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

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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.

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 (Levesque & Marshall, 2021; Maloney et al., 2017). 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

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(Mota-Rojas et al., 2021; Terrien et al., 2011). 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 (Buchholz et al., 2019; Chmura et al., 2018).

Among the behavioural aspects influenced by environmental temperature, animal movement stands out since many thermoregulatory behavioural strategies are closely related to movement (Mota-Rojas et al., 2021; Terrien et al., 2011). 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; Perea-Rodríguez et al., 2022; Tatler et al., 2021). 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 favourable 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 (Mota-Rojas et al., 2021; Terrien et al., 2011). 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, Ortega, Bertassoni et al., 2021). 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 (Attias et al., 2018; Giroux, Ortega, Bertassoni et al., 2021; Maccarini et al., 2015; Mourão & Medri, 2007). 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 (Attias et al., 2018; Camilo-Alves & Mourao, 2005). 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 (Attias et al., 2018; Camilo-Alves & Mourao, 2005; De Frenne et al., 2019; Giroux, Ortega, Bertassoni et al., 2021). 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 & Mourao, 2005; Di Blanco et al., 2017). 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 & Mourao, 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 & Mourao, 2005; Mourão & Medri, 2007). Regarding habitat selection, we expected giant anteaters to select forests during both rest and activity in cold weather (Camilo-Alves & Mourao, 2005; Giroux, Ortega, Bertassoni et al., 2021), while hot and mild weathers would lead to selection for forest areas mainly during resting (prediction 3; Camilo-Alves & Mourao, 2005). This is because forests act as thermal shelters during both cold and hot spells (De Frenne et al., 2019; Mourão & Medri, 2007), but also present physical obstacles to movement (Ferreras, 2001; Giroux, Ortega, Oliveira-Santos, et al., 2021). 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 (see Appendix, Fig. A1). 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).

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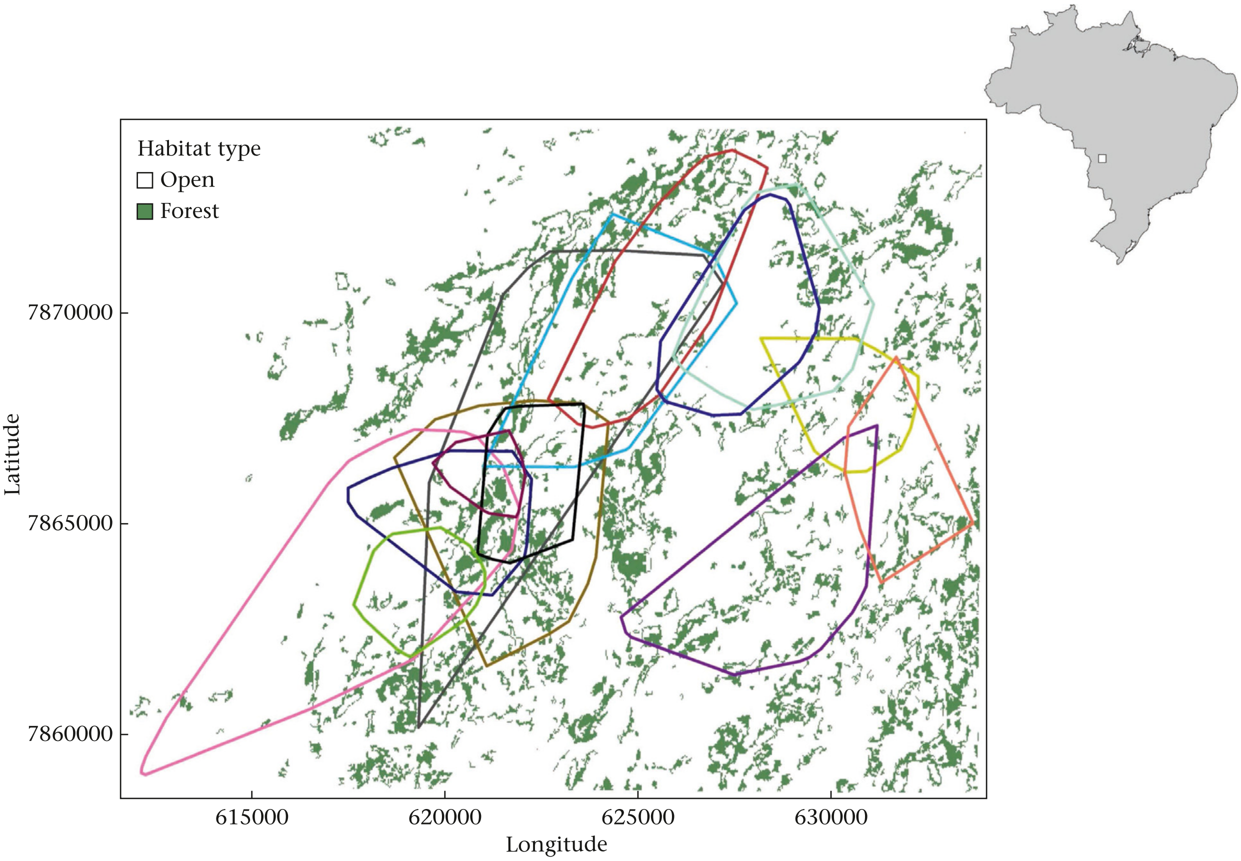

Figure 1. Land use–land cover (LULC) classification of the study area according to the Mapbiomas database, in 2015. Habitat categories are summarized as open and forested habitats, showing the naturally fragmented landscape. Each polygon represents the area used by a GPS-tracked giant anteater across the monitoring period. Inset shows a map of Brazil, indicating the study area in the Pantanal wetlands with a white square.

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. A2). 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). We provide individual information on capture date, sex, body mass, sampling regime and monitoring period in the Appendix (Table A1).

Ethical Note

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 also followed the guidelines of the Brazilian Institute of Environment and Renewable Natural Resources, under approved permits: 02014.000419/07-97 and 02001.000656/09-94.

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 centre 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: $r = 0.89$; Appendix, Fig. A3). 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 (Appendix, Fig. A4; see details on the environmental temperatures experienced by individuals in Table A2).

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%

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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' package (Hijmans et al., 2014), available in the R environment (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 behaviour. 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).

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' (McClintock & Michelot, 2020; Signer et al., 2019). Taken together, all the movement data preprocessing resulted in the elimination of 7.4% and 3.4% of locations for HMM and iSSA, respectively (see details in the Appendix, Table A3).

