (m ² /ha)	Volume médio (m ³)	Volume total (m ³ /ha)	Relação Volume/ indivíduo
A	Alto	<i>Allophylus edulis</i>	9	9.92 ± 4.85	6.56 ± 1.49	0.94 ± 0.78	0.42	4.38 ± 4.05	1.97	0.22
A	Alto	<i>Annona cacans</i>	3	15.49 ± 9.22	8.17 ± 2.36	2.33 ± 2.37	0.35	15.54 ± 17.26	2.33	0.78
A	Alto	<i>Annona emarginata</i>	2	9.6 ± 6.82	7.5 ± 3.54	0.91 ± 1.03	0.09	6.03 ± 7.64	0.60	0.30
A	Alto	<i>Campomanesia guaviroba</i>	19	8.75 ± 4.56	7.21 ± 2.09	0.76 ± 0.92	0.72	4.67 ± 7.3	4.44	0.23
A	Alto	<i>Campomanesia guazumifolia</i>	6	9.76 ± 4.03	7.08 ± 3.12	0.85 ± 0.68	0.26	5.15 ± 5.2	1.54	0.26
A	Alto	<i>Casearia decandra</i>	10	9.92 ± 3.45	7.75 ± 2.63	0.86 ± 0.54	0.43	5.33 ± 4.44	2.67	0.27
A	Alto	<i>Casearia sylvestris</i>	64	9.36 ± 4.13	6.43 ± 1.54	0.82 ± 0.76	2.63	4.07 ± 4.61	13.01	0.20
A	Alto	<i>Celtis iguanaea</i>	1	20.76	3.5	3.39	0.17	8.29	0.41	0.41
A	Alto	<i>Chrysophyllum gonocarpum</i>	8	14.53 ± 11.12	12.5 ± 7.91	2.51 ± 3.43	1.00	37.16 ± 60.07	14.86	1.86
A	Alto	<i>Cordia sellowiana</i>	1	7.77	7.0	0.47	0.02	2.32	0.12	0.12
A	Alto	<i>Diospyros inconstans</i>	6	10.07 ± 4.95	7.08 ± 1.36	0.96 ± 1.05	0.29	5.14 ± 6.04	1.54	0.26
A	Alto	<i>Duguetia lanceolata</i>	2	7.62 ± 2.77	5.25 ± 3.89	0.49 ± 0.33	0.05	2.24 ± 2.54	0.22	0.11
A	Alto	<i>Eugenia florida</i>	7	7.86 ± 2.65	6.07 ± 2.15	0.53 ± 0.36	0.19	2.5 ± 1.9	0.87	0.12
A	Alto	<i>Eugenia longipedunculata</i>	1	4.81	6.5	0.18	0.01	0.83	0.04	0.04
A	Alto	<i>Eugenia uniflora</i>	6	10.7 ± 2.94	9.25 ± 3.62	0.96 ± 0.57	0.29	6.7 ± 5.31	2.01	0.34

Tipo de recurso	Região	Espécie	N	DAP médio (cm)	Altura média (m)	Área Basal média (m ²)	Área Basal acumulada (m ² /ha)	Volume médio (m ³)	Volume total (m ³ /ha)	Relação Volume/ indivíduo
A	Alto	<i>Garcinia gardneriana</i>	5	8.12 ± 3.25	8 ± 2.85	0.58 ± 0.41	0.15	3.79 ± 3.56	0.95	0.19
A	Alto	<i>Inga marginata</i>	5	8.8 ± 5.63	6.9 ± 1.56	0.81 ± 1.08	0.20	3.8 ± 4.88	0.95	0.19
A	Alto	<i>Inga striata</i>	14	18.28 ± 12.68	8.49 ± 2.63	3.8 ± 5.14	2.66	28.86 ± 45.19	20.20	1.44
A	Alto	<i>Inga vera</i>	3	15.43 ± 7.52	13 ± 2.65	2.17 ± 2.08	0.32	17.17 ± 12.78	2.58	0.86
A	Alto	<i>Myrcia splendens</i>	1	8.12	15.0	0.52	0.03	5.43	0.27	0.27
A	Alto	<i>Myrsine umbellata</i>	4	9.32 ± 2.25	7.7 ± 0.48	0.71 ± 0.31	0.14	3.87 ± 1.83	0.77	0.19
A	Alto	<i>Pera glabrata</i>	2	10.98 ± 8.78	10 ± 5.66	1.25 ± 1.51	0.12	11.75 ± 15.55	1.17	0.59
A	Alto	<i>Protium heptaphyllum</i>	1	10.63	6.5	0.89	0.04	4.04	0.20	0.20
A	Alto	<i>Psidium guajava</i>	1	20.15	7.5	3.19	0.16	16.74	0.84	0.84
A	Alto	<i>Rhamnidium elaeocarpum</i>	2	12.48 ± 1.26	9.5 ± 0.71	1.23 ± 0.25	0.12	8.11 ± 1.03	0.81	0.41
A	Alto	<i>Sorocea bonplandii</i>	2	5.17 ± 0.34	6.75 ± 1.06	0.21 ± 0.03	0.02	1.01 ± 0.29	0.10	0.05
A	Alto	<i>Syagrus romanzoffiana</i>	31	18.95 ± 4.41	8.79 ± 3.64	2.97 ± 1.35	4.60	18.46 ± 10.61	28.62	0.92
A	Alto	<i>Tapirira guianensis</i>	5	14.44 ± 14.01	7.3 ± 2.56	2.87 ± 4.86	0.72	21.2 ± 39.89	5.30	1.06
A	Alto	<i>Trichilia catigua</i>	53	10.81 ± 7.2	8 ± 2.73	1.32 ± 2.31	3.49	9.66 ± 19.9	25.59	0.48
A	Alto	<i>Trichilia claussoni</i>	16	12.91 ± 10.67	14.13 ± 22.15	2.15 ± 3.57	1.72	68.07 ± 221.44	54.45	3.40
A	Alto	<i>Trichilia pallida</i>	2	9.31 ± 1.46	4.75 ± 3.18	0.69 ± 0.21	0.07	2.05 ± 0.82	0.21	0.10
AD	Alto	<i>Campomanesia xanthocarpa</i>	15	14.5 ± 11.54	10.07 ± 4.5	2.63 ± 4.71	1.97	28.38 ± 69.84	21.29	1.42
AD	Alto	<i>Plinia rivularis</i>	11	8.35 ± 4.53	7.5 ± 2.89	0.69 ± 0.85	0.38	4.08 ± 5.09	2.24	0.20
D	Alto	<i>Aspidosperma polyneuron</i>	1	5.51	5.5	0.24	0.01	0.92	0.05	0.05
D	Alto	<i>Cariniana estrellensis</i>	4	29.1 ± 14.91	16.38 ± 6.94	7.96 ± 6.36	1.59	106.67 ± 102.47	21.33	5.33
D	Alto	<i>Lonchocarpus cultratus</i>	24	19.78 ± 9.02	13.46 ± 4.27	3.69 ± 3.62	4.42	39.44 ± 41.71	47.33	1.97

