



Effects of air temperature on habitat selection and activity patterns of two tropical imperfect homeotherms

Nina Attias^{a,*}, Luiz Gustavo Rodrigues Oliveira-Santos^a, William F. Fagan^b,
Guilherme Mourão^c

^a Ecology Department, Federal University of Mato Grosso Do Sul, Campo Grande, MS, Brazil

^b Biology Department, University of Maryland, College Park, MD, U.S.A.

^c Embrapa Pantanal, Corumbá, MS, Brazil

ARTICLE INFO

Article history:

Received 8 June 2017

Initial acceptance 22 August 2017

Final acceptance 19 March 2018

Available online 24 May 2018

MS. number: A17-00466R

Keywords:

armadillo

GPS telemetry

Pantanal wetlands

spatial ecology

step selection functions

Xenarthra

In this study, we aimed to evaluate how air temperature is related to variation in activity patterns and habitat selection by two species of tropical armadillos, which are imperfect homeotherms. Although their behaviour is little studied, armadillos provide valuable models for understanding how physiology affects mammalian behaviour in response to environmental changes. We used GPS devices to track yellow armadillos, *Euphractus sexcinctus*, and southern three-banded armadillos, *Tolypeutes matacus*, at three sites of the Pantanal wetlands, Brazil. We used linear mixed-effects models to evaluate the variation in the timing and duration of activity patterns according to changes in air temperature. We fitted step selection functions to evaluate the effects of cover type, diel cycle and air temperature on armadillo habitat selection. Our models suggest that *E. sexcinctus* activity during the daytime decreases as air temperature increases. In contrast, *T. matacus* shows less variation, maintaining a predominantly nocturnal activity pattern. However, as air temperature decreases, activity periods of *T. matacus* are of shorter duration and peak earlier in the day. Both species should select forested areas when experiencing air temperatures outside their thermoneutral zones, as these areas act as thermal shelters. This study provides specific examples of the dynamic nature of activity patterns and habitat selection, and illustrates how thermal constraints, which vary dynamically over the daily cycle and among days, can alter behaviour. Our results highlight the importance of habitat heterogeneity for the long-term conservation of animal species that rely on behaviour to achieve adequate thermoregulation.

© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Animals use a combination of physiological, physical and behavioural processes to achieve thermal balance (Tattersall & Cadena, 2010). The question of how animals vary their behavioural patterns in response to environmental changes is central in ecology (Krebs & Davies, 1993). Because temperature can strongly affect animal behaviour and because global climate change may affect organisms directly via physiological stress, understanding the relationship between environmental conditions and behaviour is increasingly important (Gunderson & Leal, 2016; Harley, 2011). Climate change could become the major global threat to biodiversity in the next decades, surpassing habitat loss (Leadley et al., 2010).

Animal activity, behaviour and movement patterns are influenced by intrinsic (e.g. physiological and neurological state) and

extrinsic factors (e.g. presence or absence of competitors or predators, ambient temperature and rainfall; Nathan et al., 2008; Rietveld, Minors, & Waterhouse, 1993). In general, behavioural decisions are guided by trade-offs between gaining access to resources and minimizing negative effects (e.g. physiological stress), ultimately maximizing individual fitness. In addition, even though we are unable to predict whether species will be able to adapt fast enough to keep up with the rapid pace of climate change, adaptive responses could involve either microevolution and/or plasticity (which can provide shorter-term responses; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Besides microevolutionary physiological adaptations, behavioural changes may involve both timing of activity and selection of habitats (Bellard et al., 2012; Gunderson & Leal, 2016; Tattersall & Cadena, 2010).

Changes in the use of space can be accomplished through large-scale movements (e.g. migration) or finer-scale movements (e.g. habitat and microhabitat selection; Bellard et al., 2012). Habitat selection is a dynamic process that is likely to be influenced by a

* Correspondence: N. Attias, Rua das Laranjeiras 441/201, Laranjeiras, Rio de Janeiro, RJ 22240-000, Brazil.

