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**Giant anteaters' movement ecology reveals forests as a potential resource
to open-area mammals in heterogeneous landscapes**

Aline da Silva Giroux



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in heterogeneous landscapes**

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Grosso do Sul.

Advisor: Dr. Luiz Gustavo Rodrigues Oliveira-Santos

Abroad advisor: Dr. Luca Börger

Co-supervisor: Dr. Zaida Ortega Diago

Board members

Dra Marlee Turker (Netherlands)

Dra Pavla Hejcmanová (Tchéquia)

Dra Cecilia Ines Robles (Argentina)

Dr Marcos Vinícios Vieira (Brazil)

Dra Julia Emi de Faria Oshima (Brazil)

To Josie Giroux

Who introduced me to diversity and beauty of life, teaching me to treat animals and plants with kindness and compassion. Turns out I developed a little more compassion than he expected, so he had to find out a way to capture the animals that come into our house without harming them (including scorpions, spiders, snakes, and rats). Thanks dad.

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General abstract

Forests act as thermal buffers, offering milder temperatures than adjacent open areas. With the increasing frequency and intensity of extreme weather events, forests can be an important thermal shelter to wildlife. In endotherms, thermoregulatory behavioural strategies reduce the energetic costs of physiological thermoregulation. Between mammals, those with low capacity for physiologically thermoregulate should show more conspicuous thermoregulatory behaviors and, therefore, should be valuable models to understand the importance of forests as thermal shelters in a climate change world. Here, we explored the movement ecology of the giant anteater, *Myrmecophaga tridactyla*, a large mammal with low body heat production, exemplifying how forest patches can be an important thermal resource to open-area mammals living in heterogeneous landscapes. Based on GPS tracking data and movement models, we investigated (1) how much giant anteaters modulate activity and selection for forests as thermoregulatory behavioural strategies and (2) how much giant anteaters' intrinsic traits and the availability of forests influence their space use and spatial requirements. Besides a surprisingly high short-term behavioral plasticity regarding on activity, giant anteaters also showed increased selection for forests at extreme cold and hot weathers, comparing with mild ones. These animals selected forests at night when it was cold and during daylight when it was hot, while in mild temperatures they avoided forests all day long. We showed male and female giant anteaters presenting different space-use strategies, that differently scaled with body mass, and both sexes increasing home range size with decreasing proportion of forests inside their home ranges. Forests were important thermal resources at extreme weather conditions. Therefore, giant anteaters with lower access to forest patches possibly increased home range size to maximize the chances of accessing these thermal shelters. Decreasing availability of forest patches in heterogeneous landscapes can reduce the habitat thermal suitability and increase spatial requirements even to mammals that are usually found in open areas, as giant anteaters. Considering the climate change scenario, the importance of forest patches should increase to these mammals, and it need to be considered in effective management decisions.

Resumo geral

Florestas atuam como tampões térmicos, oferecendo temperaturas mais amenas que áreas abertas adjacentes. Com a crescente frequência e intensidade de eventos climáticos extremos, florestas podem ser importantes abrigos termais para a vida selvagem. Em endotermos, as estratégias de termorregulação comportamental reduzem o custo energético associado à termorregulação fisiológica. Mamíferos com baixa capacidade para termorregulação fisiológica devem mostrar comportamentos termorregulatórios mais conspícuos e, portanto, devem ser modelos valiosos para entender a importância das florestas como abrigos termais durante mudanças climáticas. Exploramos a ecologia do movimento do tamanduá-bandeira, *Myrmecophaga tridactyla*, um grande mamífero com baixa produção de calor corpóreo, exemplificando como florestas podem ser importantes recursos térmicos para mamíferos de áreas abertas vivendo em paisagens heterogêneas. Usando dados de monitoramento via GPS e modelos de movimento, investigamos (1) o quanto tamanduás bandeira modulam sua atividade e seleção por florestas como estratégias de termorregulação comportamental e (2) o quanto as características intrínsecas dos indivíduos e a disponibilidade de florestas influenciam seu uso do espaço e suas necessidades espaciais. Além de uma surpreendentemente alta plasticidade comportamental de curto prazo relativa à atividade, os tamanduás-bandeiras também mostraram aumento de seleção por florestas em extremos de frio e calor. Eles selecionaram florestas à noite em períodos de frio e à luz do dia em períodos de calor, enquanto evitaram florestas em temperaturas amenas. Machos e fêmeas apresentaram diferentes estratégias de uso do espaço, que escalaram diferentemente com a massa corpórea, e aumentaram sua área de vida com a redução de proporção de florestas nessa área. Florestas foram importantes recursos termais em temperaturas extremas. Tamanduás-bandeira com menor acesso a florestas possivelmente aumentaram sua área de vida para maximizar as chances de acessar esses abrigos térmicos. A redução da disponibilidade de florestas em paisagens heterogêneas pode reduzir a adequabilidade termal do habitat e aumentar as necessidades espaciais, mesmo para mamíferos que são usualmente encontrados em áreas abertas, como tamanduás-bandeira. Com as mudanças climáticas, a importância das florestas deve aumentar para esses mamíferos e isso precisa ser considerado em efetivas decisões de manejo.

General introduction

Forests buffer macroclimatic changes. Below forest canopies, direct sunlight, wind speed, and rain fall are strongly reduced (De Frenne et al. 2019). Compared with adjacent open areas, the understory offers a cooler microclimate when environmental temperatures are high and a warmer microclimate when environmental temperatures are low. This offset is magnified as temperatures become more extreme (De Frenne et al. 2019). Once the frequency and intensity of extreme weather events are expected to increase (IPCC 2021), forests may thus reduce the severity of climate change impacts on biodiversity (De Frenne et al. 2021). This conclusion is clear to forest animals, but the importance of forests as a thermal resource remains poor known to animals that perform most of their activities in open areas.

We used giant anteaters' movement ecology to exemplify the importance of forests to an open-area mammal living in heterogeneous landscapes. Giant anteaters present low body heat production and, consequently, low capacity for physiological thermoregulation (McNab 1984, 1985). As a compensation, this mammal rely on behavioral adjustments as an auxiliary mechanism for thermoregulation, exhibiting high behavioural plasticity in response to environmental temperature changes (Giroux et al. 2021a). This is why giant anteaters should be valuable models to understand how forests can be important thermal shelters to open-area mammals in a climate change scenario. Such as other open area mammals, giant anteaters should face a trade-off between using forests as thermal shelters and finding better conditions for displacement and foraging in open areas.

In the chapter 1 (Giroux et al. 2023), we investigated the role of forests as thermal shelters modelling the effect of the environmental temperature on the giant anteaters' selection for forests. To get an integrative understanding of giant anteaters' behavioral thermoregulation, we also evaluated how they modulate activity duration and activity period in response to environmental temperature changes. Then, in the chapter 2 (Giroux et al. 2021b), we assessed the importance of forests as a resource to this open area mammal by investigating the influence of the availability of forests on their spatial requirements. Besides, we added information about this species spatial ecology by investigating the influence of their intrinsic traits on movement patterns and home range size.

Chapter 1: Activity modulation and selection for forests help giant anteaters to cope with temperature changes

Abstract

Mammals use thermoregulatory behavioural strategies to reduce the cost of physiological thermoregulation. Environmental temperatures should, therefore, impact their decisions. We investigated the effect of environmental temperature on the movement decisions of a large mammal with low capacity for physiological thermoregulation: the giant anteater, *Myrmecophaga tridactyla*. We GPS-tracked 14 giant anteaters in the Brazilian Pantanal wetland over 5 years. We used hidden Markov models to identify two behavioural states (encamping, as a proxy of resting, and moving, as a proxy of being active) across individuals' trajectories. Then, we estimated the effect of environmental temperature on the probability of moving across the hours of the day in open and forested habitats. We also used integrated step selection analysis to understand how environmental temperature drives giant anteater's habitat selection across the day. Giant anteaters showed three important behavioural thermoregulatory strategies in response to environmental temperature changes: they modulated activity duration, completely shifted activity period on a scale of days and selected forests as thermal shelters. With increasing environmental temperature, giant anteaters increased activity duration, nocturnality and diurnal selection for forests, increasing energy intake while avoiding heat gain by solar radiation. With decreasing environmental temperature, they decreased activity duration, increased diurnality and increased nocturnal selection for forests, thus gaining heat from solar radiation when active and taking shelter in milder microclimates when resting. Besides their high short-term behavioural plasticity regarding activity, giant anteaters also used forests to thermoregulate. These results provide insights into how other mammals could respond to climate change. In particular, we highlight the importance of forests as thermal shelters, offering milder temperatures than adjacent open areas during both hot and cold weather spells. Thermal shelters will become more and more indispensable to animal thermoregulation as the frequency and intensity of extreme weather events increase.

Resumo

Mamíferos utilizam estratégias comportamentais para reduzir o custo da termorregulação fisiológica. A temperatura ambiental deve, portanto, impactar suas decisões. Investigamos o efeito da temperatura ambiental nas decisões de movimento de um grande mamífero com baixa capacidade de termorregulação fisiológica: o tamanduá-bandeira, *Myrmecophaga tridactyla*. Monitoramos 14 tamanduás-bandeira via GPS no pantanal brasileiro ao longo de cinco anos. Usamos modelos baseados em cadeia de Markov para identificar dois estados comportamentais (encampado, como uma aproximação de descanso, e movendo, como uma aproximação de atividade) ao longo das trajetórias dos indivíduos. Então, estimamos o efeito da temperatura ambiental sobre a probabilidade de mover ao longo das horas do dia em habitats abertos e florestados. Usamos a análise integrada de seleção passo a passo para entender como a temperatura ambiental influencia a seleção de habitat ao longo do dia. Os tamanduás-bandeira mostraram três importantes estratégias comportamentais em respostas às mudanças de temperatura: eles modularam a duração da sua atividade, trocaram completamente seu período de atividade em uma escala de dias e selecionaram florestas como abrigos térmicos. Com o aumento da temperatura ambiental, tamanduás-bandeira aumentaram a duração da sua atividade, a sua noturnidade e a seleção diurna por florestas, aumentando seu ganho energético e evitando o ganho de calor por radiação solar. Com a diminuição da temperatura ambiental, eles diminuíram a duração da sua atividade, aumentaram diurnidade e aumentaram a seleção noturna por florestas, ganhando calor por radiação solar quando ativos e se abrigando em microclimas mais amenos ao descansar. Apesar da alta plasticidade comportamental de curto prazo no que diz respeito à atividade, os tamanduás-bandeira ainda usaram florestas para termorregular. Esses resultados mostram como outros mamíferos poderiam responder às mudanças climáticas. Em particular, destacamos a importância das florestas como abrigos térmicos, oferecendo temperaturas mais amenas que áreas abertas adjacentes durante extremos de frio e calor. Abrigos térmicos se tornarão cada vez mais indispensáveis para a termorregulação animal à medida que a frequência e intensidade de eventos climáticos extremos aumenta.

Introduction

Environmental temperature is a major determinant of animal behaviour (Angilletta et al. 2010, Beever et al. 2017). Individuals' performance and fitness are maximized when body temperatures are close to their physiological optima (Maloney et al. 2017, Levesque & Marshall 2021). When mammals are within a species-specific range of environmental temperatures (called the thermoneutral zone: TNZ), they maintain their body temperature within optimal levels with minimal regulatory changes in metabolic heat production and evaporative heat loss (Kingma et al. 2012). As environmental temperature deviates from the TNZ, mammals do not rely exclusively on physiological mechanisms for thermoregulation, but also use behavioural adjustments as an additional thermoregulatory strategy (Terrien et al. 2011, Mota-Rojas et al. 2021). Given the ongoing increasing frequency and intensity of extreme weather events (e.g., extreme heat or cold), environmental temperature will have an increasingly stronger impact on animal behaviour and, consequently, on population dynamics and species conservation (Cohen et al. 2018, IPCC 2021). To predict the potential impacts of climate change and successfully manage future biological processes, it is fundamental to understand how environmental temperature modulates animal behaviour (Chmura et al. 2018, Buchholz et al. 2019).

Among the behavioural aspects influenced by environmental temperature, animal movement stands out since many thermoregulatory behavioural strategies are closely related to movement (Terrien et al. 2011, Mota-Rojas et al. 2021). Environmental temperature can influence, for example, the amount of time that animals spend moving, which times of the day they choose to move and where they go (Jennewein et al. 2020, Tatler et al. 2021, Perea-Rodríguez et al. 2022). Some mammals decrease movement when they are experiencing thermal discomfort, modulating activity duration in response to environmental temperature (e.g., Prajapati & Koli 2020). Many mammals also adjust their activity period as a function of environmental temperature, in order to move at times of maximum thermal comfort across the day (e.g., Levy et al. 2019). Besides, individuals that have access to a thermally heterogeneous landscape can modulate habitat selection with environmental temperature changes, searching for places with favorable thermal conditions (e.g., Mason et al. 2017).

The intensity with which environmental temperature influences animal movement depends on many factors, such as species behavioural plasticity and its physiological thermoregulatory capacity (Terrien et al. 2011, Mota-Rojas et al. 2021). In particular, members of the superorder Xenarthra, which includes armadillos (Cingulata), sloths and anteaters (Pilosa), exhibit high behavioural plasticity in response to environmental temperature changes (e.g., Attias et al. 2018, Giroux et al. 2021a). Compared with other placental mammals of similar body mass, they have a lower basal metabolic rate and lower body temperatures, due to their low-calorie diet (McNab 1984, 1985). The low body heat production leads xenarthrans to have a low capacity for physiological thermoregulation (McNab 1984, 1985), which increases the importance of behavioural adjustments for their thermoregulation.

Yellow armadillos, *Euphractus sexcinctus*, southern three-banded armadillos, *Tolypeutes matacus*, and giant anteaters, *Myrmecophaga tridactyla*, reduce activity duration with decreasing environmental temperature (Mourão & Medri 2007, Maccarini et al. 2015, Attias et al. 2018, Giroux et al. 2021a). This is because they can increase body heat conservation during rest, by adopting specific postures that reduce their surface-to-volume ratio (e.g., three-banded armadillos can ‘roll into a ball’ while anteaters cover themselves with their long furry tail; McNab 1984, 1985, Medri & Mourão 2005). They can also modulate their activity period, slightly increasing diurnality with decreasing environmental temperatures, in order to increase heat gain through solar radiation (Camilo-Alves & Mourão 2005, Attias et al. 2018). Another important response of these species to environmental temperature variations is the selection for thermal shelters in the landscape, such as burrows and forest areas (Camilo-Alves & Mourão 2005, Attias et al. 2018, De Frenne et al. 2019, Giroux et al. 2021a). Due to the intensity with which they respond to environmental temperature variation, xenarthrans are valuable models for understanding how climate changes can influence mammalian movement.

Despite the increasing number of studies in the last decade, we still lack an integrative understanding of how environmental temperature modulates giant anteaters’ movement decisions throughout the hours of the day. Here, we used global positioning system (GPS) tracking data to investigate the effects of environmental temperature on giant anteaters’ movement decisions at a fine

temporal scale (see Richter et al. 2020). Specifically, we quantified how anteaters modulate activity duration, activity period and selection for forests in response to environmental temperature variations across the day. As an important advance in relation to previous studies, we considered the effect of the interaction between environmental temperature, time of day and habitat type (open versus forested habitats) on individuals' movement when investigating both activity modulation and habitat selection. To investigate activity modulation, we identified two behavioural states (encamping, as a proxy of resting, and moving, as a proxy of being active) across individuals' trajectories by fitting a hidden Markov model (HMM; McClintock et al. 2020) and we evaluated, on both open and forested habitats, the effect of environmental temperature on the transition probabilities between the behavioural states throughout the day. Then, we used integrated step selection analysis (iSSA; Avgar et al. 2016) to assess the effect of environmental temperature on giant anteaters' habitat selection across the day, controlling for the effect of environmental temperature, time of day and habitat type on individuals' step lengths and turn angles. Finally, we checked the consistency of our results between males and females.

Given their low body heat production, we expected giant anteaters to show more conspicuous behavioural adjustments at low environmental temperatures than at high ones (McNab 1984). In relation to activity modulation, we expected that decreasing environmental temperatures would lead giant anteaters to decrease activity duration, reducing the daily probability of shifting from encamping to moving (prediction 1), in order to increase heat conservation (Camilo-Alves & Mourão 2005, Di Blanco et al. 2016). Furthermore, with decreasing environmental temperature, their activity should begin and end earlier in the day and should peak earlier, but still at night (prediction 2; Camilo-Alves & Mourão 2005, Mourão & Medri 2007). This way, individuals could expose themselves to the sun in the first hours of activity while maintaining their crepuscular–nocturnal activity period (Camilo-Alves & Mourão 2005, Mourão & Medri 2007). Regarding habitat selection, we expected giant anteaters to select forests during both rest and activity in cold weather (Camilo-Alves & Mourão 2005, Giroux et al. 2021a), while hot and mild weathers would lead to selection for forest areas mainly during resting (prediction 3; Camilo-Alves & Mourão 2005). This is because forests act as thermal shelters during both cold and hot

spells (De Frenne et al. 2019) but also present physical obstacles to movement (Ferrerias 2001, Giroux et al. 2021b). Hence, anteaters should face a trade-off between using forests to deal with thermal discomfort and finding better conditions for foraging in open areas.