Tipo de recurso	Região	Espécie	N	DAP médio (cm)	Altura média (m)	Área Basal média (m ²)	Área Basal acumulada (m ² /ha)	Volume médio (m ³)	Volume total (m ³ /ha)	Relação Volume/ indivíduo
D	Alto	<i>Ocotea corymbosa</i>	6	9.03 ± 2.31	7.58 ± 0.92	0.67 ± 0.33	0.20	3.58 ± 1.88	1.07	0.18
A	Pontal	<i>Cordia ecalyculata</i>	4	7.08 ± 0.92	6.13 ± 1.11	0.4 ± 0.1	0.08	1.74 ± 0.73	0.35	0.09
A	Pontal	<i>Duguetia lanceolata</i>	33	8.9 ± 4.2	6.06 ± 1.7	0.76 ± 0.74	1.25	3.75 ± 4.52	6.18	0.19
A	Pontal	<i>Eugenia florida</i>	10	10.56 ± 5.3	6.2 ± 2.31	1.07 ± 0.95	0.54	5.53 ± 5.91	2.77	0.28
A	Pontal	<i>Eugenia hiemalis</i>	7	5.78 ± 1.17	4.21 ± 1.04	0.27 ± 0.11	0.10	0.79 ± 0.36	0.27	0.04
A	Pontal	<i>Eugenia uniflora</i>	1	8.98	6.0	0.63	0.03	2.66	0.13	0.13
A	Pontal	<i>Ficus guaranitica</i>	2	12.47 ± 1.21	6.25 ± 0.35	1.23 ± 0.24	0.12	5.4 ± 1.34	0.54	0.27
A	Pontal	<i>Garcinia gardneriana</i>	33	8.22 ± 4.44	6.08 ± 2.18	0.68 ± 0.97	1.12	3.67 ± 7.62	6.06	0.18
A	Pontal	<i>Inga marginata</i>	1	6.88	6.5	0.37	0.02	1.69	0.08	0.08
A	Pontal	<i>Inga vera</i>	11	17.55 ± 9.53	8.14 ± 1.78	3.07 ± 2.97	1.69	16.71 ± 13.87	9.19	0.84
A	Pontal	<i>Jacaratia spinosa</i>	5	29.97 ± 10.27	10.4 ± 1.67	7.72 ± 4.95	1.93	59.77 ± 44.29	14.94	2.99
A	Pontal	<i>Myrcia splendens</i>	46	8.69 ± 3.79	5.45 ± 1.41	0.7 ± 0.68	1.62	2.91 ± 3.2	6.69	0.15
A	Pontal	<i>Myrciaria cuspidata</i>	19	9.05 ± 3.57	5.61 ± 1.34	0.74 ± 0.59	0.70	3.19 ± 3.27	3.03	0.16
A	Pontal	<i>Myrciaria floribunda</i>	77	7.17 ± 2.55	5.96 ± 1.2	0.45 ± 0.35	1.75	2.08 ± 2.01	8.02	0.10
A	Pontal	<i>Pera glabrata</i>	2	5.17 ± 0.11	5.5 ± 0.71	0.21 ± 0.01	0.02	0.81 ± 0.14	0.08	0.04
A	Pontal	<i>Protium heptaphyllum</i>	6	13.83 ± 8.45	8.67 ± 2.14	1.97 ± 2.42	0.59	12.23 ± 14.39	3.67	0.61
A	Pontal	<i>Psidium guajava</i>	1	30.89	4.0	7.49	0.37	20.99	1.05	1.05
A	Pontal	<i>Rhamnidium elaeocarpum</i>	2	11.52 ± 0.31	8.5 ± 0.71	1.04 ± 0.06	0.10	6.22 ± 0.85	0.62	0.31
A	Pontal	<i>Sorocea bonplandii</i>	3	6.01 ± 0.4	4 ± 0.5	0.28 ± 0.04	0.04	0.8 ± 0.18	0.12	0.04
A	Pontal	<i>Syagrus romanzoffiana</i>	30	20.21 ± 3.77	6.43 ± 1.85	3.32 ± 1.26	4.97	15.28 ± 7.92	22.92	0.76
A	Pontal	<i>Tapirira guianensis</i>	2	10.44 ± 8.24	5.75 ± 0.35	1.12 ± 1.35	0.11	4.69 ± 5.72	0.47	0.23

Tipo de recurso	Região	Espécie	N	DAP médio (cm)	Altura média (m)	Área Basal média (m ²)	Área Basal acumulada (m ² /ha)	Volume médio (m ³)	Volume total (m ³ /ha)	Relação Volume/ indivíduo
A	Pontal	<i>Trichilia catigua</i>	27	7.97 ± 3.04	5.41 ± 1.9	0.57 ± 0.48	0.77	2.57 ± 3.42	3.46	0.13
A	Pontal	<i>Trichilia pallida</i>	18	8.23 ± 3.68	5.44 ± 1.38	0.63 ± 0.69	0.57	2.31 ± 2.25	2.08	0.12
AD	Pontal	<i>Cabralea canjerana</i>	3	23.74 ± 31.96	8.33 ± 5.86	9.77 ± 16.55	1.47	101.57 ± 174.64	15.24	5.08
AD	Pontal	<i>Campomanesia xanthocarpa</i>	25	11.58 ± 7.18	6.74 ± 2.51	1.44 ± 1.9	1.80	9.29 ± 17.53	11.61	0.46
AD	Pontal	<i>Ficus luschnathiana</i>	1	32.66	17.0	8.38	0.42	99.69	4.98	4.98
AD	Pontal	<i>Plinia rivularis</i>	161	11.56 ± 5.46	6.43 ± 2.08	1.28 ± 1.17	10.32	6.8 ± 7.9	54.71	0.34
D	Pontal	<i>Aspidosperma polyneuron</i>	22	15.44 ± 9.83	7.68 ± 3.16	2.6 ± 3.23	2.86	18.48 ± 26.49	20.33	0.92
D	Pontal	<i>Cariniana estrellensis</i>	4	48.34 ± 32.7	17.75 ± 7.41	24.65 ± 23.98	4.93	399.52 ± 467.62	79.90	19.98
D	Pontal	<i>Lonchocarpus cultratus</i>	3	17.35 ± 3.94	8.67 ± 1.53	2.45 ± 1.02	0.37	15.56 ± 8.38	2.33	0.78
D	Pontal	<i>Ocotea corymbosa</i>	11	11.9 ± 8.89	7.45 ± 1.72	1.68 ± 2.86	0.92	11.03 ± 21.3	6.06	0.55

8 O IMPACTO DA PANDEMIA DE COVID-19 E DE OUTRAS INTERCORRÊNCIAS DE CAMPO NESSA PESQUISA

Diversas contingências, inerentes ao trabalho de campo com animais, atrasaram a coleta de dados *in situ*, iniciada em maio de 2019. Tivemos problemas com os dispositivos implantados nos dois primeiros grupos, em maio e julho de 2019. O primeiro grupo foi capturado em maio de 2019 no Parque Estadual do Morro do Diabo (33.800 ha – PEMD) e recebeu 1 GPS com acelerômetro e 2 *Daily Diaries* (DD), dispositivo que contém acelerômetro e magnetômetro, dentre outros sensores. O segundo grupo foi capturado em julho de 2019 no fragmento Ponte Branca (PBC) e recebeu 1 DD e 1 GPS com acelerômetro. Em agosto de 2019, ambos os grupos foram recapturados para recuperação dos equipamentos. No entanto, os indivíduos com DD no grupo PEMD não foram encontrados e o indivíduo com DD no grupo PBC não portava o dispositivo quando recapturado. Além disso, havia um problema não identificado anteriormente com a configuração do GPS e ambos não armazenaram nenhum dado. Tendo em vista os eventos relacionados aos DDs em campo, optamos por não utilizar este equipamento e continuar a coleta de dados utilizando apenas os dispositivos GPS/acelerômetro (TechnoSmArt, Axy Trek), o que seria suficiente para a coleta de dados relativos à análise de gasto energético, objetivo central dessa tese. Depois disso, resolvemos os problemas com este último dispositivo e os implantamos nos dois grupos monitorados no fragmento em Guareí (GUA) em setembro e outubro de 2019, que foram recuperados em janeiro e março de 2020, respectivamente.

A partir de março de 2020, devido à pandemia de COVID-19, considerando os riscos potenciais (e desconhecidos) de transmissão de coronavírus SARS-CoV-2 para primatas não humanos, as atividades de campo para captura e monitoramento dos grupos foram suspensas por seis meses (março a setembro). Durante esse período, a equipe se preparou para retornar a campo assim que possível, portando todos os equipamentos de segurança necessários que possibilitassem a retomada das pesquisas com risco minimizado. Mas este fato atrasou a coleta de dados em campo de outros grupos que eram cruciais para os objetivos deste projeto.

