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GABRIEL DA SILVA LOPES

EFEITOS DAS CONDIÇÕES CLIMÁTICAS SOBRE O COMPORTAMENTO E
DETECTABILIDADE DA PREGUIÇA-DE-COLEIRA (*BRADYPUS TORQUATUS*)

ILHÉUS – BAHIA

2022

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Dissertação apresentada à Universidade Estadual de Santa Cruz como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação da Biodiversidade.

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Ilhéus, 30 de maio de 2022

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“Pode haver 100 pessoas em uma sala, e 99 não acreditam em você, mas tudo o que você precisa é que apenas uma pessoa acredite”

Lady Gaga

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Sempre me pegava pensando no que eu iria escrever aqui quando, finalmente, chegasse a hora. E, quem diria...a hora chegou!

Chega a ser um pouco cômico, com todo respeito, pensar em como, justo no ano em que eu entrei no mestrado, fomos acometidos por uma pandemia que mudou as nossas vidas e tudo aquilo que tínhamos planejado para os próximos meses (e anos). O mestrado, sem sombra de dúvidas, foi o maior desafio que eu já passei e, não somente, por si só, mas por todo o contexto em que ocorreu. Esses 2 anos e meio foram anos bem dolorosos, pra ser sincero, especialmente o início...ficar quarentenado consigo mesmo não é lá a mais fácil das tarefas. Houve dias em que duvidei de mim mesmo, dias que pensei em desistir, dias em que tudo que eu queria era voltar pra casa da minha mãe e houve dias em que tudo era, simplesmente, insuportável demais de se aguentar. Nesses dias eu pensava numa lista de pessoas que eu decepcionaria e quem me conhece, sabe que decepcionar as pessoas é um dos meus maiores medos. Esse exercício me dava um pouco de força pra continuar e eu sou muito grato a todas essas pessoas que, inconscientemente e involuntariamente, me ajudaram, mas existem 3 pessoas que se destacam. Duas que sempre figuravam no topo da minha lista de pessoas que eu não suportaria falhar com e a terceira, a que foi responsável por eu chegar até aqui.

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“Cause in the end, the road is long but only ‘cause it makes you strong

It’s filled with peaks and twists and turns

Sometimes you have to learn to forget about it”

Marina Diamandis

RESUMO

Preguiças de três-dedos são animais heterotérmicos com temperatura corporal baixa e variável. A temperatura ambiente e radiação solar podem ser dois dos principais *drivers* de seu comportamento, já que influenciam sua taxa metabólica, temperatura corporal, ingestão de comida e, conseqüentemente, podem influenciar suas atividades e busca por conforto térmico (comportamento termorregulador). As respostas comportamentais das preguiças a estes fatores ambientes foram pouco estudadas, de forma sistemática, em campo, e podem prover informação complementar sobre sua vulnerabilidade frente às mudanças climáticas. Nós estudamos o comportamento da ameaçada preguiça-de-coleira (*Bradypus torquatus*), objetivando avaliar a influência da variação horária da temperatura ambiente e de diferentes condições climáticas (sol e nublado) sobre sua atividade, posturas e posições adotadas nas copas das árvores. Testamos, também, se esses comportamentos aumentam sua exposição à detecção humana. Performamos 350 horas de observações visuais de oito preguiças-de-coleira no norte da Bahia, de agosto a outubro de 2020, registrando seus comportamentos, posturas e posições nas copas das árvores. Também registramos o tempo gasto para visualizar cada indivíduo pela primeira vez, durante 69 dias. A temperatura ambiente positivamente influenciou os níveis de atividade das preguiças-de-coleira em condições nubladas, porém negativamente em condições de sol, uma resposta inesperada. A temperatura ambiente influenciou negativamente a frequência em que as preguiças-de-coleira adotaram a postura encolhida, e positivamente a postura estendida, em ambas condições climáticas. Isolada das condições climáticas, a temperatura ambiente, sozinha, influenciou positivamente a frequência em que as preguiças-de-coleira repousaram na copa interna, porém não afetou o uso da copa externa, assim como estes comportamentos não afetaram sua detectabilidade. Avançamos em conhecimento, indicando a direção da relação temperatura-atividade, como dependente das condições climáticas. É possível que um futuro mais quente e seco, na porção

norte da Mata Atlântica, possa reduzir os níveis de atividade e impor algumas restrições fisiológicas e comportamentais, embora possa não ocorrer um aumento na sua exposição à detecção humana.

Palavras-chave: atividade; folívoro; mamífero arborícola; radiação solar; resposta térmica

ABSTRACT

Ambient temperature and solar radiation (weather conditions) may be two of the main drivers of their behavior, since these influence their metabolic rate, body temperature, food intake and, consequently, may influence their activities, postures and their search for thermally favorable microhabitats (thermoregulatory behavior). The behavioral response of sloths to these ambient factors has been insufficiently studied in the field and can provide complementary information about their vulnerability to climate change, especially when analyzed together. We studied the behavior of the threatened maned sloth (*Bradypus torquatus*) aiming to evaluate the influence of hourly ambient temperature variation on their activities, postures, and tree crown positions under sunny and cloudy conditions. We further tested if any of these behaviors increase their exposure to human detection. We performed 350 hours of visual observation on eight maned sloths from northern Bahia, recording their behaviors, postures, and positions on tree crowns. We also recorded the time taken to visualize the sloths for 69 days. The ambient temperature positively affected the sloths' activity levels in cloudy conditions, but negatively affected it in sunny conditions, which was an unexpected response. Ambient temperature negatively affected the frequency of huddled posture and positively the frequency of extended posture in both conditions. Ambient temperature alone positively affected the frequency in which sloths rested in the inner tree crown, but no effect in use of outer tree crown was found, as well as both positions and postures did not increase their detectability. We advance in knowledge indicating that the direction of the temperature-activity relationship depends on the conditions (sunny or cloudy). It is possible that warmer and drier future climate in northern Atlantic Forest may reduce their diurnal activity levels and promote future and troubling physiological and behavioral constraints, although an increase of their exposure to human detection may not occur.

Key words: activity; arboreal mammal; folivore; solar radiation; thermal response

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INTRODUÇÃO GERAL

Maioria dos endotérmicos (*i.e.*, aqueles cuja principal fonte de calor, para regular a temperatura corporal, é endógena – aves e mamíferos) são capazes de manter suas temperaturas corporais relativamente altas e estáveis (*i.e.* homeotermia), a partir de mecanismos, principalmente, fisiológicos (Scholander, 1955). Os custos energéticos associados a estes mecanismos variam, sendo baixos e constantes dentro de uma faixa de temperaturas ambiente (zona de termoneutralidade ou ZTN), porém aumentando, consideravelmente, à medida que a temperatura ambiente se desvia dos limites da ZTN – *i.e.*, cruza os limites críticos inferior ou superior (Huey et al., 2012; Tourinho et al., 2022). Neste sentido, o emprego de estratégias comportamentais pode auxiliar estes animais a minimizar os custos energéticos da regulação da temperatura interna (Lopes and Bicca-Marques, 2017).

Mamíferos típicos, geralmente, quando expostos a temperaturas muito baixas, em geral, irão apresentar duas respostas autonômicas: vasoconstrição, reduzindo a dissipação de calor produzido e, em seguida, mecanismos de termogênese serão ativados – a termogênese por tremor, no tecido cardíaco e músculo esquelético, e a termogênese sem-tremor, no tecido adiposo marrom (Figura 1; Morrison et al., 2008; Terrien et al., 2011). O trabalho muscular, embora seja uma das mais eficientes fontes de calor interno, é uma fonte energeticamente custosa e que demanda constante ingestão de altos níveis de energia, o que é inviável para algumas espécies, principalmente aquelas de dieta baseada em alimentos energeticamente pobres (Kauffman et al., 2001). O aumento da ingestão de energia e atividade locomotora são estratégias que, também, geram calor e, portanto, são aliadas em situações como estas (Terrien et al., 2011).

Uma série de mecanismos para evitar quadros de hipertermia ou superaquecimento (Figura 1), também são empregados por mamíferos, em temperaturas muito altas. A vasodilatação próxima a superfície da pele (dissipação não-evaporativa) e a evaporação através da perda de água por respiração e/ou pele (dissipação evaporativa), são mecanismos fisiológicos autônomos empregados na redução da temperatura interna (Norris and Kunz, 2012). Embora seja uma forma eficiente, a dissipação evaporativa de calor impacta diretamente o balanço hídrico do animal, pode resultar numa perda excessiva de água e, também, tem alto custo calórico (Mota-Rojas et al., 2021). Espécies com excesso de pelos possuem, ainda, dificuldade para dissipar o calor, que em maioria dos casos fica restrita ao suor nas regiões periféricas do corpo (Šumbera et al., 2007). Inversamente ao quadro de hipotermia, aqui, a redução na ingestão de energia e na atividade locomotora, são algumas estratégias que diminuem a produção de calor durante risco de hipertermia (Terrien et al., 2011).

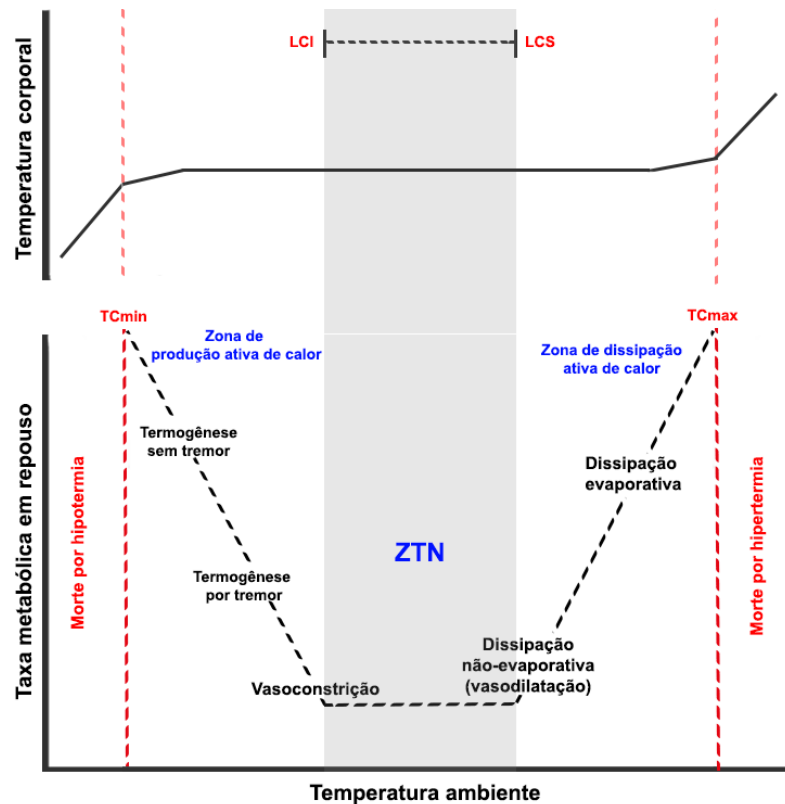


Figura 1 – Relação entre temperatura ambiente, taxa metabólica em repouso e temperatura corporal de um mamífero típico (i.e., homeotérmico), e suas respostas termo efetoras. São apresentados mecanismos autonômicos que são ativados, à medida que a temperatura ambiente desvia dos limites críticos inferior (LCI) e superior (LCS) da zona de termoneutralidade (ZTN, faixa cinza) e se aproxima das temperaturas críticas para o óbito do organismo, por hipotermia (TCmin) e hipertermia (TCmax). Entre os limites críticos da ZTN e das temperaturas críticas para óbito, o organismo ativará mecanismos termo efetores específicos para cada situação (ver texto). Adaptado de Almeida & Branco (2006) e Cannon & Nedergaard (2011).

Mamíferos heterotérmicos: os arborícolas folívoros

Uma pequena parcela de mamíferos, devido a fatores ecológicos, possuem dificuldade na regulação de suas temperaturas corporais, a qual varia relativamente, caracterizando a heterotermia (McNab, 1978). Diversas linhagens de mamíferos evoluíram para viver nos dosséis florestais e subsistir de folhas de árvores – folivoria arborícola, como primatas, coalas, preguiças e marsupiais (Eisenberg, 1978). Além destes animais possuírem restrições energéticas associadas a uma fonte de alimento nutricional e energeticamente pobre, os animais folívoros arborícolas apresentam, também, pouca variação no tamanho corporal, visto como uma otimização energética, possuindo tamanho suficiente para processar a matéria vegetal, porém leves o bastante para acessar o dossel (Cork and Foley, 1991; Eisenberg, 1978).