Methods

Study Area

We conducted this study in an extensively managed cattle ranch (19°18'9"S, 55°47'4"W) located in the Pantanal wetlands, midwest of Brazil (Fig. 1). The climate is semihumid tropical, with cold fronts causing abrupt drops in temperature during a few days throughout the year (Fig. 2). Air temperatures can exceed 40 °C in the summer and drop to 0 °C in the winter (Alvares et al., 2013). The landscape is naturally fragmented (Fig. 1), composed of a mosaic of semideciduous forests, scrub forests, scrub grasslands and open grasslands partially flooded with permanent and temporary salty and freshwater lakes (Evans & Costa, 2013).

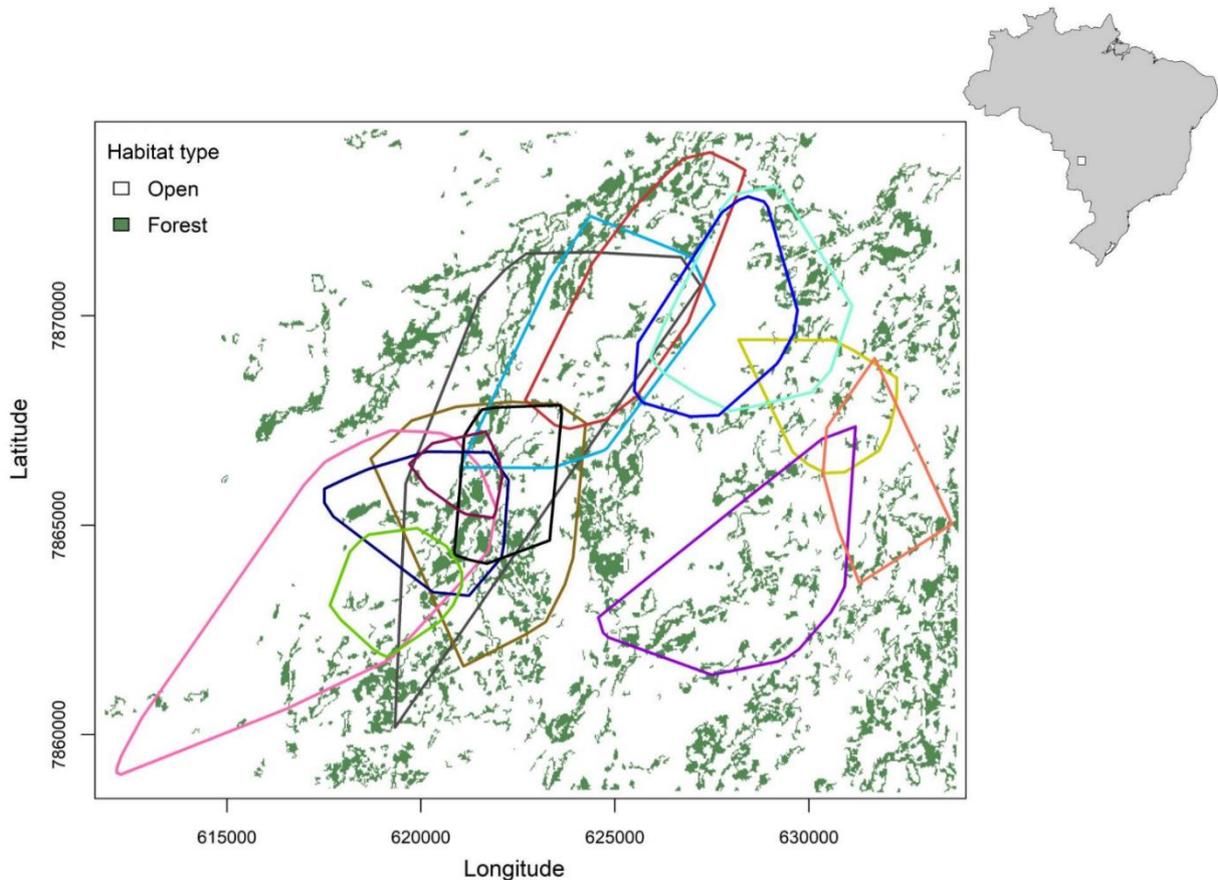


Figure 1. Land-use land-cover (LULC) classification of the study area according to the Mapbiomas database, in the year of 2015. Habitat categories are summarized as open and forested habitats, showing

the naturally fragmented landscape. Each polygon represents the area used by a GPS-tracked giant anteater across the monitoring period. Inset shows a map of Brazil, indicating the study area in the Pantanal wetlands with a white square.

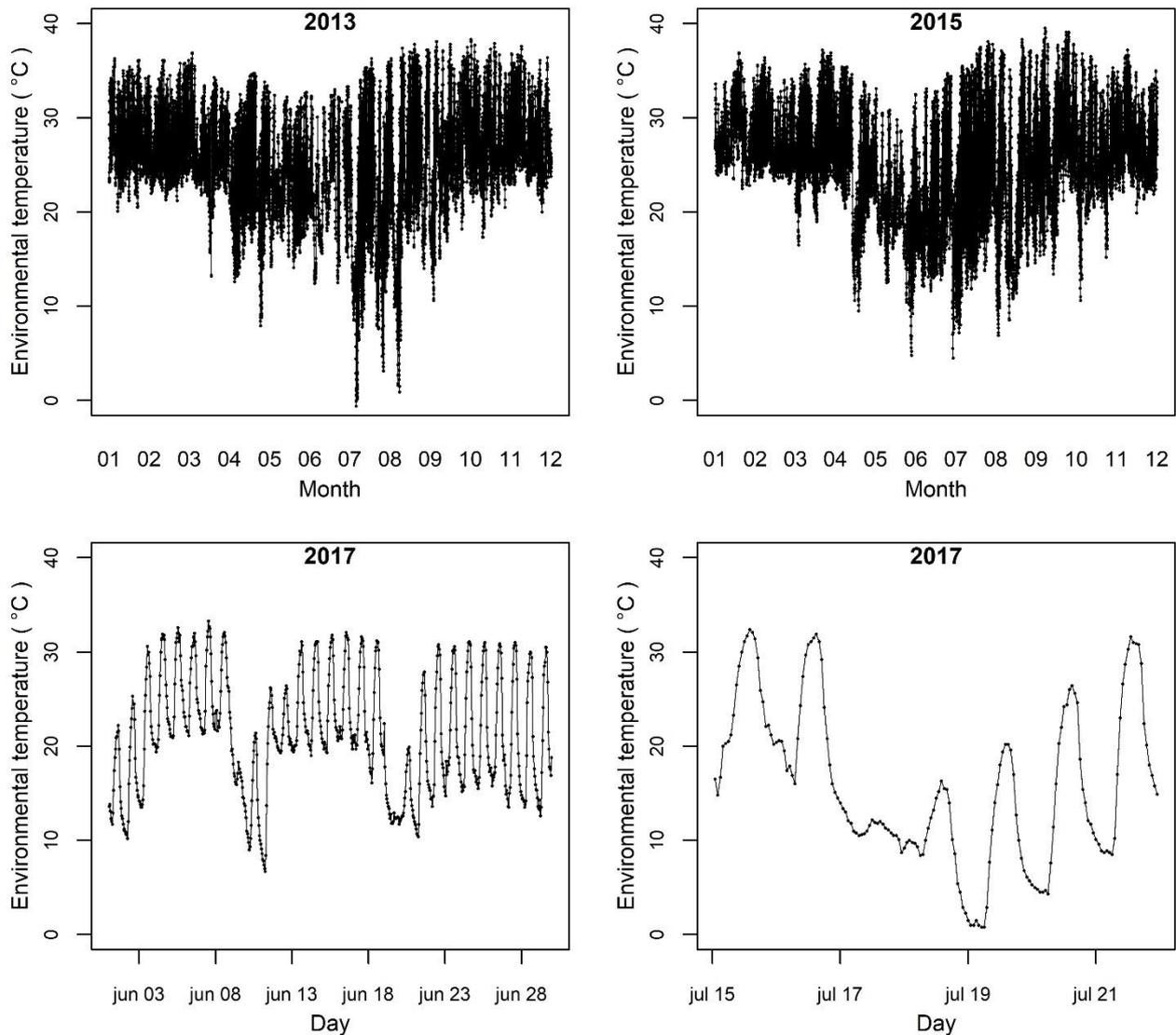


Figure 2. Variogram of the environmental temperature in Pantanal wetlands, Brazil, across the study period. The top graphics show how environmental temperature varied across the years of 2013 and 2015, where it is possible to see abrupt drops in environmental temperature caused by cold fronts. The bottom graphics show in detail the high thermal amplitude of the study area across a month and a week of 2017.

Capture and Movement Data Collection

From 2013 until 2017, we searched for giant anteaters by pick-up trucks at low speed (maximum of 20 km/h) and captured them with long-handled dip-nets. We sedated them following the protocol described

by Kluyber et al. (2021). During anaesthesia, we identified individuals' sex, measured their body mass and evaluated their health condition. We equipped 14 healthy adult giant anteaters (six males and eight females) with a GPS harness (TGW-4570-4 Iridium GPS, Telonics, Mesa, AZ, U.S.A.; Appendix, Fig. 3). We programmed the GPSs to record giant anteaters' geographical locations at fixed intervals varying between 20 and 30 min (Appendix, Table A1). The individual monitoring period varied between 51 and 509 days (mean = 262 days), resulting in a total number of 204 005 locations across 3671 monitoring days (Appendix, Table A1). Capture and tracking procedures did not harm or injure the giant anteaters, and none of the tracking devices exceeded 3% of the animals' body mass. We conducted all procedures in accordance with the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes, 2016). We provide individual information on capture date, sex, body mass, sampling regime and monitoring period in the Appendix Table A1.



Figure 3. Healthy adult giant anteater equipped with a Global Positioning System harness (GPS; TGW-4570-4 Telonics) in Baía das Pedras ranch, Pantanal wetlands, Brazil.

Environmental Data Collection

We recorded the hourly air temperatures provided by a meteorological station of the National Institute of Meteorology of Brazil (INMET) throughout the whole monitoring period so we could determine the

environmental temperature associated with all individuals' locations. The meteorological station was located 85 km from the center of the study area. The difference between the mean altitude of the study area and the altitude of the meteorological station was 38 m. To verify that the meteorological station provided a good representation of the macroclimate of our study area, we checked the correlation between environmental temperatures recorded by two meteorological stations 110 km apart from each other and differing 40 m on altitude, both located on the Pantanal wetlands, and we found a strong positive correlation (Pearson correlation: $r = 0.89$; Figure 4). During the monitoring period, mean environmental temperature was 22.5 °C, showing an approximately normal distribution ranging from 0.8 °C to 40.2 °C (Figure 5; see details on the environmental temperatures experienced by each individual in Appendix Table A2).

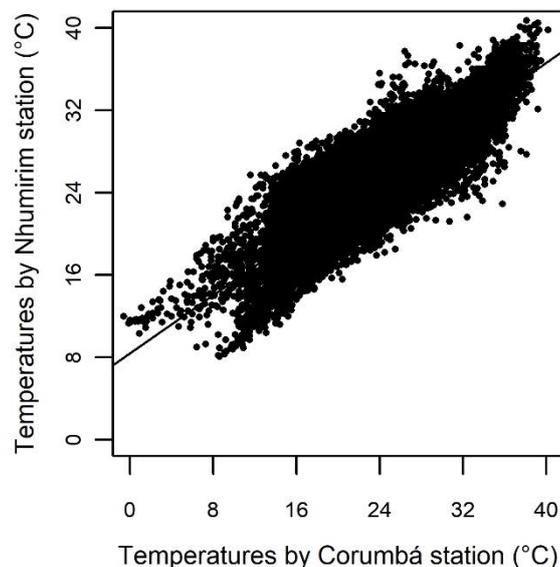


Figure 4. Relationship between temperature measurements of two meteorological stations 110 km apart from each other and differing 40 m on altitude, both located in Pantanal wetlands, Brazil

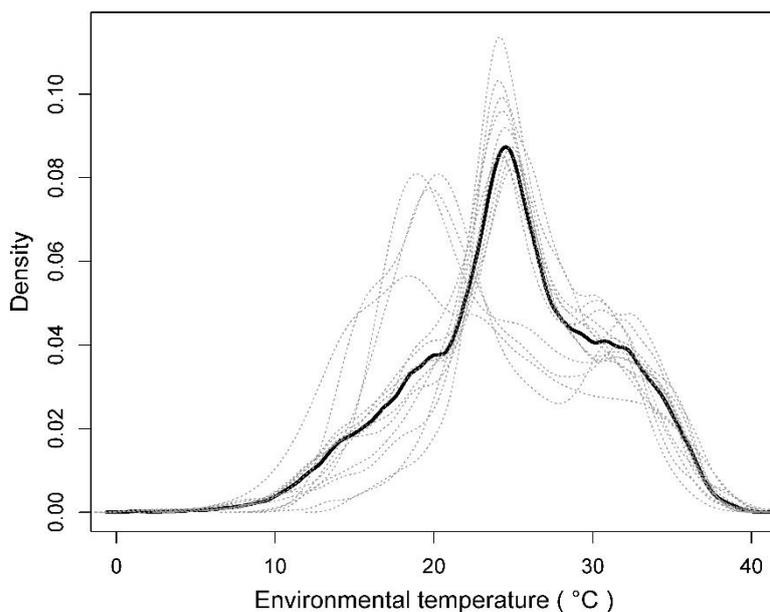


Figure 5. Density distribution of environmental temperatures experienced by each individual (dashed lines) and by the population (continuous line) in the study area across the monitoring period.

We used the land use–land cover (LULC) classification from MapBiomas (Collection 5, LULC classification with 30×30 m pixels, <https://mapbiomas.org>). We summarized the landscape into two categories: open areas (scrub grasslands, open grasslands, and areas without vegetation cover) and forests (semideciduous forests and scrub forests). Of our study area, 88% corresponded to open areas and 12% to forests (Fig. 1). We also identified the habitat type associated with all individuals' locations. On average, 32% of the locations occurred in forest areas, varying from 10.8% to 55.1% across individuals (Appendix, Table A2). Our classification intended to identify as forests the areas with some thermal buffering capacity in comparison to adjacent open areas (De Frenne et al. 2019). However, we recognize that such complex landscapes could offer other thermal buffering opportunities that we could not map, such as shadows of isolated trees, very tall grasses, and flooded grasses (e.g., Milling et al. 2018; Verzuh et al. 2021). We performed map processing using the 'raster' R package (Hijmans et al. 2014, R Core Team 2019).

Movement Data Preprocessing

Movement data need to fulfil some fundamental requirements to be suitable for both HMM and iSSA: the data should provide a reliable representation of animal movement and the measurement error in positions should be negligible (Patterson et al. 2017). To meet these requirements, we preprocessed the movement data using the R package 'adehabitatLT' (Calenge 2006). We removed the first two monitoring days to exclude the potential capture and handling effects on animal behavior. Then, we removed the top 5% of steps with highest velocities since these abnormally fast steps are unrealistic and commonly associated with GPS reception failures (see Patterson et al. 2017).

Another important requirement for both HMM and iSSA is that the sampling rate should be regular (Patterson et al. 2017). However, some GPS failures produced monitoring gaps much longer than the sampling interval, making it necessary for some additional data preprocessing. HMM uses continuous trajectories as input, and its Markovian dependency structure assumes that the trajectories are independent of each other, not allowing for multiple trajectory bursts from the same individual (see McClintock & Michelot 2020). Because of this, we decided to use in HMM the largest portion of each

individual's trajectory whose sampling rate was regular (standard deviation <10 min) for at least 99.9% of locations. We individually selected these regular trajectory portions using the R package 'adehabitatLT' (Calenge 2006). On the other hand, iSSA uses trajectory steps (i.e., the straight line between two consecutive locations) as input and does not require continuity between them (see Signer et al. 2019). Thus, for iSSA, we split each individual trajectory in several bursts whose sampling rate ranged from 15 to 35 min, allowing for some tolerance around the mean sampling rate (i.e., 25 min). We split the trajectories using the R package 'AMT' (Signer et al. 2019). The movement data preprocessing resulted in the elimination of 7.4% and 3.4% of locations for HMM and iSSA, respectively (Table A3).

