

The role of environmental temperature on movement patterns of giant anteaters

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Abstract

Mammals can show conspicuous behavioral responses to thermal variation, including changes in movement patterns. We used an integrative approach to understand how environmental temperature can drive the movement behavior of a mammal with low capacity for physiological thermoregulation, the giant anteater (*Myrmecophaga tridactyla*). We tracked 52 giant anteaters in 7 areas throughout the Brazilian savannah. We estimated the distance moved, area used, use of forest areas, and mean environmental temperature for each monitoring day of each individual. We modeled these data with Mixed Structural Equations — considering the possible interactions between our variables and controlling for sex and body mass. Giant anteaters reduced displacement and increased forest use with decreasing environmental temperature, probably because of their low body heat production. It is possible that

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they reduce distance moved and area used by reducing the duration of activity. With decreasing temperature, forest habitats become warmer than open ones, besides buffer rain and chilly winds. Reducing displacement and using forests are important strategies to reduce body heat loss and the energetic costs of thermoregulation. However, decreasing movement can limit food access and, consequently, fitness. Therefore, we highlight the importance of forests as thermal shelters. With increasing frequency and intensity of extreme weather events, we showed the need to preserve forest patches to offer suitable conditions for tropical mammals' behavioral thermoregulation. In this context, policies favoring deforestation on Brazilian territory are especially worrisome. Finally, we emphasize the need of integrative approaches to understand the complex interactions between organisms and the environment.

Key words: behavioral thermoregulation, biologging, habitat use, mixed structural equations, movement ecology

INTRODUCTION

The spatial and temporal distribution of animals results from the interaction between physiological and environmental conditions that drive animal behavior (Börger *et al.* 2008; Nathan *et al.* 2008). Intraspecific behavioral variations are commonly influenced by intrinsic factors, such as sex (Viana *et al.* 2018), body mass (Rosten *et al.* 2016), and personality (Spiegel *et al.* 2017). Moreover, extrinsic factors, such as habitat composition, predation risk, and weather conditions interact with intrinsic traits, driving animal behavior (Fortin *et al.* 2005; Pigeon *et al.* 2016; Mangipane *et al.* 2018). In face of the forecasts for climate and land use changes, we need to understand how environmental changes shape animal behavior to successfully predict and manage future biological processes (Rutz & Hays 2009; Schwenk *et al.* 2009).

Environmental temperature stands out among the climatic parameters that can shape animal decision-making, and the understanding of its influence on endotherm behavior is increasing (Angilletta *et al.* 2010). Mammals, for example, do not rely exclusively on physiological mechanisms for thermal regulation but also use behavioral strategies, which can directly drive their movement patterns (Angilletta *et al.* 2010; Terrien *et al.* 2011). To enhance heating or cooling, the individuals can modulate displacement, activity period and activity duration (Terrien *et al.* 2011). Another example of behavioral strategy to thermoregulation is the use of microhabitats that work as thermal refuges (Terrien *et al.* 2011). This occurs because in a complex landscape, subjected to a given macroclimate, there is a complex arrangement of microclimate conditions that the individuals can access to perform their activities and to rest (Angilletta *et al.* 2010; Terrien *et al.* 2011). Furthermore, some behavioral responses to environmental temperature may have indirect influence on individual movement, such as using specific energy-conserving postures to limit heat dissipa-

tion or maximize heat gain from the surrounding habitat. Generally, these postures can only be performed if the animal is standing still (Terrien *et al.* 2011). Therefore, environmental temperature can drive direct or indirect shifts in the movement patterns of mammals (Campos *et al.* 2014).

Behavioral strategies can reduce the metabolic costs of mammal thermoregulatory responses but can also imply energetic costs, for example, by limiting the access of individuals to food resources (Angilletta 2009; Terrien *et al.* 2011). Modulating displacement and habitat use, 2 common mechanisms of mammalian behavioral thermoregulation, is associated with both costs and benefits. For example, decreasing displacement decreases the energy consumed and allows performing most of the energy-conserving postures (McNab 1984; Terrien *et al.* 2011). However, while moving, animals increase their chances of obtaining feeding resources and increase endogenous heat production due to muscular activity (Burt 1943; Angilletta *et al.* 2010). In addition, microhabitats that offer high availability of thermal shelters could present low availability of food resources (Mourão & Medri 2007). Depending on intrinsic characteristics of the individuals, environmental temperature, and the landscape opportunities, certain behavioral choices should be energetically more favorable than others, and the resulting thermoregulatory behavior should represent a solution for the trade-off between costs and benefits (Huey & Slatkin 1976; Angilletta *et al.* 2010). From an energetic perspective, we expect mammals to increase displacement and use microhabitats with greater food availability whenever environmental temperatures are within their thermoneutral zone (Angilletta *et al.* 2010; Mitchell *et al.* 2018). As operative temperatures deviate from the set-point body temperatures and the energetic costs of thermoregulation increase (Angilletta *et al.* 2010), we expect mammals reducing displacement, and increasing the use of thermal shelters (van Beest *et al.* 2011; Street *et al.* 2016).