Dentre as características compartilhadas entre os arborícolas folívoros, podemos citar as taxas metabólicas notavelmente reduzidas, além de adaptações anatômicas para otimizar a digestão da matéria vegetal, comportamentos associados à aquisição de recursos e termorregulação e padrão de atividade reduzido (Briscoe et al., 2014; Cliffe et al., 2014; Cork and Foley, 1991; MacLennan, 1984; Pauli et al., 2014). Inclusive, estudos com arborícolas

folívoros de vida-livre, apontam baixas taxas metabólicas mesmo com deslocamentos consideráveis e outras atividades sendo performadas (Nagy and Martin, 1985; Nie et al., 2015; Pauli et al., 2016; Pontzer et al., 2010). Pauli et al. (2016) sugere que estes animais reduzam seus gastos energéticos através de um relaxamento do controle termorregulatório e redução de movimento para compensar a paisagem energeticamente pobre, investindo, ainda, em estratégias comportamentais para auxiliar na redução desses gastos.

A preguiça-de-três-dedos

As preguiças de três-dedos (gênero *Bradypus*) são exemplos de animais endotérmicos e heterotérmicos, extremamente especializados ao estilo de vida estritamente arborícola e dieta folívora (Cliffe et al., 2018; Giné et al., 2015; McNab, 1978; Pauli et al., 2016). Se comparado a outros mamíferos, estes animais possuem temperatura corporal baixa e variável (27.7 – 36.8 °C; Goffart, 1971; Kredel, 1928; McNab, 1978), baixos níveis de atividade (20.9 – 45%; Chiarello, 1998; Giné et al., 2015; Montgomery and Sunquist, 1978; Oliveira Bezerra et al., 2020; Urbani and Bosque, 2007), baixas porcentagens de massa muscular, taxa metabólica extremamente baixa e a mais baixa taxa de digestão dentre todos mamíferos (Cliffe et al., 2018; Foley et al., 1995; McNab, 1978; Pauli et al., 2016). Estas restrições impostas pelo seu modo de vida estritamente arborícola e hábito folívoro, acabam por trazer limitações no controle da temperatura interna (Cliffe et al., 2018, 2015). Inclusive, contradizendo o que se espera de um animal tipicamente endotérmico-homeotérmico, a relação temperatura ambiente – metabolismo das preguiças-de-três-dedos exhibe um padrão inverso, assemelhando-se a o que, geralmente, é observado em ectotérmicos-heterotérmicos (Figura 2; Cliffe et al., 2018).

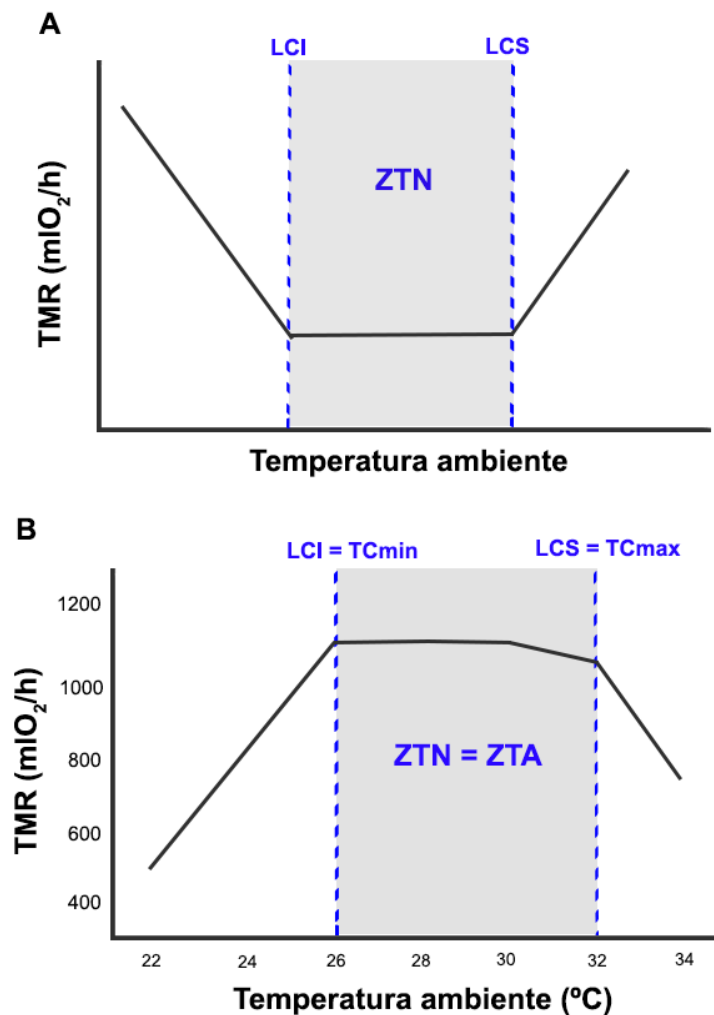


Figura 2 - Relação entre temperatura ambiente e taxas metabólicas. (A) Taxa metabólica em repouso (TMR) de um endotérmico típico e de (B) *Bradypus variegatus*, onde a zona termoneutra (ZTN) = zona termoativa (ZTA). LCI e LCS representam os limites críticos inferior e superior, respectivamente, que para *B. variegatus* coincidem com as temperaturas críticas mínima (TCmin) e máxima (TCmax) para o óbito. Adaptado de Tourinho et al. (2022) e (A) Huey et al. (2012) e (B) Cliffe et al. (2018).

Estudos que ilustram as respostas da preguiça-de-três-dedos às temperaturas muito altas são, geralmente, restritos a laboratório e animais de cativeiro, tornando difícil extrapolar estes resultados para a vida-livre (Britton and Atkinson, 1938; Cliffe et al., 2018). Britton e Atkinson

(1938) sugerem que preguiças-de-três-dedos tem pouca habilidade na dissipação do calor, apesar do estudo ter sido realizado de forma que os indivíduos não podiam escapar da incidência direta da luz solar e altas temperaturas ($> 40^{\circ}\text{C}$), resultando no óbito de alguns deles. Devido às suas restrições, as preguiças de três-dedos, também, tem pouca habilidade em produzir calor, quando expostas a temperaturas mais frias, mesmo performando atividade. Inclusive, Chiarello (1998) sugere que para evitar temperaturas mais frias, nas regiões montanhosas do Espírito Santo, a preguiça-de-coleira invista mais em atividades diurnas, do que noturnas, uma estratégia observada em outros mamíferos catemerais (Curtis et al., 1999; Curtis and Rasmussen, 2006).

A temperatura ambiente e a exposição à luz solar são dois dos principais *drivers* da temperatura interna, taxas metabólicas, níveis de atividade e ingestão de alimento das preguiças-de-três-dedos (Britton and Atkinson, 1938; Cliffe et al., 2015; Giné et al., 2015; Montgomery and Sunquist, 1978). Em estudos laboratoriais com *Bradypus variegatus*, Cliffe et al. (2018) constatou que a temperatura interna de *Bradypus variegatus*, aumenta linearmente com a temperatura externa, enquanto a taxa metabólica é reduzida tanto em baixas ($< 22 - 26^{\circ}\text{C}$), quanto altas ($> 30^{\circ}\text{C}$) temperaturas externas, gerando uma curva em forma de “U” invertido (Figura 2b). Essa faixa de pico metabólico ($26 - 30^{\circ}\text{C}$), interessante, corresponde às temperaturas diurnas médias nas florestas tropicais, sob as quais as preguiças-de-três-dedos são mais ativas e se alimentam mais (zona termoativa; Chiarello, 1998; Cliffe et al., 2015; Giné et al., 2015). Estudos envolvendo *B. variegatus* de vida livre revelam, também, uma taxa metabólica de campo baixa com provável ligação à regulação da temperatura corporal e aos seus baixos níveis de atividade (Pauli et al., 2016).

O uso de estratégias comportamentais

Segundo Pauli et al. (2016) espécies mais especializadas se apoiam mais fortemente em estratégias comportamentais e termorreguladoras para diminuir seus gastos energéticos diários totais. Os ajustes comportamentais fornecem suporte aos mecanismos autonômicos e facilitam a perda ou conservação de calor (Terrien et al., 2011). Desta forma, como as preguiças-de-três-dedos possuem pouca habilidade em produzir calor, mesmo performando atividade alimentar, e sua temperatura interna oscila com a temperatura ambiente, alguns ajustes comportamentais são esperados a fim de conservar calor, bem como promover sua perda e evitar superaquecimento (Kredel, 1928; McNab, 1978; Montgomery and Sunquist, 1978). Tais comportamentos termorreguladores podem ser expressados na forma de seleção de microhabitat, bem como faixas de hora com temperaturas favoráveis, ajustes posturais ou de orientação do corpo – aumentando ou diminuindo a superfície corporal exposta à radiação solar (Chiarello, 1998; Cliffe et al., 2018; Terrien et al., 2011). Neste sentido, a radiação solar é uma importante aliada de alguns destes comportamentos, já que pode favorecer o ganho de calor, principalmente, sob temperaturas baixas (Lopes and Bicca-Marques, 2017).

O ajuste postural é um mecanismo comportamental empregado pelas preguiças-de-três-dedos a fim de facilitar suas trocas de calor com o ambiente (Cliffe et al., 2015; Urbani and Bosque, 2007). Quando exposta a temperaturas altas, em laboratório, *B. variegatus* frequentemente adotou uma postura esticada, possivelmente para facilitar a perda de calor, enquanto o oposto foi observado sob baixas temperaturas (Cliffe et al., 2018). É importante notar que essas respostas não, necessariamente, refletem o que acontece em vida livre, onde os animais tem a possibilidade de selecionar outros microhabitats, termicamente mais favoráveis, e estão sujeitos a outras variáveis climáticas além da temperatura ambiente. Neste sentido, a incidência de luz solar pode incitar respostas diferentes, das observadas em laboratório, nos animais. Preguiças-de-três-dedos frequentemente adotaram, após eventos de chuva, uma

postura mais esticada sob a presença de sol – *basking*, possivelmente para secar a pelagem e se aquecer, sugerindo o emprego desta postura no ganho de calor (Montgomery and Sunquist, 1978; Urbani and Bosque, 2007). Por outro lado, quando expostas a temperaturas mais frias e na ausência de sol, estes animais adotam uma postura mais encolhida, dificultando assim a perda de calor para o meio (Urbani and Bosque, 2007).

Interessantemente, preguiças de três-dedos tendem a escolher copas de árvores com maior grau de exposição ao sol, alternando, dentro da copa, entre locais mais expostos, quando necessita aumentar sua temperatura interna e, menos expostos ao sol, quando estão aquecidas o suficiente (Montgomery and Sunquist, 1978). Urbani e Bosque (2007), inclusive, observaram esse comportamento no norte da Venezuela, onde a temperatura média atingiu os 19°C e as preguiças usaram mais os estratos superiores. O oposto foi observado, na planície brasileira, em Mamirauá, onde as temperaturas variaram entre 21 – 41°C e as preguiças usaram mais o estrato médio das árvores, sugerindo uma evitação a luz solar direta quando a temperatura externa já estava alta (de Queiroz, 1995).

A termorregulação comportamental no contexto das mudanças climáticas: custos e possíveis impactos sobre as preguiças

A termorregulação comportamental, tem sido citada como uma estratégia-chave que pode proteger os animais frente às futuras mudanças climáticas (Briscoe et al., 2014; Ellis et al., 2010; Kearney et al., 2009). O entendimento dessas interações entre os organismos e as variáveis climáticas tomou um tom urgente, a partir do cenário de mudanças climáticas, já que as respostas destes animais terão profundas implicações para a conservação (Kearney et al., 2009). Kearney et al. (2009) sugerem que, em zonas tropicais, a prioridade será evitar o aumento excessivo da temperatura interna e, que a eficácia dos comportamentos termorreguladores está

fortemente ligada a disponibilidade de sombra e, conseqüentemente, da extensão de cobertura vegetal. Além da redução de cobertura vegetal estar ligada à disponibilidade de microhabitats, pode também alterar o microclima do habitat dessas espécies (Prevedello et al., 2019). Nos trópicos, o desflorestamento, geralmente, ocorre através de incêndios, contribuindo, ainda, na emissão de gases do efeito estufa (Gatti et al., 2021). Alguns modelos climáticos, inclusive, preveem um aumento substancial na temperatura ambiente para a Mata Atlântica, com os modelos mais extremos sugerindo aumento de até 5.6°C (Marengo et al., 2010; Montero et al., 2018; Vale et al., 2021).