Finally, because both HMM and iSSA are not defined when step length is zero (0.25% of our observations), we set the length of these steps to the smallest nonzero distance that was recorded (i.e., 1 m). This procedure was performed along HMM and iSSA, respectively using the R packages 'momentuHMM' and 'AMT' (Signer et al. 2019, McClintock & Michelot 2020). Taken together,

Hidden Markov Model

We used HMM to understand whether and how giant anteaters modulate activity duration and activity period in response to environmental temperature changes (i.e., to evaluate predictions 1 and 2; see McClintock et al. 2020). By modelling the movement data as correlated random walks, HMM enables the estimation of latent behavioural states (McClintock et al. 2012). We modelled the transition probability between behavioural states in response to environmental temperature throughout the time of day on both open and forested habitats (e.g., Patterson et al. 2009, see details below).

For the HMM, we considered the observed time series movement data as a bivariate state described by two movement variables: step length and turning angle (see also Morales et al 2004, McClintock et al. 2012). We calculated step length as the Euclidean distance between successive relocations and turning angle as the change in bearing between steps. We characterized each behavioural state using the state-dependent probability distribution of step lengths (assuming a gamma distribution) and turning angles (assuming a von Mises distribution). We assumed two biologically meaningful behavioural states: encamping and moving (see Pohle et al. 2017). The encamping state (proxy of

resting) was expected to be described by shorter step lengths (slower displacement) with wide turning angles (little to no directional persistence), and the moving state (proxy of active) was expected to be described by longer step lengths (faster displacement) with small turning angles (high directional persistence; Morales et al. 2004, McClintock et al. 2012).

The HMM was fitted by numerical maximization of the likelihood function (MacDonald & Zucchini 2016) using the ‘momentuHMM’ R package (McClintock & Michelot 2020). We provided a set of biologically realistic initial parameter values of steps length and turning angle distributions, as required by the numerical optimizer. We based the initial parameters on the observed mean and standard deviation of step lengths and on the observed mean and variance of turning angles. Once we fitted the model, we used the Viterbi algorithm to predict the most likely sequence of behavioural states, i.e., to attribute a behavioural state to each observed step (Langrock et al. 2012, MacDonald & Zucchini 2016). This way, we could visually distinguish the behavioural states on each individual trajectory and visually check for potential misclassifications, since we expected that encamping would coincide with spatially aggregated points and that moving would coincide with dispersed points.

As part of the HMM framework, we used a logit link to model the transition probabilities between behavioural states as a function of environmental temperature, time of day, habitat used (open versus forest) and the possible interactions between these variables (MacDonald & Zucchini 2016). We included time of day as a circular covariate (over 24 h periods) using a trigonometric link function (‘cosine’ function; Leos-Barajas et al. 2017). We determined whether it was possible to statistically discern the effect of covariates on transition probabilities between behavioural states based on whether the 95% confidence intervals (CIs) of the beta parameters overlapped zero (Patterson et al. 2017). To better visualize the covariate effects, we plotted their influence on the behavioural states’ stationary probability, which represents the equilibrium of the Markov process (Patterson et al. 2009).

We accounted for individual heterogeneity in movement and state-switching dynamics as a random effect (see McClintock 2021). We examined the goodness of fit of the model by assessing quantile–quantile plots, pseudo-residual plots and autocorrelation plots (Patterson et al. 2017). We

checked the consistency of our results by separately running two additional models, identical to the model described above, but with one using only females' movement data and another using only males' movement data.

Integrated Step Selection Analysis

We used iSSA to understand whether and how environmental temperature influences giant anteater habitat selection across the day (i.e., to evaluate prediction 3). The iSSA is a model that compares the habitat used by the individuals whenever they perform a step to the available habitats at alternative locations that the individuals could have reached in alternative steps (Thurfjell et al. 2014, Avgar et al. 2016). This analysis allows to determine whether a habitat type was used more frequently than expected given its availability (i.e., selected), used less frequently than expected given its availability (i.e. avoided) or used as available. We performed the iSSA using the 'amt' R package (Signer et al. 2019).

For each observed step, we randomly created 30 alternative steps by drawing step lengths from a gamma distribution and turning angles from a von Mises distribution (Fortin et al. 2005). Both distributions were fitted by maximum likelihood to the values of step length and turning angle observed in the individuals' original trajectory (Fortin et al. 2005). Despite this empirical parametrization, it is still challenging to create a good representation of available habitats using alternative steps when the animals could travel faster and more directionally in certain environmental conditions (e.g. more permeable landscapes) than others (Forester et al. 2009, Avgar et al. 2016). To account for this, iSSA assumes that animal movement can be represented by a separable model, the product of two kernels: a habitat-independent movement kernel (a function governing movement in the absence of habitat selection) and a habitat selection kernel (Avgar et al. 2016, Signer et al. 2019).

The available habitats at alternative steps (scored as 0) were compared with the habitat used in the observed step (scored as 1) at each step performed by each individual using a conditional logistic regression (CLR; Fortin et al. 2005). We relied on a CLR because the response variable is binary (used or available habitat) and 'conditional', because it is conditioned to each step of each individual. We simultaneously estimated the effect of environmental temperature, time of day and habitat type (open

versus forest) on individuals' movements (allowing the interaction of these variables with step length and turning angle) and on habitat selection. We extracted the covariate values from the end of each step since we were mainly interested in how environmental temperature influences individuals' decision making about where to go across the time of the day (see Avgar et al. 2016). We included time of day as a trigonometric harmonic to respect the circular nature of circadian time (cosine ($\text{hour}/24 \times 2 \times \pi$); Signer et al. 2019). Finally, we evaluated the lower and upper confidence intervals of the estimates to determine the significance of the effects, and we checked the consistency of our results between individuals' sex.

Results

Hidden Markov Model

The two behavioural states were well differentiated by HMM, since the confidence intervals for their attributes did not overlap (Fig. 6, Table 1). As expected, one of the states (encamping) presented shorter step lengths and very wide turning angles (i.e., slow undirected movement), while the other one (moving) was characterized by longer step lengths and turning angles concentrated at zero (i.e., fast directed movement; Fig. 6, Table 1). On average, 53% of individual location points corresponded to the moving state, varying from 21% to 65% among individuals.

Table 1. Estimates and 95% confidence intervals of the parameters that describe each giant anteater behavioral state (*Myrmecophaga tridactyla*; encamping and moving). Step lengths were modeled with gamma distribution, and turning angles were modeled with von Mises distribution.

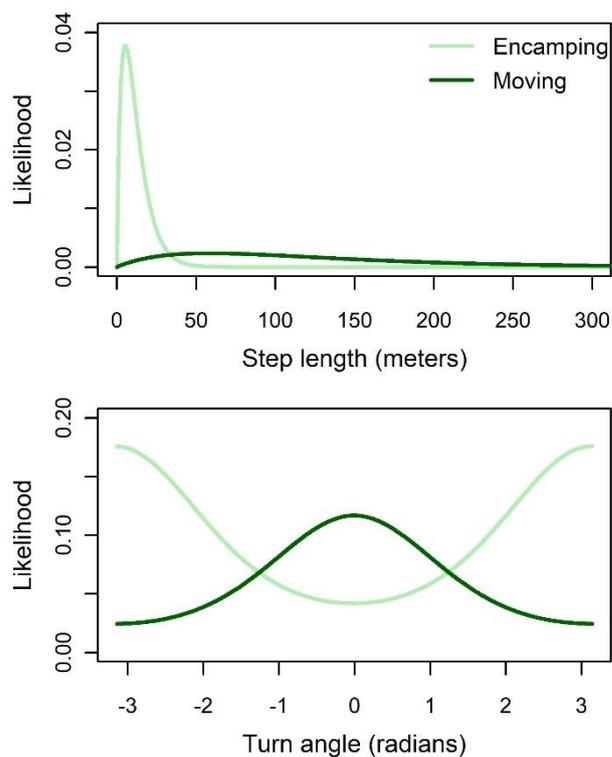


Figure 6. Probability distribution of observed step lengths and turning angles of giant anteaters at two behavioral states (encamping and moving).

Estimated parameter	Encamping	Moving
Step length mean (meters)	11.74 (11.67; 11.80)	121.63 (120.94; 122.32)
Step length SD (meters)	8.69 (8.62; 8.75)	87.45 (86.78; 88.11)
turning angle mean (radians)	3.13 (3.11; 3.14)	- 0.01 (- 0.02; 0.01)
turning angle concentration (radians)	0.72 (0.71; 0.73)	0.78 (0.77; 0.79)

The transition probabilities between giant anteaters' behavioural states were influenced by the interaction between environmental temperature, time of day and habitat used (Table 2). As environmental temperature decreased, giant anteaters decreased overall probability of moving and showed a progressively earlier peak probability of moving (i.e., they decreased activity duration and increased diurnality). Both these effects were observed in open and forested habitats. As an example, when temperatures were high (i.e., 30 °C), giant anteaters varied their

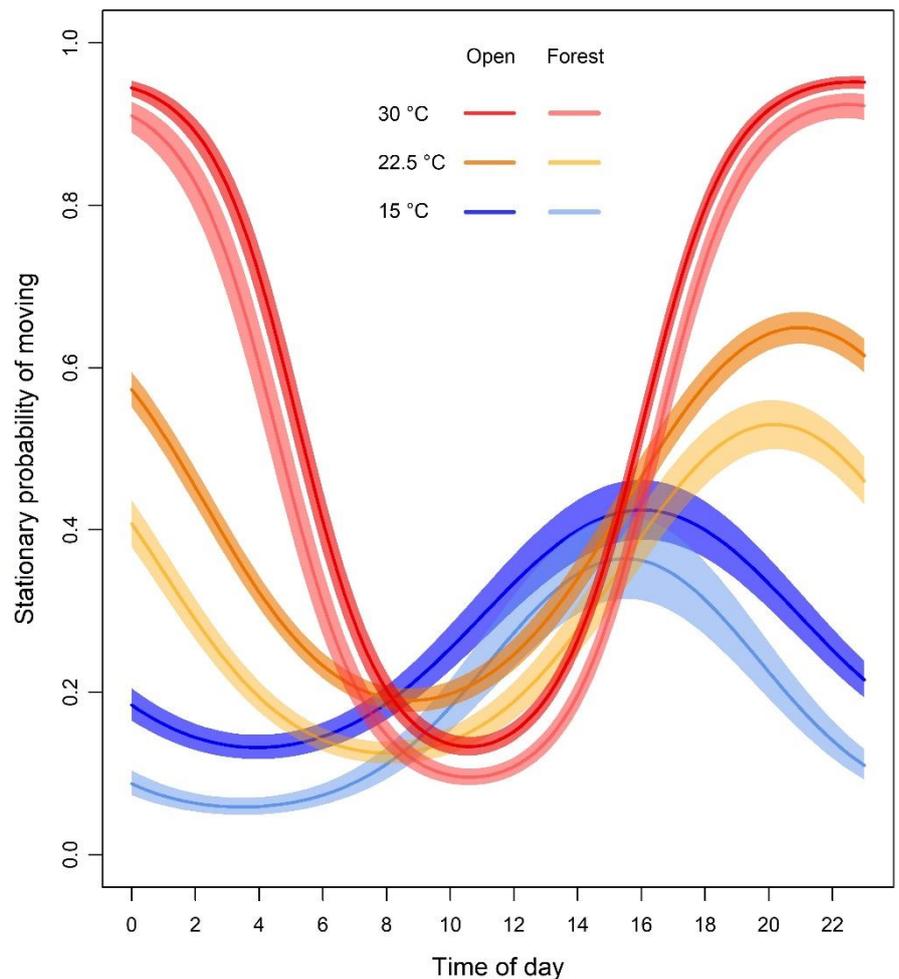


Figure 7. Stationary probability of moving of giant anteaters as a function of the time of day under three temperature conditions (cold [15 °C], mild [22.5 °C], and hot [30 °C]) and in two habitats types (open areas, darker colors, and forests, lighter colors). 15 °C and 30 °C respectively represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C). The colored bands represent 95% confidence intervals.

probability of moving between 10% and 95% throughout the day and they were mostly nocturnal, with higher probability of moving between 20 and 2 hours (Fig. 7). In contrast, when temperatures were low (i.e., 15 °C), giant anteaters varied their probability of moving from 5% to 45% throughout the day and they were diurnal, presenting higher probability of moving between 13 and 17 hours. Meanwhile, at mild temperatures (i.e., 22.5 °C), they showed an intermediate overall probability of moving and were also nocturnal, with activity peak between 19 hours and midnight (Fig. 7). The high short-term thermal amplitude of the study area (Fig. 2) indicates that giant anteaters' activity adjustments in response to environmental temperature changes should happen on a scale of days (see Fig. 8 as an example).

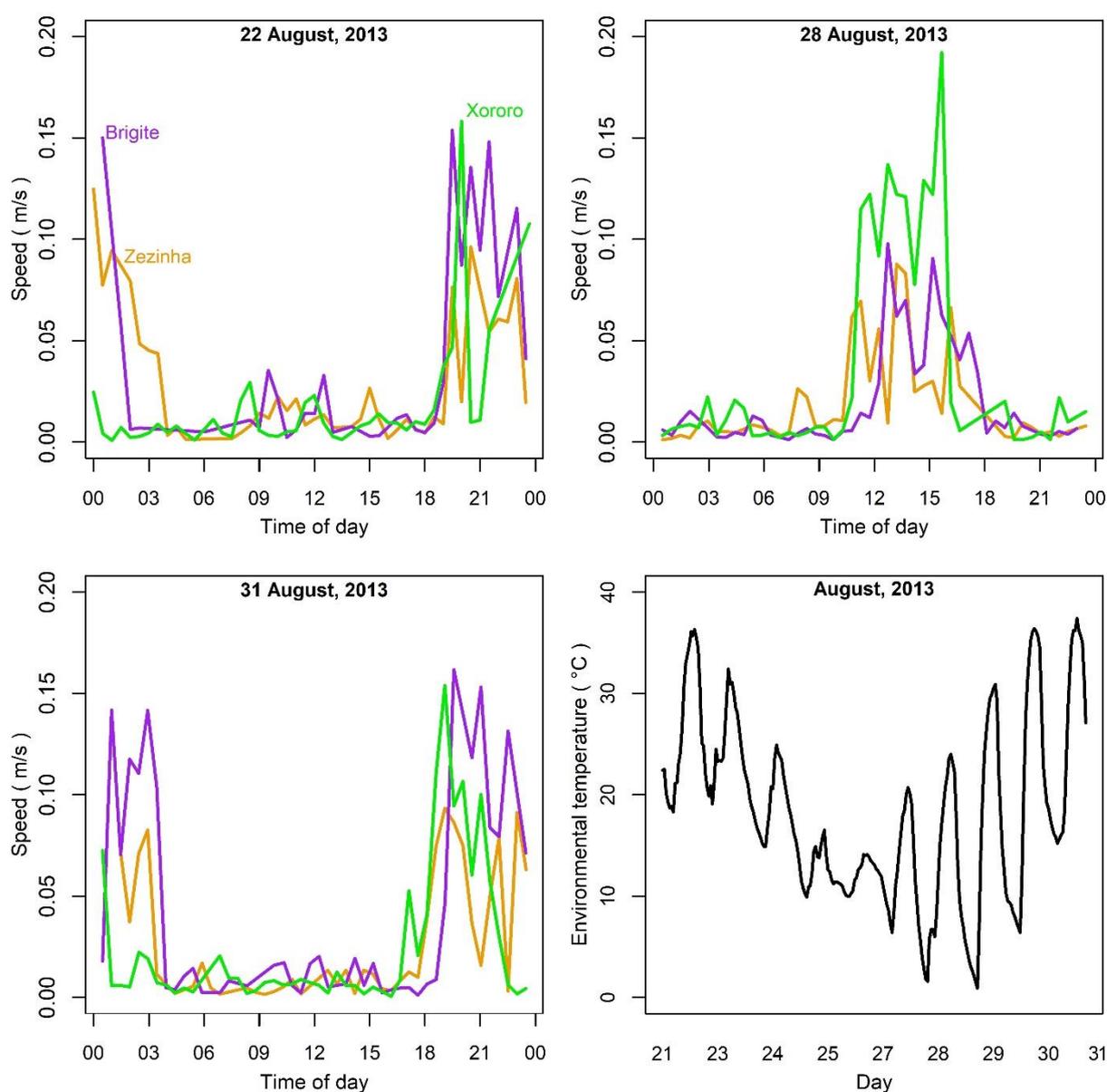


Figure 8. Giant anteaters speed (meters/second) across time of day on 22, 28 and 31 August 2013, as well as the variogram of the environmental temperature in the study site in this period. The three

individuals monitored in this period (Brigite, Zezinha, and Xororo were nocturnal on 22 August, when it was hot, diurnal on 28 August, when it was cold, and then nocturnal on 31 August, when it got hot again. This example shows that giant anteaters can switch activity period from nocturnal to diurnal and vice-versa in a scale of days as a response to abrupt drops in environmental temperature.