The Xenarthra (Mammalia)—superorder of basal placental mammals that includes armadillos (Cingulata), sloths, and anteaters (Pilosa)—may be quite sensitive to variations in environmental temperature (Camilo-Alves & Mourão 2006; Maccarini *et al.* 2015; Attias *et al.* 2018). Due to their low-calorie diet, they present a lower basal metabolic rate and lower body temperatures than other placental mammals of similar body mass (McNab 1984, 1985). Because of their reduced body heat production, xenarthrans present a low capacity for physiological thermoregulation (McNab 1984, 1985). Besides physiological strategies, these animals exhibit a wide variety of conspicuous behavioral responses to environmental temperature variation, which contribute to their thermoregulation and modulate their movement (Camilo-Alves & Mourão 2006; Attias *et al.* 2018). Therefore, xenarthrans are valuable models for understanding how environmental temperature changes can influence mammalian behavior and, consequently, how this climatic parameter can drive their movement patterns.

Xenarthrans modulate their activity in response to environmental temperature variation. Yellow armadillos increase their activity duration and diurnality on cold days, possibly to increase sun exposure (Maccarini *et al.* 2015; Attias *et al.* 2018). In contrast, southern three-banded armadillos and giant anteaters reduce the total duration of activity on cold days. This is probably because part of their strategies to reduce thermal conductance is related to specific body postures that hinders their displacement (Camilo-Alves & Mourão 2006; Attias *et al.* 2018). While one rolls into a ball, the other covers itself with its long furry tail (McNab 1984, 1985; Medri & Mourão 2005). The use of thermal shelters also has been demonstrated in xenarthrans. Although armadillos usually use dens as thermal shelters and anteaters do not, the use of forest patches is important to both. Under extreme environmental temperatures, southern 3-banded armadillos [*Tolypeutes matacus* (Desmarest, 1804)] increase their selection strength for forests (Attias *et al.* 2018), which buffer temperature variation (Lin *et al.* 2017; De Frenne *et al.* 2019). Analogously, giant anteaters (*Myrmecophaga tridactyla* Linnaeus, 1758) and yellow armadillos [*Euphractus sexcinctus* (Linnaeus, 1758)] increase forest use at low environmental temperatures (Camilo-Alves & Mourão 2006; Attias *et al.* 2018). Despite the existing evidence on the causal relationship of environmental temperatures on changes in xenarthran behavior, previous studies have focused only on evaluating one specific movement aspect at a time (e.g. distance moved or habitat use), limiting a comprehensive understanding of this process. Hence, an integrative perspective is necessary to