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 McClintock et al., 2012; Morales et al., 2004). 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; McClintock et al., 2012; Morales et al., 2004).

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, pseudoresidual 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 (Avgar et al., 2016; Thurfjell et al., 2014). 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 (Avgar et al., 2016; Forester et al., 2009). 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 (hour/24 × 2 × 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. 2, Appendix, Table A4). 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. 2, Appendix, Table A4). On average, 53% of individual location points corresponded to the moving state, varying from 21% to 65% among individuals.

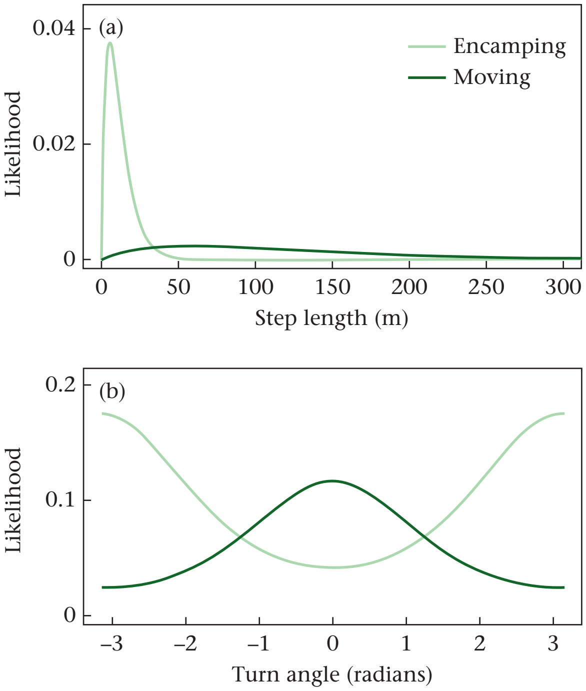

Figure 2. Probability distribution of observed step lengths (above) and turning angles (below) of monitored giant anteaters. Lines represent the estimated densities of each behavioural state (encamping and moving).

The transition probabilities between giant anteaters' behavioural states were influenced by the interaction between environmental temperature, time of day and habitat used (Table 1). 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 probability of moving between 10% and 95% throughout the day and they were mostly nocturnal, with higher probability of moving between 2000 and 0200 hours (Fig. 3). 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 0200 and 1700 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 1900 hours and midnight (Fig. 3). The high short-term thermal amplitude of the study area (Appendix, Fig. A1) indicates that giant anteaters' activity adjustments in response to

Table 1
Estimates (95% confidence interval, CI) of the effect of environmental temperature, time of day and habitat type (open and forest; using open as the reference category) as well as their interactions on transition probabilities between giant anteaters behavioural states

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)**

Significant effects are shown in bold.

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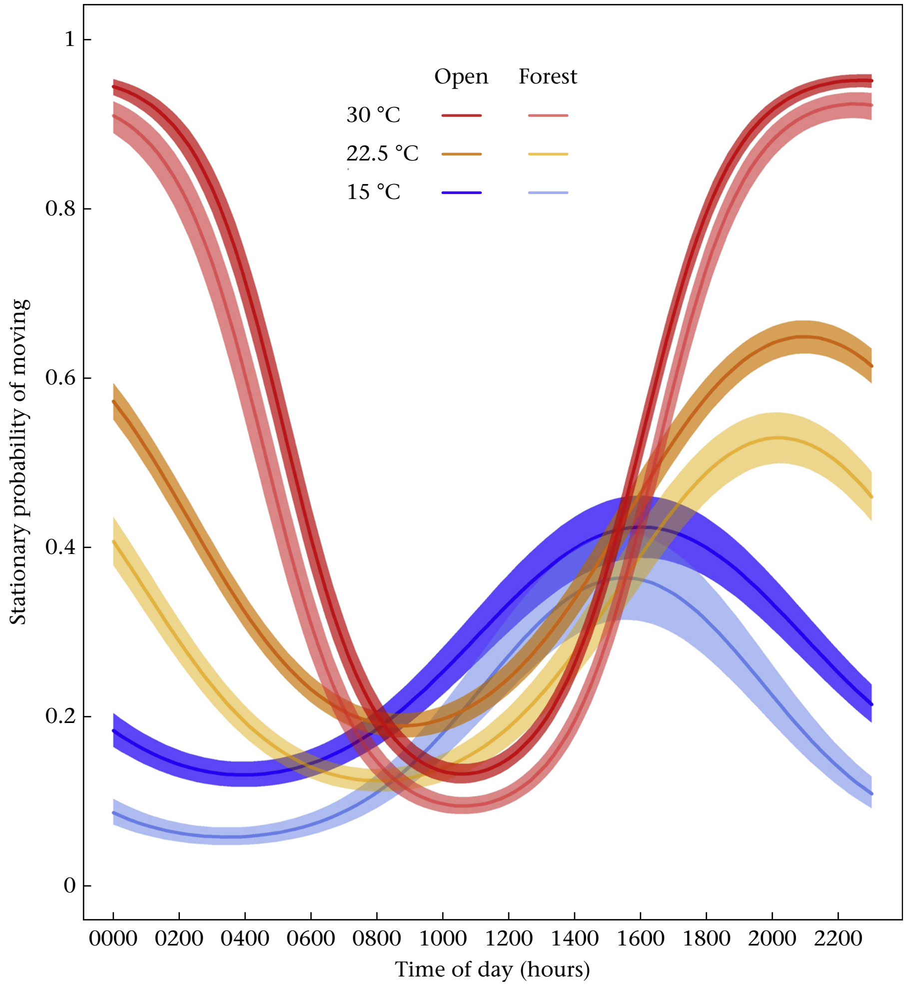

Figure 3. Stationary probability of moving by giant anteaters as a function of time of day under three temperature conditions (cold: 15 °C; mild: 22.5 °C; hot: 30 °C) and in two habitats (open areas: darker colours; forests: lighter colours). Temperatures 15 °C and 30 °C, respectively, represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C). The coloured bands represent the 95% confidence intervals.

environmental temperature changes should happen on a scale of days (see Appendix, Fig. A5 as an example).

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 1). 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 1, Fig. 3). 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. A6).

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 4, 5, Appendix, Table A5). 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, which indicates an increase in diurnal activity and nocturnal rest. These effects could be observed on both open and forested habitats. 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 4, 5).