The effect of habitat type on the giant anteaters' probability of moving depended on environmental temperature and time of day, as indicated by the significant interaction coefficients (Table 2). However, the direction of this effect was consistent across the conditions experienced by the individuals. Regardless of environmental temperature and time of day, giant anteaters presented a higher probability of moving (i.e., being active) in open areas, and, consequently, a higher probability of encamping (i.e., resting) in forests (Table 2, Fig. 7). Besides, the influence of the interaction between environmental temperature, time of day and habitat used on giant anteaters' probability of moving was similar between males and females (see Appendix Fig. A1).

Table 2. Estimates (95% CI) of the effect of environmental temperature, time of day, and habitat type (open and forest; using open as the reference category), and their interactions, on transition probabilities between giant anteater behavioral states. The significant effects are represented in bold.

Covariate	Estimated effect (95% CI)	
	encamping to moving	moving to encamping
Temperature	0.001 (0.001; 0.001)	-0.002 (-0.002; -0.002)
Time of day	-0.892 (-1.012; -0.771)	0.466 (0.353; 0.580)
Habitat	-0.614 (-0.825; -0.403)	0.072 (-1.246; 0.270)
Temperature * time of day	0.002 (0.002; 0.002)	-0.002 (-0.002; -0.002)
Temperature * habitat	0.001 (0.001; 0.001)	0.001 (0.001; 0.001)
Habitat * time of day	-0.300 (-0.344; -0.255)	0.130 (0.062; 0.198)
Temperature * time of day * habitat	0.001 (0.001; 0.001)	0.001 (0.001; 0.001)

Integrated Step Selection Analysis

The iSSA suggested that giant anteaters' step lengths and turning angles are influenced by the interaction

between environmental temperature, time of day and habitat used (Figs 9, 10, Appendix Table A4). Decreasing environmental temperature led animals to increase step lengths and decrease turning angles at daylight, as well as decrease step lengths and increase turning angles during night, indicating an increase in diurnal activity and nocturnal rest. These effects could be observed on both habitat types. For example, at 30 °C, giant anteaters were faster and more directional at midnight, compared with noon. In contrast, at 15 °C, the animals were faster and more directional at noon than at midnight (Figs 9, 10).

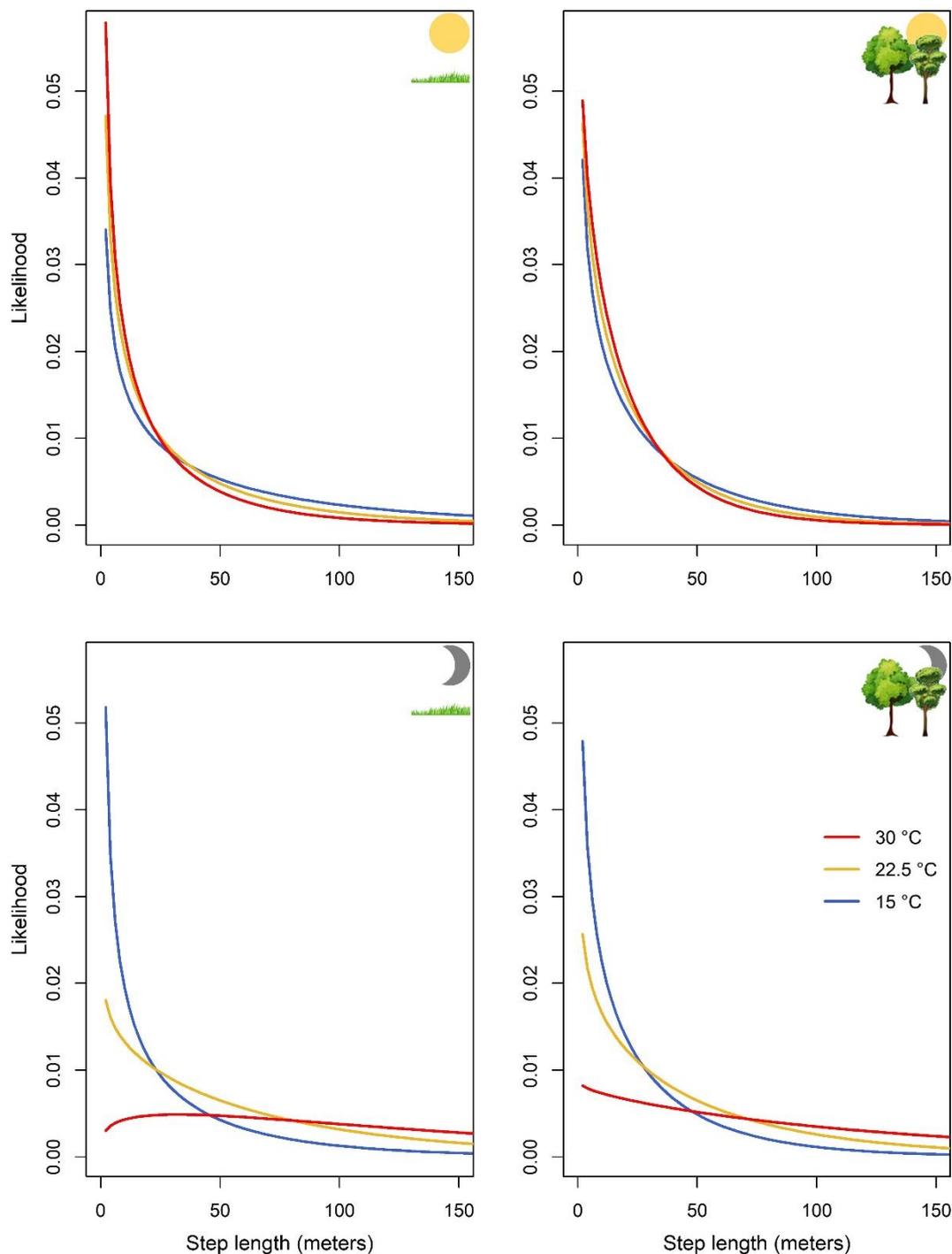


Figure 9. Probability distribution of giant anteaters' step lengths under three temperature conditions

(cold [15 °C], mild [22.5 °C], and hot [30 °C]), at two times of the day (noon above and middle night bellow), and in two habitat types (open areas, left, and forests, right). 15 °C and 30 °C respectively represent 1.25 standard deviations below and above the mean environmental temperature experienced by the individuals (22.5 °C).

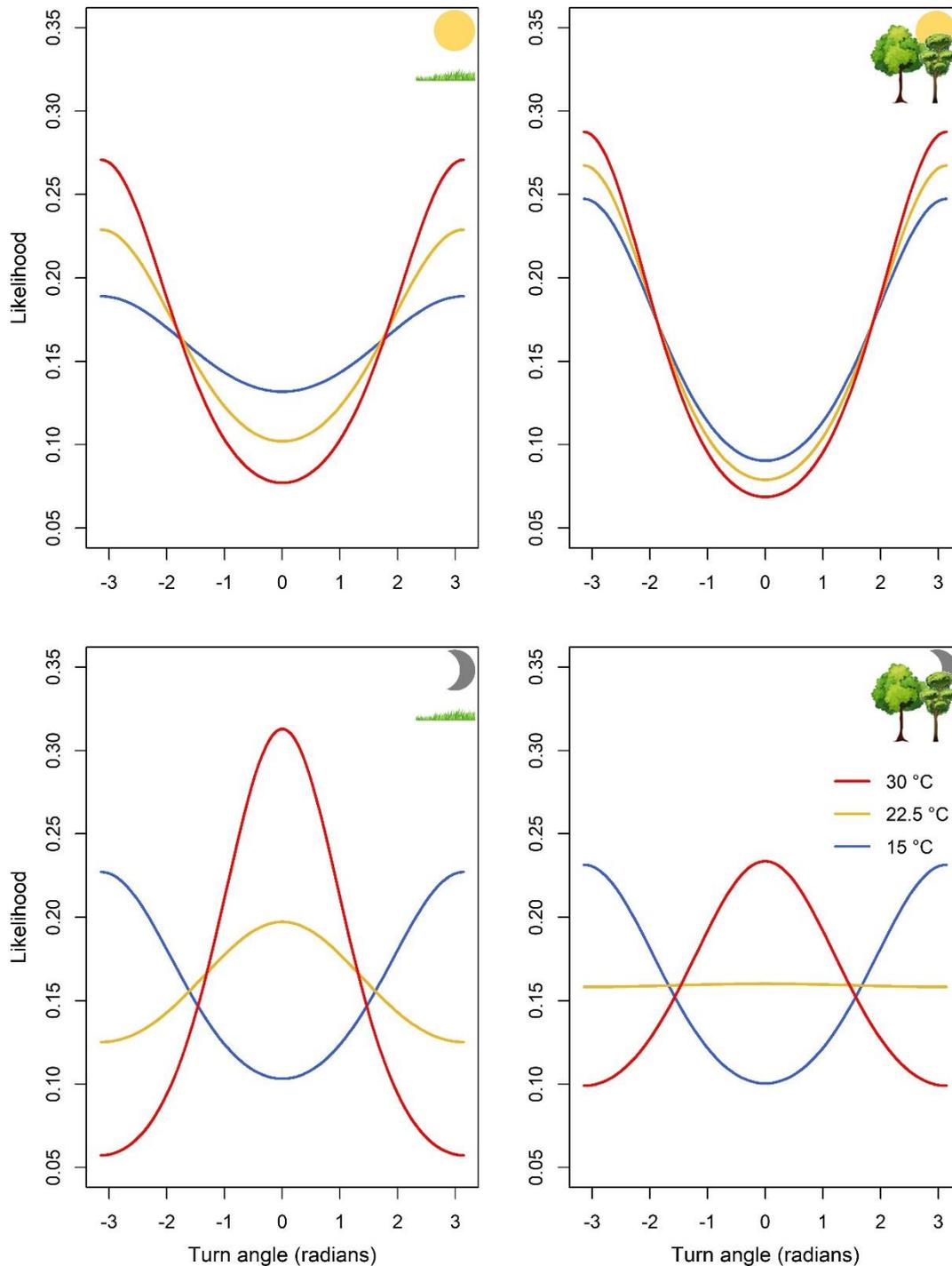


Figure 10. Probability distribution of giant anteaters' turning angles under three temperature conditions (cold [15 °C], mild [22.5 °C], and hot [30 °C]), at two times of the day (noon above and midnight bellow), and on two habitat types (open areas, left, and forests, right). 15 °C and 30 °C respectively

represent 1.25 standard deviations below and above the mean environmental temperature (22.5 °C).

The effect of the habitat type on individuals' step lengths and turning angles depended on environmental temperature and time of day (see significant interaction coefficients in the Appendix Table A4). However, note that, regardless of environmental temperature and time of day, the animals presented longer step lengths and smaller turning angles in open areas than in forests (Figs 9, 10), reinforcing that giant anteaters tend to be active in open areas and to rest in forests.

Controlling for the effect of the environmental covariates on giant anteater movements (see Figs 9, 10, Appendix Table A4), the iSSA showed that the interaction between environmental temperature and time of day modulated the selection strength for forests, relative to open habitats (Table 3, Fig. 11). With increasing environmental temperature, giant anteaters increased selection for forests during daylight and reduced selection for forests at night. Interestingly, as environmental temperature decreased, individuals showed the opposite pattern, increasing selection for forests at night and reducing it during daylight (Table 3, Fig. 11). For instance, at 30 °C, giant anteaters selected forests between 9 and 15 hours (with a selection peak at noon), but strongly avoided forests for most of the day, with a peak of avoidance at midnight (Fig. 11). In contrast, at 15 °C, they selected forests between 18 and 6 hours, with peak of selection at midnight and peak of avoidance at noon. At 22.5 °C, the individuals used forests as available between 9 and 15 hours, avoiding them during most of the daytime. Males and females presented similar responses (Appendix, Fig. A2).

Table 3. Estimates (95% CI) of the effect of environmental temperature, time of day, and habitat type (open areas, as the reference category, and forests), and their interactions on giant anteaters' habitat selection. The significant effects are represented in bold.

Covariate	Estimated effect (95% CI)	p value
habitat	-0.247 (-0.256; -0.157)	0.006
habitat * temperature	-0.020 (-0.023; -0.017)	<10⁻⁸
habitat * time of day	1.183 (1.056; 1.310)	<10⁻¹⁶
Habitat * temperature * time of day	-0.064 (-0.069; -0.059)	<10⁻¹⁶

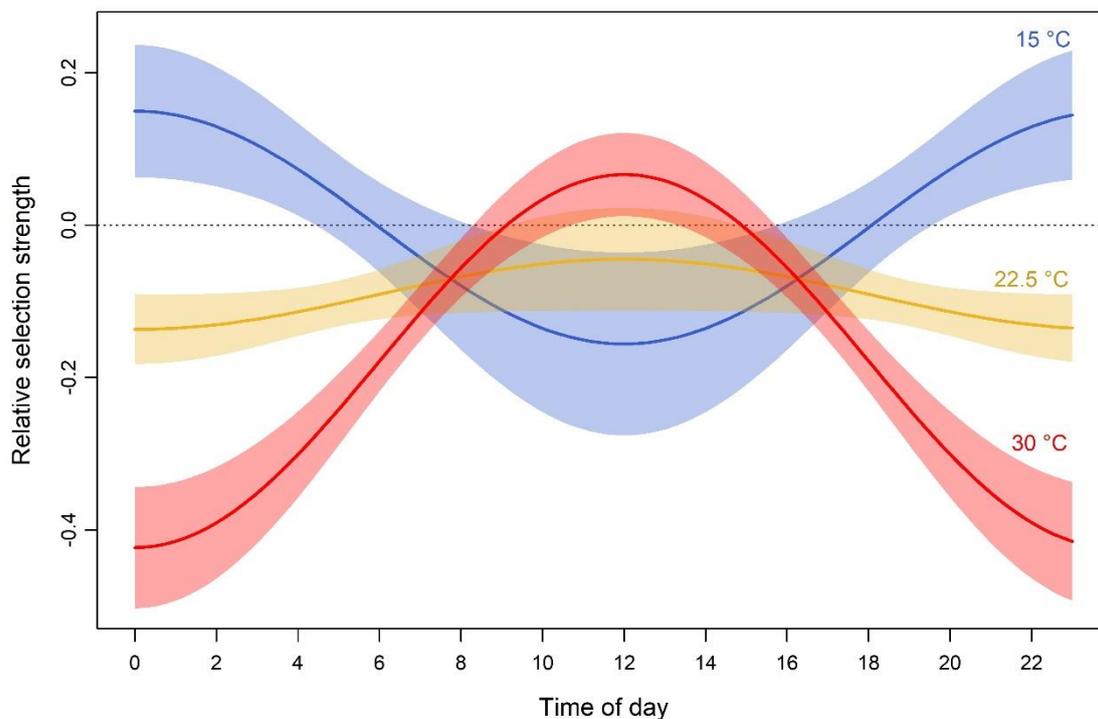


Figure 11. Selection strength of giant anteaters for forests, relative to open habitats, as a function of time of day on three environmental temperatures (cold [15 °C], mild [22.5 °C], and hot [30 °C]). The colored bands represent the 95% confidence intervals. 15 °C and 30 °C respectively represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C).

Discussion

We evaluated long-term fine-scale movement data of giant anteaters in a well-preserved naturally fragmented landscape under a wide variety of environmental temperatures. We used powerful statistical models to uncover how environmental temperature influences individuals' activity patterns and habitat selection. HMM allowed us to understand the effect of environmental temperature on individuals' activity duration and activity period in both open and forested habitats (McClintock et al. 2020). The iSSA made it possible to understand how complex interactions between environmental temperature, habitat type and time of day influence individuals' step lengths and turning angles, confirming HMM results and adding insights to giant anteater movements (Avgar et al. 2016). Importantly, iSSA allowed us to investigate how the effect of environmental temperature on giant anteaters' habitat selection changes throughout the day (Avgar et al. 2016, see Richter et al. 2020). With these powerful tools, we

were able to identify the high behavioural plasticity of giant anteaters in response to environmental temperature fluctuations. Finally, our results for males and females were very similar, indicating that environmental temperature is an important driver for movement strategies of both sexes.