Uma vez que: (1) preguiças, no geral, no que tange a padrões de gasto energético e termorregulação, estão mais próximas dos ectotérmicos-heterotérmicos, os mecanismos comportamentais da termorregulação assumem uma relevante importância; (2) a condição de tempo (sol, nublado ou chuva) altera a forma como a temperatura ambiente é percebida, podendo em conjunto (interação aqui definida como condições climáticas) induzir respostas diferentes nos animais (Norris and Kunz, 2012), preguiças-de-três-dedos podem estar, particularmente, vulneráveis às mudanças climáticas. Os aumentos de temperatura previstos para ocorrer na Mata Atlântica, nas próximas décadas (Montero et al., 2018; Vale et al., 2021), podem afetar diretamente o comportamento desses animais.

Visto que a atividade de preguiças-de-três-dedos é estimulada pela temperatura ambiente (Giné et al., 2015), seria plausível pensar que, neste cenário futuro, tornar-se-iam mais ativas, porém para prevermos uma resposta mais fidedigna seria necessário, antes, considerar o efeito conjunto da radiação solar e entender seus efeitos sobre esses animais. Outra hipótese possível seria um maior uso dos estratos mais baixos e/ou internos das copas das árvores, visto que as, já altas, temperaturas ambientes seriam intensificadas com a presença de sol. Assim, um entendimento detalhado de como os organismos controlam sua exposição a condições climáticas é de grande importância para prever suas performances frente às mudanças

climáticas previstas, permitindo a proteção e conservação de habitats que fornecem refúgio adequado (Huey et al., 2012).

O uso de estratégias comportamentais na termorregulação pode, ainda, ser associado a custos como tempo de forrageio perdido e aumento dos riscos de predação, bem como ser restrito a disponibilidade de microhabitats favoráveis (Briscoe et al., 2014; du Plessis et al., 2012). Desta forma, compensações podem surgir, quando alguns comportamentos interferem em outros, levando os animais a tomarem escolhas que facilitem respostas a uma demanda, em detrimento de outras (Glass et al., 2021; Lima and Dill, 1990). Por exemplo, um bom local para se expor ao sol (*basking*), seria uma área aberta no estrato mais alto/externo do dossel, o que poderia tornar o animal mais exposto a predadores aéreos. Por outro lado, o uso dos estratos mais baixos para evitar o excesso de radiação solar poderia aumentar a exposição a predadores terrestres e, até mesmo, a caçadores (Milling et al., 2017). Este último cenário torna-se ainda mais preocupante quando consideramos os aumentos de temperatura previstos, o que, neste caso, poderia, indiretamente, torná-las mais vulneráveis.

A preguiça-de-coleira *Bradypus torquatus* Illiger, 1811 (Pilosa: Bradypodidae) é uma das quatro espécies existentes de preguiças de três-dedos, e a única espécie continental ameaçada de extinção (Chiarello & Moraes-Barros, 2014). É o maior e mais, morfológica e filogeneticamente, distinto membro da família Bradypodidae (Delsuc et al., 2019a; Presslee et al., 2019a). A espécie é endêmica da Mata Atlântica brasileira e vulnerável a extinção devido sua restrita e fragmentada área de ocupação (Chiarello & Moraes-Barros, 2014; Hirsch & Chiarello, 2012). Desflorestamento, fragmentação de habitat, caça e acidentes rodoviários são listados como as principais ameaças à espécie (Chiarello & Moraes-Barros, 2014; Superina et al., 2010).

Embora os impactos de variáveis climáticas sob o comportamento destes animais já tenham sido estudados, o efeito conjunto da temperatura ambiente e condições de tempo (i.e., condições climáticas) nunca foram analisados, e podem trazer respostas diferentes daquelas já descritas para esses fatores separados. Desta forma, objetivamos analisar a influência da temperatura ambiente nas atividades diurnas da preguiça-de-coleira, posturas e posições nas copas das árvores, em condições de tempo ensolaradas e nubladas. Também objetivamos analisar se estes comportamentos tornavam as preguiças-de-coleira mais expostas a detecção humana e, conseqüentemente, mais vulneráveis a atividades de caça e captura.

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CHAPTER 1

HOW THE SYNERGISTIC EFFECT OF WEATHER CONDITIONS AFFECTS MANED SLOTHS' BEHAVIOR AND DETECTABILITY?

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A maned sloth performing basking behavior at Reserva Sapiranga, northern Bahia. Photo by: Cosme Guimarães.

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ABSTRACT

Ambient temperature and solar radiation (weather conditions) may be two of the main drivers of their behavior, since these influence their metabolic rate, body temperature, food intake and, consequently, may influence their activities, postures and their search for thermally favorable microhabitats (thermoregulatory behavior). The behavioral response of sloths to these ambient factors has been insufficiently studied in the field and can provide complementary information about their vulnerability to climate change, especially when analyzed together. We studied the behavior of the threatened maned sloth (*Bradypus torquatus*) aiming to evaluate the influence of hourly ambient temperature variation on their activities, postures, and tree crown positions under sunny and cloudy conditions. We further tested if any of these behaviors increase their exposure to human detection. We performed 350 hours of visual observation on eight maned sloths from northern Bahia, recording their behaviors, postures, and positions on tree crowns. We also recorded the time taken to visualize the sloths for 69 days. The ambient temperature positively affected the sloths' activity levels in cloudy conditions, but negatively affected it in sunny conditions, which was an unexpected response. Ambient temperature negatively affected the frequency of huddled posture and positively the frequency of extended posture in both conditions. Ambient temperature alone positively affected the frequency in which sloths rested in the inner tree crown, but no effect in use of outer tree crown was found, as well as both positions and postures did not increase their detectability. We advance in knowledge indicating that the direction of the temperature-activity relationship depends on the conditions. It is possible that warmer and drier future climate in northern Atlantic Forest may reduce their diurnal activity levels and promote future and troubling physiological and behavioral constraints, although an increase of their exposure to human detection may not occur.

Key words: activity; arboreal mammal; folivore; solar radiation; thermal response

INTRODUCTION

The exposure to extreme temperatures is greatly stressful for animals and can lead to hypo or hyperthermia, harming countless internal processes and, ultimately, leading to death, thus thermoregulation is a key process to maintain body homeostasis (Terrien *et al.* 2011a). Most mammals are able to maintain a relatively high and constant body temperature (i.e., homeothermy), mainly from physiological processes (e.g., shiver, sweating, panting, non-shivering thermogenesis; Scholander, 1955). However, these mechanisms are accompanied by high costs of energy and, in this context, behavioral strategies may help offset these energetic costs (Lopes & Bicca-Marques 2017). At the same time, a smaller fraction of mammals is unable to sustain a constant body temperature, which oscillates with ambient temperature (heterothermy; McNab, 1978), relying greatly on behavioral strategies such as activity and postural adjustments, and the selection of microhabitats (Hetem *et al.* 2016; Norris & Kunz 2012).

Exposure to direct solar radiation via postural adjustments (basking) is a common thermoregulatory strategy in heterothermic animals (Coppola *et al.* 2019; Geiser *et al.* 2002; Grigg *et al.* 1992). Exposure to sunlight can reduce the energy expenditure in thermoregulation when environmental temperatures are low, and this behavior is one of the most effective ways for warming and rewarming among heterothermic animals (Coppola *et al.*, 2019; Hanya *et al.*, 2007; Takemoto, 2004; Terrien *et al.*, 2011). As the body temperature of heterothermic animals oscillates with ambient temperature, some thermoregulatory behaviors to avoid overheating are also expected (Sunday *et al.* 2014). In order to dissipate body heat and avoid excessive heat gain, these animals should pick shaded/cooler areas, while regions with high incidence of solar radiation should be chosen in order to raise body temperature (Terrien *et al.*, 2011). On the other

hand, shrunken postures should be adopted to minimize heat loss, especially at low ambient temperatures and in the absence of sunlight (Norris & Kunz 2012). Activity is also sensitive to these variables, and mammals can shift it by choosing a time range with more favorable ambient temperatures to carry out their activities (Norris & Kunz 2012; Terrien *et al.* 2011a).

Three-toed sloths (*Bradypus* spp.) are examples of heterothermic mammals (Cliffe *et al.* 2018). Limitations in controlling body temperature are linked to constraints imposed by their low-calorie diet, low metabolic rate, and low percentage of muscle mass, which are associated to their strictly arboreal and folivore habits (Cliffe *et al.* 2015, 2018). Indeed, their metabolic rate is reduced at both low ($< 22 - 26\text{ }^{\circ}\text{C}$) and high ($> 30\text{ }^{\circ}\text{C}$) ambient temperatures, a relationship that shows an inverse pattern from that observed in typical endotherms-homeotherms and approaches what is observed in ectotherms-heterotherms (Cliffe *et al.* 2018). Moreover, they present low activity levels (Chiarello 1998; Giné *et al.* 2015; Oliveira Bezerra *et al.* 2020) and body temperature, ranging from $27.7\text{ }^{\circ}\text{C}$ to $36.8\text{ }^{\circ}\text{C}$ ($27.7 - 36.8\text{ }^{\circ}\text{C}$; Goffart, 1971; Kredel, 1928; McNab, 1978).

Weather variables, such as ambient temperature and solar radiation (henceforth referred to as weather conditions), were already pointed out as two of the main drivers of sloths' body temperature, metabolic rates and activity levels (Britton & Atkinson 1938; Cliffe *et al.* 2018; Giné *et al.* 2015; Montgomery & Sunquist 1978). More precisely, body temperature shows a linear increase at ambient temperature, which also stimulates food intake, probably because of increased fermentation rates (Cliffe *et al.* 2015; Giné *et al.* 2015). Studies with three-toed sloths, under laboratorial or captive conditions, also indicate that body temperature varies with direct sunlight exposure and ambient temperature, and a continued exposure to direct sunlight may result in a 4 to $6\text{ }^{\circ}\text{C}$ rise in deep body temperature (Britton & Atkinson 1938; Britton & Kline 1939). Montgomery & Sunquist (1978) observed that free ranging sloths' maximum body temperature were lower on rainy days, especially when rain came during daylight, compared to

sunny days, suggesting a dependence on sunlight to raise their body temperature. Sloths tended to choose tree crowns with a higher degree of exposure to sunlight in cooler environments, as observed by Urbani & Bosque (2007), where the mean ambient temperature during the study was 19 °C and sloths used the upper tree strata more often. On the other hand, in the warmer Brazilian lowland, which ranges from 21 °C to 41 °C (de Queiroz, 1995), sloths mainly used the middle tree strata, suggesting an avoidance of the direct solar radiation when the ambient temperature was already high.

Behavioral thermoregulation has been cited as a key strategy that may protect animals in light of future climate changes (Briscoe *et al.* 2014; Ellis *et al.* 2010; Kearney *et al.* 2009). In terms of energetic costs and thermoregulation, sloths are closer to ectotherms-heterotherms than to endotherms-homeotherms, so their behavior assumes relevant importance (Cliffe *et al.* 2018). The worst scenario for the Brazilian Atlantic Forest predicts an increase up to 5.6 °C in ambient temperature, and some authors already suggest that avoiding overheating will be top priority (Kearney *et al.* 2009; Marengo *et al.* 2010; Vale *et al.* 2021). This worrying perspective paints a tone of urgency in understanding the interactions between these animals and climatic variables, not only separated but taking into consideration their joint effects, so we can have a more reliable picture of how these animals control their exposure and respond to these variables.