Então, em setembro/2020 pudemos retomar as expedições de campo e coletamos dados de mais dois grupos, novamente no fragmento PBC (PBC01 e PBC02). A partir daí, o plano seria fazer novas tentativas de captura de grupos no PEMD, uma vez que teríamos essa área como ‘controle’, por se tratar de um remanescente de floresta de grande porte, bem preservado e o único com população viável de mico-leão-preto. Porém, devido às restrições ao desenvolvimento de pesquisas com mamíferos nessa Unidade de Conservação (cf. Portaria Normativa FF/DE-329 de 14 /05/2021), que se mantiveram até setembro/2021, tivemos que focar em outra área na tentativa de aumentar o tamanho amostral para a pesquisa. A partir de abril/2021, concentramos esforços de captura em um segundo fragmento na região do Pontal do Paranapanema, denominado Santa Maria (SMA, 505 ha). Nesse período, também realizamos as coletas de dados relativas à caracterização de vegetação em todos os sete fragmentos florestais da região que integram o último capítulo. As tentativas de captura em SMA foram mantidas, sem sucesso, até setembro quando, enfim, pudemos realizar expedições no PEMD novamente.

Em novembro/2021, por fim, capturamos um grupo no PEMD e instalamos o equipamento contendo GPS e acelerômetro (AxyTrek, TechnoSmArt, Itália) no macho, coincidentemente o mesmo em que o DD havia sido instalado em 2019, mas que havia desaparecido. A captura desse grupo também tinha como objetivo a coleta de dados comportamentais, simultaneamente à coleta de dados de movimentação pelo equipamento, seguindo a mesma programação utilizada anteriormente. Por isso, acompanhamos o grupo *in loco* para registrar dados de comportamento ao longo de uma semana. A coleta de dados comportamentais desses micos teve por objetivo de validar algoritmos (LoCoD's, *sensu* Wilson et al., 2018) que estão sendo desenvolvidos para a identificação de comportamentos com base nos dados de acelerômetro.

Apesar de se tratar de um grupo numa nova área, que poderia aumentar nosso tamanho amostral para as análises de uso do espaço, movimento e gasto energético, esses dados estão sendo utilizados exclusivamente para a identificação de comportamentos nos dados dos acelerômetros e não foram incluídos nas demais análises relativas aos objetivos dos capítulos 3 e 4. Consideramos que o período de 18

meses nos quais não pudemos realizar pesquisas no PEMD afetou o grau de habituação desse grupo e avaliamos que nossa presença influenciou o deslocamento diário dos animais. Diante do atraso na coleta desses dados, essas análises para identificação de comportamento e gasto energético comportamento-específico de micos-leões-pretos selvagens e cativos não puderam ser incorporadas à tese, por falta de tempo hábil para finalização e discussão dos resultados.

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10 ANEXOS

10.1 ANEXO I: AVALIAÇÃO DA QUALIDADE DO HÁBITAT PARA MICOS-LEÕES-PRETOS (*LEONTOPITHECUS CHRYSOPYGUS*) EM FRAGMENTOS FLORESTAIS DE DISTRIBUIÇÃO ATUAL E POTENCIAL

O material apresentado a seguir apresenta os métodos utilizados e respectivos resultados relativos à caracterização e avaliação do hábitat para o mico-leão-preto, realizado em 11 fragmentos florestais presentes em sua área de distribuição. O texto integra o TCC que está sendo elaborado pela aluna de graduação em Ciências Biológicas, Catarina Ferraz de Camargo Cibim, da UNESP Rio Claro, sob minha orientação.

10.1.1 METODOLOGIA

10.1.1.1 ÁREA DE ESTUDO

O estudo foi realizado num total de 11 áreas, sendo sete delas na região do Pontal do Paranapanema, uma na bacia do Médio Paranapanema, no município de Lençóis Paulista e três na bacia do Alto Paranapanema, nos municípios de Guareí, Angatuba e Buri. Desse total, três áreas não apresentam ocorrência de MLP. Todas as áreas são localizadas no interior do estado de São Paulo, Brasil.

As áreas localizadas no Pontal do Paranapanema foram: Parque Estadual do Morro do Diabo (que aqui trataremos como PMD), cinco fragmentos de Mata Atlântica distribuídos ao seu redor e o corredor ecológico implantado pelo IPÊ – Instituto de Pesquisas Ecológicas (**Figura 1**). O clima da região, em geral, tem duas estações bem demarcadas: o verão quente e úmido, podendo chegar a 32,3°C, enquanto o inverno é seco e frio, atingindo em média 11,1°C (FARIA et al., 2006).

O PMD (33.800 ha; 22°32'43"S, 52°18'17"O), decretado em 1986, localiza-se no município de Teodoro Sampaio, SP, e possui a maior área preservada contínua de Mata Atlântica de interior do estado, abrigando a maior população de micos-leões-pretos conhecida, estimada em cerca de 1200 indivíduos, com densidade populacional de 0.035

ind/ha, e grupos com a média de 5.22 indivíduos (PARANHOS, 2006). A área de vida dos micos no local equivale a cerca de 1.38 km² (VALLADARES-PADUA, 1993).

Três dos fragmentos fazem parte da Estação Ecológica do Mico-Leão-Preto (ESEC MLP, 6.677 ha), unidade de proteção integral criada por Decreto em 2002 (BRASIL, 2002). São eles: Água Sumida (AGS, 1.199 ha, 22°16'57"S, 52°19'49"O), Ponte Branca (PBC, 1.306 ha, 22°24' S, 52°30' O) e Tucano (TUC, 2.115 ha, 22°29'10" S, 52°27'53" O), distribuídos nos municípios de Euclides da Cunha Paulista, Marabá Paulista e Presidente Epitácio (ICMBIO, 2007). Os outros dois fragmentos menores ao redor do parque são privados (<500 ha cada), sendo localizados na Fazenda Ribeirão Bonito (FRB, 22°30' S, 52°20"O), em Teodoro Sampaio e na Fazenda Santa Maria (SMA, 22°14'18"S, 52°18'27"O) em Presidente Epitácio. Atualmente, sub-populações de MLP estão presentes em apenas três desses cinco fragmentos: PBC, SMA e FRB (GARBINO et al., 2016).

O corredor ecológico (COR), previsto no Plano de Manejo da Estação Ecológica Mico-Leão-Preto (2007), foi implantado para unir o PMD a um dos fragmentos da ESEC, o TUC. Para a conexão, através de projetos do Instituto IPÊ, já foram plantadas 2,4 milhões de árvores em cerca de 12 quilômetros (1,3 mil hectares), conectando pequenos remanescentes florestais entre as áreas (IPÊ, 2020). Nessa área, a população de MLP não é registrada há mais de 10 anos, sendo considerada extinta localmente (GARBINO et al., 2016) ainda não há ocorrência de MLP.

O município de Lençóis Paulista (22°48' S, 48°55' O) localiza-se na borda leste do Planalto Ocidental de São Paulo e a área de estudo está localizada na Fazenda Rio Claro (FRC). O clima da região apresenta temperatura média do mês mais quente superior a 22°C e do mês mais frio, inferior a 18°C. Dois períodos bem distintos são caracterizados: um seco e frio (abril a setembro) e outro quente e úmido (outubro a março). A FRC é de propriedade da Suzano S.A. e possui 12.000 hectares, sendo destes 1.324 ha de Mata Atlântica do Interior, divididos em cinco corredores de mata ciliar distribuídos entre plantios de eucalipto. As matas acompanham as bacias dos Rios Claro e Palmital (MEDICI, 2001). A ocorrência de MLP nesta área é reportada desde a década de 1990 (VALLADARES-PÁDUA & CULLEN JR., 1994) possibilitando estudos e práticas de

manejo como a translocação de um grupo deste fragmento para a Fazenda Mosquito, em Narandiba, no ano de 1995 (MEDICI, 2003).