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 A5). 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 4, 5), 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 4, 5, Appendix, Table A5), the iSSA showed that the interaction between environmental temperature and time of day modulated the selection strength for forests, relative to open habitats (Table 2, Fig. 6). 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 2, Fig. 6). For instance, at 30 °C, giant anteaters selected forests between 0900 and 1500 hours (with a selection peak at noon), but strongly avoided forests for most of the day, with a peak of avoidance at midnight (Fig. 6). In contrast, at

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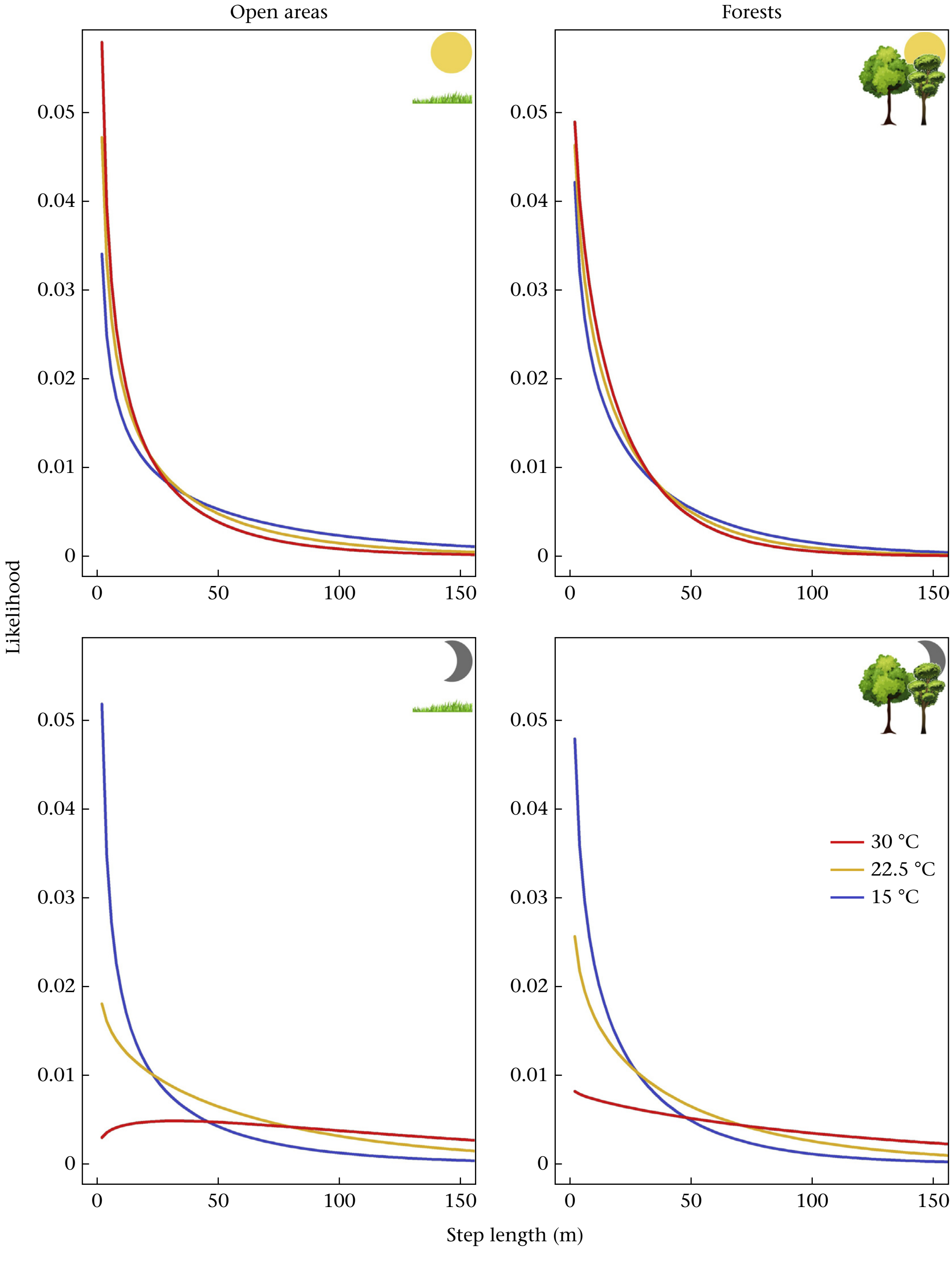

Figure 4. Probability distribution of step lengths of giant anteaters under three temperature conditions (cold: 15 °C; mild: 22.5 °C; hot: 30 °C) at two times of the day (noon above; middle of night below) and in two habitat types (open areas, forests). Temperatures 15 °C and 30 °C, respectively, represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C).

15 °C, they selected forests between 1800 and 0600 hours, with peak of selection at midnight and peak of avoidance at noon. At 22.5 °C, the individuals used forests as available between 0900 and 1500 hours, avoiding them during most of the daytime. Males and females presented similar responses (Appendix, Fig. A7).