Climate changes might not only directly bring consequences on sloths' behavior, but also indirectly make them more vulnerable to human pressures, such as hunting. Since behavioral strategies in thermoregulation might be associated to an increased risk of predation (du Plessis *et al.* 2012), maybe climatic variables, through its effects on behavior, make sloths more detectable to predators or hunters. For example, if sloths descend to the lower/internal forest strata to avoid sunlight during warm hours, it is possible that in an even warmer weather in the future sloths use this stratum more frequently, becoming easier to be spotted by terrestrial predators or humans.

The maned sloth, *Bradypus torquatus* Illiger, 1811 (Pilosa: Bradypodidae), is one of the four extant species of three-toed sloths and the unique continental sloth considered threatened with extinction (Chiarello & Moraes-Barros, 2014). This species is endemic to the Brazilian Atlantic Forest (Hirsch & Chiarello, 2012) and vulnerable to extinction due to its restricted and fragmented occupancy area (Chiarello & Moraes-Barros, 2014). Deforestation, habitat fragmentation, hunting and road accidents are listed as the main threats (Chiarello & Moraes-Barros, 2014; Superina et al., 2010). It is the largest, most morphological and phylogenetically distinct member of the Bradypodidae family (Delsuc *et al.* 2019; Presslee *et al.* 2019). Although the effects of ambient temperature and conditions (sunny, cloudy, or rainy) on sloths' behavior are known, the joint effect of these variables have never been studied in free ranging sloths. As the three-toed sloths are potentially sensitive to fluctuations in temperature and conditions, the maned sloth may be particularly vulnerable in the face of global climate changes and landscape changes occurring in the Atlantic Forest (Tourinho *et al.* 2022). Additionally, changes in the activity levels, forest strata selection and frequency of postures adopted might make them more detectable and vulnerable to human pressures, such as hunting.

In this study, we aimed to analyze the influence of hourly ambient temperature on maned sloths' diurnal activities, postures, and tree crown positions, under sunny and cloudy conditions (henceforth referred to only as conditions). We also aimed to explore if these behaviors lead to a greater exposure of the animals to human detection. Considering that three-toed sloths are poor regulators of body temperature and need to save energy, we expected that free ranging maned sloths would exhibit behavioral (Figure 1A and B), postural (Figure 1C and D) and positional (Figure 1E and F) responses depending on ambient temperature. Moreover, given the additional effect of direct and indirect solar radiation, we expected differences in the behavior performed in cloudy and sunny periods (Figure X). In lower temperatures, we expected sloths to be more active, adopting a more extended posture and using more external parts of the tree

crown during sunny rather than cloudy days. In higher temperatures, we expected sloths to be less active, adopting a more huddled posture and using more internal parts of the tree crown during sunny rather than cloudy days because the presence of sun should imply an extra heat gain in an already warm condition. Regarding species' detectability, we expected that the use of inner tree crown and extended posture would increase the exposure of maned sloths to humans, which may make them more susceptible to capture and hunting.

PREDICTIONS

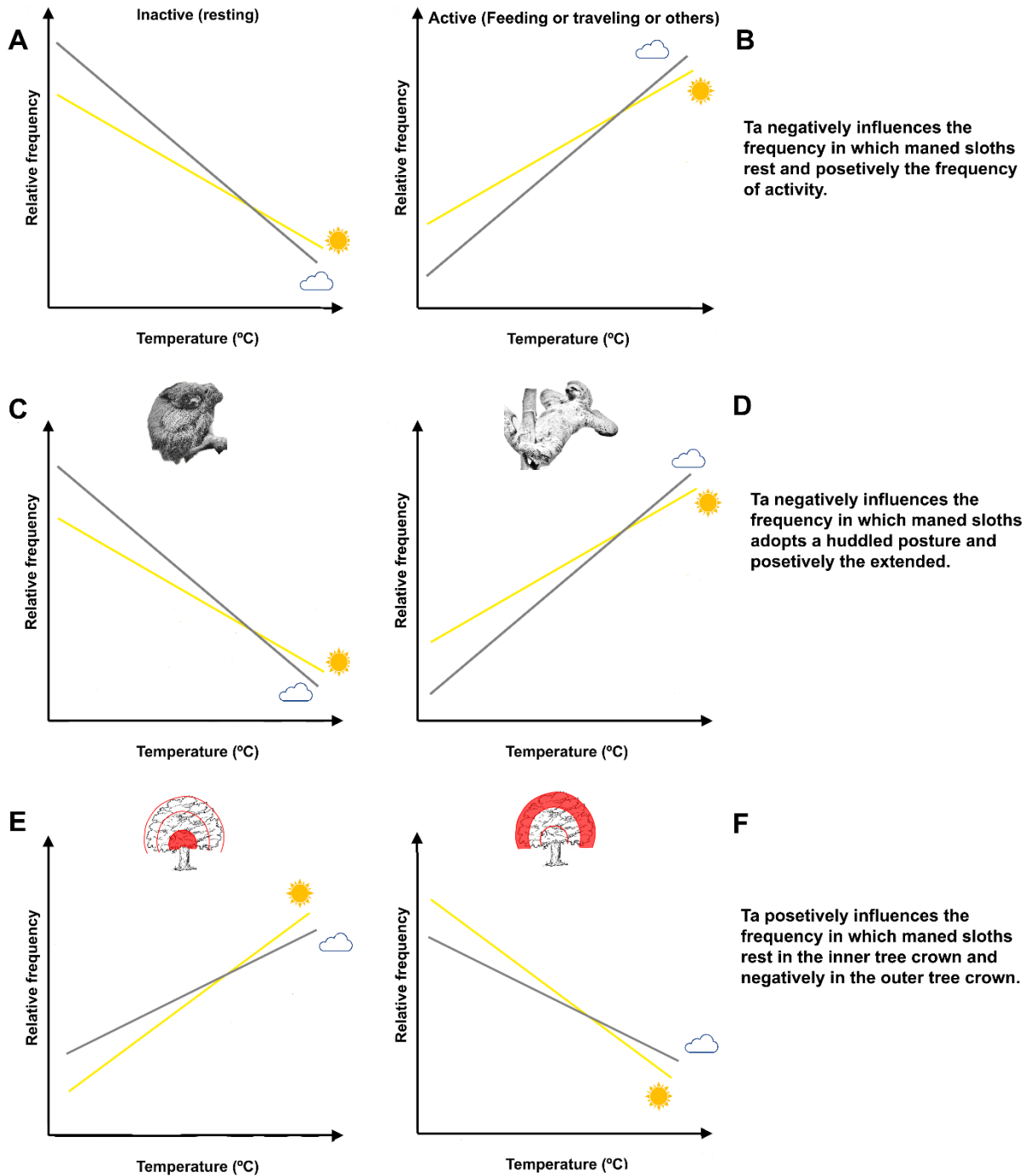


Figure 1: Predictions regarding the effects of ambient temperature (x axis) and conditions (yellow line for sunny and gray line for cloudy and rainy) in maned sloths' activity levels (A – B), postures (C – D) and tree crown positions (E – F). Differences in slopes indicate that at a lower temperature, sloths should be more active, adopt more extended posture and use more external parts of the tree crown during sunny rather than cloudy days, while the opposite should

be true at higher temperatures. Crossed lines indicate that, at some point, these behaviors should be performed less frequently under sunny conditions to avoid overheating.

METHODS

Study site

The study was conducted in the Sapiranga Reserve (12° 34' 04" S, 38° 02' 31" W; Figure 2), located in Mata de São João, Bahia, Brazil. This natural reserve is currently managed by the local government, receives many tourists and suffers with urban expansion problems. Despite several families living inside the reserve and a high degree of human interference, no information about hunting activities reached the research team during the study. On the other hand, while conducting this research, we observed the presence of domestic dogs within the forest fragment, forest clearing, selective cutting and intentional fires.

The vegetation is composed of a secondary forest fragment (~560 ha) on the Brazilian coastal sandbank, with vegetation structure typical of the *restinga* forest, mixed with ombrophilous forest. The vegetation is composed of Rainforest tree species and herbaceous vegetation, with canopy height of 11 to 13 m and few trees reaching more than 20 m (L. Mureb, unpublished data, 2022). The Reserve also contains some small open areas, including shrubs, urban areas, trails and roads (Juncá 2006). The climate is humid and tropical, with average monthly temperature ranging between 21 °C to 32 °C, and rainfalls throughout the whole year, with a monthly rate of 84 mm (WeatherSpark, 2020). The mean temperature during the period of this study (August to November 2020) was 26.9 °C, with minimum of 21.6 °C and maximum of 32.8 °C, and the daytime period occurred between 05h20 a.m. and 05h40 p.m. Two potential predators of three-toed sloths are known to circulate in the study area, which are the ocelot *Leopardus pardalis*, that has nocturnal habits (de Oliveira *et al.* 2013; Moreno *et al.* 2006;

Wang 2002) and the diurnal spectacled owl *Pulsatrix perspicillata* (Vasconcelosa *et al.* n.d.; Voirin *et al.* 2009), nonetheless none of these were sighted during this study.

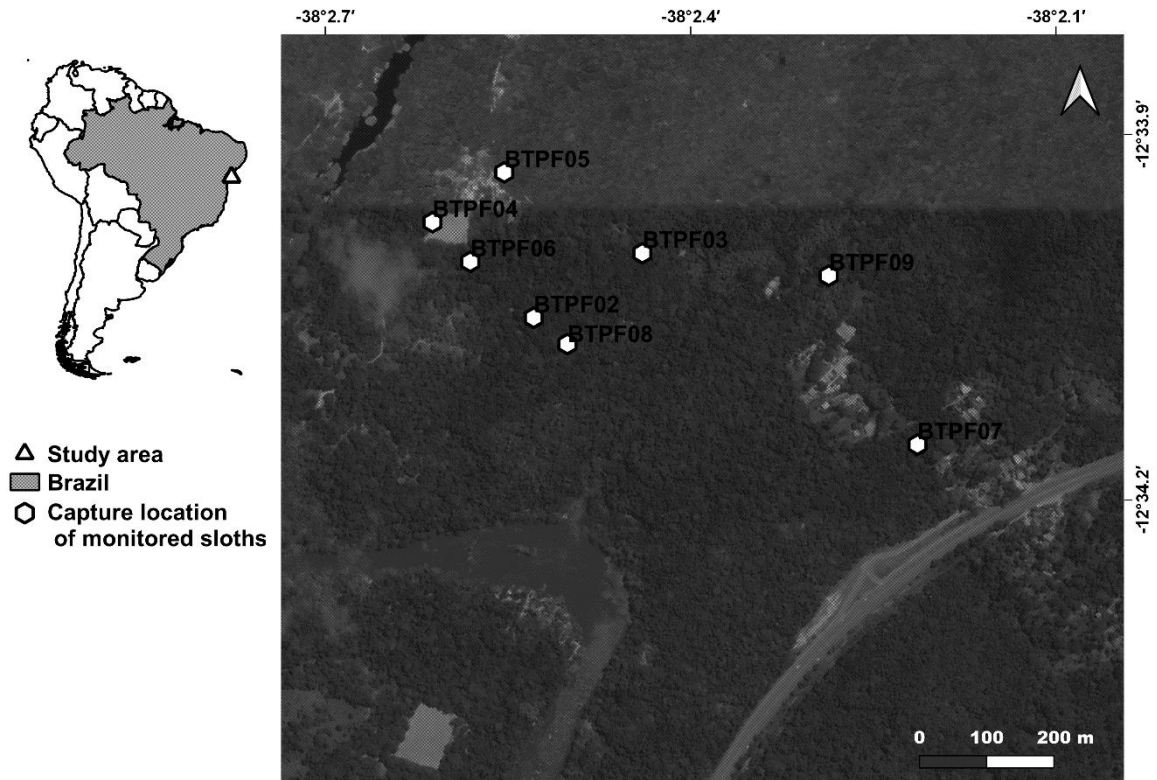


Figure 2: Location of the study site (left), the Sapiroanga Reserve (white triangle), northern Bahia, Brazil. Red circles on the right represent the location where the maned sloths were captured and released (Google Earth, 2022).