O município de Guareí encontra-se ao sul do estado de São Paulo. O clima é tropical, com temperaturas variando entre 17°C e 27°C na estação chuvosa e entre 13°C e 26°C na estação seca. O município é composto por áreas urbanas e grandes áreas rurais, devido à forte atividade agrícola e agropecuária na região, e está na bacia dos rios Guareí e Areia Branca. A área de estudo (GUA) encontra-se numa propriedade privada (Fazenda Santo Antônio - 23°24'55"S 48°14'31"O) compreendendo 100 hectares de Floresta Atlântica Semidecidual secundária e está a 11,2 km de distância da Estação Ecológica de Angatuba, a qual abriga a população de MLP mais próxima. Relatos de moradores sobre observações de MLP em Guareí permitiram que a população presente no município fosse recentemente descoberta (CULOT et al, 2015).

A espécie foi registrada na Estação Ecológica de Angatuba (ANG) em 2001 (MEDICI et al., 2003). A mata ciliar do Rio Guareí promove a conectividade dos fragmentos florestais do município de Guareí com a Estação Ecológica de Angatuba, Unidade de Conservação com 1.394,15 ha (CULOT et al., 2015). O estudo foi realizado na floresta ripária que compreende 82,91 ha (23°27'28"S 48°23'58"O).

Em Buri, localizada ao sul das cidades de Angatuba e Guareí, foi confirmada a existência de 18 grupos de MLP em 15 fazendas na região no ano de 2003 (LIMA et al., 2003). A área de estudo é a Fazenda Garibaldi (GRB), que se localiza-se na floresta ripária do município e compreende 100,2 ha (23°47'26"S 48°35'15"O).

Em geral, todos os fragmentos são cercados por áreas de pasto, plantações de cana-de-açúcar, milho ou eucalipto. A temperatura média anual e a precipitação anual total da região do Alto Paranapanema e do Pontal do Paranapanema são, respectivamente, 21,9°C e 25°C; 1067,9 mm e 1595,2 mm, (Agrometeorological Monitoring System, 2021).

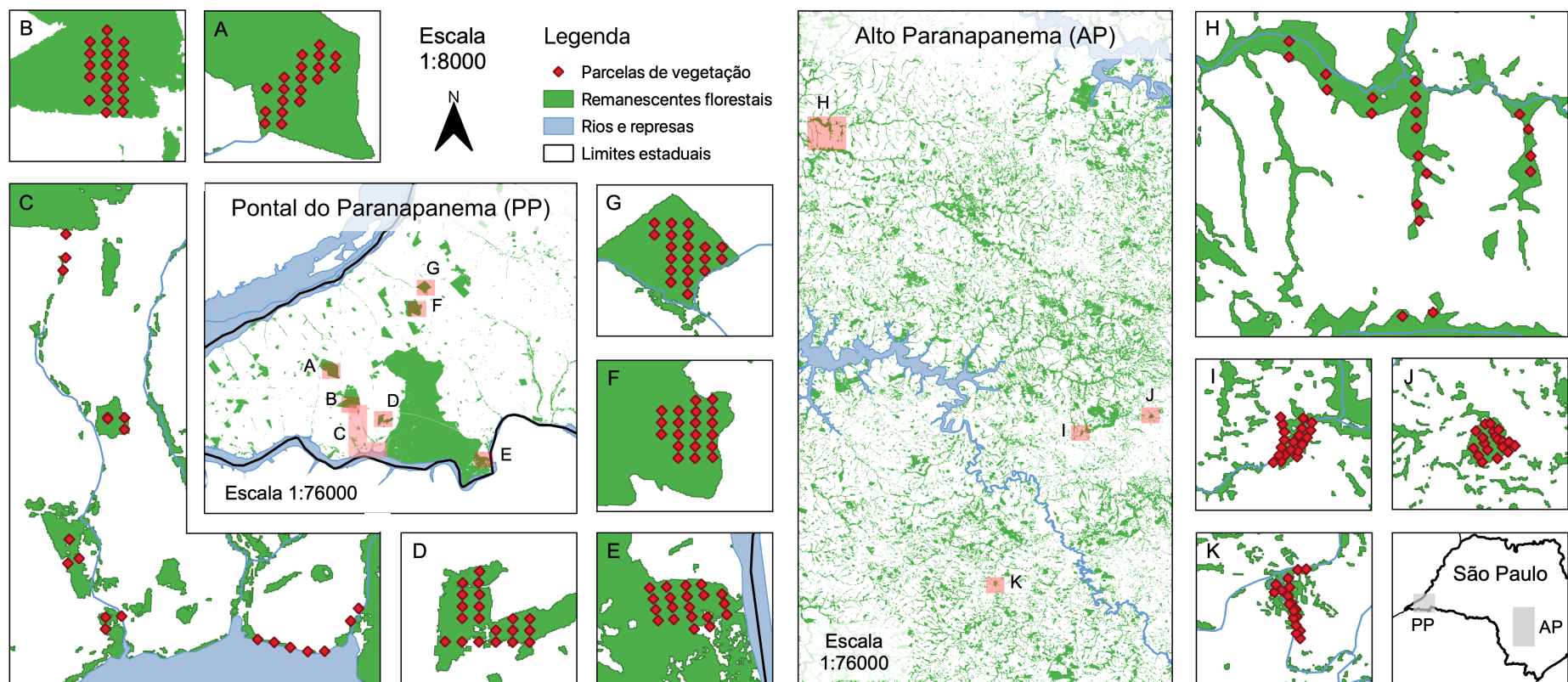


Figura 1. Mapa das onze áreas de estudo no Pontal do Paranapanema (esquerda, A-G) e Alto Paranapanema (direita, H-K), São Paulo, Brasil. Fonte: Gabriela Cabral Rezende.

10.1.1.2 COLETA DE DADOS

Foram distribuídas sistematicamente 20 parcelas de 10m x 10m em cada área, distanciando cerca de 400 m entre si (CAIAFA & MARTINS, 2007). Dentro das parcelas, cada árvore ou palmeira com perímetro a 1,30 m de altura do solo (perímetro à altura do peito - PAP) ≥ 14 cm (ou Diâmetro à Altura do Peito – DAP $\geq 4,45$ cm) tiveram seus dados coletados correspondentes às variáveis apresentadas na **Tabela 1** (SOARES et al., 2006). Cada árvore amostrada recebeu uma plaqueta de alumínio com um número de identificação e nos casos em que houve ramificações vivas a 1,30 m de altura, foram todas medidas.

Tabela 1. Variáveis medidas e estimadas para a caracterização da estrutura florestal em cada local de estudo.

Variável medida	Variável estimada
Número de árvores por parcela (com DAP ≥ 4.45 cm)	Densidade média ($\pm$ desvio padrão) de árvores (árvores/m ²)
Espécies de árvores e palmeiras	Riqueza Diversidade
Perímetro à Altura do Peito (PAP) das árvores (cm)	DAP médio ($\pm$ desvio padrão) por fuste (cm) Área basal total (m ² /ha) Área basal média (m ²)
Altura das árvores (m)	Altura média ($\pm$ desvio padrão) por indivíduo (m) Volume total (m ³ /ha) Volume médio ($\pm$ desvio padrão) por indivíduo (m ³)

10.1.1.3 ANÁLISE DOS DADOS

A partir dos dados coletados, as variáveis estimadas e as médias $\pm$ desvio padrão foram calculadas no programa FITOPAC versão 2.1 (SHEPHERD, 2010).