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

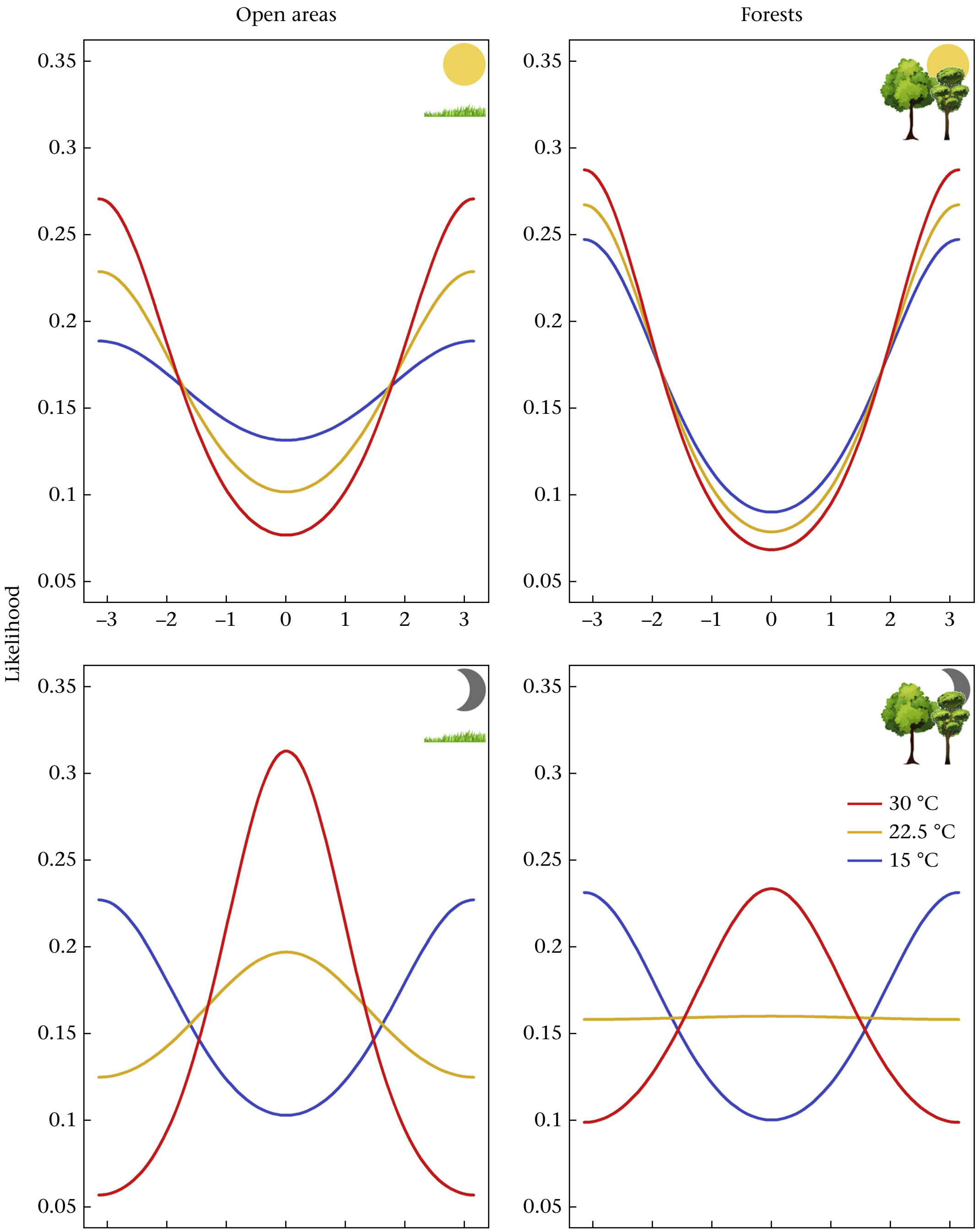

Figure 5. Probability distribution of turning angles of giant anteaters under three temperature conditions (cold: 15 °C; mild: 22.5 °C; hot: 30 °C) at two times of the day (noon above; midnight below) and in two habitat types (open areas, forests). Temperatures 15 °C and 30 °C, respectively, represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C).

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

Table 2

Estimates (95% confidence interval, CI) of the effect of environmental temperature, time of day and habitat type (open areas as the reference category and forests) as well as their interactions on habitat selection of giant anteaters

Covariate	Estimated effect (95% CI)	*P*
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)**	**$<10^{-16}$**

Significant effects are shown in bold.

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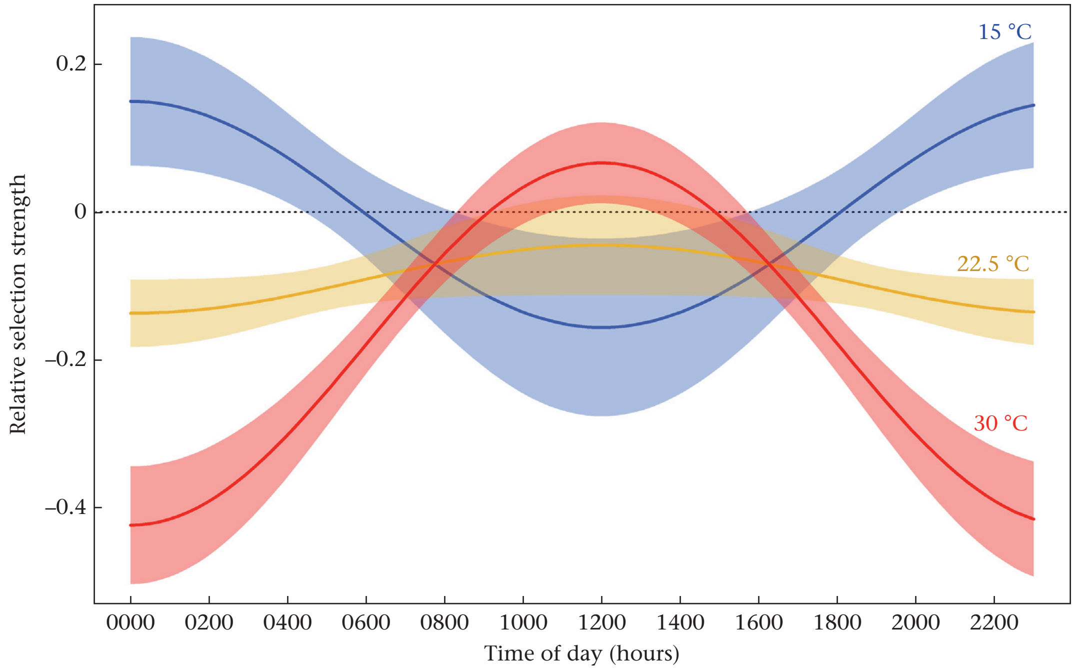
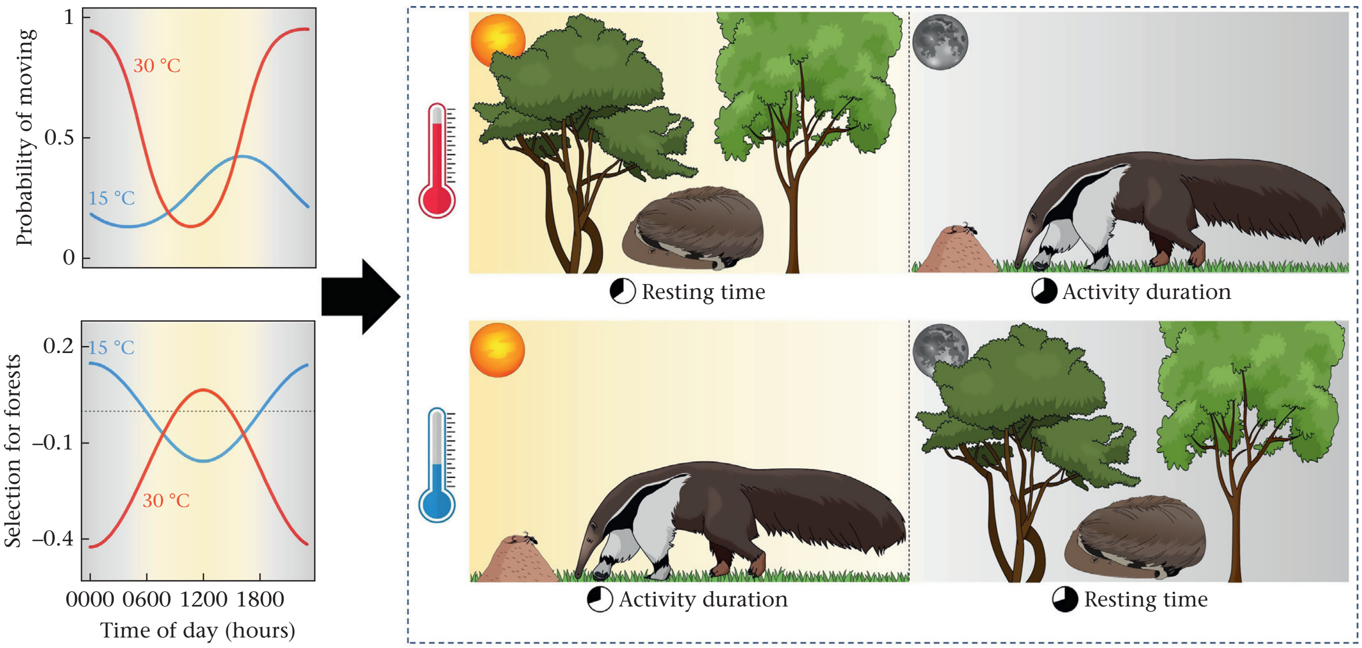