Capture and tagging

We captured eight maned sloths in March 2020 (Table 1), following the methodology described by Cassano *et al.* (2011). The animals were restrained in the tree top and their claws were immobilized using Velcro® straps (7 cm width), then they were conducted to the ground inside a permeable raffia bag (1 x 0.5 m), previously sanitized with a chlorine-based solution. Once on the ground, a band was placed over the animals' eyes to diminish the stress during the process, and information regarding sex, weight and body measurements were obtained. The

maned sloths were equipped with radio-backpacks (3 Telenax TGB325/304BF and 5 Telenax TGB325/311B) weighting 70 g, which represents less than 2% of the species average weight, as recommended by the Sikes and Animal Care and Use Committee of the American Society of Mammalogists (2016). After receiving the radio-backpack, we removed their blindfolds and the Velcro® straps, and immediately released the animal at the bottom of the same tree where it was captured.

Table 1. Sex and age classes, monitoring period and sampling effort during focal animal observations of maned sloths in the Sapiranga reserve, northern Brazilian Atlantic Forest.

Animal	Sex	Age classes	Period	Days	Hours
BTPF02	Male	Adult	18/08/2020 to 30/09/2020	5	44
BTPF03	Male	Subadult	17/08/2020 to 28/09/2020	5	41
BTPF04*	Female	Adult	14/08/2020 to 24/09/2020	5	45
BTPF05	Female	Adult	12/08/2020 to 26/10/2020	5	45
BTPF06	Female	Adult	19/09/2020 to 24/09/2020	5	45
BTPF07*	Female	Adult	13/08/2020 to 22/09/2020	5	44
BTPF08	Male	Adult	21/08/2020 to 29/09/2020	5	45
BTPF09	Female	Adult	20/08/2020 to 22/10/2020	5	41
Total				40	350

* Asterisk indicates females performing parental care during the period of observation.

Data collection

Radio-tracking and behavioral records

We monitored the maned sloths from August to November 2020 using *focal animal observations and single daily record monitoring*. We categorized the animals' postures as (1) huddled (tight-ball aspect) or (2) extended (limbs spread), an adapted classification from Cliffe et al. (2018; Figure 3A). We categorized animals' positions in the tree crown as inner (between the first and second bifurcation of tree branches) or outer (in the terminal branches portion) tree crown (adapted from Johansson 1974; Figure 3B).

To proceed with the *focal animal observations*, we preliminarily sorted one tagged animal to be monitored continuously in each sampling day. The animal sorted was located with a VHF receiver (TR-4; Telonics Inc., Mesa, Arizona) connected to a directional two-element antenna (RA-23 K; Telonics Inc., Mesa, Arizona) applying the homing technique (Mech 1983). After visually locating the animal, we consistently followed it in two time series, from 7h00 a.m. to 12h00 p.m. and 1h00 p.m. to 5h00 p.m. We observed the focal animal with binoculars (Bushnell 10 x 50 mm) and recorded the first visible behavior, posture and position exhibited at each 10-min interval, following the scan sampling method (Figure 3; Altmann, 1974). We categorized the animals' behaviors as feeding (when biting, chewing, reaching for or swallowing food), traveling (any type of displacement, whether horizontal or vertical), resting (stationary, sleeping or awake but engaged in no activity), or others (any activity not mentioned before, *e.g.*, breastfeeding, auto-grooming). We followed this method until monitoring each sloth for 5 days, totalizing 350 hours of observation (Table 1).

For the *single daily record monitoring*, each animal was located daily for 58 days, totalizing 408 registers. Through the homing technique, we defined the probable tree(s), pointed by the VHF signal, and from there we started the visual search (limited to 90 minutes). The first

visible behavior, posture and position exhibited were recorded, together with the time spent to visualize the animal. The condition at the time which the animal was sighted was also recorded. We named this method as *single daily record monitoring*, since we took only one record for each animal per day.

We recaptured and removed the radio collars at the end of the sampling period, and no injuries were observed. The licenses to carry these procedures and research were provided by the Chico Mendes Institute for Biodiversity Conservation (No. 67274-1) and the State University of Santa Cruz Ethics Committee on Animal Use (No. 022/20).

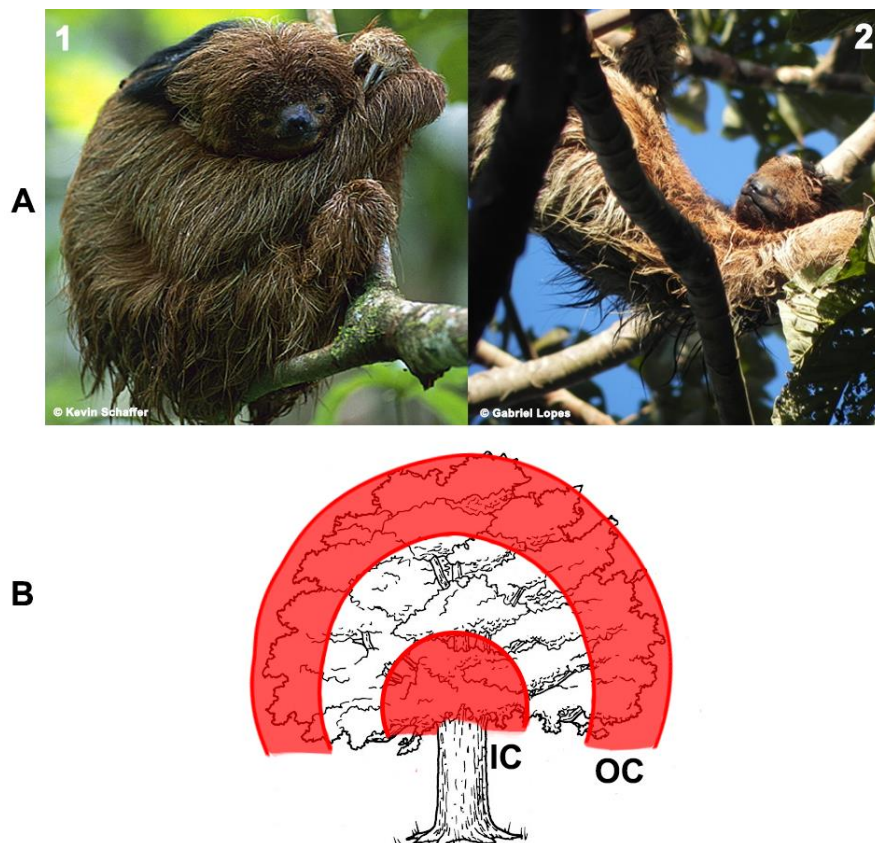


Figure 3: (A) Categories of postures adopted by maned sloths used for this study: 1. Huddled and 2. Extended (adapted from Cliffe et al., 2018). (B) Categories of tree crown positions: IC – inner tree crown and OC – outer tree crown (adapted from Johansson, 1974).

Ambient temperature recording

We placed data loggers (Hobo pedant UA-002-08), one for each month of monitoring, inside the forest fragment studied, 5 m above the ground (nearly the mean canopy height of the forest fragment), approximately at a central point to all capture sites, which recorded the ambient temperature (in °C) at every 10 minutes, simultaneously to the behavioral records. In addition, we recorded the conditions at every 10 minutes during *focal animal observations* in two categories: sunny and cloudy conditions. For the *single daily record monitoring* we recorded the condition at the time the animal was sighted. We considered sunny hours as when the greater part (> 50%) of the scans in that 1-hour interval occurred under clear sky with no clouds blocking the sunlight, and cloudy hours when the sunlight was totally or partially blocked by clouds for most of the time (> 50%). We did not consider hours in which the two conditions occurred equally.

Data analysis

We used data from *focal animal observations* to evaluate the influence of the ambient temperature and condition on the behavior, posture, and position of the maned sloths. We calculated the mean ambient temperature and the relative frequency of each behavior, posture, and position during each hour of observation, for each animal. These relative frequencies were estimated by dividing the number of records included in each category by the total number of observations at each sampling hour. Since the engagement in active behaviors can influence animal posture and position on tree crowns (e.g., the animal may adopt a more spread posture to reach its food), we only considered the postures and positions displayed during resting. We constructed Generalized Linear Mixed Models (GLMM) using the relative frequency of each behavioral (feeding, traveling, resting and others), postural (huddled and extended) and positional (inner and outer) categories as response variables (each category of behavior, posture,

and position was analyzed in a separated model selection), and the interactions between hourly mean temperature and predominant condition as predictor variables. We used interactive models and binomial distributions and included the individual sloths as random effect. This decision was made to deal with individual characteristics that could affect our results (Table 1). For each response variable, we constructed a null model, considering only the ambient temperature as the predictor variable, and a model considering the interaction between weather conditions (full model).

We used data from *single daily records monitoring* to evaluate if the posture and position of maned sloths influenced their visibility from the ground. We only used registers in which sloths were visualized in the inner or outer tree crown and adopting huddled or extended postures. For this, we constructed four GLMMs using detectability (i.e., 90 minutes minus the time spent to visualize the sloths) as the response variable and individual sloths as a random effect: (1) a null model, (2) a model considering only sloths' posture (huddled and extended), (3) one considering only positions (inner tree crown and outer tree crown) and (4) a full model with the interaction between position and posture. To handle problems of overdispersion with our response variable, we used a negative binomial distribution (Lindén & Mäntyniemi 2011). For this purpose, all models were constructed using the 'glmer.nb' function from the package 'lme4'.

We performed a model selection to identify the best fit model using the 'model.sel' function from the package 'MuMIn'. We used delta AIC (≤ 2) to identify selected models, and the Akaike weight to identify a 'best fit' (large difference in w_i) when two or more models were selected (ω_i ; Wagenmakers & Farrell 2004). Finally, we looked at the 95% confidence intervals, for each parameter of each best fit model, to check if the effect (coefficient) of the response variable was different than zero. All the analyses were run in R software (Britton & Kline 1939; Cliffe *et al.* 2015, 2018; Giné *et al.* 2015).

RESULTS

Influence of ambient temperature on the sloths' behavior, posture, and position

In general, we collected 2.266 records of behavior from focal animal observations. Ambient temperature measured by the dataloggers ranged from 21.7 to 32.9 °C. The mean hourly ambient temperature was higher between 10h00 a.m. and 2h00 p.m., although it widely varied in each sampling hour. The model including weather conditions interaction was the only one selected for resting behavior (Table 2), and the 95% IC for all coefficients (ambient temperature, conditions and interaction) did not include the zero (Appendix S1a). Frequency of resting increased with ambient temperature on cloudy days, while the opposite was observed on sunny days (Figure 4). For the three active behaviors (feeding, moving and others), both the model considering ambient temperature in interaction with conditions and one considering only ambient temperature were selected. Although weights (ω_i) were relatively similar (Table 2), the 95% IC for the coefficients estimated in all models included the zero (Appendix S1 b – d), indicating great uncertainty about the estimated effects.

Both models including ambient temperature in interaction with conditions and the one considering only ambient temperature were selected for the huddled posture. However, the weight for the first model was remarkably higher than the second one (Table 2), thus we chose the model including the interaction between both response variables, in which the 95% IC for all coefficients did not include the zero (Appendix S2a). For the extended posture, only the model with interaction was selected, and, besides that, the 95% IC of all its coefficients did not include the zero (Appendix S2b). Frequency of resting in huddled posture decreased both in sunny and cloudy conditions, while the opposite occurred for extended posture (Figure 5).

Finally, the models considering only the ambient temperature were selected, both for inner tree crown and outer tree crown. However, only the 95% IC for coefficients of the inner

tree crown selected model did not include zero (Appendix S3a and b). Temperature played a positive effect on the frequency in which maned sloths rested on the inner tree crown (Figure 6).

Table 2. Ranking of the competing Generalized Linear Mixed Models fitted to characterize effects of conditions in sloths' behavior, posture, and positions. Monitored maned sloths (8) were placed as random effect, and a binomial distribution was used to perform the GLMMs.