Para comparar a comunidade de árvores de todas as áreas e entre as áreas com presença e ausência de micos-leões-pretos, foi calculada a riqueza e diversidade de espécies através de curvas de acumulação interpoladas (rarefação) e extrapoladas (predição) corrigidas por *Hill numbers*, construídos no iNEXT package (Hsieh et al. 2016)

no programa RStudio versão 3.6.0 (R Studio Team 2019). Esse método padroniza amostras com base no tamanho ou integridade das mesmas, facilitando a comparação de dados de biodiversidade (CHAO et al., 2014). Os *Hill numbers* utilizados nos cálculos foram: $q = 0$ (riqueza de espécies), $q = 1$ (diversidade de Shannon), e $q = 2$ (diversidade de Simpson). Quando $q = 0$, a diversidade é representada sem dar peso à abundância de espécies (Jost 2006; Tuomisto 2010), enquanto em $q = 1$, a diversidade apresenta um peso para cada espécie de acordo com sua abundância dentro da comunidade, assim baseando-se mais em espécies comuns (JOST, 2007), e em $q = 2$, há maior peso para a abundância de espécies raras, fornecendo assim uma medida do número de espécies dominantes (JOST, 2010; CHAO et al., 2012). As comparações das curvas de diversidade foram baseadas na sobreposição das estimativas do intervalo de confiança de 95% (CHAO & CHIU, 2016).

Com o objetivo de analisar se haviam diferenças entre as características estruturais (altura e DAP) das árvores nos fragmentos estudados foi realizada uma análise dos pressupostos de normalidade dos dados por meio do teste de Shapiro-Wilk e de homogeneidade de variância por meio do teste de Levene (HAUKOOS & LEWIS, 2005). Considerando os pressupostos atendidos e não atendidos, foi realizado o teste de Kruskal Wallis para comparar a média das alturas e o post-hoc de Dunn para comparação par a par entre os fragmentos.

A fim de comparar as áreas com presença e ausência de MLP segundo as espécies vegetais usadas por eles para alimentação e como dormitórios, foi utilizado o banco de dados do Laboratório de Primatologia da UNESP Rio Claro para filtrar a presença dessas espécies em cada área. A partir disso, foram calculadas e comparadas a densidade e diversidade dessas espécies, além da comparação das características estruturais (altura e DAP) utilizando testes de Mann-Whitney. Os cálculos foram feitos no programa R Studio versão 3.6.0 (R Studio Team 2019).

10.1.2 RESULTADOS

Ao todo foram registradas 274 espécies arbóreas distribuídas em 54 famílias na caracterização vegetal das áreas do Pontal e Alto Paranapanema. Destas, 14,9% (N= 41 spp.) foram espécies utilizadas para alimentação e 6,9% (N= 19 spp.) como dormitório. Foi encontrada uma maior riqueza de espécies na região do Alto Paranapanema (225 spp., 82% da riqueza estimada) quando comparada à região do Pontal (158 spp., 57,6% da riqueza estimada). Das 274 espécies levantadas, as duas regiões compartilham apenas 109 spp. (39,7%).

As espécies *Eugenia subterminalis*, *Plinia rivularis* e *Myrcia guianensis* apresentaram maior abundância no Pontal (421, 161 e 84 indivíduos, respectivamente), enquanto *Gymnanthes klotzschiana* e *Dahlstedtia floribunda* apresentaram maior abundância no Alto Paranapanema (82 e 81 indivíduos, respectivamente).

As variáveis estimadas foram dispostas nas **Tabelas 2 e 3** seguindo os respectivos fragmentos de cada região.

Tabela 2. Dados coletados e variáveis estimadas dos sete fragmentos de estudo no Pontal do Paranapanema, sendo AS = Água Sumida, COR = corredor, PB = Ponte Branca, PMD = Parque Estadual Morro do Diabo, RB = Ribeirão Bonito, SMA = Santa Maria e TUC = Tucano.

	AGS	COR	PBC	PMD	RBN	SMA	TUC
Nº de indivíduos	278	190	294	256	243	315	375
Nº de espécies	45	60	51	73	57	50	34
Nº de famílias	22	23	22	25	24	22	17
Densidade média (árvores/m ²)	0,139 (±0,04)	0,095 (±0,05)	0,147 (±0,04)	0,128 (±0,02)	0,121 (±0,04)	0,157 (±0,05)	0,187 (±0,06)
DAP médio (cm)	10,8 (±8,3)	12,7 (±8,01)	10,8 (±7,9)	13,2 (±10,3)	10,1 (±6,05)	9,5 (±6,25)	9,7 (±6,4)
Área basal total (m ² /ha)	2033	1694	2078	2841	1298	1471	1996
Área basal média (m ²)	14,6 (±38,6)	17,2 (±22,8)	14,1 (±29,2)	22,1 (±43)	10,6 (±15,3)	0,93 (±12,7)	10,7 (±20,8)
Altura média (m)	7,5 (±3,2)	5,7 (±1,7)	6,6 (±2,4)	6,9 (±3,7)	6,15 (±1,8)	5,8 (±2,03)	6,2 (±1,6)
Volume total (m ³ /ha)	188,8	760,0	150,9	236,6	70,53	815,7	113,1
Volume médio (m ³)	13,5 (±6,7)	77,5 (±10,8)	10,2 (±32,3)	18,4 (±56,1)	58 (±11,3)	51,7 (±12,5)	61 (±17,9)

Tabela 3. Dados coletados e variáveis estimadas dos quatro fragmentos de estudo no Alto Paranapanema, sendo ANG = Angatuba, FRC = Fazenda Rio Claro (Lençóis Paulista), GRB = Garibaldi (Buri), GUA = Guareí.

	ANG	FRC	GRB	GUA
Nº de indivíduos	567	366	386	364
Nº de espécies	81	93	63	82
Nº de famílias	31	35	23	27
Densidade média	0,219	0,149	0,141	0,156
(árvores/m²)	(±0,09)	(±0,05)	(±0,05)	(±0,03)
DAP médio (cm)	12,4	13,3	13,8	14,2
	(±75,1)	(±12,8)	(±10,7)	(±11,7)
Área basal total (m²/ha)	3655	4028	3397	4180
Área basal média (m²)	16,6	26,9	24	26,7
	(±21,6)	(±88,7)	(±5,4)	(±54,6)
Altura média (m)	7,8	10,2	7,2	8,8
	(±2,3)	(±6,9)	(±2,2)	(±5,3)
Volume total (m³/ha)	242,0	530,9	235,1	456,5
Volume médio (m³)	11	35,5	16,6	29,2
	(±1,6)	(±1,5)	(±4,9)	(±8,2)

Os testes pareados comparando os fragmentos para cada variável analisada (**Tabela 4**) demonstraram que, em relação ao DAP, área basal média, volume médio, área basal total e volume total, os fragmentos do Alto Paranapanema não diferenciaram um do outro, enquanto os fragmentos do Pontal demonstraram diferenças entre si e principalmente entre as duas regiões, com exceção do PMD, que não diferiu dos fragmentos do Alto Paranapanema, mas sim dos fragmentos do Pontal. O corredor também apresentou essa exceção para as variáveis DAP e área basal média, se assemelhando aos fragmentos do Alto Paranapanema. Em relação à altura, poucos fragmentos não se diferenciaram significativamente, como GRB, GUA e AGS entre as duas regiões, GUA e ANG no Alto Paranapanema, e PMD e COR no Pontal. Para densidade, COR diferiu de todos os fragmentos, assim como ANG (exceto de SMA e TUC), enquanto para TUC foi a única variável que se assemelhou a todos os fragmentos do Alto Paranapanema.

Tabela 4. Valores de *p* obtidos nos testes pareados comparando cada fragmento para as variáveis: **(a)** Diâmetro à altura do peito (DAP); **(b)** área basal média (BA), **(c)** volume médio, **(d)** altura, **(e)** densidade, **(f)** área basal total (T.BA) e **(g)** volume total (T.Vol.). A cor amarela representa os fragmentos da região do Alto Paranapanema, a cor azul, os fragmentos da região do Pontal e a cor verde, a comparação entre fragmentos de diferentes regiões.