With decreasing environmental temperature, giant anteaters reduced daily activity duration regardless of the habitat used, which indicates that they increased rest time, as we expected in prediction 1. This is because, as a behavioural strategy to offset the low production of body heat and keep their bodies warm, giant anteaters lie down and cover themselves with their long furry tail, which reduces their thermal conductance, but also prevents their movement (McNab 1984, Medri & Mourão 2005). In accordance, previous studies showed giant anteaters reducing activity duration, distance moved, and area used with decreasing temperature (Camilo-Alves & Mourão 2005, Di Blanco et al. 2016, Giroux et al. 2021a). Other mammals have also been reported decreasing daily activity duration in response to decreasing environmental temperature (Evans et al. 2016, Hume et al. 2020, Tatler et al. 2021), including members of superorder Xenarthra (Attias et al. 2018). Staying still displaying heat-conserving postures is a common strategy used by mammals to cope with low environmental temperatures (Terrien et al. 2011). However, by reducing locomotor activity, animals compromise foraging behavior, and, consequently, energy intake (Abrahms et al. 2021). Therefore, long periods of low environmental temperatures could lead mammals to energetic deficit, reducing individuals' performance and fitness (Mota-Rojas et al. 2021).

As a second strategy to face decreasing environmental temperature in both open and forested habitats, giant anteaters increased diurnality, as expected based on prediction 2. Surprisingly, we found that giant anteaters were capable of completely switching their activity period, from nocturnal on warm and mild days to diurnal on cold days. When moving, many mammals increase heat exchange by exposing a larger body surface to the environment, contrasting with their resting period when they can display tight, closed body postures for heat conservancy (Mota-Rojas et al. 2021). Thus, selecting daylight hours to move increases heat gain by solar radiation, which is an advantage at low temperatures (e.g., van der Vinne et al. 2014, Attias et al. 2018). Similarly, mammal species have been recorded

increasing their nocturnality to deal with weather warming (Davimes et al. 2017, Levy et al. 2019). The search for times with milder temperatures to be active can also lead mammals to seasonally switch activity period, from diurnal in winter to crepuscular/nocturnal in summer (Finn et al. 2022). However, completely shifting the activity period from nocturnal to diurnal or vice versa on a scale of days demands high short-term behavioural plasticity, an uncommon phenomenon for mammals and, to our knowledge, a result never observed in giant anteaters (see Camilo-Alves & Mourão 2005, Mourão & Medri 2007, Di Blanco et al. 2016). As this species has a low production of body heat (McNab 1984), and environmental temperature may drop suddenly in the Pantanal due to cold fronts, this short-term behavioural response can be an efficient energetic strategy for them.

Forests played a fundamental role as thermal shelters for giant anteaters, being selected for rest in cold and hot weather, but not in mild weather (partially agreeing with prediction 3). Giant anteaters increased selection for forests during daylight when it was hot whereas they increased selection for this habitat at night when it was cold. The use of thermal shelters reduces the thermal difference between the animals' bodies and the environment, reducing heat exchange (De Frenne et al. 2019). This behaviour helps maintain individuals' body temperature within optimal levels as environmental temperatures deviate from their TNZ (Mota-Rojas et al. 2021). However, when the habitat used as thermal shelter does not coincide with the one that is usually used for foraging, animals must choose between food resource acquisition and thermoregulation. In this case, thermal shelters will be selected mainly for resting, which is the case in the giant anteater (also see Haase et al. 2020, Verzuh et al. 2021). It is worth noting that the daily mean selection for forests was smaller at high environmental temperatures (also see Giroux et al. 2021a). Nevertheless, throughout the hours of the day, positive coefficients of selection for forests were observed at low and high environmental temperatures, but not at mild ones. This result highlights the importance of considering fine-scale temporal dynamics to understand habitat selection (see Richter et al. 2020). Giant anteaters probably show the highest selection for forests in the cold due to their low capacity for body heat production, but they also select forests to avoid overheating at high temperatures. In mild weather, they behave like a typical open-area mammal all day long, avoiding forest

or, at most, using it as available during rest.

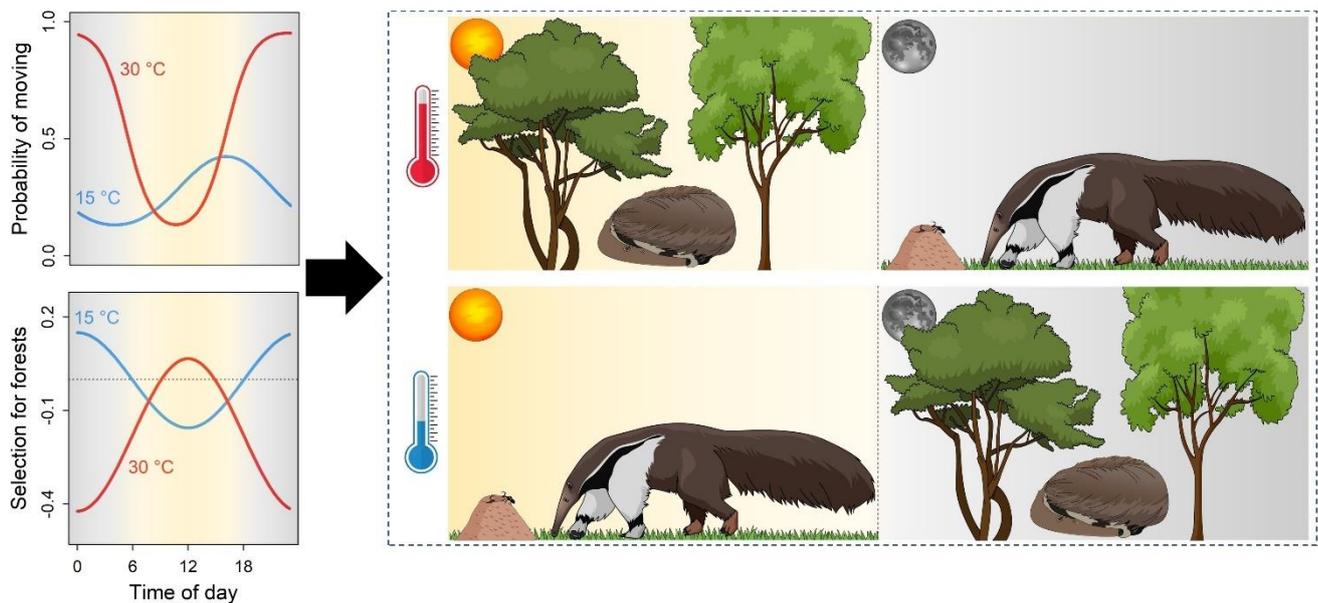
Our work suggests that reducing availability of forest patches in heterogeneous landscapes would compromise giant anteater's thermoregulation. Similarly to giant anteaters, many other open-area mammals living in heterogeneous landscapes increase selection for forests as environmental temperature deviates from their TNZ (e.g., Ewald et al. 2014, Marchand et al. 2014, Street et al. 2015), even when forests are not their preferred habitat to forage (e.g., Street et al. 2016). This is because forests act as thermal shelters for both cold and hot weather, not only offering milder temperatures than adjacent open areas, but also offering protection against rain, chilly winds, and solar radiation (De Frenne et al. 2019). Based on predictions of increasing frequency and intensity of extreme cold and hot weather events (IPCC 2021), we expect open-area mammals to increase demand for forest patches as thermal shelters, especially on hot days and cold nights. Therefore, the rapid and intense global loss of forests and its consequences for wildlife are worrisome (De Frenne et al. 2021, Giroux et al. 2021b). In the Brazilian territory, where this study was conducted, massive agricultural expansion has caused extensive habitat degradation and dramatically decreased forest patches on savannah areas, both in number and size (Reynolds et al. 2016, Tollefson 2018). Under this current deforestation scenario, the opportunities that the landscape offers for mammals' behavioural thermoregulation are decreasing while extreme weather events are becoming more frequent (De Frenne et al. 2021).

Conclusion

We combined two powerful statistical models to understand how environmental temperature modulates the movement decisions of a large mammal. Due to their low capacity for physiological thermoregulation, giant anteaters conspicuously responded to environmental temperature variations. Besides being relevant for monitoring and understanding giant anteater behavior, this work provides insights into how other mammals might respond to climate changes. To deal with thermal discomfort, giant anteaters showed three important behavioural thermoregulatory strategies: they modulated activity duration, shifted activity period, and increased selection for forests (Fig. 12). The long-term impact of these behavioural adjustments on individuals, populations and communities is still unknown and should

be the focus of future studies. We highlight that, despite their high behavioural plasticity regarding activity, giant anteaters still need forests as thermal shelters. Therefore, we make it clear that forest conservation should be increasingly prioritized as we face climate changes and effective management efforts must consider the indispensability of forests for animal thermoregulation.

Activity modulation and selection for forests as behavioral thermoregulatory mechanisms



Forests act as thermal shelters, providing thermoregulation opportunities to face climate change

Figure 12. Take-home illustration showing how giant anteaters adjust their activity and selection for forests to deal with temperature changes.

Appendix

Table A1. Individual characteristics of the captured giant anteaters (*Myrmecophaga tridactyla*) as well as monitoring effort and sampling regime.

Id	Capture date	Sex	Body mass (kg)	Sampling regime (min)	Monitoring period (days)
Annie	06/20/2015	F	30.0	20	84.0
Berenice	10/25/2015	F	39.0	20	386.0
Brigite	07/31/2013	F	26.3	30	339.7
Buba	07/08/2015	F	30.0	20	69.1
Henriqueta	08/15/2014	F	28.1	20	159.9
Justin	05/31/2016	M	30.0	20	144.7
Kiko	10/25/2015	M	35.0	20	363.2
Lubetta	06/19/2015	F	28.0	20	51.0
Mariah	09/26/2016	F	33.3	20	122.4
Pdg	06/18/2015	M	36.0	20	509.7
Xororo	07/25/2013	M	37.2	30	387.8
Zezipha	07/27/2013	F	35.0	30	279.8
Fergus	07/01/2016	M	35.0	20	378.0
Jacques	07/31/2016	M	25.0	20	366.7

Table A2. Weather and habitat conditions experienced by the giant anteaters (*Myrmecophaga tridactyla*) across their monitoring period.

Id	Environmental temperature (median)	Environmental temperature (range)	Forest use
Annie	22.6 °C	11.6 °C - 36.0 °C	35.8%
Berenice	22.1 °C	4.5 °C - 39.5 °C	55.1%
Brigite	22.5 °C	0.9 °C - 38.3 °C	59.7%
Buba	22.3 °C	13.9 °C - 35.8 °C	26.1%
Henriqueta	23.7 °C	14.2 °C - 35.8 °C	32.1%
Justin	22.5 °C	4.5 °C - 39.5 °C	34.4%
Kiko	22.1 °C	4.5 °C - 39.5 °C	26.9%
Lubetta	23.4 °C	14.2 °C - 36 °C	19.1%
Mariah	26.0 °C	10.6 °C - 39.5 °C	45.23%
Pdg	24.0 °C	4.5 °C - 40.2 °C	22.3%
Xororo	23.9 °C	0.2 °C - 38.3 °C	21.9%
Zezinha	24.8 °C	0.9 °C - 38.3 °C	32.9%
Fergus	22.9 °C	0.8 °C - 39.5 °C	38.9%
Jacques	22.9 °C	0.8 °C - 38.1 °C	10.8%

Table A3. Number of observations of the original movement data of GPS-tracked giant anteaters (*Myrmecophaga tridactyla*) in comparison to the number of observations used in the Hidden Markov Model (HMM) and in the integrated Step-Selection Analysis (iSSA).

Id	Original number of observations	HMM number of observations	iSSA number of observations
Annie	4529	3983	4274
Berenice	27162	26042	26740
Brigite	11857	10092	11105
Buba	788	408	528
Henriqueta	8717	8627	8677
Justin	10273	10104	10104
Kiko	25866	25680	25741
Lubetta	521	361	382
Mariah	8730	8612	8612
Pdg	32908	30039	31525
Xororo	16733	15203	16868
Zezipha	11604	9793	10027
Fergus	27139	26921	26921
Jacques	17178	13108	15632

Table A4. Estimates (95% CI) of the effect of step lengths (sl) and turning angles (ta), as well as their interactions with environmental temperature, time of day, and habitat type (open and forest; using open as the reference category) on movement of giant anteaters (*Myrmecophaga tridactyla*). Significant effects are highlighted in bold.

Covariate	Estimated effect (95% CI)	P value
sl	0.004 (0.004; 0.004)	<10 ⁻¹⁶
log (sl)	-0.595 (-0.605; -0.585)	<10 ⁻¹⁶
cos (ta)	-0.859 (-0.868; -0.850)	<10 ⁻¹⁶
sl * temperature	-0.001 (-0.001; -0.001)	<10 ⁻¹⁶
log (sl) * temperature	0.024 (0.024; 0.024)	<10 ⁻¹⁶
cos (ta) * temperature	0.026 (0.026; 0.026)	<10 ⁻¹⁶
sl * habitat	-0.011 (-0.012; -0.010)	<10 ⁻¹⁶
log (sl) * habitat	0.280 (0.250; 0.310)	<10 ⁻¹⁶
cos (ta) * habitat	-0.103 (-0.116; -0.090)	0.0057
sl * time of day	-0.015 (-0.015; -0.015)	<10 ⁻¹⁶
log (sl) * time of day	-0.445 (-0.447; -0.443)	<10 ⁻¹⁶
cos (ta) * time of day	-0.978 (-1.006; -0.950)	<10 ⁻¹⁶
sl * temperature * time of day	0.001 (0.001; 0.001)	<10 ⁻¹⁶
log (sl) * temperature * time of day	0.027 (0.027; 0.027)	<10 ⁻¹⁶
cos (ta) * temperature * time of day	0.057 (0.056; 0.058)	<10 ⁻¹⁶
sl * temperature * habitat	0.001 (0.001; 0.001)	0.0004
log (sl) * temperature * habitat	-0.009 (-0.011; -0.008)	<10 ⁻¹¹
cos (ta) * temperature * habitat	-0.004 (-0.005; -0.003)	0.0007
sl * time of day * habitat	0.004 (0.003; 0.005)	0.0054
log (sl) * time of day * habitat	0.367 (0.362; 0.372)	<10 ⁻¹⁵
cos (ta) * time of day * habitat	0.476 (0.421; 0.531)	<10 ⁻¹⁶
sl * temperature * time of day * habitat	0.001 (0.001; 0.001)	<10 ⁻¹¹
log (sl) * temperature * time of day * habitat	-0.022 (-0.023; -0.021)	<10 ⁻¹⁶
cos (ta) * temperature * time of day * habitat	-0.021 (-0.022; -0.020)	<10 ⁻¹⁶

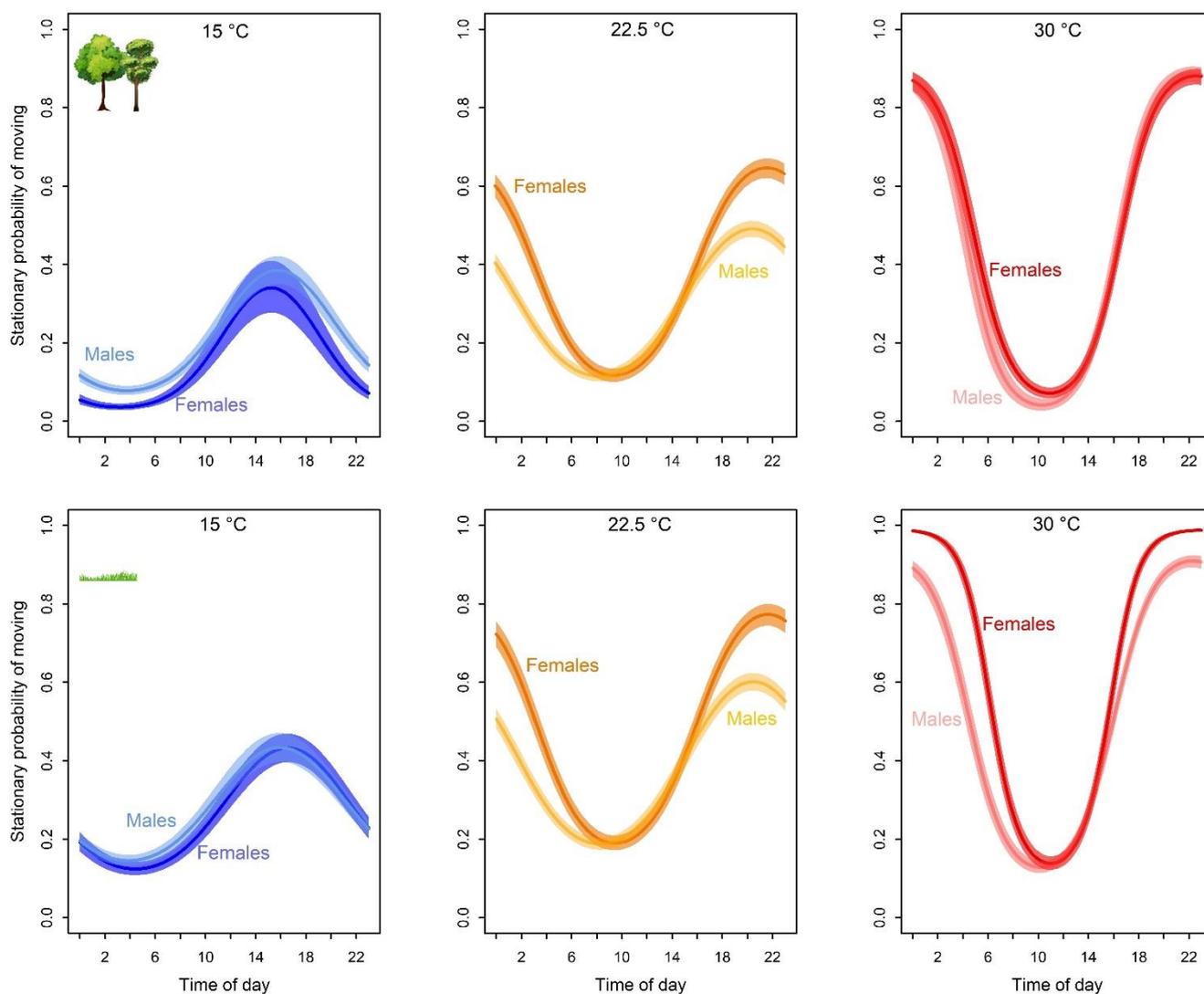


Figure A1. Stationary probability of moving of males and females' giant anteaters (*Myrmecophaga tridactyla*) as a function of time of day under three temperature conditions (cold [15 °C], mild [22.5 °C], and hot [30 °C]) and in two habitats (open areas, bottom graphics, and forests, top graphics). 15 °C and 30 °C respectively represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C). The colored bands represent the 95% confidence intervals.