Pattern/ Response variable		Candidate model	Coeff. Temp.	Coef. Sun.	Df	AICc	Δ AICc	ω_i
Behavior	Resting	T_a*Cond.	-0.328	- 10.972	5	297.7	0	0.766
		T _a	-0.113		3	300.1	2.37	0.234
		Null			2	392.3	94.5	0
	Feeding	T_a	-0.089		3	218.6	0	0.598
		T_a*Cond.	-0.027	5.563	5	219.4	0.8	0.402
		Null			2	282.0	63.4	0
	Traveling	T_a*Cond.	0.549	11.633	5	60.5	0	0.595
		T_a	0.231		3	61.3	0.77	0.404
		Null			2	72.5	11.97	0.001
	Others	T_a*Cond.	0.494	4.244	5	68.8	0	0.504
		T_a	0.272		3	69.1	0.32	0.429
		Null			2	72.9	4.05	0.067
Posture	Huddled	T_a*Cond.	-0.697	- 14.455	5	180.5	0	0.694
		T _a	-0.462		3	182.2	1.64	0.306
		Null			2	277.1	96.5	0
	Extended	T_a*Cond.	0.598	- 16.380	5	259.5	0	0.995
		T _a	0.355		3	270.0	10.54	0.005
		Null			2	413.9	154.4	0
Position	Inner crown	T_a	1.385		3	19.2	0	0.865
		T _a *Cond.	0.007	< 0.01	5	22.9	3.71	0.135
		Null			2	71.4	52.12	0
	Outer crown	T_a	-0.019		3	236.9	0	0.852
		T _a *Cond.	0.080	3.743	5	238.5	3.51	0.148

		Null	2	355.6	118.71	0
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‡ Models account for the effects of ambient temperature (T_a) on the behavior and posture of maned sloths in sunny and cloudy conditions (Cond.). Degrees of freedom (df), Corrected Akaike information criterion (AICc), change in AICc relative to the highest ranked model ($\Delta AICc$) and AICc weight (ω_i).

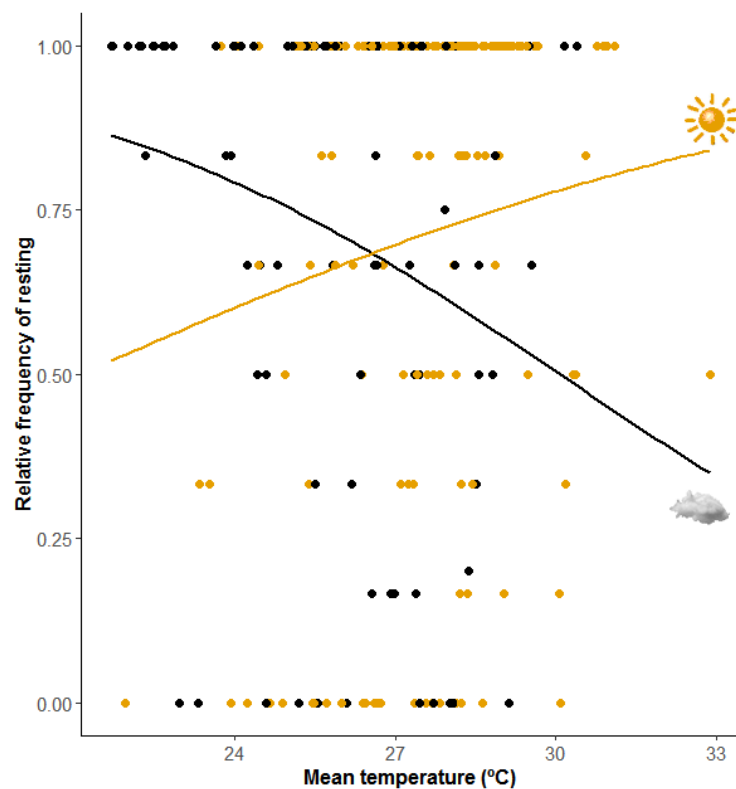


Figure 4: Relation (lines) between frequency of resting by *Bradypus torquatus* and mean ambient temperature in hourly intervals under sunny (yellow lines) and cloudy (black lines) conditions. Points represent the observed values.

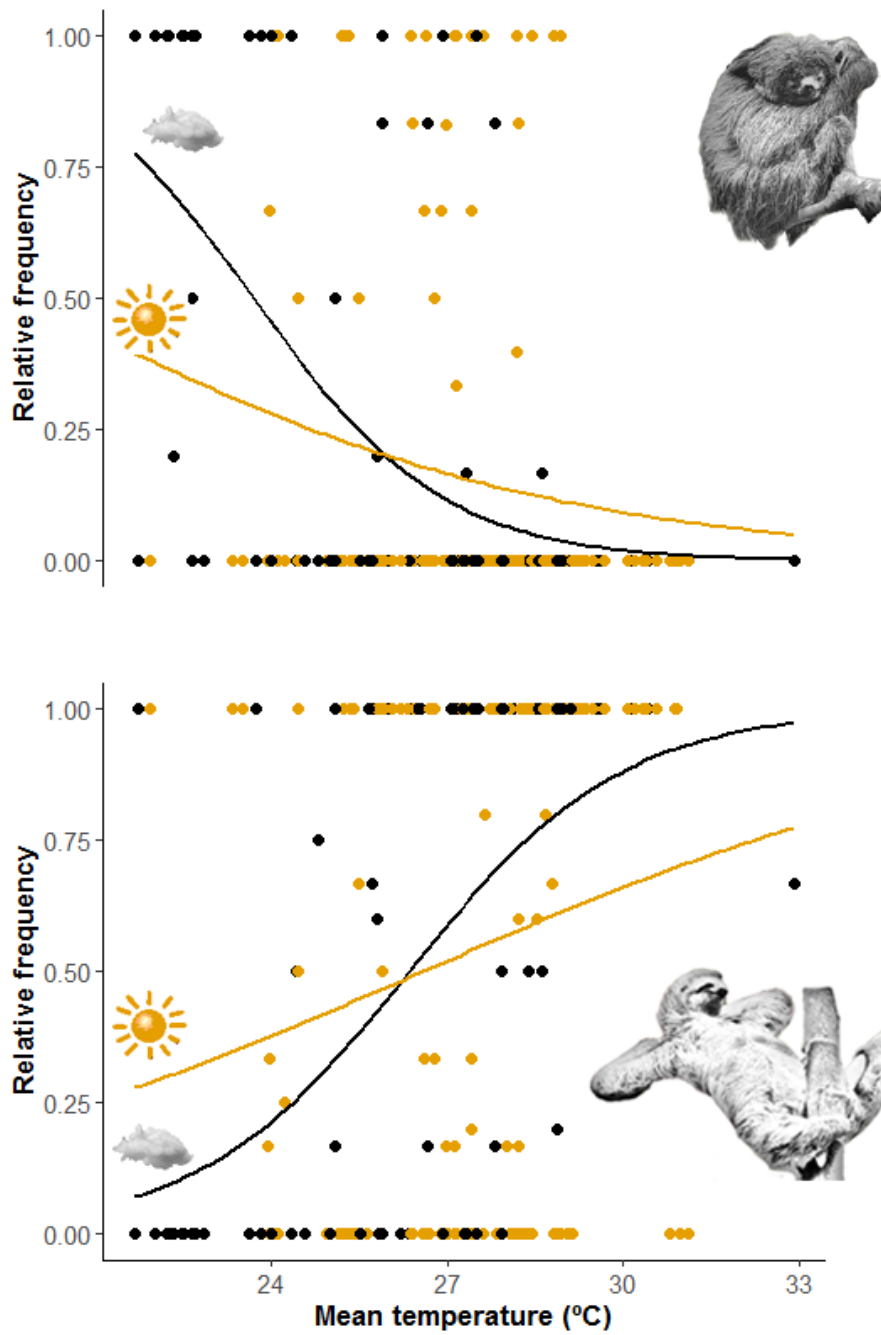


Figure 5: Relation (lines) between the frequency of resting in huddled (A) and extended (B) postures, for *Bradypus torquatus*, and the mean ambient temperature, in hourly intervals, on sunny (yellow lines) and cloudy (black lines) conditions. Points represent the observed values.

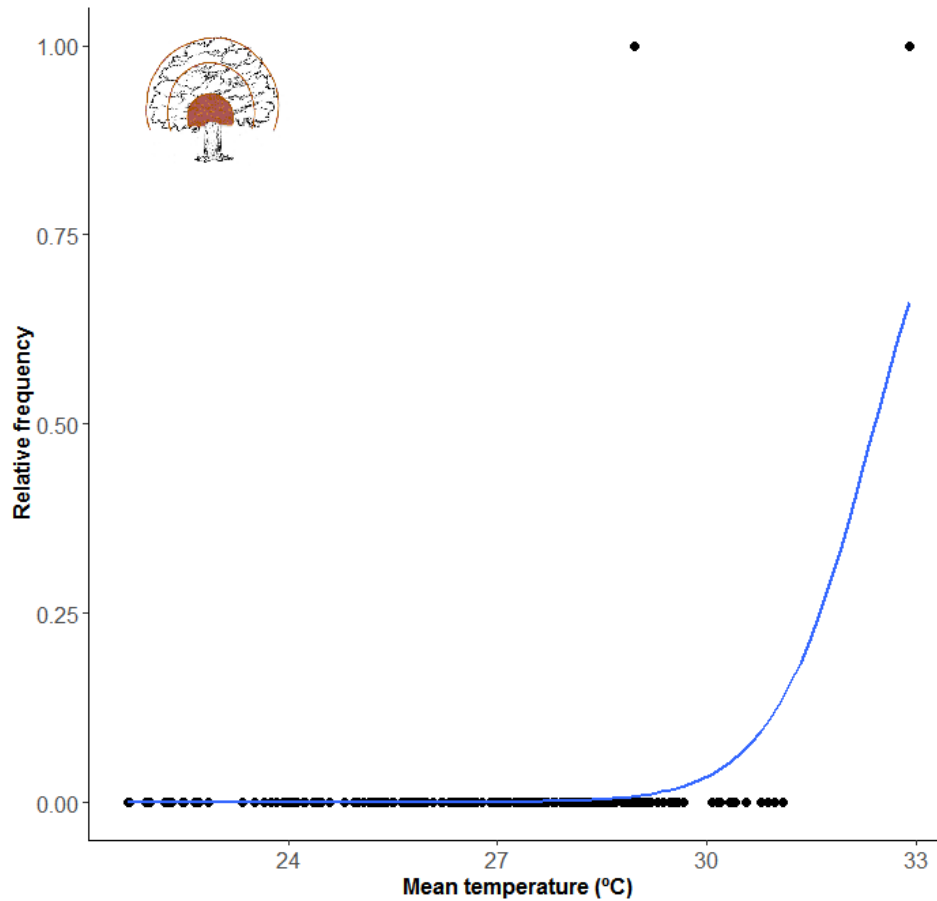


Figure 6: Relation (blue line) between the frequency of resting in the inner tree crown by *Bradypus torquatus* and the mean ambient temperature in hourly intervals. Points represent the observed values.

Influence of animal posture and position on the sloths' detectability

The maned sloths were visualized in 88% of the 407 *single daily records* ($n = 360$). The models explaining the variation of sloths' detectability as a function of position in the tree crown and as a function of position interacting with posture were selected and had relatively similar weight (Table 3). Nevertheless, the 95% IC for the coefficients estimated in all models included the zero (Appendix S4), indicating great uncertainty about the estimated effects.

Table 3. Ranking of the four competing Generalized Linear Mixed Models fitted to characterize effects of posture and position on tree crown on sloths' detectability. Monitored maned sloths (8) were placed as random effects and a negative binomial distribution was applied to the models.

Model rank	Candidate model	df	AICc	ΔAICc	ω_i
1	Detectability ~ position	4	2063.4	0	0.589
2	Detectability ~ position*posture	6	2064.1	0.72	0.411
3	Detectability ~ posture	4	3215.9	1152.5	0
4	Detectability ~ 1	3	3259.7	1196.3	0

‡ Models account for the effects of posture and position on animals' detectability. Degrees of freedom (df), Corrected Akaike information criterion (AICc), change in AICc relative to the highest ranked model (Δ AICc) and AICc weight (ω_i).

DISCUSSION

The findings reported here show that maned sloths spend most of their daytime resting, and that resting behavior most frequently occurs in an extended posture and in the outer tree crown. Our results also indicated that ambient temperature increased the sloths' activity level in cloudy conditions and decreased their activity level in sunny conditions. Regarding postures, ambient temperature increased the frequency of resting in extended posture, and decreased the frequency of resting in huddled posture, with stronger responses under cloudy conditions for both postures. Regarding position in the tree crown, only the frequency of resting in the inner

tree crown was positively affected by the ambient temperature. Finally, neither posture nor position affected sloths' detectability.