(a) Diâmetro à altura do peito (DAP)

DAP	AGS	ANG	COR	FRC	GRB	GUA	PBC	PMD	RBN	SMA
ANG	0.000									
COR	0.016	0.712								
FRC	0.003	0.524	0.984							
GRB	0.000	0.664	0.427	0.299						
GUA	0.003	0.985	0.712	0.712	0.686					
PBC	0.807	0.000	0.025	0.012	0.000	0.003				
PMD	0.006	0.701	0.945	0.984	0.435	0.811	0.012			
RBN	0.984	0.000	0.009	0.003	0.000	0.001	0.701	0.004		
SMA	0.807	0.000	0.001	0.000	0.000	0.000	0.463	0.001	0.868	
TUC	0.532	0.000	0.000	0.000	0.000	0.000	0.268	0.000	0.664	0.784

(b) Área basal

BA	AGS	ANG	COR	FRC	GRB	GUA	PBC	PMD	RBN	SMA
ANG	0.000									
COR	0.016	0.712								
FRC	0.003	0.524	0.984							
GRB	0.000	0.664	0.427	0.299						
GUA	0.003	0.985	0.712	0.712	0.686					
PBC	0.807	0.000	0.025	0.012	0.000	0.003				
PMD	0.006	0.701	0.945	0.984	0.435	0.811	0.012			
RBN	0.984	0.000	0.009	0.003	0.000	0.001	0.701	0.004		
SMA	0.807	0.000	0.001	0.000	0.000	0.000	0.463	0.001	0.868	
TUC	0.532	0.000	0.000	0.000	0.000	0.000	0.268	0.000	0.664	0.784

(c) Volume

Vol.	AGS	ANG	COR	FRC	GRB	GUA	PBC	PMD	RBN	SMA
ANG	0.000									
COR	0.621	0.007								
FRC	0.000	0.621	0.005							
GRB	0.001	0.817	0.019	0.528						
GUA	0.040	0.688	0.122	0.341	0.699					
PBC	0.747	0.000	0.303	0.000	0.000	0.011				
PMD	0.588	0.022	0.741	0.010	0.040	0.271	0.273			
RBN	0.228	0.000	0.076	0.000	0.000	0.002	0.344	0.072		
SMA	0.024	0.000	0.006	0.000	0.000	0.000	0.040	0.006	0.380	
TUC	0.082	0.000	0.019	0.000	0.000	0.000	0.150	0.019	0.730	0.528

(d) Altura

Alt.	AGS	ANG	COR	FRC	GRB	GUA	PBC	PMD	RBN	SMA
ANG	0.001									
COR	0.000	0.000								
FRC	0.000	0.000	0.000							
GRB	0.818	0.000	0.000	0.000						
GUA	0.136	0.898	0.000	0.000	0.074					
PBC	0.000	0.000	0.000	0.000	0.000	0.000				
PMD	0.001	0.000	0.054	0.000	0.001	0.000	0.278			
RBN	0.000	0.000	0.011	0.000	0.000	0.000	0.021	0.705		
SMA	0.000	0.000	0.693	0.000	0.000	0.000	0.000	0.041	0.016	
TUC	0.000	0.000	0.000	0.000	0.000	0.000	0.056	0.975	0.442	0.000

(e) Densidade

Dens.	AGS	ANG	COR	FRC	GRB	GUA	PBC	PMD	RBN	SMA
ANG	0.006									
COR	0.003	0.000								
FRC	0.655	0.033	0.001							
GRB	0.978	0.020	0.006	0.654						
GUA	0.309	0.043	0.000	0.659	0.621					
PBC	0.655	0.025	0.002	0.926	0.799	0.659				
PMD	0.655	0.001	0.003	0.302	0.654	0.043	0.244			
RBN	0.415	0.001	0.018	0.170	0.523	0.037	0.185	0.654		
SMA	0.468	0.056	0.001	0.748	0.550	0.974	0.709	0.136	0.090	
TUC	0.034	0.495	0.000	0.149	0.092	0.239	0.149	0.006	0.005	0.244

(f) Área basal total

T.BA	AGS	ANG	COR	FRC	GRB	GUA	PBC	PMD	RBN	SMA
ANG	0.001									
COR	0.072	0.000								
FRC	0.012	0.649	0.000							
GRB	0.007	0.513	0.000	0.921						
GUA	0.007	0.649	0.000	0.627	0.362					
PBC	0.649	0.004	0.072	0.039	0.021	0.006				
PMD	0.060	0.175	0.001	0.540	0.487	0.097	0.128			
RBN	0.072	0.000	0.955	0.000	0.000	0.000	0.022	0.000		
SMA	0.222	0.000	0.443	0.000	0.000	0.001	0.110	0.001	0.443	
TUC	0.916	0.002	0.039	0.007	0.007	0.007	0.912	0.058	0.017	0.100

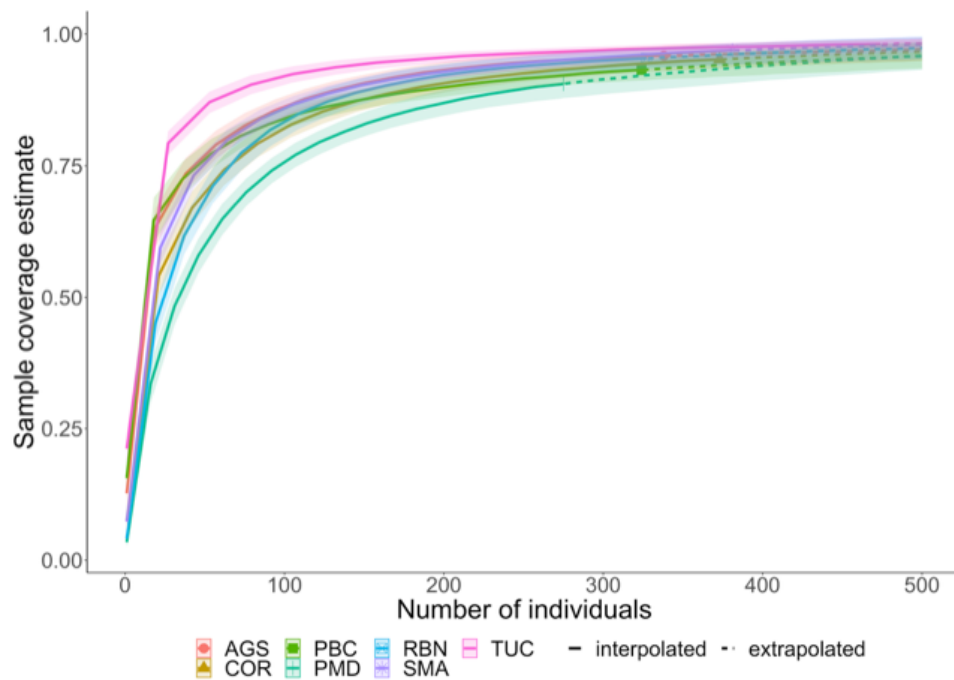
(g) Volume total

T.Vol.	AGS	ANG	COR	FRC	GRB	GUA	PBC	PMD	RBN	SMA
ANG	0.033									
COR	0.005	0.000								
FRC	0.004	0.317	0.000							
GRB	0.117	0.684	0.000	0.154						
GUA	0.013	0.083	0.000	0.669	0.083					
PBC	0.968	0.035	0.003	0.012	0.045	0.002				
PMD	0.125	0.676	0.000	0.196	0.921	0.067	0.142			
RBN	0.022	0.000	0.341	0.000	0.000	0.000	0.033	0.000		
SMA	0.079	0.000	0.142	0.000	0.000	0.000	0.121	0.001	0.602	
TUC	0.345	0.000	0.017	0.000	0.002	0.001	0.536	0.012	0.082	0.270

As curvas de amostragem corrigidas por Hill Numbers demonstraram que a estimativa de cobertura de todas as áreas foi acima de 80% (**Figura 2**). As curvas de diversidade demonstraram que os fragmentos com maior riqueza de espécies e diversidade de Shannon no Pontal foram, respectivamente, o Parque Estadual Morro do Diabo, o corredor ecológico e Ribeirão Bonito, sendo que desses, apenas no corredor não há a presença de micos-leões-pretos. O fragmento com menores valores número de riqueza de espécies e diversidade de Shannon foi Tucano (**Figura 3**).