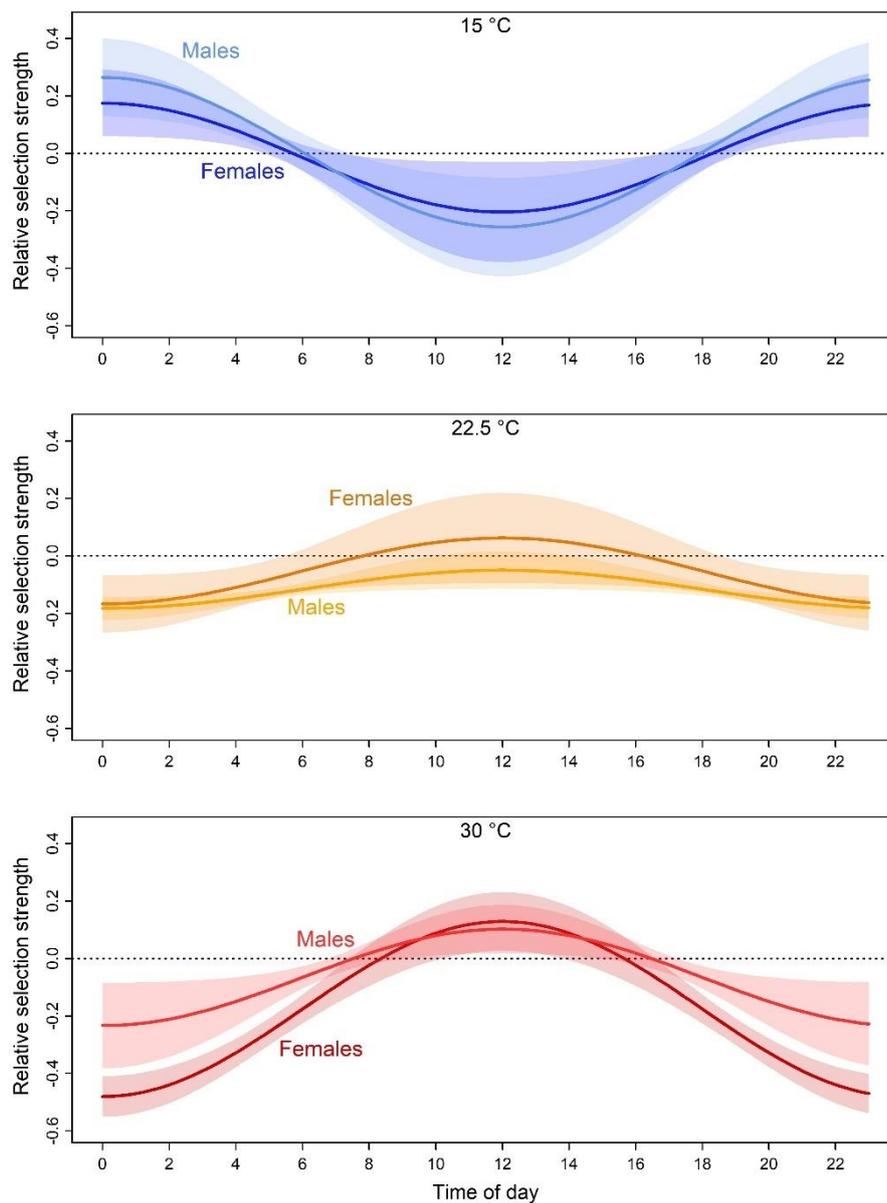


Figure A2. Selection strength of males and females' giant anteaters (*Myrmecophaga tridactyla*) for forests, relative to open habitats, as a function of time of day on three environmental temperatures (cold [15 °C], mild [22.5 °C], and hot [30 °C]). The colored bands represent the 95% confidence intervals. 15 °C and 30 °C respectively represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C).

Chapter 2: Sexual, allometric and forest cover effects on giant anteaters' movement ecology

Abstract

Knowing the influence of intrinsic and environmental traits on animals' movement is a central interest of ecology and can aid to enhance management decisions. The giant anteater, *Myrmecophaga tridactyla*, is a vulnerable mammal that presents low capacity for physiological thermoregulation and uses forests as thermal shelters. Here, we aim to provide reliable estimates of giant anteaters' movement patterns and home range size, as well as untangle the role of intrinsic and environmental drivers on their movement. We GPS-tracked 19 giant anteaters in Brazilian savannah. We used a continuous-time movement model to estimate their movement patterns (described by home range crossing time, daily distance moved and directionality), and provide an autocorrelated kernel density estimate of home range size. Then, we used mixed structural equations to integratively model the effects of sex, body mass and proportion of forest cover on movement patterns and home range size, considering the complex net of interactions between these variables. Male giant anteaters presented more intensive space use and larger home range than females with similar body mass, as it is expected in polygynous social mating systems. Males and females increased home range size with increasing body mass, but the allometric scaling of intensity of space use was negative for males and positive for females, indicating different strategies in search for resources. With decreasing proportion of forest cover inside their home ranges, and, consequently, decreasing thermal quality of their habitat, giant anteaters increased home range size, possibly to maximize the chances of accessing thermal shelters. As frequency and intensity of extreme weather events and deforestation are increasing, effective management efforts need to consider the role of forests as an important thermal resource driving spatial requirements of this species. We highlight that both intrinsic and environmental drivers of animal movement should be integrated to better guide management strategies.

Resumo

Conhecer a influência de características intrínsecas e ambientais no movimento animal é de central interesse para ecologia, além de ter grande utilidade para decisões de manejo. O tamanduá-bandeira, *Myrmecophaga tridactyla*, é uma espécie vulnerável que apresenta baixa capacidade de termorregulação fisiológica e usa florestas como abrigos termais. Aqui, pretendemos prover estimativas confiáveis dos padrões de movimento e área de vida dos tamanduás-bandeira, bem como desemaranhar o papel de fatores intrínsecos e ambientais influenciando sua movimentação. Monitoramos 19 tamanduás-bandeira na savana brasileira. Usamos modelos de movimento em tempo contínuo para estimar seus padrões de movimento (descritos pelo tempo de cruzamento da área de vida, distância diária movida e direcionalidade), e provemos uma estimativa de área de vida baseada em uma função kernel controlada por autocorrelação. Então, nós usamos equações estruturais mistas para integrativamente modelar os efeitos do sexo e massa corpórea dos indivíduos, assim como da proporção de cobertura florestal em suas áreas de vida, nos padrões de movimento e tamanho da área de vida, considerando a complexa rede de interação entre essas variáveis. Machos apresentaram mais intenso uso do espaço e maior área de vida que fêmeas com massa corpórea similar, como esperado em um sistema de acasalamento polígino. Machos e fêmeas aumentaram o tamanho das suas áreas de vida com o aumento da massa corpórea, mas a alometria da intensidade de uso do espaço foi negativa para machos e positiva para fêmeas, indicando diferentes estratégias de busca de recursos. Com a diminuição da proporção de florestas dentro das suas áreas de vida e a consequente redução da adequabilidade termal do habitat, os tamanduás-bandeira aumentaram o tamanho da sua área de vida, possivelmente para maximizar as chances de acessar abrigos termais. Com o aumento da frequência e intensidade de eventos climáticos extremos em um cenário de desmatamento, efetivos esforços de manejo precisam considerar o papel das florestas como um importante recurso termal influenciando os requerimentos especiais das espécies. Destacamos que ambos os fatores intrínsecos e ambientais influenciam o movimento animal e devem ser integrados para a melhor tomada de decisões de manejo.

Introduction

Animal movement is a key process of ecology, driving survival and fitness (Morales et al. 2010). Individuals' movement patterns shape their home range, which can be defined as the part of their cognitive map that they choose to be continuously updated (Gautestad 2011, Powell & Michael 2012). The home range should offer the needed conditions for basic activities of food gathering, mating, and caring for young (Burt 1943). Describing movement patterns and estimate home range size allow us better understanding animals' ecology and spatial requirements to make appropriate management decisions that can help to preserve wildlife (Börger et al. 2008, Allen & Singh 2016). Such knowledge has become even more important as human actions are increasingly endangering natural systems (Nathan et al. 2008, Doherty et al. 2021). Theoretical and empirical studies have more often focused on understanding 'typical' movement of a species than understanding its variation (Shaw et al. 2020). However, both movement patterns and home range size widely vary between individuals within a population, and these variations are commonly influenced by intrinsic and environmental traits (Börger et al. 2008, Nathan et al. 2008).

Sex and body mass are among the main intrinsic traits driving intraspecific variations on animal movement (Vieira et al. 2019). The mating system and the associated reproductive tactics employed by males and females within a species influence the evolutionary selection of various characters (Gaulin & FitzGerald 1986). This can result in sex-related metabolic, cognitive, and behavioral differences that should be reflected on movement patterns and, consequently, on home range size (McLoughlin & Ferguson 2000). Body mass, in turn, has direct influence on the individual's body mechanics and physiology (Wilson et al. 2015, Daley & Birn-Jeffery 2018). Besides, body mass can drive movement patterns and home range size by influencing individuals' energetic requirements (McNab 1963, Rosten et al. 2016), foraging experience (Papastamatiou et al 2011, Viswanathan et al. 2011), and/or orientation ability (Ross et al., 2012). Therefore, the animal movement allometry relative to individuals' body mass is commonly found (e.g., Rosten et al. 2016). Among environmental traits shaping animals' movement patterns and home range size, the proportion of available forest cover stands out to animals that habit

heterogeneous landscapes and use forests as resource (Mancinelli et al. 2018, Mangipanea et al. 2018).

The influence of intrinsic and environmental traits on animal movement is being increasingly better understood as technological advances on tracking methods increase (Shaw et al. 2020). Although the analysis of movement data is still challenging (Cagnacci et al. 2010, Fleming et al. 2019), the recent implementation of continuous-time movement models on understanding movement patterns and on estimating home range size has allowed great advances (Fleming & Calabrese 2016, Katzner & Arlettaz 2020). For high-quality GPS tracking data of range-resident individuals, these models allow the estimation of descriptors of movement patterns such as home range crossing-time, daily distance moved and directionality (Fleming et al. 2014). These descriptors bring insights on underlying movement processes determining home range and can be used to provide an autocorrelated kernel density estimator of home range size (Fleming et al. 2014). However, previous research has focused on evaluating one specific movement metric at a time (Morato et al. 2016, De la Torre & Rivero 2019), disregarding the possible causal relationships of the descriptors of movement patterns with each other and with home range size. Both accurate estimates of animal movement, based on movement models, and integrative approaches that consider the complex network of relations between the variables can help us to understand the effect of intrinsic and environmental traits on movement patterns and home range size.

The giant anteater (*Myrmecophaga tridactyla*) is a vulnerable mammal whose movement patterns and home range size have been previously studied to better guide its management and conservation (Miranda et al. 2014, Bertassoni & Ribeiro 2019). Their original spatial distribution covered from Belize to the south of South America, excluding the Andes (Miranda et al. 2014). While some populations are already locally extinct, others are facing habitat loss, wildfires, roadkills, conflicts with dogs and other threats (Miranda et al. 2014). In this scenario, their low reproductive rate and long periods of parental care make giant anteaters conservation status even more worrisome (Rodrigues et al. 2008, Miranda et al. 2015). Despite being commonly associated with open habitats (Eisenberg & Redford 1999), forests have a fundamental role in giant anteater thermoregulation (Giroux et al. 2021a, Giroux et al. 2023). This is because giant anteaters present reduced body heat production (McNab 1984) and low capacity

of physiological thermoregulation, and forests act as important thermal shelters. Besides showing smaller environmental temperature variation than adjacent open areas, forest patches buffer rain and chilly winds and offer protection against solar radiation (De Frenne et al. 2019). Therefore, it is also worrying that deforestation may be reducing the habitat thermal quality for these animals across their current distribution (Zepetello et al. 2020).

Despite the efforts to understand giant anteaters' movement ecology, previous estimates of their home range size have ignored the intrinsic autocorrelation of high-resolution movement data and have not been based on movement models, probably generating underestimated results (Fleming & Calabrese 2016, Bertassoni & Ribeiro 2019). While some studies showed no evidence of sexual effects on their movement (Di Blanco et al. 2017, Giroux et al. 2021a), other ones showed males presenting longer daily activity time (Di Blanco et al. 2017, Bertassoni et al. 2020) and using larger areas than females (Bertassoni et al. 2020). Because of their sexual size dimorphism (Giroux et al. 2021a), the possible influence of body mass on movement needs to be considered when assessing sexual effects. Besides, although we know that giant anteaters select forests to set their home ranges and allocate time within it (Bertassoni et al. 2020), we still ignore if the proportion of forest cover within home ranges influences their movement patterns and spatial requirements. Here we used a continuous-time movement model to offer reliable estimates of giant anteaters' movement patterns (specifically home range crossing-time, daily distance moved and directionality) and home range size. Then, we investigated the effect of sex, body mass and proportion of forest cover on giant anteaters' movement patterns and home range size. Using an integrative approach, we were able to uncover all these effects simultaneously, controlling for the possible relations among descriptors of movement pattern and with home range size.

Due to their probably polygynous social mating system (Desbiez et al. 2020), we expected male giant anteaters to increase their chances of mating opportunities by moving longer daily distances and using larger home ranges than females (Fig. 1b, d; Clutton-Brock et al. 1989). We also expected an allometric scaling between body mass and movement, since larger bodied individuals have higher energetic requirements than smaller ones (Isaac et al. 2012). Larger giant anteaters should increase the

intensity of space use, increasing home range crossing-time and daily distance moved while decreasing directionality. This is because this increasing space use should increase the individuals' chances to find food resources – mainly ants and termites – spread on the landscape (Fig. 1a, b, c; Redford 1985, Isaac et al. 2012, Fleming et al. 2014). Besides, it is reasonable to expect that larger animals will require more space to meet their energetic requirements (Isaac et al. 2012), so they would also increase home range

size with increasing body mass (Fig. 1d). We expect that increasing proportion of forest inside home range will lead animals to increase home range crossing time, decreasing daily distance moved and directionality, because the forests' three-dimensional structure should present physical obstacles to displacement, imposing more friction than open grasslands (Fig. 1e, g; Ferreras 2001). Finally, lower proportions of forest inside home range would decrease the animal's access to thermal shelters, decreasing the habitat thermal quality. It could lead animals to increase their spatial requirements, increasing home range size (Fig. 1h; Said et al. 2009).