E-mail address: nina.attias@gmail.com (N. Attias).

variety of temporally variable factors, like temperature (Sunde, Thorup, Jacobsen, & Rahbek, 2014). Furthermore, diel cycles of activity allow animals to modulate their behaviour according to predictable environmental changes and to choose the appropriate time for a given response or activity (Aronson et al., 1993). Ambient temperature can exert strong, direct, short-term effects on endogenous circadian rhythms, altering diel activity patterns (Rietveld et al., 1993).

The superorder Xenarthra (Mammalia) comprises armadillos (Cingulata), anteaters and sloths (Pilosa) and contains some of the most morphologically specialized terrestrial extant mammals (Möller-Krull et al., 2007). Armadillos possess low body temperatures (i.e. 32.7–35.5 °C), low basal metabolic rates (i.e. ~50% of what would be expected for a nonxenarthran placental mammal with similar body mass) and high thermal conductance (i.e. 130–200% of what would be expected for a nonxenarthran placental mammal with similar body mass). Like the other xenarthrans, armadillos are considered imperfect homeotherms. That is, even though armadillos are able to generate body heat like other placental mammals, they have a limited capacity to regulate it (McNab, 1985). Armadillos build burrows that they use to rest, to shelter from predators and to avoid adverse environmental conditions (McDonough & Loughry, 2008). Animals that take refuge when conditions are not suitable for activity are good models for understanding how thermal constraints can affect animal behaviour (Gunderson & Leal, 2016). As burrowing, imperfect homeotherms, armadillos should present conspicuous behavioural responses (entering or exiting burrows) to air temperature changes and, as such, are valuable models for understanding how physiology affects decision making in mammals (Maccarini, Attias, Medri, Marinho-Filho, & Mourão, 2015).

Instead of a dense layer of fur, armadillos possess a carapace composed of osteoderms that covers most of their body surface. The presence of this carapace confers armadillos a high thermal conductance and brings important physiological and ecological consequences (Superina & Loughry, 2012; Tattersall & Cadena, 2010). The thermoneutral zone is defined as the ambient temperature range where the animal's metabolic rate is independent of temperature (McNab, 2002). The increased thermal conductance provided by the presence of the carapace results in an increase of armadillos' lower limit of thermoneutrality and leads to small differences between body temperature and environment (McNab, 1985, 2002). Because this lower limit is high in armadillos, the ambient temperature is often below it, even in tropical regions. Consequently, armadillos often need to expend more energy to keep their body heat than if the ambient temperature were within their narrow thermoneutral zone (McNab, 1985).

Metabolic thermoregulation is especially costly from an energetic standpoint (Liwanag, 2010), especially for these low-metabolism, imperfect homeotherms. To reduce such energetic costs, xenarthrans can adopt behavioural strategies to overcome unfavourable environmental conditions and mitigate thermal limitations. Variations in habitat use and activity patterns have been recorded for xenarthrans such as screaming hairy armadillos, *ChaetophRACTUS vellerosus*, giant anteaters, *Myrmecophaga tridactyla*, and yellow armadillos, *Euphractus sexcinctus*, as responses to temperature variation (e.g. Greigor, 1985; Maccarini et al., 2015; Mourão & Medri, 2007).

Here, we aim to evaluate whether air temperature drives variation in activity patterns and habitat selection by two species of imperfect homeotherms (*E. sexcinctus* and three-banded armadillos, *Tolypeutes matacus* Desmarest, 1804) in a tropical region. The six-banded armadillo (*E. sexcinctus*) is known to be a diurnal and conspicuous burrowing species, widely distributed throughout Brazil and other parts of South America. This 4.4 kg armadillo is an

opportunistic carnivorous–omnivorous species (Medri, Mourão, & Rodrigues, 2011) that has a basal metabolic rate of 42% and a thermal conductance of 172% of what would be expected for a non-xenarthran placental mammal of its size (McNab, 1985). It is found in open areas, savannahs, shrublands, dry and semideciduous forests (Eisenberg & Redford, 1999). Roig (1969) proposed that 30 °C would be its optimal ambient temperature, and the graphical inspection of Figure 2D of the work of McNab (1980) indicates that its thermal neutral zone ranges from 26 °C to about 34 °C. Nevertheless, *E. sexcinctus* has been recorded active at instant air temperatures between 13.2 and 36.2 °C in the Pantanal wetlands of Brazil (Maccarini et al., 2015; see Methods for area description).