Já no Alto Paranapanema, a Fazenda Rio Claro demonstrou maiores índices de riqueza de espécies e diversidade de Shannon, ultrapassando os índices do PMD, incluindo nessa comparação como grupo externo. Guareí foi o segundo fragmento com maiores índices de diversidade, sendo estes muito próximos aos do Parque. Nesta região, a Fazenda Garibaldi em Buri foi o fragmento com índices de diversidade mais baixos, sendo ainda assim superiores aos demais fragmentos do Pontal (**Figura 4**).

(a)



(b)

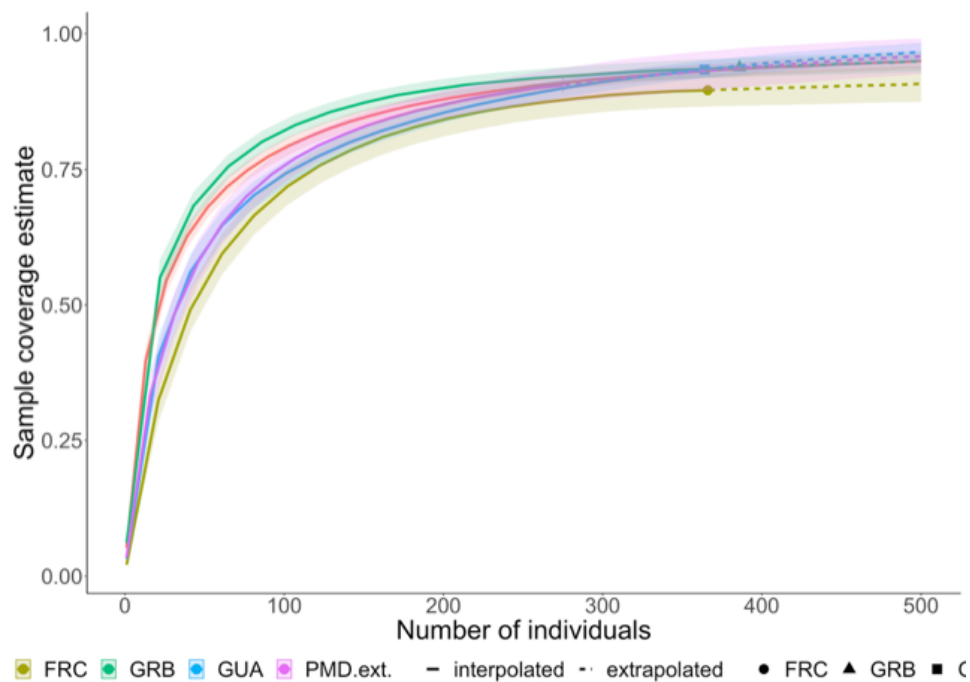


Figura 2. Curvas de amostragens rarefeitas (linhas sólidas) e extrapoladas (linhas tracejadas) baseadas na cobertura de cada fragmento em função do tamanho das amostras, com intervalos de confiança de 95% (áreas sombreadas). **(a)** fragmentos da região do Pontal do Paranapanema **(b)** fragmentos da região do Alto Paranapanema.

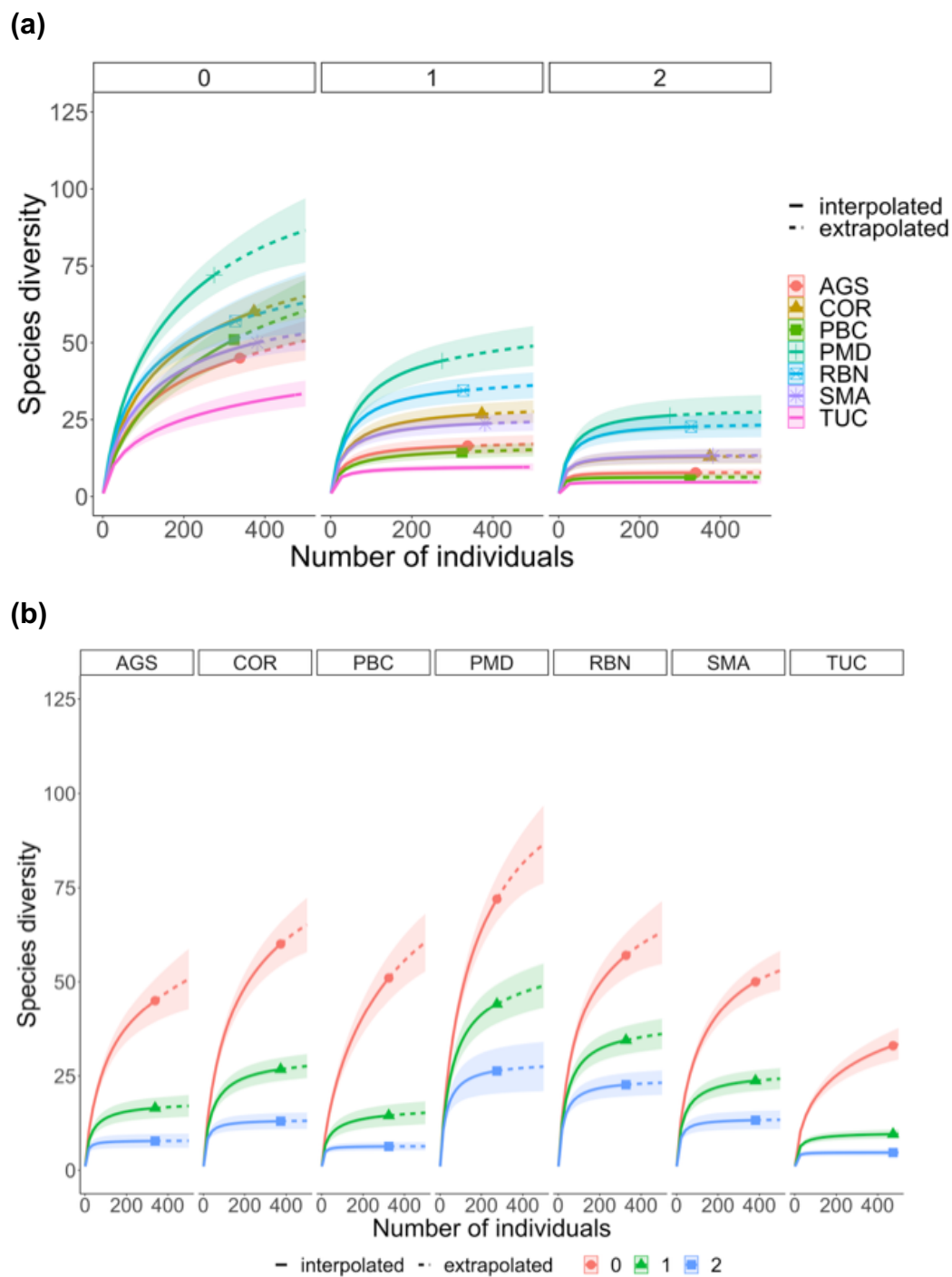


Figura 3. Curvas de rarefação (segmento de linha sólida) e extrapolação (segmentos de linha pontilhada) com intervalos de confiança de 95% (áreas sombreadas) baseadas na amostragem dos fragmentos do Pontal. **(a)** Curvas por ordem de diversidade: $q = 0$ (riqueza de espécie, painel esquerdo), $q = 1$ (diversidade de Shannon, painel do meio) e $q = 2$ (diversidade de Simpson, painel direito). **(b)** Curvas de diversidade com base na amostragem de cada fragmento.