Figure 6. Selection strength of giant anteaters for forests, relative to open habitats, as a function of time of day on three environmental temperatures (cold: 15 °C; mild: 22.5 °C; hot: 30 °C). The coloured bands represent the 95% confidence intervals. Temperatures 15 °C and 30 °C, respectively, represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C).

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



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

Figure 7. Take-home illustration showing how giant anteaters use activity modulation and selection for forests as behavioural thermoregulatory mechanisms.

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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., 2017; Giroux, Ortega, Bertassoni et al., 2021). 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 cold (Terrien et al., 2011). However, by reducing locomotor activity, animals compromise foraging behaviour, 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. Attias et al., 2018; van der Vinne et al., 2014). 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 & Mourao, 2005; Di Blanco et al., 2017; Mourão & Medri, 2007). 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, Ortega, Bertassoni et al., 2021). 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 fragmented landscapes would compromise giant anteater's thermoregulation. Similarly to giant anteaters, many other open-area mammals living in fragmented landscapes increase selection for forests as environmental temperature deviates from their TNZ (e.g. Ewald et al., 2014; Marchand et al., 2015; 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, Ortega, Oliveira-Santos, et al., 2021). 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).

Conclusions

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 behaviour, 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. 7). 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.

Author Contributions

A.G. and L.G.R.O.-S. conceptualized the article. A.L.J.D. acquired funding for, participated in and supervised the giant anteater data collection. A.G. conducted analysis, created figures and wrote the original draft. L.G.R.O.-S. provided feedback on data analyses. Z.O. provided important suggestions and feedback regarding thermal

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ecology. All authors reviewed and edited the manuscript, substantially improving it.

Data Availability

Giant anteaters are listed as a vulnerable species across their distribution. Therefore, location data of this species are sensitive. All movement data used in analyses are available for visualization from the Movebank database (www.movebank.org; study name: Myrmecophaga tridactyla Pantanal). Data download requests may be sent to the Center for Species Survival Brazil (SSC) – International Union for Conservation of Nature (IUCN) (csebrasil.contato@gmail.com / fabiana@cpsg.org).

Declaration of Interest

None.

Acknowledgments

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Appendix

Table A1
Individual characteristics of the captured giant anteaters as well as monitoring effort and sampling regime

ID	Capture date	Sex	Body mass (kg)	Sampling regime (min)	Monitoring period (days)
Annie	20 Jun 2015	F	30.0	20	84.0
Berenice	25 Oct 2015	F	39.0	20	386.0
Brigite	31 Jul 2013	F	26.3	30	339.7
Buba	8 Jul 2015	F	30.0	20	69.1
Henriqueta	15 Aug 2014	F	28.1	20	159.9
Justin	31 May 2016	M	30.0	20	144.7
Kiko	25 Oct 2015	M	35.0	20	363.2
Lubetta	19 Jun 2015	F	28.0	20	51.0
Mariah	26 Sep 2016	F	33.3	20	122.4
Pdg	18 Jun 2015	M	36.0	20	509.7
Xororo	25 Jul 2013	M	37.2	30	387.8
Zezinha	27 Jul 2013	F	35.0	30	279.8
Fergus	1 Jul 2016	M	35.0	20	378.0
Jacques	31 Jul 2016	M	25.0	20	366.7

Table A2
Weather and habitat conditions experienced by giant anteaters across their monitoring period

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

Table A3
Number of observations of the original movement data of GPS-tracked giant anteaters in comparison to the number of observations used in the hidden Markov model (HMM) and in the integrated step selection analysis (iSSA)

ID	Number of observations		
	Original	HMM	iSSA
Annie	4529	3983	4274
Berenice	27 162	26 042	26 740
Brigite	11 857	10 092	11 105
Buba	788	408	528
Henriqueta	8717	8627	8677
Justin	10 273	10 104	10 104
Kiko	25 866	25 680	25 741
Lubetta	521	361	382
Mariah	8730	8612	8612
Pdg	32 908	30 039	31 525
Xororo	16 733	15 203	16 868
Zezinha	11 604	9793	10 027
Fergus	27 139	26 921	26 921
Jacques	17 178	13 108	15 632

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Table A4
Estimates and 95% confidence intervals of the parameters describing giant anteater behavioural states (encamping and moving)

Estimated parameter	Encamping	Moving
Step length mean (m)	11.74 (11.67; 11.80)	121.63 (120.94; 122.32)
Step length SD (m)	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)

Step lengths were modelled with gamma distribution, and turning angles were modelled with von Mises distribution.