In contrast, the southern three-banded armadillo (*T. matacus*) is restricted to the dry forests of western Brazil, Bolivia, Paraguay and Argentina (Wetzel, Gardner, Redford, & Eisenberg, 2008). Like its congener, this species can roll into a ball as a defence mechanism. *Tolypeutes matacus* weighs ca. 1.1 kg and is classified as an opportunistic insectivore (Bolkovic, Caziani, & Protomastro, 1995). It has one of the lowest basal metabolic rates among armadillos (i.e. 31% of what would be expected for a mammal of its size) and a thermal conductance of 133% of that expected (McNab, 1980). When resting, it can use burrows and other types of shallow shelters (Attias, Miranda, Sena, Tomas, & Mourão, 2016). In the studied areas, this species is mostly nocturnal (Attias, 2017), although its activity pattern may be influenced by temperature and rainfall (Eisenberg & Redford, 1999). To date, many aspects of its biology and ecology are poorly known. Eisentraut (1932) stated that between 16 °C and 28 °C, *T. matacus* maintains a constant body temperature of about 32 °C, but its body temperature increases if the ambient temperature becomes higher than 28 °C. However, the graphical inspection of Figure 1A in McNab (1980) indicates that the thermal neutral zone of *T. matacus* ranges from 28 °C to about 34 °C.

Because the diel activity pattern adopted by an animal is one of the most effective and generalized ways to minimize the influence of unfavourable biotic and abiotic factors (Layne & Glover, 1985), we expect armadillos to alter their activity patterns to avoid physiologically unfavourable ambient temperatures. Shifts in timing of behaviours (on a daily and/or seasonal scale) could help species cope with changes in cyclical abiotic factors (such as temperature). In a climate change scenario, animals could adjust their daily activity rhythms to match the energetic costs of a different climatic condition (Bellard et al., 2012). We hypothesize that, on days with low temperatures, armadillos should increase their activity during the warmest hours of the day. Moreover, because different habitats are subject to different levels of solar radiation and have different capabilities to buffer the ambient temperature, we hypothesize that armadillos may select different habitats as a function of air temperature, allowing them to control their body temperature by spending more time in cooler or warmer habitats as conditions dictate. We expect these relationships because thermoregulation appears to be the most important proximate factor influencing habitat selection by terrestrial heterotherms (Reinert, 1993), and is thus likely to affect the behaviour of imperfect homeotherms as well. In particular, we expect armadillos to shift between open areas and forested areas to find microclimates closer to their thermoneutral zone. Because forested areas tend to act as temperature buffers, being cooler than open vegetation habitats on hot days and warmer on cold days (Mourão & Medri, 2007), we expect armadillos to select forested habitats or habitats with denser vegetation cover on those days featuring extreme air temperatures (either unusually hot or unusually cold) in comparison to typical conditions in the Pantanal. This behaviour should facilitate armadillo thermoregulation without the increased cost of metabolic changes imposed on animals with low basal metabolic rates and low-energy diets.