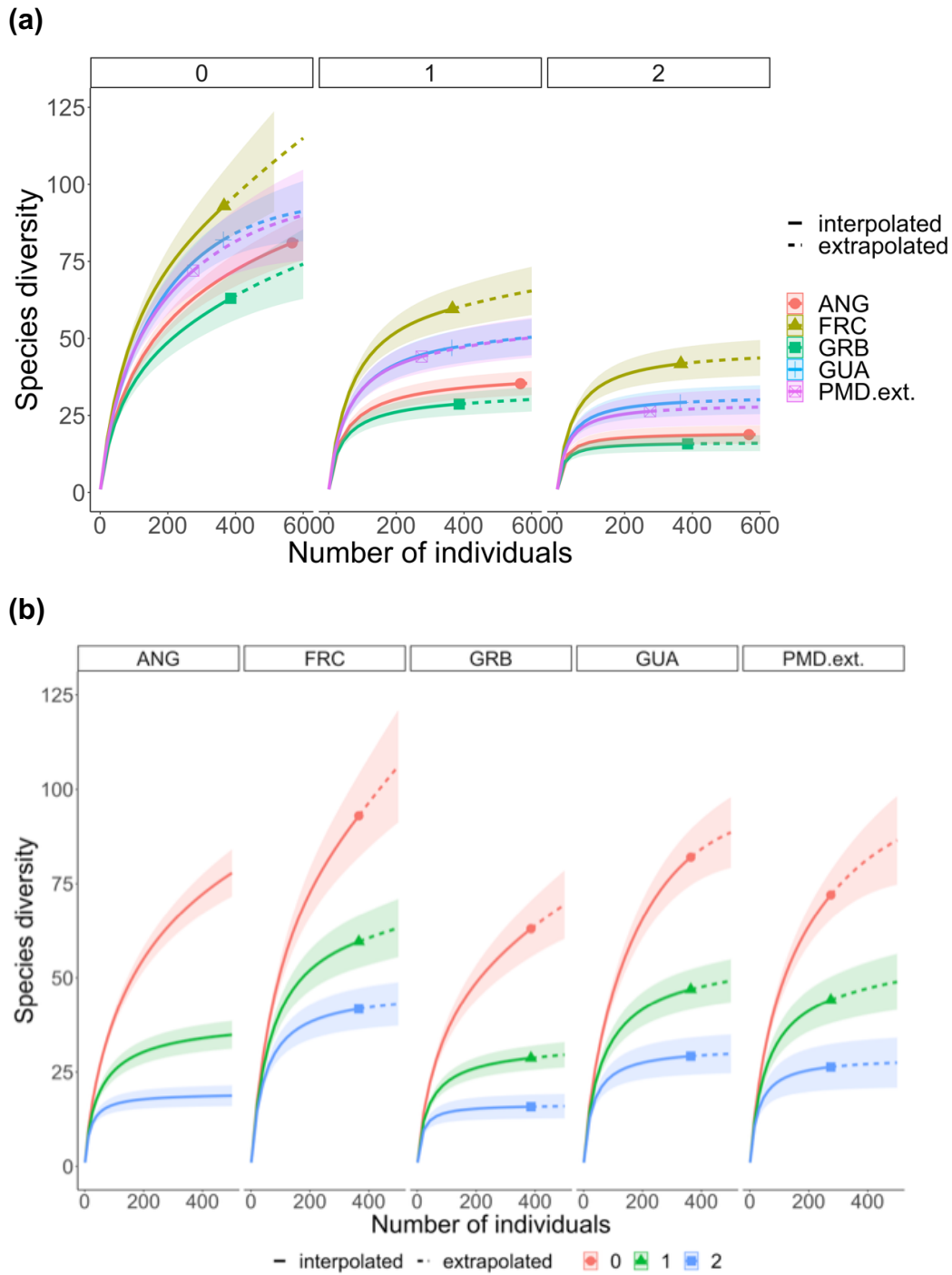


Figura 4. Curvas de rarefação (segmento de linha sólida) e extrapolação (segmentos de linha pontilhada) com intervalos de confiança de 95% (áreas sombreadas) baseadas na amostragem dos fragmentos do Alto Paranapanema e do Parque Estadual Morro do Diabo. **(a)** Curvas por ordem de diversidade: $q = 0$ (riqueza de espécie, painel esquerdo), $q = 1$ (diversidade de Shannon, painel do meio) e $q = 2$ (diversidade de Simpson, painel direito). **(b)** Curvas de diversidade com base na amostragem de cada fragmento.

10.2 ANEXO II: CERTIFICADO DA COMISSÃO DE ÉTICA NO USO DE ANIMAIS

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UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
Campus de Rio Claro

COMISSÃO DE ÉTICA
NO USO DE ANIMAL
CEUA – IB – UNESP – CRC

ANIMAIS DE VIDA LIVRE
DECISÃO CEUA Nº 12/2018

Instituição: UNESP – IB – CRC	Departamento: Zoologia
Data de Registro CEUA: 07.02.2018	
CERTIFICADO	
Certificamos que o Projeto de Pesquisa intitulado "Uso de habitat, padrões de movimento e gasto energético pelo mico-leão-preto (<i>Leontopithecus chrysopygus</i>) em diferentes contextos de fragmentação", protocolo nº 0993, sob responsabilidade de Gabriela Cabral Rezende (Pesquisadora Responsável) e Laurence M. V. Culot (Orientadora), que envolve a produção, manutenção e/ou a utilização de animais pertencentes ao filo Chordata, subfilo Vertebrata (exceto o homem), para fins de pesquisa científica (ou ensino) – encontra-se de acordo com os preceitos da Lei nº 11.794 de 8 de outubro de 2008, do Decreto nº 6.899 de 15 de julho de 2009, e com as normas editadas pelo Conselho Nacional de Controle da Experimentação Animal (CONCEA).	
Subprojeto(s) vinculado(s): ==.==	

Colaboradores:	Silvia Bahadian Moreira, Danilo Simonini Teixeira e Ariovaldo Pereira da Cruz Neto
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A Comissão de Ética no Uso de Animal - CEUA do Instituto de Biociências da UNESP – Campus de Rio Claro, em sua **36ª reunião ordinária**, realizada em **06.06.2018**.

(x)	Aprovou o Projeto de Pesquisa acima citado, ratificando o parecer emitido pelo relator.
()	Desde que atendidas as pendências apontadas na reunião (vide anexo), aprova o Projeto de Pesquisa acima citado (prazo máximo de 30 dias).
()	Referendou o Projeto de Pesquisa acima citado, ratificando o parecer emitido pelo relator.
()	Aprovou retornar ao interessado para atendimento das pendências encontradas (prazo máximo de 30 dias).
()	Não Aprovou.
()	Retirou , devido à permanência das pendências.

Vigência da autorização	15/03/18 a 20/01/2021
Finalidade	() Ensino (X) Pesquisa Científica
Nº da Solicitação ou Autorização SISBIO	41375-6 E 62116-1
Atividade (s)	(x) Captura (x) Coleta de espécimes () Marcação () Outras (especificar)
Espécies/Grupos Taxonômicos	Leontopithecus chrysopygus (mico-leão-preto)
Local (is) de realização das atividades	Fragmentos florestais no Pontal do Paranapanema e matas ciliares do Rio Guareí e Rio Claro.

Objetivo Acadêmico:	() TCC () Mestrado (x) Doutorado () Outros- iniciação Científica
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Rio Claro, 06/06/2018

Prof. Dr. Marco Aurélio Pizo Ferreira
Coordenador