Table A5
Estimates (95% confidence interval, CI) of the effect of step length (SL) and turning angle (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

Covariate	Estimated effect (95% CI)	*P*
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)**	**$<10^{-16}$**

Significant effects are shown in bold.

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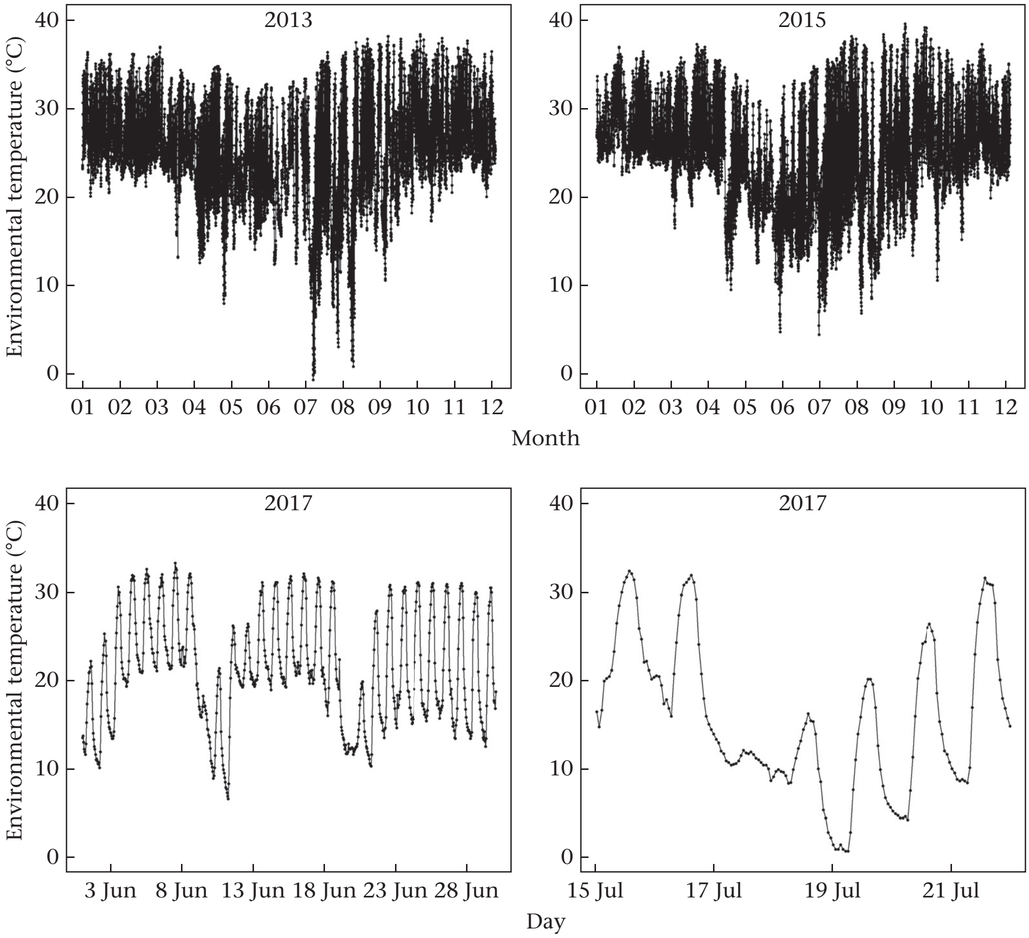

Figure A1. Variogram of the environmental temperature in Baía das Pedras ranch, Pantanal wetlands, Brazil, across the study period. The top graphics show how environmental temperature varied across 2013 and 2015, where it is possible to see abrupt drops in environmental temperature caused by cold fronts. The bottom graphics show in detail the high thermal amplitude of the study area across a month and a week in 2017.

Figure A2. Healthy adult giant anteater equipped with a GPS harness (TGW-4570-4 Telonics) in Baía das Pedras ranch, Pantanal wetlands, Brazil.

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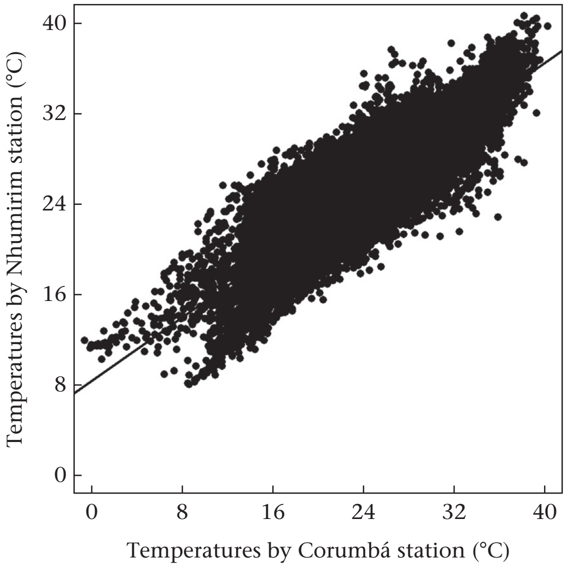

Figure A3. Relationship between temperature measurements of two meteorological stations 110 km apart from each other and differing 40 m on altitude, one in Nhumirim Ranch (18°98′5″S, 56°61′9″W) and another in Corumbá city (19°00′2″S, 57°67′5″W), both located in the Mato Grosso do Sul state, Pantanal wetlands, Brazil (Pearson correlation: $r = 0.89$).

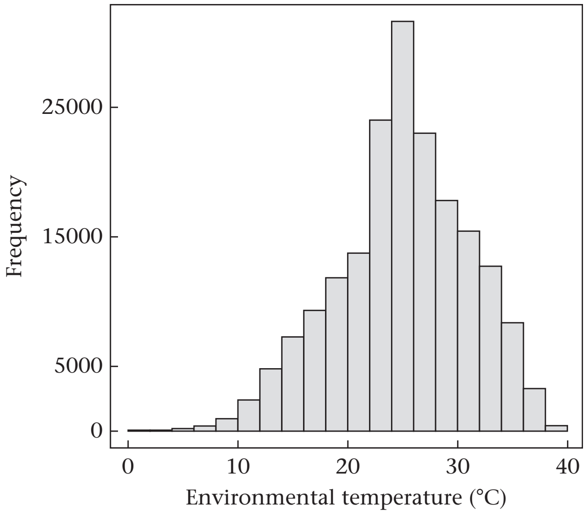

Figure A4. Histogram of the environmental temperatures experienced by GPS-tracked giant anteaters across their monitoring period in Baía das Pedras ranch, Pantanal wetlands, Brazil.