Methods

Study site

We carried the study out in two savannah areas in the Brazilian territory: (1) Santa Barbara Ecological

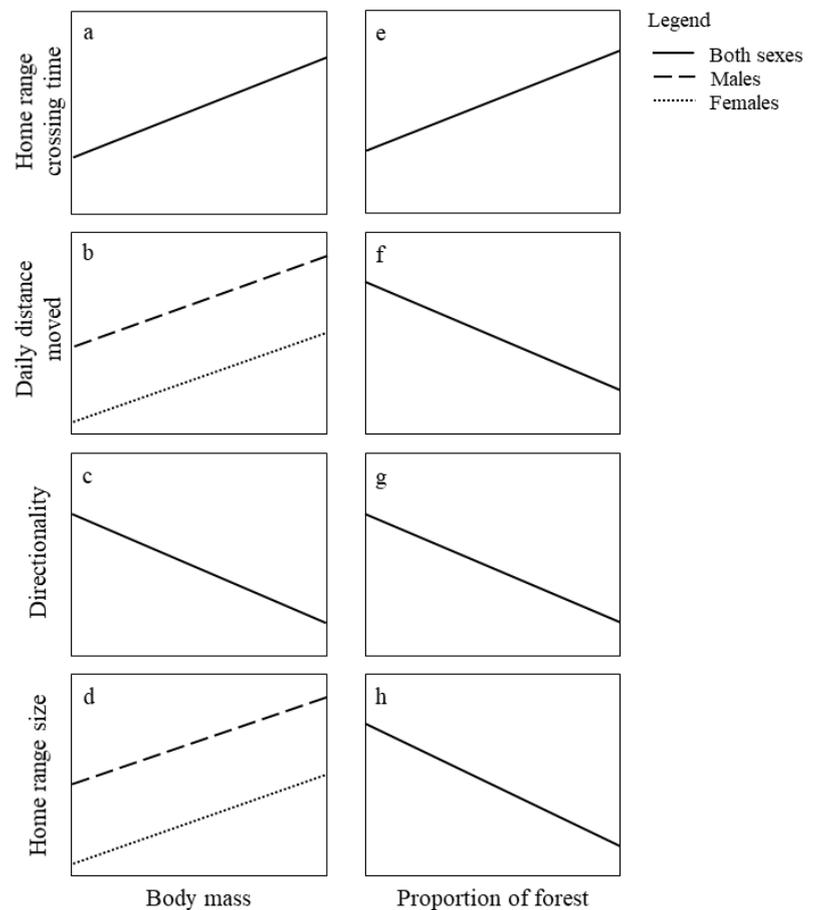


Figure 1. Hypothetical direction and shape of the expected effects of intrinsic (sex and body mass) and environmental traits (proportion of forest cover inside home range) on three descriptors of movement patterns (home range crossing time, daily distance moved, and directionality) and home range size of giant anteaters.

Station, São Paulo state (22° 48' 59" S, 49° 14' 12" W) and (2) Baía das Pedras ranch, Mato Grosso do Sul state (19° 18' 9" S, 55° 47' 4" W). The study areas have a tropical climate, with rainy summers and dry winters (Alvares et al. 2013). The landscape of both studied areas is composed of mosaics of open grasslands, scrublands, savannahs, and woodlands (Abdon et al. 1995, Durigan et al. 2007). The landscape of Santa Barbara Ecological Station also includes anthropic elements, such as exotic forests of *Pinus* sp. and *Eucalyptus* sp., as well as highways (Durigan et al. 2007). Baía das Pedras Ranch is located within the Pantanal wetland, and it presents a naturally fragmented landscape with permanent and temporary salty and freshwater ponds, where open grasslands are subjected to seasonal flooding (Abdon et al. 1995).

We classified the landscapes using georeferenced maps (LANDSAT 7 TM) and the MapBiomias database (Collection 5; Souza et al. 2020). To test the effect of the forest cover in movement patterns and home range size of giant anteaters, we summarized the observed habitats in two categories: forest or non-forest (Fig. 2). Forest areas included woodland savannahs, woodlands, riparian forests, regenerating arboreal vegetation and exotic forests. Non-forest areas included open grasslands, scrublands, open savannahs, and areas without vegetation cover. We calculated the proportion of forest cover within each individual home range dividing the number of pixels classified as forest by the total number of pixels. We performed satellite image processing and supervised classifications using raster (Hijmans et al 2014), maptools (Bivand & Lewin-Koh 2016), and rgdal (Bivand et al. 2015) packages available in the R environment (R Core Team 2019).

Capture and Data Collection

We searched for giant anteaters by horse or by pickup vehicle at low speed (maximum of 20 km/h). Once we saw the anteaters, we captured them using dip nets, dart-guns, or a blowpipe. Anteaters were immobilized and sedated following the protocol described by Bertassoni et al. (2020) in Santa Barbara Ecological Station and following the protocol described by Kluyber et al. (2021) in Baía das Pedras Ranch. Each captured individual was sexed, weighted, and equipped with a global positioning system (GPS) harness during anesthesia. We conducted a T test (Young 1998) to compare the mean body mass

between individuals of our two study areas (see Fig 3 in results section). None of the tracking devices exceeded 3% of the animals' body mass. The procedures were performed under the license numbers SISBIO 16010-1 and SISBIO 38326-5 (Chico Mendes Institute for Biodiversity Conservation). After completing their recovery from the anesthesia, we released the giant anteaters at the site of capture for movement GPS-tracking (see Fig. 2).

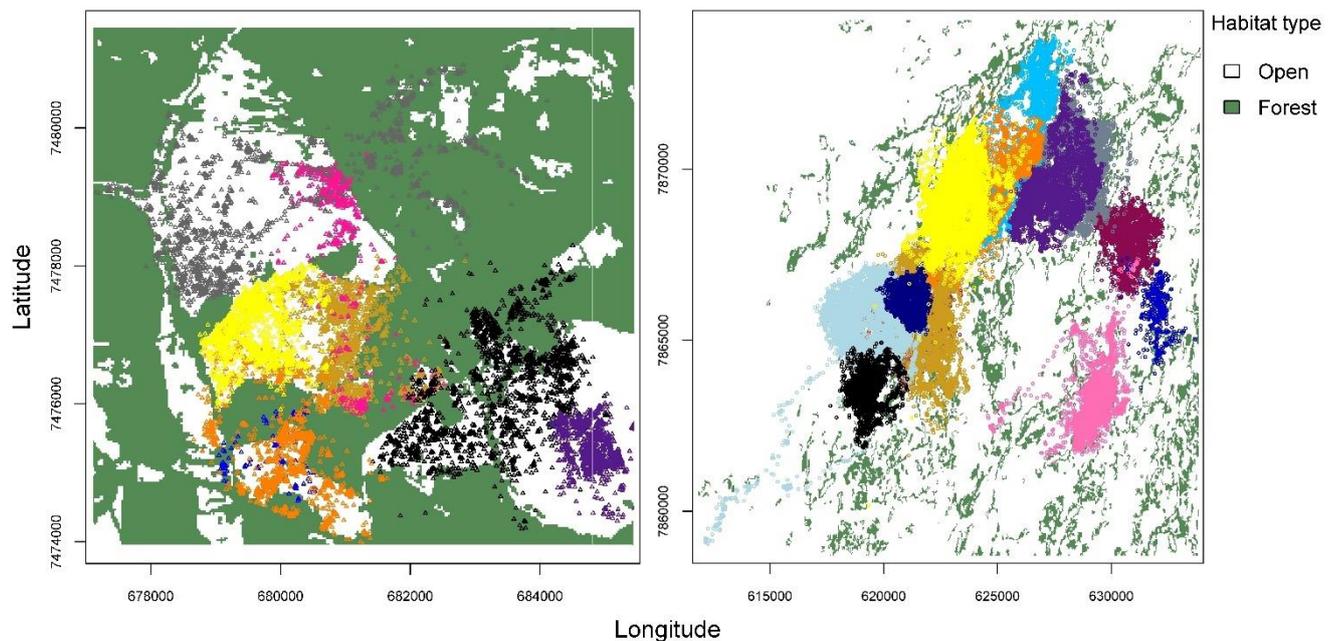


Figure 2. Study sites' maps showing the mosaic of forests (green) and open areas (white) in Santa Bárbara Ecological Station (left) and Baía das Pedras ranch (right). Colored points represent individuals' location points, with one colour to each individual.

Movement patterns and home range analysis

We described animals' movement patterns and estimated home range size using the *ctmm* R package (Fleming et al. 2015, Calabrese et al. 2016). We first examined the empirical variogram of each individual tracking data to check for an asymptote (Fleming et al. 2014), as it is an evidence of range residence and a premise for the movement parameters estimation (Calabrese et al. 2016). Because tracking data with such short sampling intervals are inherently autocorrelated, we also used the variogram to investigate the autocorrelation structure of data, obtaining starting values for the variance and autocorrelation timescales. Then, we fitted continuous-time movement models to the individuals' location data via maximum likelihood. Among the fitted models, we included the Brownian motion

model (BM), the Ornstein-Uhlenbeck model (OU), the Integrated OU model (IOU) and the Ornstein-Uhlenbeck-F model (OUF; Fleming et al. 2014). We ranked the movement models based on the second order Akaike Information Criterion (AIC_C ; Burnham & Anderson 2002) and selected the one with the best fit for each individual anteater data set.

For those animals that better fitted OUF model, we obtained the three descriptors of individuals' movement patterns: home range crossing time (timescale of autocorrelation in position), daily distance moved and directionality (direction persistence timescale), as well as their confidence intervals (Fleming 2014). For those animals that showed range residence (i.e., better fitted OU or OUF models), we used the ninety-five per cent area corrected autocorrelated kernel density estimator (AKDEc 95%) to estimate the individuals' home range size and its confidence limits. AKDEc is a nonparametric home-range estimator that assumes the data represent a sample from a nonstationary, autocorrelated, continuous movement process (Fleming & Calabrese 2017). This estimator allows movement models to be fitted to data with different temporal structures (e.g., irregular sampling regime, gaps, and short sampling time). Also, AKDEc allows to compare home ranges of individuals with different monitoring times. This is because AKDEc extrapolates the data, basing itself on parameters of the model selected for each individual data set, to provide reliable home range estimates (Fleming & Calabrese 2017).

Structural Equation Modeling

We used mixed Structural Equations Modeling (mixed-SEM) [64] to investigate: (1) the effect of intrinsic traits (individuals' sex and body mass) in movement patterns and home range size and (2) the effect of an environmental trait (proportion of forest cover inside the individuals' home range) in movement patterns and home range size. Because the descriptors of movement patterns can be related to each other, and can modulate home range size, we controlled for these possible relationships in an integrative approach (see Fig. 4). In this approach, the same variable could simultaneously act as response in an equation and as predictor in another one (Fig. 4; Kline 2015). Mixed-SEM allowed us to disentangle a complex net of interactions, estimating the indirect, direct, and total effects among variables (Lefcheck 2016). Indirect effects were estimated by the product of the direct effects that

compose them, and total effects were given by the sum of direct and indirect effects (Stolzenberg 1980, Hayes & Preacher 2010).

Mixed-SEM was fitted using the R package PiecewiseSEM (Lefcheck 2016, Heck et al. 2001). We included random variables in the model to account for the hierarchical structure of our data (i.e., individuals' intercepts were nested within the sites; see Lefcheck 2016). We also took into consideration the uncertainty associated with the estimated values of movement patterns and home range size. Accordingly, we used an autoregressive error structure to weigh the contribution of the values of the response variables for the inverse of its variance in the corresponding equations (Sterne et al. 2001, Lin & Chu 2020). We standardized the estimated coefficients to allow comparison between the different parameters (Grace et al. 2018). Finally, we checked the global goodness-of-fit of our mixed-SEM by a Fischer's C test, which measures the discrepancy between predicted and observed covariance matrices of our causal predictions (Holst & Budtz-Jørgensen 2013).

Results

General results

We GPS-tracked 19 individuals – six individuals (three males and three females) in Santa Barbara Ecological Station (SP) in 2015, and 13 individuals (eight males and five females) in Baía das Pedras Ranch (MS) between 2013 and 2017. The individuals weighed between 21.6 kg and 38.7 kg (mean = 32.5 kg). Individuals' body mass was similar for both study areas (t test; $t = -0.69$; $df = 12.53$; $p = 0.50$; Fig. 3). The GPS devices recorded location points at intervals ranging between 20 and 70 minutes. The monitoring time varied between individuals, ranging from 45 to 136 days in Santa Barbara Ecological Station (mean = 90 days) and from 69 to 509 days in Baía das Pedras

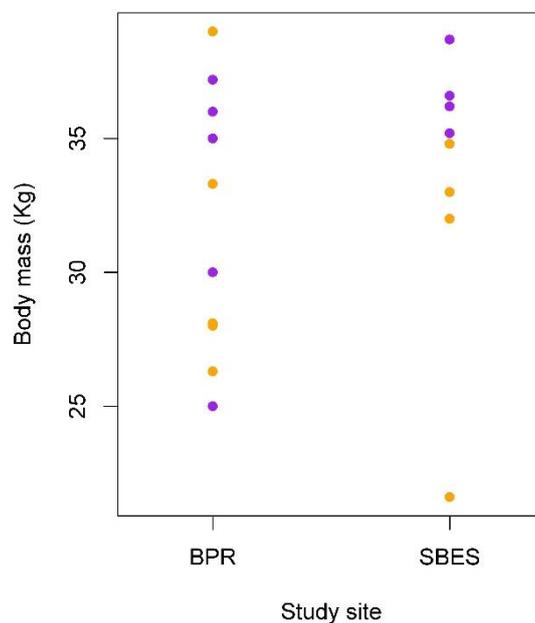


Figure 3. Body mass of male (purple) and female (orange) giant anteaters monitored at Baía das Pedras ranch (BPR) and Santa Bárbara Ecological Station (SBES).

ranch (mean = 371.5 days). The total dataset consisted of 213,901 locations. We provided individual information on sex, body mass, sample regime and monitoring time in Appendix Table A1.

The individuals' empirical variogram showed the plotted semi-variance reaching an asymptote on a timescale that roughly corresponded to the home-range crossing time. Therefore, all the monitored giant anteaters showed constrained space use and were defined as range residents. For all individuals, the highest ranked movement model was the OUF – that considers autocorrelation in both location and velocity (Fleming et al. 2014). The estimates of home range crossing time, daily distance moved, directionality, and home range size varied between individuals (Table 1). The mixed-SEM explained a substantial amount of the observed variation in home range crossing time ($R^2 = 0.67$), daily distance moved ($R^2 = 0.72$), directionality ($R^2 = 0.88$), and home range size ($R^2 = 0.81$).

Table 1. Estimates and confidence intervals of movement patterns (described by home range crossing time, daily distance moved and directionality) and home range size of giant anteaters (*Myrmecophaga tridactyla*).

	Minimum (95% CI)	Mean	Maximum (95% CI)
Home range crossing time (days)	0.26 (0.23 - 0.29)	2.15	10.58 (7.01 - 15.96)
Daily distance moved (km)	5.41 (3.74 - 7.08)	8.01	12.04 (11.90 - 12.19)
Directionality (min) ^a	1.64 (0.94 - 2.87)	13.82	34.9 (31.76 - 38.37)
Home range (km ²)	1.44 (1.09 - 1.84)	8.94	20.74 (15.26 - 27.06)

^a Directionality was measured as the timescale of the persistence in direction.

Intrinsic effects on movement patterns and home range size

Home range crossing time and daily distance moved had positive influence of sex, with males presenting higher values than females (Fig 4; β_1 and β_2 , respectively; Fig 5a, b). The effect of body mass in home range crossing time and daily distance moved depended on the sex, and it was negative for males (Fig 4; β_3 and β_5 , respectively; Fig 5a, b) and positive for females (Fig 4; β_4 and β_6 , respectively; Fig 5a, b).

Directionality was indirectly driven by sex through daily distance moved (Fig 4; $\beta_2 * \beta_7 = -1.56$; Fig 5c). The effect of body mass on directionality was also given indirectly via daily distance moved (Fig 4; $\beta_5 * \beta_7$ for males, and $\beta_6 * \beta_7$ for females), and it was equal to 1.29 for males and -0.50 for females (Fig 5c). The effect of both sex and body mass on home range size was mediated by home range crossing time, daily distance moved and directionality. The total effect of sex on home range size was given by $\beta_1 * \beta_8 + \beta_2 * \beta_7 * \beta_9 = 0.45$ (males > females; Fig 4; Fig 5d). The total effect of body mass on home range size was given by $\beta_3 * \beta_8 + \beta_5 * \beta_7 * \beta_9 = 0.41$ for males, and $\beta_4 * \beta_8 + \beta_6 * \beta_7 * \beta_9 = 1.27$ for females (Fig 4; Fig 5d).