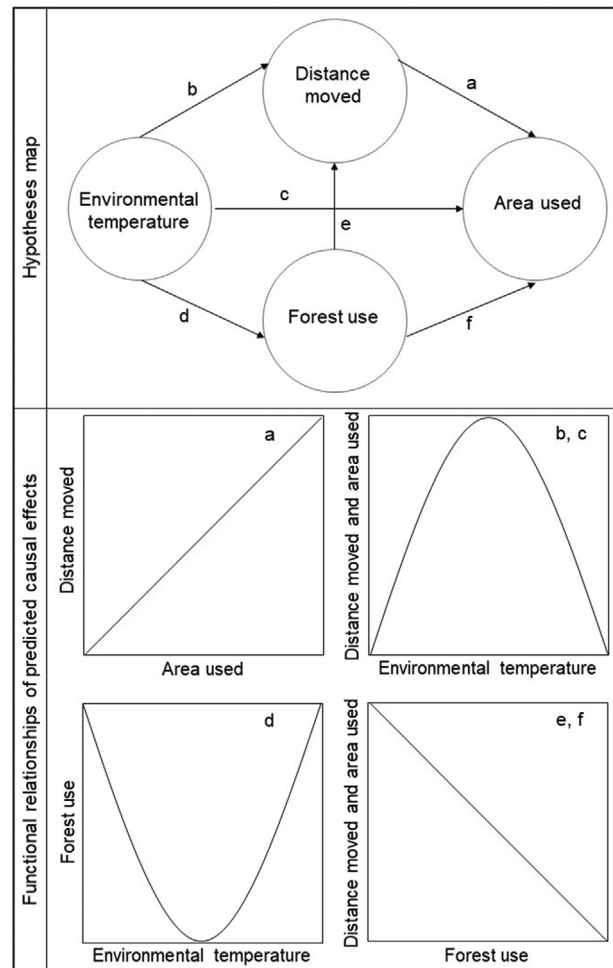


Figure 1 Hypotheses map integrating the effects of environmental temperature to the movement patterns of giant anteaters (*Myrmecophaga tridactyla*). Considering that distance moved and area used are positively correlated (a), we expect giant anteaters to decrease both distance moved and area used in extreme environmental temperatures (b,c). We also expect them to increase the use of forest habitats under extreme environmental temperatures (d). Furthermore, by increasing forest use, we expect giant anteaters to reduce their distance moved and area used (e,f).

evaluate the influence of environmental temperature on the movement patterns of these animals.

We use giant anteaters as a model organism to understand how environmental temperature can shape movement behavior, disentangling 3 of its main components: distance moved, area used, and habitat use. Considering the common positive relationship between distance moved and area used (Rosten *et al.* 2016; Fig. 1a), and because giant anteaters modify their

activity with environmental temperature (Camilo-Alves & Mourão 2006), we expect them to decrease distance moved and area used when environmental temperatures are extreme (Fig. 1b,c). Because forests act as thermal shelters (Mourão & Medri 2007), we also expect giant anteaters to increase forest use under extreme temperatures (Fig. 1d). As giant anteaters normally use forests to rest and open areas for activity (Medri & Mourão 2005), we predict they would reduce displacement (reducing both distance moved and area used) when increasing the forest use, when compared to open areas (Fig. 1e,f).

MATERIALS AND METHODS

Study sites

The study was carried out in 7 savannah areas along the Brazilian territory: (1) the peri-urban area of Boa Vista city, Roraima state (2°49'10"N, 60°40'17"W); (2) the peri-urban area of Rondonópolis city, Mato Grosso state (18°28'15"S, 54°38'08"W); (3) Emas National Park, Goiás state (18°15'50"S, 52°53'33"W); (4) Serra da Canastra National Park, Minas Gerais state (20°18'16"S, 46°35'56"W); (5) Santa Barbara Ecological Station, São Paulo state (22°48'59"S, 49°14'12"W); (6) Baía das Pedras Ranch, Mato Grosso do Sul state (19°18'9"S, 55°47'4"W), and (7) Nhumirim Ranch, Mato Grosso do Sul state (18°59'6"S, 56°37'24"W). Our study sites span over an extensive area of the species distribution (Fig. 2), which occurs from the south of Guatemala to the north of Argentina (Eisenberg & Redford 1999).

The landscape of all studied sites is composed of mosaics of open grasslands, scrublands, savannahs and woodlands (Abdon *et al.* 1998; Ramos-Neto & Pivello 2000; Durigan *et al.* 2007; Couto-Junior *et al.* 2010; Campos & Barbosa 2011; Rohling & da Silva 2012). Besides these habitat types, the landscape of Santa Barbara Ecological Station also includes anthropic landscape elements, such as exotic forests of *Pinus* sp. and *Eucalyptus* sp. (Durigan *et al.* 2007). At Baía das Pedras Ranch and Nhumirim Ranch, the open grasslands are subjected to seasonal flooding, with permanent and temporary salty and freshwater ponds that create a naturally fragmented landscape (Abdon *et al.* 1998; Fig. 2).

All study sites have a tropical climate, with rainy summers and dry winters. Maximum temperatures often exceed 40 °C, while the absolute minimum is close to 0 °C at some sites (Alvares *et al.* 2013). To test our hypotheses in this wide range of study areas with potentially complex land use, we classified the observed habitats in 2 categories: forest or non-forest. We classified as forest

all canopy areas with some thermal buffering capacity in comparison to adjacent open areas (De Frenne *et al.* 2019), which were 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.

Capture and movement data collection

Between 2002 and 2017, we tracked 52 adult giant anteaters (29 males and 23 females), with uniformly distributed body mass (mean = 32.5 kg, range = 21 to 41 kg; Table 1). We searched for giant anteaters by horse or by pickup trucks at low speed (maximum of 20 km/h) during daytime, mainly in days with milder temperatures. Once we saw the anteaters, we performed captures using dip nets, dart-guns, or a blowpipe. Anteaters were sedated with an intramuscular injection of a combination of tiletamine and zolazepan, known as Zoletil, in a concentration of 2 mg/kg. The anesthetic induction took between 4 and 6 min. All the procedures were conducted in accordance with the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes 2016) and were approved by the Brazilian government (capture authorizations: COTEC 429/2014 D23/2013 PGH, SISBIO 38326-5, SISBIO 16010-1, SISBIO 13994-1, IBAMA 02038.000114/06-90, IBAMA 02014.000419/07-97, IBAMA 02014.002009/05-64, IBAMA 02001.000656/09-94). The captured individuals were sexed, weighed, and equipped with GPS-harnesses during anesthesia. None of the tracking devices exceeded 3% of the animals' body mass. The GPS devices were programmed to record location points (hereafter relocations) at intervals ranging from 5 to 60 minutes, depending on the study site (Table 1).