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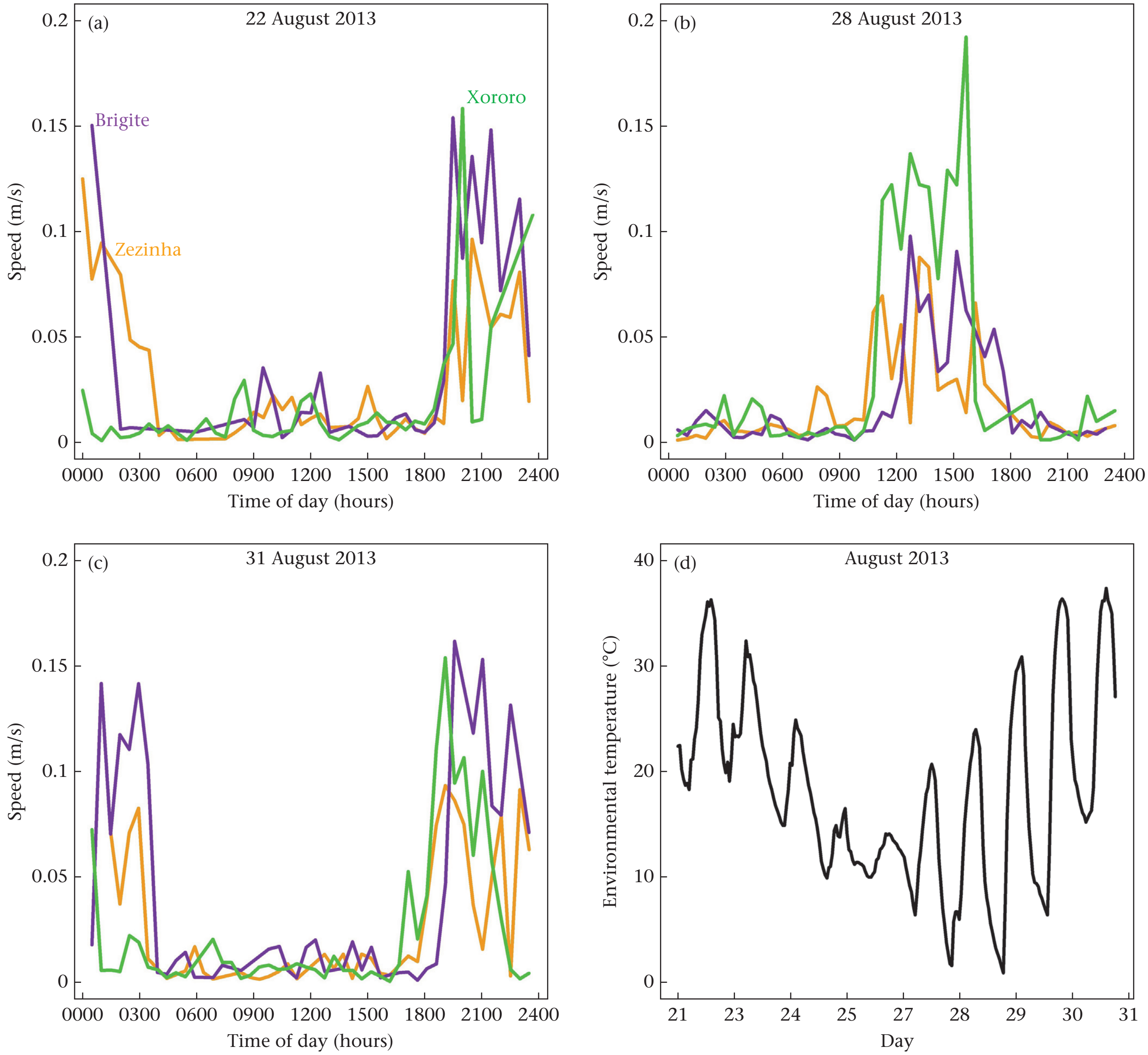

Figure A5. Giant anteaters speed (m/s) across time of day on (a) 22 August 2013, (b) 28 August 2013 and (c) 31 August 2013, as well as the variogram of the environmental temperature in the study site from 22 August 2013 to 31 August 2013 (d). The three individuals monitored in this period (Brigite: purple; Zezinha: yellow; Xororo: green) 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, demonstrating that giant anteaters can switch activity period from nocturnal to diurnal and vice versa on a scale of days in response to abrupt drops in environmental temperature.