Sloths are animals critically limited by the low rates of energy acquisition and rest most of the time, a characteristic commonly shared with other arboreal mammalian folivores (Eisenberg 1978). Indeed, the frequency of resting exhibited by maned sloths reported here (74%) was similar to that expected for this species (74 – 83.8%; Chiarello, 1998; Giné et al., 2015) and other arboreal mammalian folivores, such as its congener *Bradypus variegatus* (72.9 – 74.9%; Oliveira Bezerra et al., 2020; Urbani & Bosque, 2007), the thin-spined porcupine *Chaetomys subspinosus* (74%; Giné et al., 2012), the eastern woolly lemur *Avahi laniger* (82.2%; Faulkner & Lehman, 2006). Nevertheless, we expected a positive influence of ambient temperature on sloths' activity levels regardless of conditions, as the temperature and/or solar radiation may directly stimulate the sloths' metabolic rate, food intake and activity (Britton & Kline, 1939, Cliffe et al. 2018, Cliffe et al. 2015, Giné et al. 2015). Surprisingly, our results indicated that hourly mean ambient temperature increased activity levels only under cloudy conditions, the opposite occurring in sunny hours. While this may contradict the general expectation for an arboreal mammalian folivore, including previous results reported for *Bradypus torquatus* through the diel cycle (Giné et al., 2015), our results show a depression of activity (in hour intervals) imposed by heat.

Laboratorial studies have shown that temperature has an inhibitory effect over *B.variegatus* metabolism under 22°C and above 30°C, and it is interesting to note that our registers occurred exactly inside this range of ambient temperatures where sloths' metabolic rate reaches its peak in laboratory – the so called thermoactive zone (TAZ; Cliffe et al., 2018). In natural environments, not only the ambient temperature itself induces responses in organisms, but also its combinations with solar radiation and other environmental variables, such as wind speed (Norris & Kunz 2012), which was not replicated in laboratorial studies.

Despite very few behavioral observations with ambient temperature $> 30^{\circ}\text{C}$ were registered during this study, it is possible that the combined effect of ambient and solar radiation may have caused this physiologic-behavioral or only behavioral response. Thus, considering that high temperatures lead to an inhibition of the metabolic rate (Cliffe et al. 2018) and sloths apparently have difficulty losing an excess of body heat quickly (Britton & Atkinson 1938), we hypothesized that they reduced activity in short intervals to avoid overheating from the synergistic effect of ambient temperature and solar radiation, since activity tends to raise body temperature – especially during daylight (Weinert & Waterhouse 1998). It could be possible that a depression in metabolism caused this decline in activity, but it is a winding path trying to extrapolate laboratorial results to free-ranging animals and, thus, we will assume this was a purely behavioral response.

As we expected, maned sloths rely on changes in posture to benefit heat exchange with the environment. Shrunken posture is adopted more frequently at lower ambient temperatures and in cloudy conditions, a strategy to diminish heat loss (Cliffe et al., 2018; Terrien et al., 2011; Urbani & Bosque, 2007) that is less frequent on sunny days. The opposite is observed for the extended posture, which was more adopted during sunny conditions, rather at lower temperatures than in cloudy conditions. Although we cannot infer if the maned sloths were really performing basking behavior (since data do not necessarily indicate that they were exposed to direct incidence of sunlight), they do take advantage of solar radiation (both direct and indirect incidence) to warm their bodies during lower temperatures. These results suggest that sunlight may provide an extra source of heat, which these animals try to take advantage of when ambient conditions are cooler by increasing the exposed body surface (Urbani & Bosque 2007). Moreover, differences in the slope of the response curve suggest that sloths seem to adopt the extended posture more cautiously during sunny conditions. We believe that this slower increase could be a way to avoid a faster overheating provoked by solar radiation during

already warm periods, reinforcing, once again, the idea that the combination of solar radiation and ambient temperature provokes behavioral changes in sloths.

Our selected model regarding position in the tree crown shows a positive relation between ambient temperature and the usage frequency of the inner tree crown, which drastically increases in temperatures above 29 – 30°C. This could suggest that maned sloths look for shaded areas under higher ambient temperatures to find milder thermal conditions, but this result must be read carefully, as we have had very few observations at high temperatures (Figure 6). Several mammals are known to shelter in shaded areas under hot weather and sunny conditions, reducing the risk of hyperthermia, water loss and excessive evaporative respiration (Clarke & Fraser 2004; Kosheleff & Anderson 2009; Norris & Kunz 2012; Sato 2012; Terrien *et al.* 2011). Chimpanzees (*Pan troglodytes*) have been observed to become more terrestrial at high ambient temperatures and chacma baboons (*Papio ursinus*) take advantage of thermal microclimates by resting in the shade during midday (Hill 2006; Takemoto 2004). Although the outer tree crown can offer more exposure to sun, we did not find any effect of temperature on the frequency in which maned sloths rested in this region. It is possible that, due to the forest's short stature and opening, sloths could expose themselves to higher temperatures and/or solar radiation at other forest strata levels (e.g., middle), maybe hampering the detection of this type of relation. It is worth remembering that our study site has diverse types of environments, going from predominantly open areas to areas with higher tree density, with heights rarely reaching 20 m (Mureb *et al.*, unpublished data, 2022).

Hunting is listed as a threat to the maned sloth, and even though they are not aimed by hunters, they may be victims of opportunistic hunting (Superina *et al.* 2010). Although some behaviors may lead maned sloths to a greater exposure to predators or humans, our results indicate that sloths' positions in the tree crown have no effect on their detectability by humans, as well as their postures and interactions between position and posture. Nonetheless, sloths use

the inner tree crown more often when ambient temperature is high, and although its use may not interfere with their detectability, it could make it easier for them to be captured. Opportunistic encounters (i.e., when there is no initial goal in finding the animal) may lead to capture, persecution, and even injuries by curious people, thus educational work on this subject is of integral importance for protecting these animals.

These ambient temperature effects on sloths' behaviors could be even more significant in a warmer future. Climatic changes caused by anthropic activities are probably the largest disturbance provoked by humans to the environment (Deutsch *et al.* 2008). The study area (northern Bahia) is predicted to be 1.8 – 5°C warmer until 2100 and to present a decrease in rainfalls (Marengo *et al.* 2010; Montero *et al.* 2018). This is even more worrying when we consider that most areas predicted to become climatically suitable for this species are highly deforested (Tourinho *et al.* 2022). The maned sloth already suffers with the deforestation pressure, since it is strictly arboreal, thus, besides reducing its habitat, it could also reduce the climatic suitability in certain areas. Our results suggest that maned sloths could already change their habits, being less active in increasing ambient temperature under sunny conditions during the diurnal period to avoid heat stress. Since maned sloths are cathemeral animals, this future climate scenario could bring more nocturn rather than diurnal habits as a way to prevent an excessive increase in body temperature during their activities (Chiarello, 1998; Pinder, 1985). Future high ambient temperatures could also lead maned sloths to use the inner tree crown more frequently, which could favor opportunistic capture.

Our findings provide a more complete insight about the effects of weather variables on maned sloths' behavior. Although it's known that increasing ambient temperatures may stimulate activity in sloths, here we show that its combination with solar radiation may actually reduce diurnal activity. Besides that, resting postures, more than the position in the tree crown, constitute an important behavioral mechanism for heat exchange and thermal maintenance.

Although the use of the inner tree crown is influenced only by the ambient temperature, the postures adopted by them are influenced both by ambient temperature and conditions, which apparently potentialize the heat gain. It is possible that a warmer and drier future in the already warm northern Atlantic Forest may bring some changes in maned sloths' behaviors, such as reduced diurnal activity levels and a higher use of inner tree crown, although a rise of their exposure to human detection may not occur. The maned sloth is already a threatened species that might deal with one more factor that may affect their physiology, metabolism, and behavior (Deutsch *et al.* 2008). However, the information provided by this study could, and should, be combined with spatial data on climate to predict impacts of increased temperature on this species thermoregulation and habitats that will remain providing suitable climatic refuges (Kearney *et al.* 2009; Tourinho *et al.* 2022).