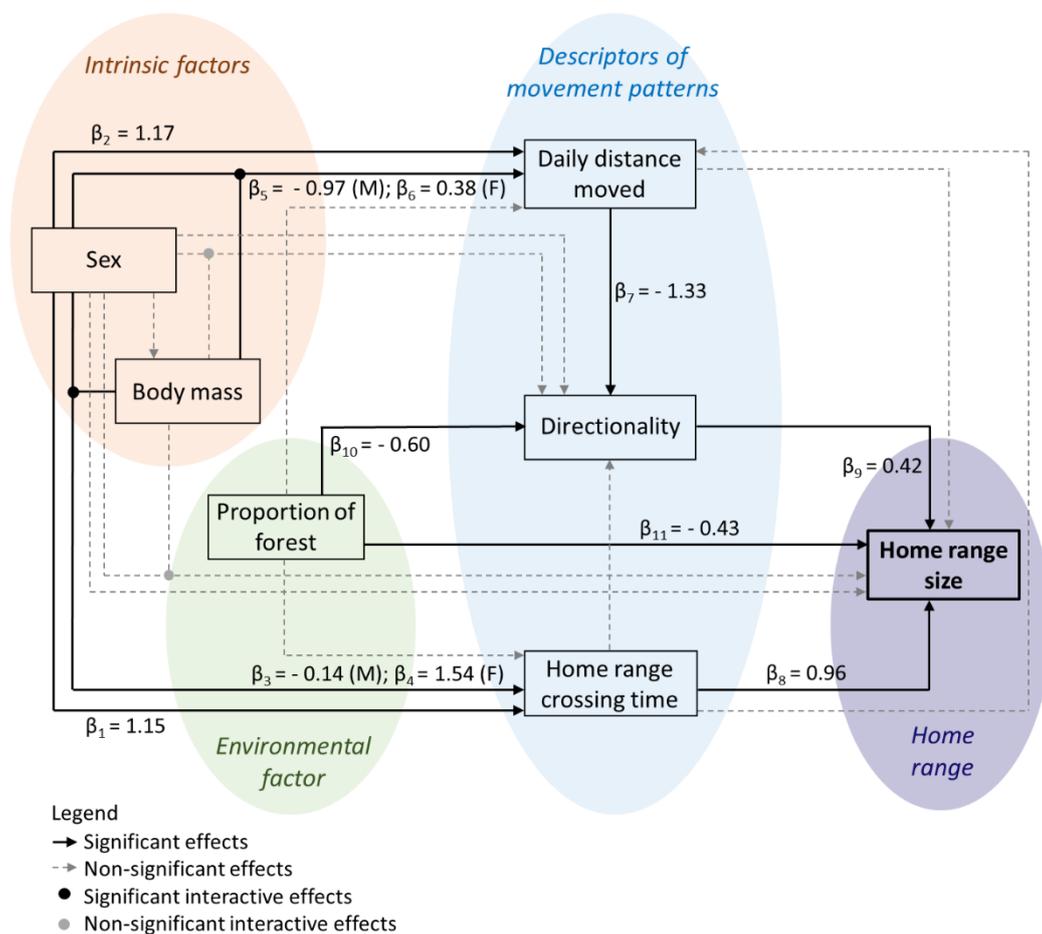


Figure 4. Schematic representation and estimated coefficients of intrinsic (sex and body mass) and environmental effects (proportion of forests) on movement patterns (described by home range crossing time, daily distance moved and directionality) and home range size of giant anteaters, as well as of the relationships between the descriptors of movement patterns to each other and with home range size. The standardized coefficients (β) represent the relative strength of significant effects.

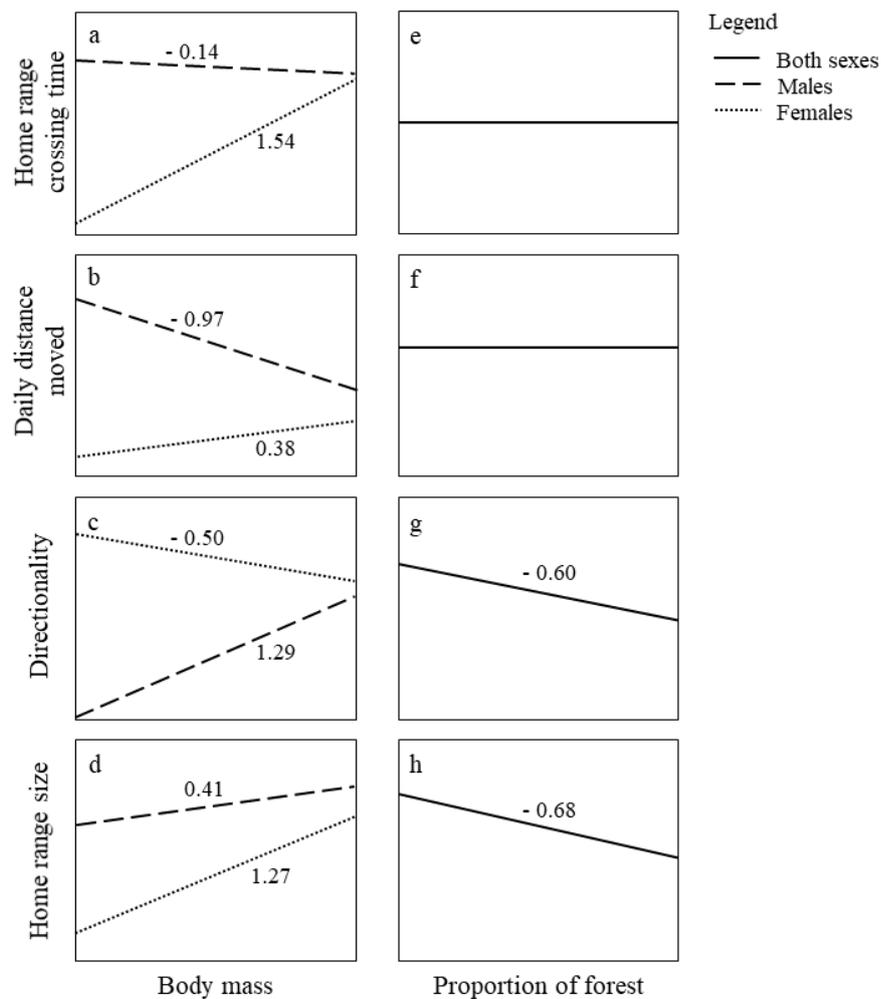


Figure 5. Graphical representation of the shape and direction of the effects of intrinsic and environmental traits on movement patterns and home range size of giant anteaters (*Myrmecophaga tridactyla*). Intrinsic traits are represented by sex and body mass. The environmental trait is represented by the proportion of forest cover within individuals' home ranges. Movement patterns are described by home range crossing time, daily distance moved and directionality. Estimated coefficients are provided above tendency lines for each relationship.

Environmental effect on movement patterns and home range size

The proportion of forest cover within the individuals' home range ranged between 0.17 and 0.88 (mean = 0.42). The proportion of forest had no influence on home range crossing time or daily distance moved (Fig 4; Fig 5e, f), however, it negatively influenced directionality (Fig 4; $\beta_{10} = -0.60$; Fig 5g). It means that individuals whose home range presented a higher proportion of forest cover showed less directionality – i.e., more tortuous movements – than individuals occupying areas with a low proportion

of forests. The total effect of the proportion of forest cover on home range size resulted of the sum of its direct effect (Fig 4; β_{11}) with indirect effects, mediated by directionality (Fig 4; $\beta_{10} * \beta_9$), totaling an effect of - 0.68 (Fig 4; Fig 5h). In other words, individuals increased home range size with a decreasing proportion of forests inside it.

Discussion

As far as we know, we provided here for the first-time movement model-based estimates of home range crossing time, daily distance moved and directionality for giant anteaters, allowing a better characterization of the species' movement patterns. Once home range crossing time indicates the timescale of autocorrelation in position, our results show that, on average, a two-days interval between consecutive relocations is necessary to consider them spatially independent (Fleming & Calabrese 2017). However, previous studies using GPS devices have adopted monitoring regimes much shorter than that and unconsidered the spatial autocorrelation of data (Bertassoni & Ribeiro 2019, Bertassoni et al. 2020), probably leading to underestimating results. This is an important factor explaining why our estimates of daily distance moved, and home range size were, in average, bigger than those provided by recent studies (Bertassoni & Ribeiro 2019, Bertassoni et al. 2020), once AKDEc incorporates and controls for the autocorrelation in both location and velocity (Fleming & Calabrese 2017). Other possible explanations to this discrepancy can be related to the intrinsic characteristics of monitored individuals and the environmental characteristics associated with the site and period of monitoring.

The use of mixed-SEM allowed us to disentangle the effects of sex, body mass and proportion of forest on movement patterns and home range size, simultaneously estimating the direction and intensity of direct and indirect effects. The three descriptors of movement patterns (home range crossing time, daily distance moved and directionality) mediated the effects of sex and body mass on home range size, illustrating the importance of integrating these relationships in the same model (Lefcheck 2016). We were able to clarify the sexual effects on movement patterns and home range size by considering body mass effects and the interactions between individuals' sex and body mass. Even though the intraspecific effect of body mass on movement patterns and home range size is generally weak in

mammals (McLoughlin & Ferguson 2000), we were still able to detect it with this integrative approach. To our best knowledge, this is the first record of allometric scaling in the movement patterns and home range size in giant anteaters. On the other hand, environmental traits, such as the proportion of forest cover, are common direct drivers of mammal's home range size at the individual level (McLoughlin & Ferguson 2000), and our model provided additional details, showing the direct and indirect paths of this effect. Despite the great explanatory power of our model, we recognize that there must be other intrinsic and environmental factors influencing giant anteaters' movement that we did not investigate here, and some of them may even seasonally change.

In general, male giant anteaters presented more intensive space use than females with similar body mass, showing longer home range crossing-time, longer daily distance moved and smaller directionality. Besides, males also exhibited larger home ranges than females. We expected males moving longer distances and occupying larger areas than females. However, it was surprising that they also took more time to cross their areas and were less directional at doing it. The higher intensity of space use and larger home range in males than females are, probably, strategies to increase the chances to find receptive females on landscape (Clutton-Brock 1989). This is because the home range of a male giant anteater usually overlaps with the home range of several females (Medri & Mourão 2006). Hence, males could increase their chances of finding receptive females exploiting their home ranges and increasing their home ranges size to include more females inside it. In line with these results, male giant anteaters were recorded presenting longer activity time and larger home range than females (Bertassoni et al. 2020). Therefore, we reinforced the idea that giant anteaters present a polygynous social mating system, with a male mating with more than one female (Clutton-Brock 1989, Desbiez et al. 2020).

Female giant anteaters behaved as expected, increasing the intensity of space use with increasing body mass. This is probably related to an increase in the search for food resources (Fleming et al. 2014), once larger animals have higher energetic requirements (Isaac et al. 2012). For species that have their food resources unpredictably spread on the landscape, such as the invertebrate nests that giant anteaters' prey upon, the intensity of utilization of food resources depends on the intensity of use of space that

provides physical access to those resources (De Knegt et al. 2007, Augustine & Derner 2013). Besides, female giant anteaters also increased home range size with increasing body mass, showing a second strategy to increase the access to food resources: increasing the size of the space used to find those resources. A positive allometric scaling of both intensity of space use and home range size has been found in some mammals (Cameron & Spencer 1985, Duncan et al. 2015), including other xenarthrans with myrmecophagous diets such as giant armadillos (*Priodontes maximus*; Desbiez et al. 2019) and southern three-banded armadillos (*Tolypeutes matacus*; Attias et al. 2020). This relationship indicates that the search for energetic resources is one of the main factors driving female giant anteaters' movement across body mass.

On the other hand, males did not display the same pattern. With increasing body mass, males reduced intensity of space use and increased home range size. This reveals a change of males' movement strategy guided by body mass: while small males used their small areas intensively, large males ranged over large areas with comparatively lower intensity of use. Considering a limited quantity of metabolic energy available for movement (Sparrow & Newell 1998), animals moving close to their limit capacity should experiment a trade-off between the intensity of use and the area size, and this can be the case of male giant anteaters. Both strategies can increase the access to both food resources spread on the landscape and receptive females (Shepard et al. 2013). Meanwhile, small males could minimize the chances of agonistic interactions with other males if they use smaller areas than the big ones (Rocha & Mourão 2006, Kreutz et al. 2009). Further studies, such as behavioral assessments, will help us to confirm these hypotheses and better understand the species' reproductive biology.

As we expected, male and female giant anteaters reduced the directionality as the proportion of forest patches inside their home ranges increased, probably due to the physical obstacles that forests impose to displacement (Ims 1995). Similarly, small mammals have presented shorter step lengths and higher tortuosity within forest areas (Wells et al. 2006), and African wild dogs have shown that the movement permeability of the vegetation decreases with its increasing density (Abrahms et al. 2015). However, it is worth noting that, contrary to our expectations, a greater proportion of forest inside the

home ranges did not influence the home range crossing time or daily distance moved.

Decreasing the proportion of forest inside giant anteaters' home range led males and females to an increase in the home range size. This is probably because giant anteaters present a low capacity for physiological thermoregulation (McNab 1984), and less forest implies less access to thermal shelters and, consequently, a reduced habitat thermal quality (Giroux et al. 2021a, Giroux et al. 2023). As a result, animals would increase the home range size as a strategy to maximize the chances of accessing this thermal resource. Supporting this idea, the increase of home range size with decreasing habitat quality has been widely documented for terrestrial vertebrates (Ofstad et al. 2016, Gardiner et al. 2019, Mayer et al. 2019). Furthermore, the importance of forests as thermal shelters has also been shown for other mammals (Melin et al. 2014, Attias et al. 2018), and it should increase with the predicted increasing frequency of extreme weather events (Meehl et al. 2000). In the Brazilian territory, where this study was conducted, massive agricultural expansion has caused extensive habitat degradation and dramatically decreased forest patches on savannah areas in number and size (Tollefson et al. 2018, Reynolds et al. 2016). In this current deforestation scenario, our results bring an important implication for giant anteaters' management: the minimal area needed to preserve a given giant anteaters' population should increase as the proportion of forests inside it decreases.

Conclusion

We brought reliable measures of giant anteaters' movement patterns and home-range size, showing that their movements are influenced by sex, body mass and proportion of forest cover; and revealed two important strategies used by giant anteaters to maximize the access to resources: they modulate movement patterns, increasing space use intensity, and/or increasing home range size. This information contributes to the understanding of giant anteaters' spatial ecology and can help define the spatial scale of effective management efforts for their conservation, especially as the anthropogenic impacts on landscapes increase. We highlight the need to consider the sexual differences on movement strategies and the role of forests as an important thermal resource driving giant anteaters' spatial requirements (also see Desbiez et al. 2020). We strongly suggest that management efforts should focus on maintaining

the giant anteaters' access to forest patches inside their home ranges to provide environmental conditions for behavioral thermoregulation. Both intrinsic and environmental traits driving animal movement should be integrated when establishing conservation strategies for populations and species.

Appendix

Table A1. Intrinsic characteristics and monitoring information of tracked giant anteaters.

Id	Site	Sex	Body Mass (kg)	Sampling Regime (minutes)	Monitoring time (days)	Number of points
1	MS	F	30	20	84.03	4529
2	MS	F	39	20	386.04	27162
3	MS	F	26.3	30	339.72	11857
4	MS	F	30	20	69.06	788
5	MS	F	28.1	20	159.94	8717
6	MS	M	30	20	144.73	10273
7	MS	M	35	20	363.16	25866
8	MS	F	33.3	20	122.45	8730
9	MS	M	36	20	509.74	32908
10	MS	M	37.2	30	387.77	16733
11	MS	F	35	30	279.75	11604
12	MS	M	35	20	378	27139
13	MS	M	25	20	365	17178
14	SP	F	34.8	40	44.6	839
15	SP	M	35.2	60	136.08	2467
16	SP	M	36.6	40	90	1608
17	SP	F	33	60	107.63	2019
18	SP	M	36.2	70	106.38	2091
19	SP	F	21.6	60	80.27	1393

General Conclusion

We explored giant anteaters' movement ecology, showing how this big size mammal use behavioral adjustments to thermoregulate as well as how their movement patterns and spatial requirements are influenced by intrinsic and environmental traits. Importantly, forest patches were important thermal shelters to giant anteaters at extremes environmental temperatures, and the availability of forests was a strong driver of giant anteaters' spatial requirements. Because of their low capacity for physiological thermoregulation, giant anteaters were excellent models to exemplify how forest patches can be an important thermal resource to open-area mammals living in heterogenous landscapes. This work gives us the insight that the climate change scenario should make forest patches increasingly important to mammals' thermoregulation, even those usually found in open areas. This is why the conservation of forest patches should be increasingly prioritized in heterogeneous landscapes. To face climate change, it is mandatory consider the importance of forests as thermal resources.

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