Furthermore, even though both species face similar thermo-regulatory constraints, they present subtle physical (i.e. body mass, carapace anatomy), physiological (i.e. thermal conductance) and ecological (i.e. diet specialization, predation susceptibility) differences. Hence, the two species can present distinct behavioural responses to temperature variation, potentially increasing or decreasing their niche overlap, exacerbating or offsetting ecological interactions (e.g. predator–prey, intraguild competition; Creel, Creel, Creel, & Creel, 2016). Thus, we hypothesize that *E. sexcinctus* might need to be more flexible in relation to its activity period than *T. matacus*. This would be due to *E. sexcinctus*'s relatively higher thermal conductance and tendency to forage in open habitats, which could make it more vulnerable to temperature variations. This could potentially alter the degree of overlap of the temporal niche dimension between the two species.

METHODS

Study Area

This study was carried out at three sites, 120–350 km apart, located in the Pantanal wetlands of midwestern Brazil (Fig. 1). The Pantanal is a large Neotropical wetland, extending 210 000 km² over Brazil, Bolivia and Paraguay (Mittermeier et al., 2003). Its climate is classified by Köppen's system as tropical subhumid (Aw), with well-defined rainy (October–March) and dry (April–September) seasons and average annual rainfall of 1100 mm. Summers are hot and rainy with maximum temperatures that often exceed 40 °C. Except during cold fronts coming from the south, when air temperature can drop abruptly, winters are hot and dry. The annual mean minimum temperature is about 20 °C, but the absolute minimum is close to 0 °C (Calheiros & Fonseca, 1996). Nevertheless, the Pantanal wetlands of Brazil should follow the global trend, with an estimated mean warming ranging from 5–7 °C until the end of this century (Marengo, Alves, & Torres, 2016).

The Nhimirim Ranch (site 1; 18°59'26"S; 56°39'14"W) is an experimental station of the Brazilian Agricultural Research Corporation - Embrapa Pantanal, with an area of 43 km² and an altitude of 98 m above sea level (Fig. 1), located in Corumbá municipality, Mato Grosso do Sul state. This almost pristine landscape comprises a natural mosaic of habitat types, consisting of large natural grassland areas, permanent and temporary ponds surrounded by native grassland vegetation, and savannah and woodland areas (Abdon, Silva, Pott, Pott, & Silva, 1998; Fig. 2a). At this site, we captured and monitored *E. sexcinctus* in undisturbed areas (i.e. all of the above-mentioned habitat types).

The Santa Teresa Ranch (site 2) is located in the Serra do Amolar Mountain Range, in Corumbá municipality, Mato Grosso do Sul state, in the western limits of the Brazilian Pantanal (18°17'51"S, 57°30'35"W; Fig. 1). The variable relief in the area (90–1000 m of altitude) influences the vegetation structure. The nonflooded areas are dominated by deciduous and semideciduous forests, while pastures and humid and dry savannahs occupy the areas subjected to flooding (Tortato, Layme, Crawshaw, & Izzo, 2015; Fig. 2b). This private property is part of the Network for the Protection and Conservation of Serra do Amolar and only 3% of its 630 km² were converted into exotic pasture (*Brachiaria* spp.) for cattle ranching. At this site, we captured and monitored *T. matacus* at the lowest-altitude areas, in both disturbed and undisturbed habitats.

The Duas Lagoas Ranch (site 3; 16°10'13"S, 58°11'12"W) is located in the transition zone between the Pantanal and Cerrado ecoregions, in Cáceres municipality, Mato Grosso state (Fig. 1). This 74 km² ranch is owned by the private company Floresteca. Its main economic activity is a teak plantation (*Tectona grandis*; 42 km²), but there are also areas of exotic pasture (*Brachiaria* sp.) dedicated to

cattle ranching (12 km²) and a small sugarcane plantation (0.24 km²; Fig. 2c). Besides these areas, the ranch encompasses 16.3 km² of native remnants of cerrado woodland, scrub savannah, grassland and gallery forest. At this ranch, we captured and monitored *T. matacus* almost exclusively at disturbed areas.