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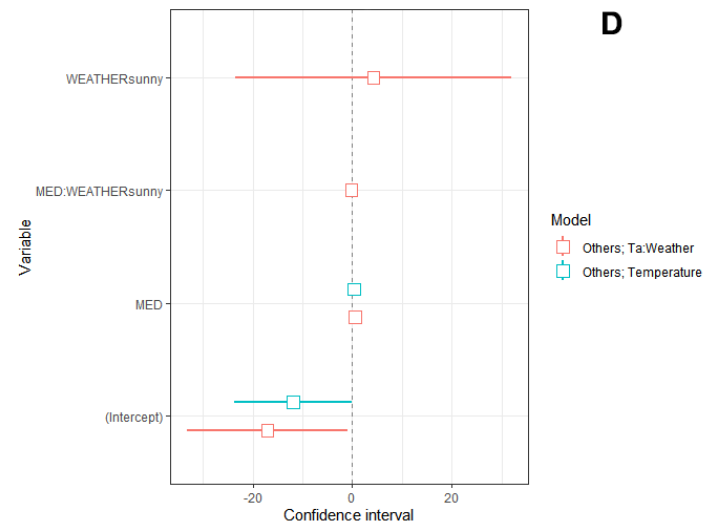
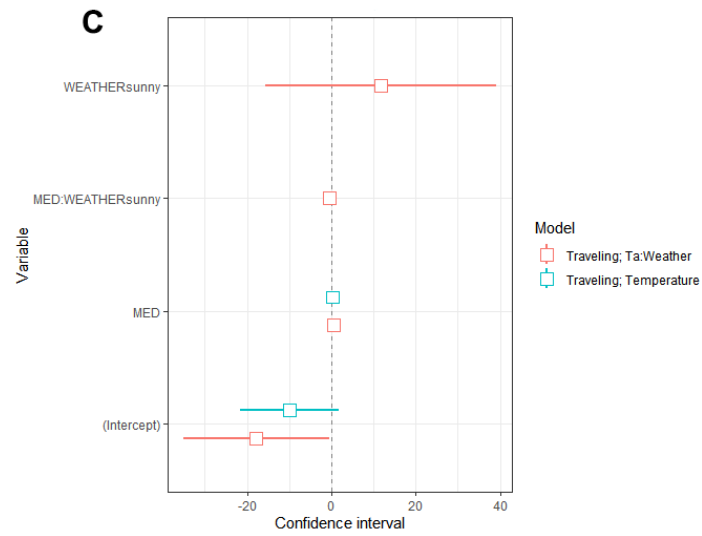
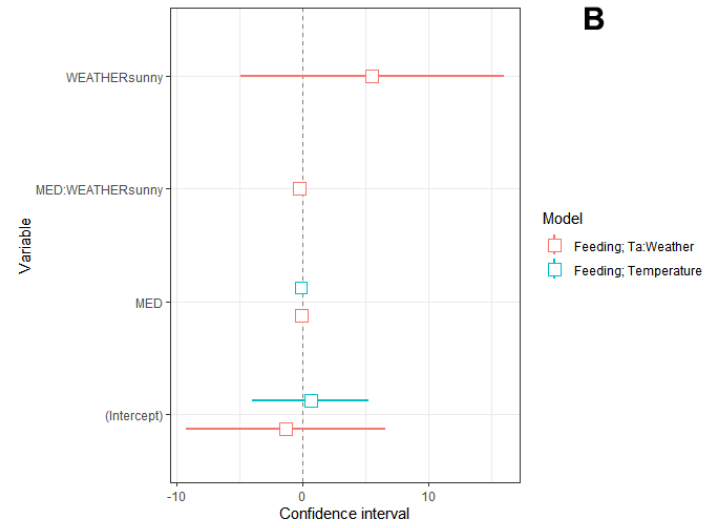
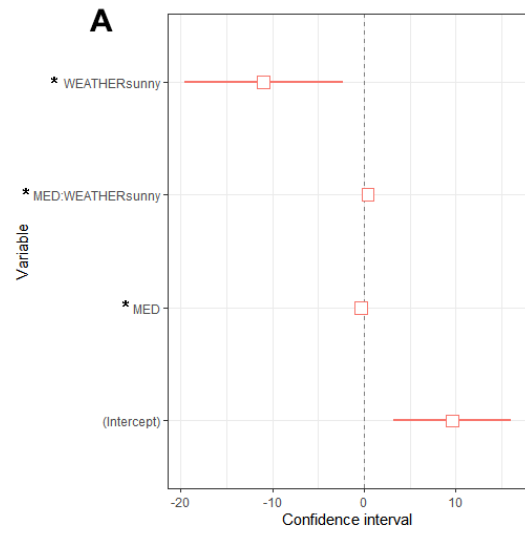
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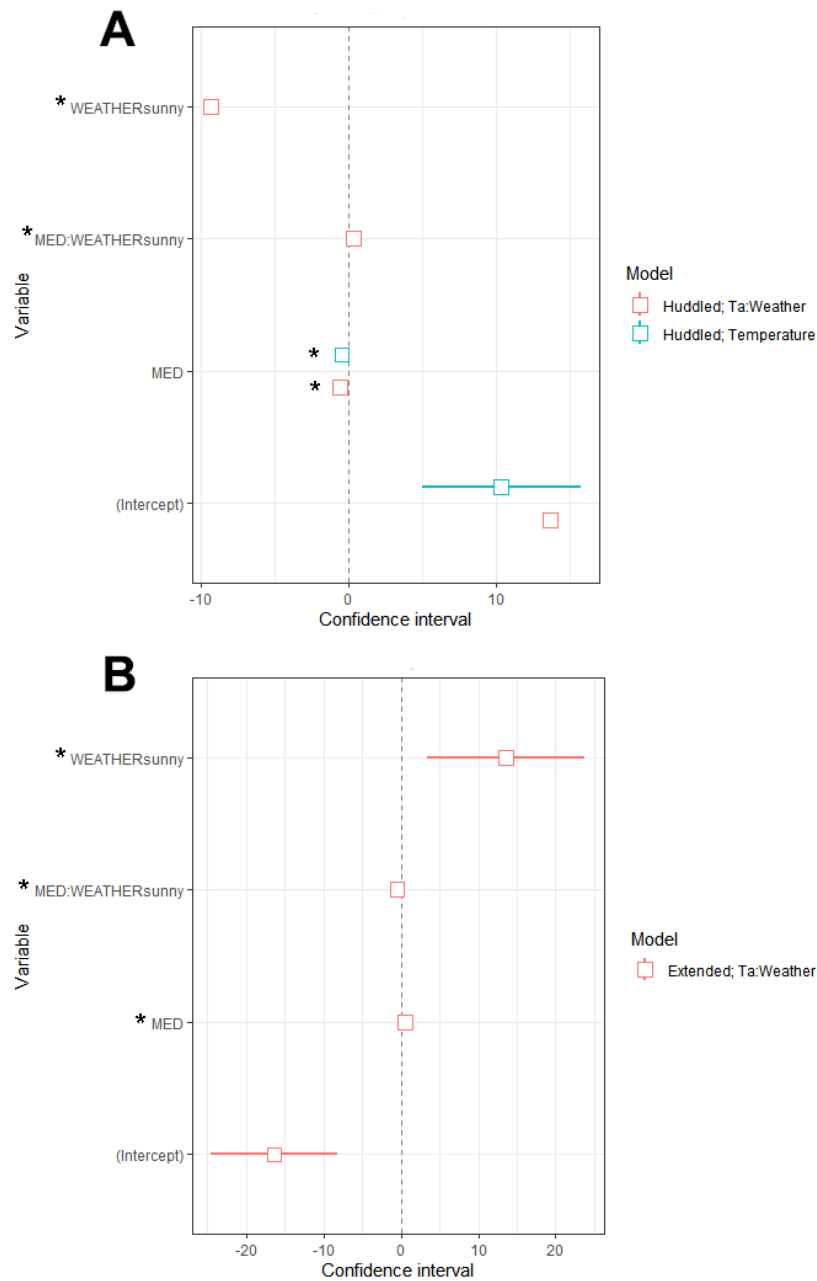
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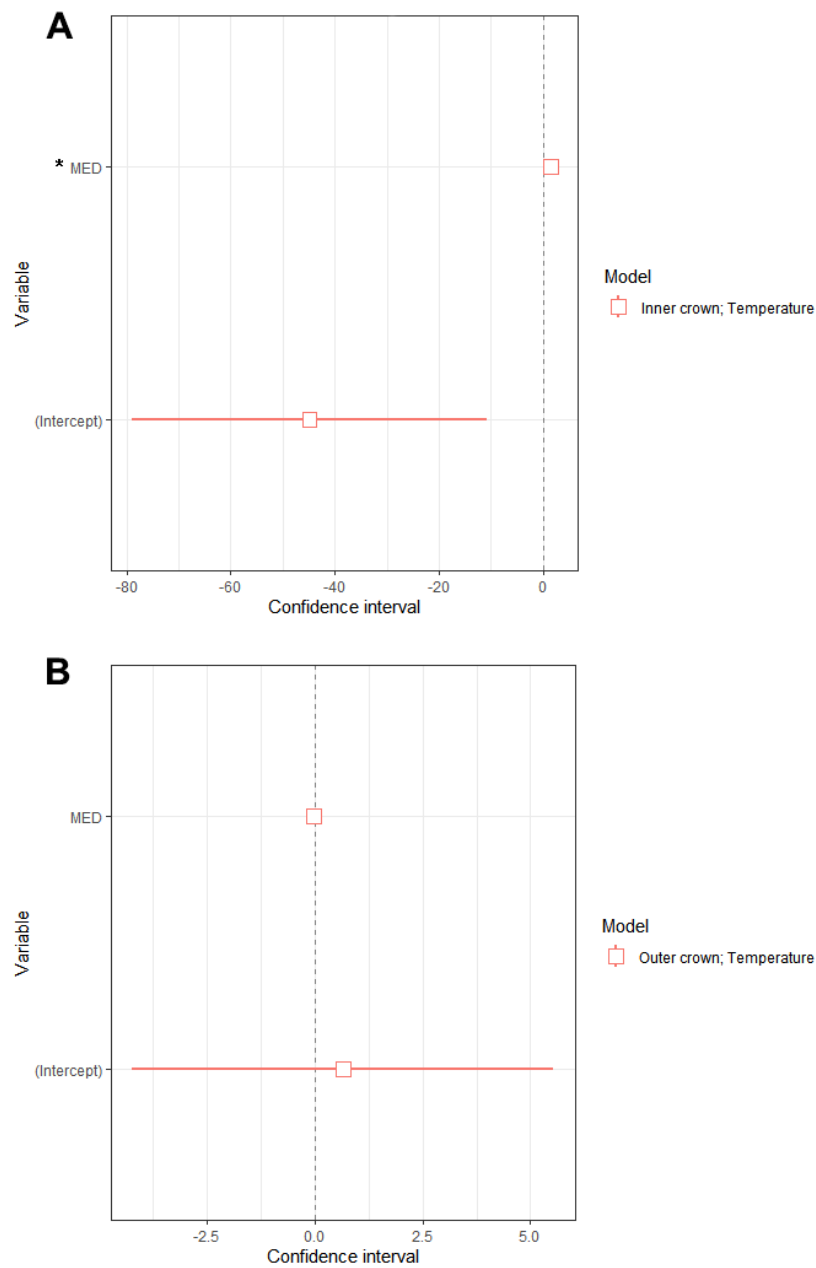
SUPPORTING INFORMATION



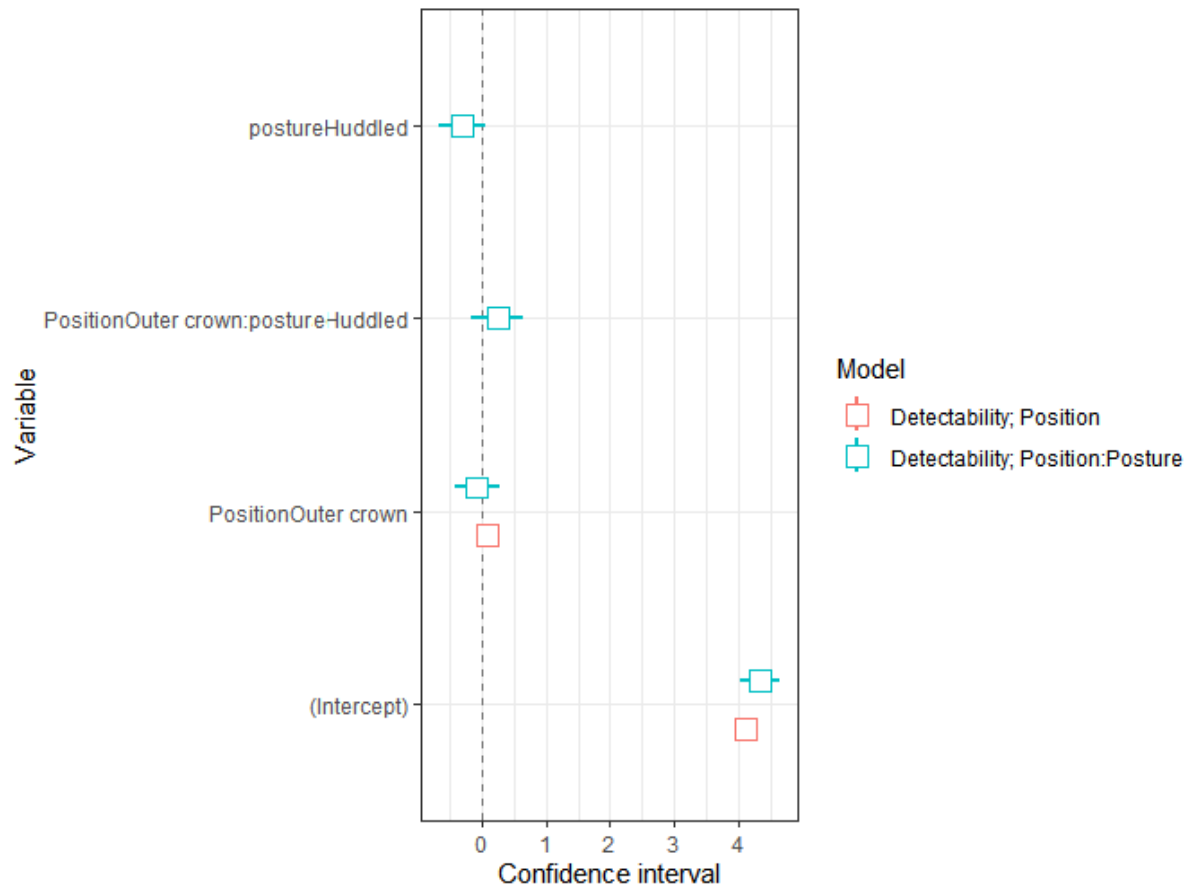
S1: Confidence intervals for each parameter of each selected model regarding the effects of T_a in interaction with conditions (pink) and/or the effect of only T_a (blue) on maned sloths' behavior: (a) resting, (b) feeding, (c) traveling and (d) others. Asterisks indicates variables which CI did not overlapped the zero. "MED" represents the variable mean ambient temperature, while "WEATHER" regards the categories sunny or cloudy.



S2: Confidence intervals for each parameter of each selected model regarding the effects of T_a in interaction with conditions (pink) and/or the effect of only T_a (blue) on maned sloths' postures during rest: (a) huddled and (b) extended. Asterisks indicates variables which CI did not overlapped the zero. "MED" represents the variable mean ambient temperature, while "WEATHER" regards the categories sunny and cloudy.



S3: Confidence intervals for each parameter of each selected model regarding the effects of T_a in interaction with conditions (pink) and/or the effect of only T_a (blue) on maned sloths' positions on tree crown: (a) inner and (b) outer tree crown. Asterisks indicates variables which CI did not overlapped the zero. "MED" represents the variable mean ambient temperature, while "WEATHER" regards the categories sunny and cloudy.



S4: Confidence intervals for each parameter of each selected model regarding the effects of maned sloths' position on the tree crown (pink) and its interaction with postures (blue) adopted by them on their detectability.