Daily movement estimates

We investigated the influence of environmental temperature on giant anteater's movement patterns at a daily scale (see Morales *et al.* 2010). The daily scale allows us to make good estimates of distance moved, area used, and habitat use over the course of a complete cycle of activity (from the beginning of activity to the end of the resting period). The giant anteaters' activity is usually crepuscular and nocturnal, beginning in the early evening and ending early in the morning (Medri & Mourão 2005). Thus, we considered the operational day of giant anteaters to be initiated at 1800 hours and finished at 1759 hours of the next day, which comprises a complete circadian cycle.

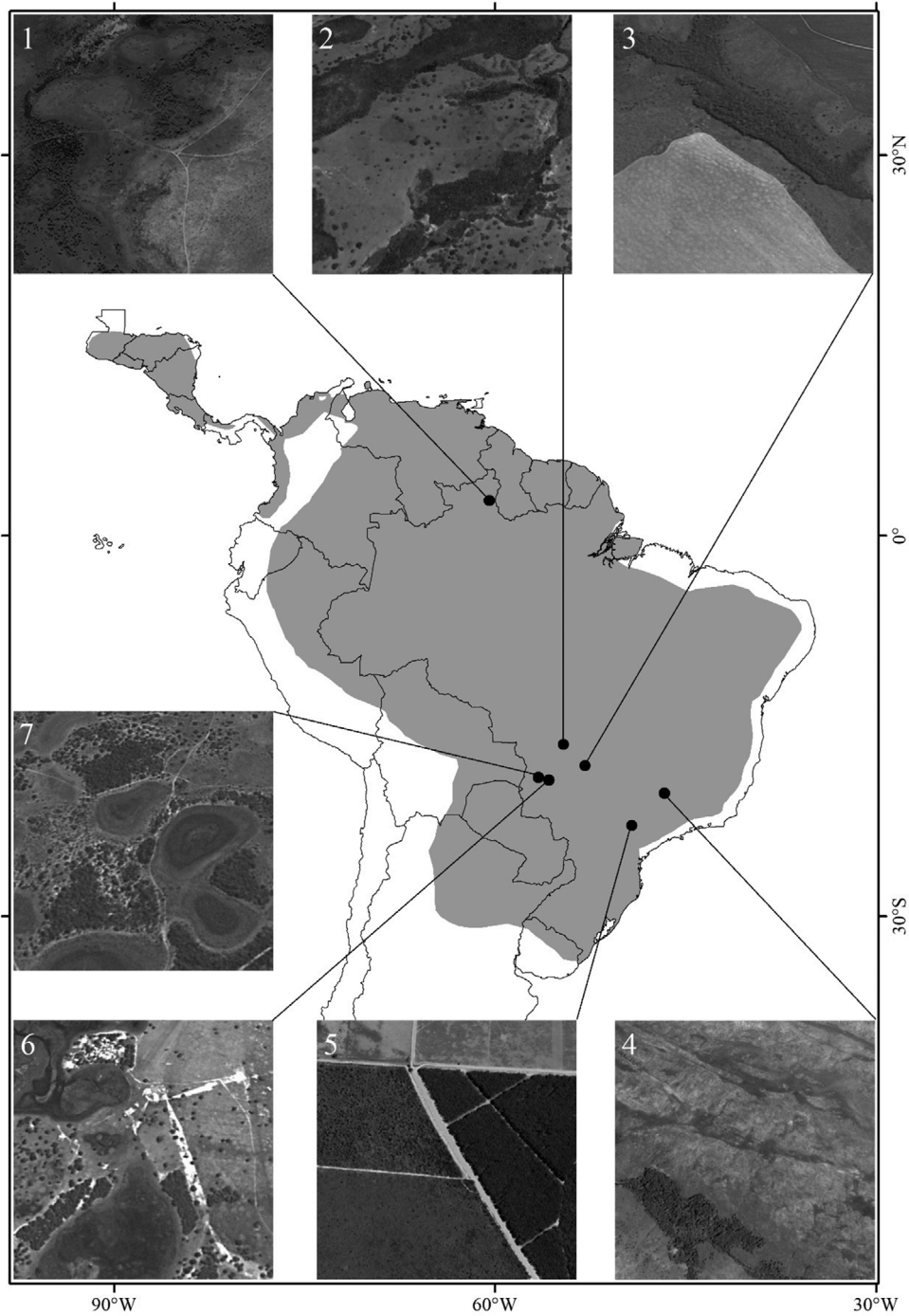


Figure 2 Study sites (black circles), covering a large part of the distribution of giant anteaters (*Myrmecophaga tridactyla*) (grey area; IUCN 2014). Map insets contain LANDSAT satellite images of each study site: (1) peri-urban area of Boa Vista city, (2) peri-urban area of Rondonópolis city, (3) Emas National Park, (4) Serra da Canastra National Park, (5) Santa Barbara Ecological Station, (6) Baía das Pedras Ranch, and (7) Nhumirim Ranch.

Table 1 Individual characteristics of the giant anteaters (*Myrmecophaga tridactyla*) captured and monitored at each study site as well as monitoring effort and protocol

Site	Number of individuals by sex	Body mass (mean and range; kg)	Mean monitoring duration (days)	Range monitoring duration (days) [†]	Sample regime (min) [‡]
1	2 F, 1 M	30.5 (27–32)	18.2	17–19	30
2	0 F, 1 M	25.0	39.8	—	20
3	3 F, 7 M	31.8 (24–40)	2.9	1–7	60
4	1 F, 1 M	31.5 (31–32)	4.1	2–7	15
5	4 F, 4 M	35.0 (21–39)	87.7	8–140	5
6	8 F, 6 M	31.6 (25–39)	257.6	50–486	20
7	5 F, 9 M	35.3 (25–41)	13.6	3–53	10

[†]Minimum and maximum number of individual monitoring days. [‡]Time interval between GPS fixes (minutes).

Because days with less than 10 relocations would fail to represent the daily movement of giant anteaters (see Börger *et al.* 2006), we excluded these days from the analysis. Then, we used the R package *trajr* to characterize the daily trajectories of individuals (McLean & Skowron Volponi 2018; R Core Team 2019). We discretized each daily trajectory to 20-min interval fixes, standardizing the daily sample size of relocations for all individuals. This procedure allows us to control for the potential effect of the daily sample size.