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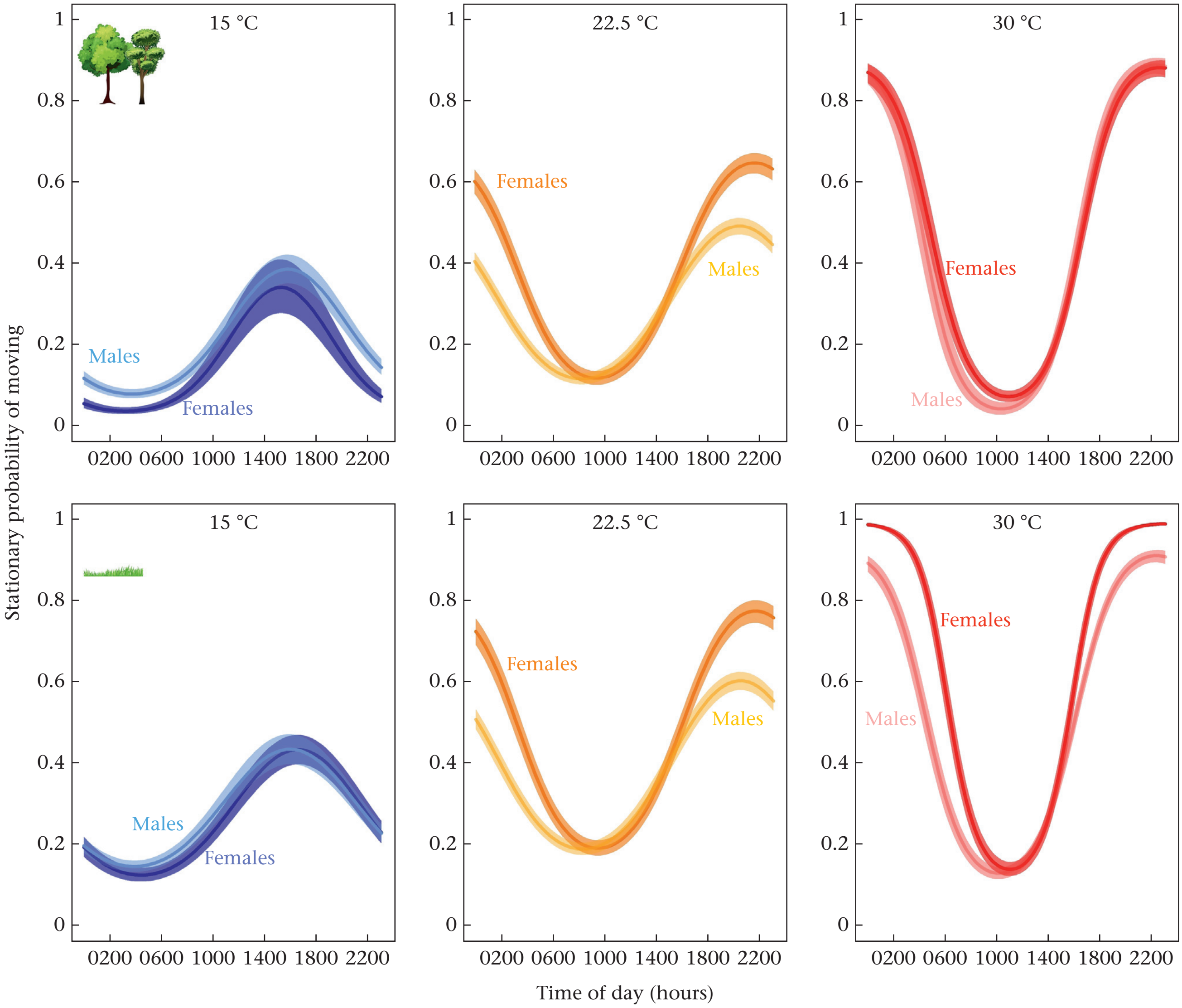

Figure A6. Stationary probability of moving by male and female giant anteaters as a function of time of day under three temperature conditions (cold: 15 °C; mild: 22.5 °C; hot: 30 °C) and in two habitats (open areas, bottom; forests, top). Temperatures 15 °C and 30 °C, respectively, represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C). The coloured bands represent the 95% confidence intervals.

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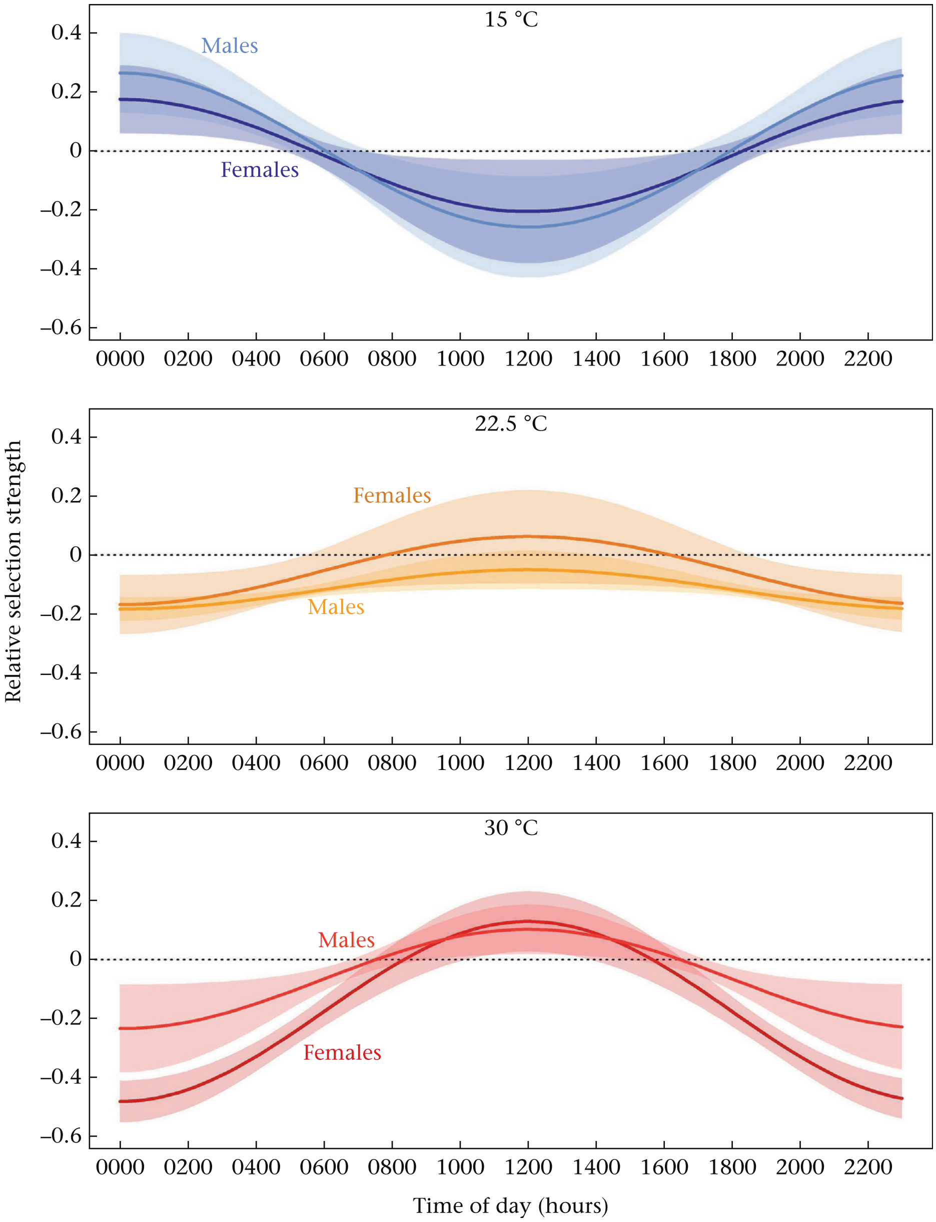

Figure A7. Selection strength of male and female anteaters for forests, relative to open habitats, as a function of time of day on three environmental temperatures (cold: 15 °C; mild: 22.5 °C; hot: 30 °C). The coloured bands represent the 95% confidence intervals. Temperatures 15 °C and 30 °C, respectively, represent 1.25 standard deviations below and above the mean environmental temperature experienced by individuals (22.5 °C).

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