Using the individuals' standardized trajectories, we computed daily estimates of: (1) distance moved, (2) area used, and (3) intensity of use of forested habitats (hereafter forest use). Distance moved was measured as the sum of Euclidean distances between consecutive relocations. Area used was estimated through a minimum convex polygon (MCP) including 95% of relocations. Despite overestimating home range, MCP was chosen as it is appropriate for day range estimations when sample sizes are small (Seaman *et al.* 1999; Boyle *et al.* 2009). The daily estimates of the giant anteater's distance moved (mean = 2143 m, range = 26 to 12 175 m) and area used (mean = 0.3 km², range = 0 to 5.1 km²) were highly variable with a left skewed distribution. Forest use was measured as the ratio between the number of relocations found inside forest habitats and the total number of relocations of the day (ranging from 0 to 1).

Environmental temperature data collection and daily mean estimate

Hourly air temperature measurements were recorded by 6 automatic meteorological stations of the National Institute of Meteorology of Brazil (INMET) and ranged

from –0.6 to 42.2 °C during our monitoring period. The closest meteorological station to each study site was selected for local temperature characterization. The Euclidean distance between the center of the study areas and the closest meteorological station ranged from 3 to 90 km (mean = 42 km; Table S1, Supporting Information). The difference between the mean altitude of the study areas and the altitude of the corresponded meteorological stations did not exceed 40 m (Table S1, Supporting Information). To assess if the temperatures of the meteorological stations could provide a good representation of the macroclimate experienced by animals in the study sites, we conducted 2 tests. In 2 of our study sites, we estimate the correlation between temperature measurements provided by the GPS harnesses that were equipped with temperature sensors ($N = 12$) and those provided by the closest meteorological station ($r_{\text{pearson}} < 0.80$; Figs S1 and S2, Supporting Information). In addition, we checked the correlation between temperatures recorded by 2 meteorological stations 110 km apart from each other ($r_{\text{pearson}} = 0.89$; Fig. S3, Supporting Information). These tests ensured the reliability of the meteorological stations' temperature data for macroclimate characterization.

We estimated the average air temperature during 24-h periods that corresponded to the giant anteaters' operational days. Although we did not use to the daily minimums and maximums temperatures experienced by the animals at each day in our analysis, we graphically show (Fig. S4, Supporting Information) that, at our study sites, where the climate is tropical, daily mean temperatures offer a good representation of minimum and maximum temperatures of the day. In other words, days with low mean temperature usually offered colder mornings and colder nights than days with high mean temperature. Therefore, in our case, the daily mean air temperature (hereafter

environmental temperature), which it ranged from 7.0 to 36.1 °C during our monitoring period, is a suitable proxy of the macroclimate conditions of the day.

Structural equation modeling

In order to obtain an integrative view of the effect of environmental temperature on the movement of giant anteaters (specifically distance moved, area used, and forest use), we used mixed Structural Equations Modeling (mixed-SEM; Kline 2016). Mixed-SEM was estimated using the PiecewiseSEM package (Lefcheck 2016) available in the R environment (R core Team 2019). The estimated coefficients were standardized to allow comparison between the parameters. We checked for model adjustment of our mixed-SEM, which measures the discrepancy between predicted and observed covariance matrices of our causal predictions, based on Fischer's C test (Holst & Budtz-Jørgensen 2013).

We chose mixed-SEM because it allowed us to include random variables to deal with the hierarchical structure of our data (i.e. daily replications were nested within individuals and individuals' replication were nested within the sites). This nesting structure deals with individual and spatial autocorrelation of the data. The temporal autocorrelation between successive sampling days within individuals was controlled using a first-order autoregressive autocorrelation term (Lefcheck 2016). The mixed-SEM allowed us to estimate the indirect, direct, and total effects among variables. 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). The standard error of indirect effects was estimated using the bootstrap method (Preacher & Hayes 2004).

In addition, we included in the model 2 variables intrinsic to the animals to act as control: sex and body mass. We believe that sex can be related to individual body mass (sexual size dimorphism, Lindenfors *et al.* 2007), and that both sex and body mass should explain part of variability observed in movement, as found in many mammals' species (e.g. Vieira *et al.* 2019 and Lidgard *et al.* 2020).

RESULTS

Control variables

Males were larger than females ($\beta_1 = 0.08$, $R^2 = 0.45$, $P = 0.01$). While males had mean body mass of 35 kg (ranging from 25 to 41 kg), females had mean body mass of 32 kg (ranging from 21 to 39 kg). Neither sex nor body

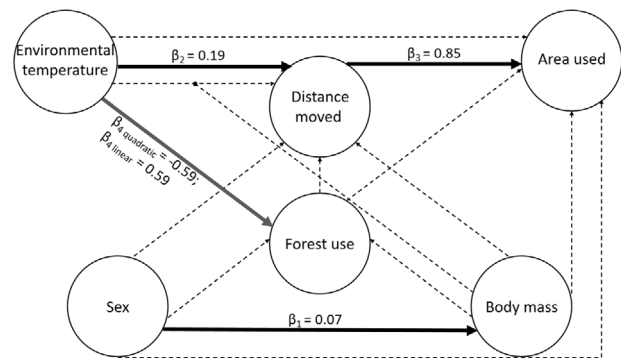


Figure 3 Estimated coefficients by a mixed-Structural Equations Model, integrating how environmental temperature variation drives 3 aspects of the movement (distance moved, area used, and habitat use) of giant anteaters (*Myrmecophaga tridactyla*), while controlling for the effect of intrinsic variables (sex and body mass). Positive effects are indicated by black arrows and negative effects by grey arrows. Dashed arrows indicate non-significant effects ($P > 0.05$). The black point indicates a non-significant interactive effect between body mass, environmental temperature, and distance moved. The standardized coefficients (β) represent the relative strength of effects. β_1 to β_3 are the coefficients of linear regressions. β_4 quadratic and β_4 linear are the quadratic and linear coefficients of a quadratic equation, respectively.

mass influenced distance moved ($P_{\text{sex}} = 0.43$, $P_{\text{bodymass}} = 0.54$), area used ($P_{\text{sex}} = 0.08$, $P_{\text{bodymass}} = 0.35$) or forest use ($P_{\text{sex}} = 0.11$, $P_{\text{bodymass}} = 0.09$). In addition, body mass had no influence in the effect of environmental temperature on distance moved (interactive effect, $P = 0.9$, Fig. 3).

Effects of environmental temperature on movement

The model revealed a positive and linear influence of environmental temperature on distance moved ($\beta_2 = 0.19$, $P < 0.01$; Figs 3 and 4). The effect of environmental temperature on area used did not occur directly ($P = 0.08$), but it occurred indirectly, mediated by distance moved, and it was also linear and positive ($\beta_2 \times \beta_3 = 0.16$, $P = 0.01$; Figs 3 and 4). Environmental temperature had a negative quadratic effect on the use of forest habitats (β_4 quadratic = -0.59 , β_4 linear = 0.59 , $P = 0.01$; Figs 3 and 4). Forest use had no effect on distance moved ($P = 0.92$) or area used ($P = 0.56$). Our model explained a substantial amount of the observed variation in distance moved ($R^2 = 0.56$), area used ($R^2 = 0.87$), and forest use ($R^2 = 0.47$).

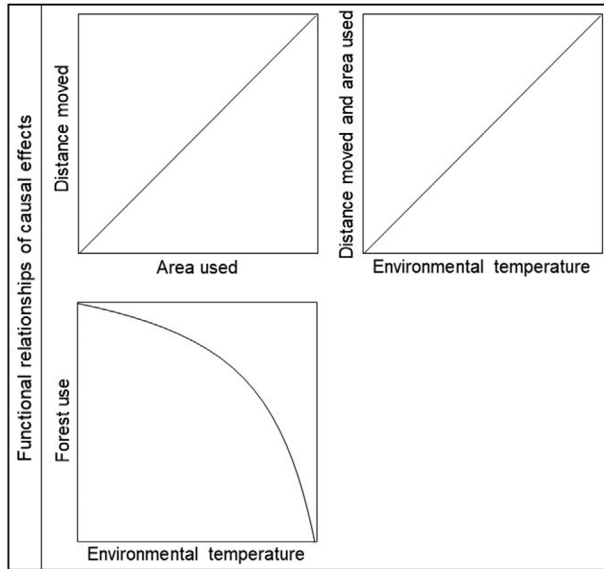


Figure 4 Shape of the estimated relationship between distance moved and area used, as well as of the estimated total effects of environmental temperature on the descriptive variables of giant anteater's (*Myrmecophaga tridactyla*) movement (distance moved, area used, and forest use). The effect of environmental temperature on the area used was mediated by the distance moved (Fig. 3).

Overall, our results show that giant anteaters increased both their distance moved and area used with increasing environmental temperature (Fig. 4). Besides, increasing environmental temperature also led them to decrease forest use, increasing the use of open areas (Figs 3 and 4). On the other hand, with decreasing environmental temperature, giant anteaters moved shorter distances, used smaller areas, and increased the use of forest patches inside their home ranges.

DISCUSSION

In this study, we tracked individuals from different localities over a period of 15 years, which allowed us to obtain a representative sample of the movement patterns of giant anteaters under a wide variety of environmental conditions. These data represent a large number of individuals, including both sexes and almost the whole range of body mass expected for adult wild giant anteaters (22–45 kg; Eisenberg & Redford 1999). The use of mixed-SEM allowed us to disentangle the effects of the environmental temperature variation on 3 different aspects of animal movement: distance moved, area used, and habitat use. By standardizing the number of reloca-

tions, we were able to analyze movement data with different sampling protocols (see Börger *et al.* 2006). Our approach also allowed us to include intrinsic variables that could mask the effects of environmental temperature on movement, such as sex and body mass. Furthermore, we were able to compare the direction and intensity of direct and indirect effects of the environmental temperature on animal movement. Hence, our approach provided a more comprehensive understanding of animal movement, as it considers the effects of many factors in the same model. Only with this integrative approach could we characterize movement patterns and disentangle their relationships with environmental temperature while considering the intrinsic characteristics of the organism (see Lefcheck 2016).

Sexual size dimorphism, with larger males, is common among mammalian species (Lindenfors *et al.* 2007) in which males provide little or no parental care (Trivers 1972). This is the case of the giant anteaters, which are essentially solitary and whose parental care is provided only by females (Eisenberg & Redford 1999). In addition, the opportunity for sexual selection on male size is expected in species with a polygynous mating system where body mass influences the access of males to receptive females (Trivers 1985). Despite the sexual size dimorphism, male and female giant anteaters had similar movement patterns. We would expect larger animals moving more than small ones because they require more space to meet their energetic requirements (McNab 1963; Isaac *et al.* 2012). However, giant anteaters have a low basal metabolic rate (McNab 1984) and the influence of their body mass on their energetic demand should be smaller than on mammals with higher metabolic rates (see Nagy 2001). Thus, this intraspecific effect might not be large enough to be detected within this body mass range.

Contrarily to our expectations, giant anteaters increased their displacement (both distance moved and area used) and the use of open areas with the increasing environmental temperature. We expected that increasing temperature would lead giant anteaters to decrease displacement (to decrease muscular heat production) and increase forest use (since forests are thermal buffers and offer protection against solar radiation) to avoid overheating (Lin *et al.* 2017; De Frenne *et al.* 2019). However, giant anteaters present a low metabolic rate and low body temperature (McNab 1984), which could help them prevent overheating within the thermal range experienced in this study. This species increases its activity duration on hot days (Camilo-Alves & Mourão 2006), which could allow them to travel longer distances and, consequently, occupy larger areas. In addition, on hotter days,

giant anteaters can increase their nocturnality, (Mourão & Medri 2007), avoiding direct solar radiation. Hence, they can explore open areas, which are habitats likely to present high food resource availability (Redford 1985). However, it is possible that environmental temperatures higher than the range that we recorded here could lead giant anteaters to overheating, constraining their movements and leading to increase in forest use.

As we predicted, giant anteaters exhibited 2 important behavioral strategies to reduce body heat loss and the energetic costs of thermoregulation with decreasing environmental temperature: they reduced displacement and increased forest use. We believe that reducing the distance moved and area used on colder days could be due to the reduction in the duration of activity. Both giant anteaters and three-banded armadillos have been recorded to reduce their activity duration on cold days (Camilo-Alves & Mourão 2006; Attias *et al.* 2018). These animals can reduce their thermal conductivity while inactive by altering body posture (McNab 1984, 1985; Medri & Mourão 2005). Also corroborating our results, previous studies showed that both giant anteaters and yellow armadillos increase the selection strength of forests on cold days (Camilo-Alves & Mourão 2006; Attias *et al.* 2018). Forest habitats buffer rain and chilly winds, thus offering feasible shelters against low environmental temperatures (Lin *et al.* 2017; De Frenne *et al.* 2019). Furthermore, McNab (1984) showed that the body temperature of a giant anteater can drop by 2.7 °C at low environmental temperatures (<15 °C). Due to their low metabolic rate and their low body temperature, giant anteaters are particularly adversely affected by low environmental temperatures and forest patches are extremely important for their thermoregulation.

Here, we showed how unsuitable environmental temperatures can constrain mammals' movement, decreasing their access to energetic resources in the landscape and, consequently, their fitness. We also underscored the importance of habitat heterogeneity for mammal thermoregulation. Giant anteaters seem to be more susceptible to cold than to heat, probably due to their low production of body heat (McNab 1984). However, it is reasonable to expect that mammal species with high metabolic rates would also decrease their movement and increase forest use on very hot days, since both strategies also help avoid overheating (Mitchell *et al.* 2018). In the Pantanal, one of our study sites, the forest areas were recorded to be up to 5 °C warmer in the coldest days of monitoring and up to 8 °C cooler in the hottest days, when compared to adjacent open areas (Mourão & Medri 2007). The importance of forests as thermal shelters for thermoregulation

on both cold and hot days has been shown for other xenarthrans such as the three-banded armadillo (Attias *et al.* 2018). In addition, other mammals, like the moose (*Alces alces*), have been recorded using forests as thermal shelters at high temperatures (Melin 2014). Hence, it is possible that even mammals with low metabolic rates could use forests patches also to avoid overheating when environmental temperatures of open areas are so high that their ability to dissipate heat is insufficient (Lovegrove *et al.* 2012).

The frequency and/or intensity of extreme weather events is predicted to increase in future years due to climate change (Meehl *et al.* 2000; Coumou & Rahmstorf 2012). This implies that mammals would rely even more on forests to deal with more frequent unsuitable thermal conditions. Hence, preserving forest patches will be essential for animal conservation (Mourão & Medri 2007; Desbiez & Medri 2010), even for species commonly associated with open habitats, like giant anteaters (Eisenberg & Redford 1999). This species is listed as Vulnerable by IUCN and, in several parts of its geographical distribution, it is in danger of extinction due to loss of savannah areas (Miranda *et al.* 2014). In the Brazilian territory, where this study was conducted, massive agricultural expansion has dramatically decreased forest patches on savannah areas (Tollefson 2018) and the current government is even encouraging a rapid expansion of deforestation (Rochedo *et al.* 2018). We emphasize the need to preserve forest patches to offer suitable conditions for behavioral thermoregulation of tropical mammals. Furthermore, linking animal movement and environmental conditions by integrating the variables that drive their relationships, as we did here, is needed to predict how mammals will respond to deforestation and climate change. This response will depend on the metabolic traits of the species. Next steps should focus on generating simulations that will lead to predictions on how habitat selection varies depending on environmental temperature and forest loss for different mammal species.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Distance between the study site and its corresponding meteorological station as well as the areas' elevation

Figure S1 Comparing temperature measurements between the meteorological station and GPS harness temperature sensor in São Paulo state.

Figure S2 Comparing temperature measurements between the meteorological station and the GPS harness temperature sensor in Mato Grosso state.

Figure S3 Comparing temperature measurements between two meteorological stations 110 km apart.

Figure S4 Relationship between the mean air temperature of the day with minimum and maximum daily temperatures.

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