Using RapidEye satellite imagery (taken in 2011), the habitat types of the study areas were summarized into habitat categories as follows: forest, grassland (combining exotic and native grasslands in one category), shrubland and sugarcane plantation (Fig. 2). Some habitat types were not available at all study sites: native grasslands were only available at sites 1 and 2, shrublands only at site 1, and sugarcane plantations only at site 3. We used this classification to make inferences about the density of arboreal vegetation cover in each habitat type and their potential temperature-buffering effect. We considered forested areas as areas of high arboreal cover and temperature-buffering potential (sensu Mourão & Medri, 2007), areas of shrubland and sugarcane plantation as areas with intermediate arboreal cover and comparatively lower temperature-buffering potential and grassland areas as areas with reduced or no arboreal cover directly subjected to daily fluctuations of temperature.

Ethical Note

This study was performed under License No. 39872-3 (Chico Mendes Institute for Biodiversity Conservation). All procedures were accompanied or performed by a veterinarian and followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research, the ASAB/ABS Guidelines for the use of animals in research, and were approved by the ethics committee of the Federal University of Mato Grosso do Sul (process 570/2013).

Capture and Tracking Methods

We captured animals by hand during surveys performed by foot, horse, all-terrain vehicles or pickup trucks. At site 1, from February to August 2014, we captured and tracked 17 *E. sexcinctus*. Of these, 10 were males (nine adults, one cub) and seven were adult females (Supplementary Material 1). We captured and monitored 21 *T. matacus*, 10 at site 2 (four adult males, three adult females, two subadult females, one female cub), from November 2014 to April 2015, and 11 at site 3 (six adult males, four adult females, one subadult male), from June to August 2015 (Supplementary Material 1). Age class was determined based on body mass. *Euphractus sexcinctus* weighing less than 2 kg were classified as cubs (Medri, 2008). For *T. matacus*, we defined adults as individuals weighing more than 1 kg and subadults as weaned individuals weighing less than 1 kg.

Captured animals were temporarily contained in ventilated plastic boxes or cloth bags until processing. Information on age, sex and mass were obtained for each individual. We equipped the animals with a package containing a glue-on VHF radio (model R1920, Advanced Telemetry Systems, Inc., Isanti, MN, U.S.A.) and a GPS tracking device (noncommercial prototype used in other studies of the Wildlife Laboratory of Embrapa Pantanal, e.g. Oliveira-Santos, Forester, Piovezan, Tomas, & Fernandez, 2016). The package mass (~50 g) corresponded to up to 4% of *T. matacus* body mass and 1% of *E. sexcinctus* body mass. We attached the tracking devices to the tail of *E. sexcinctus* using adhesive tape (Maccarini et al., 2015) and to the posterior part of the pelvic shield of *T. matacus*, using flexible cyanoacrylate super glue and/or epoxy resin, following a protocol commonly used for hard-shelled turtles (e.g. Seminoff, Resendiz, & Nichols, 2002). This procedure did not prevent *T. matacus* from rolling into a ball. All individuals were monitored through GPS telemetry, using a 5 min interval between fixes. We tracked animals



Figure 1. Location of the Pantanal wetlands (grey area) in South America and of the three study sites: (1) Nhimirim Ranch; (2) Santa Teresa Ranch; (3) Duas Lagoas Ranch.

daily, at varying times between 0600 and 2200 hours, to ensure GPS functioning, assess animal welfare and locate resting sites.

Even though all the procedures described above could be accomplished under physical restraint, some of the animals were anaesthetized through an intramuscular injection in the hindlimbs to enable the collection of biological samples used in other studies. Eleven individuals of *E. sexcinctus* and 19 of *T. matacus* were anaesthetized with a combination of ketamine (Quetamina® 10%; Vetnil, Louveira, SP, Brazil), 30 mg/kg for *E. sexcinctus* and 25 mg/kg for *T. matacus*, xylazine 0.5 mg/kg (Rompun® 2%; Bayer, Shawnee Mission, KS, U.S.A.), midazolam 0.5 mg/kg (Dormire® 0.5%; Cristalia, Itapira, SP, Brazil) and atropine 0.02 mg/kg (Atropina® 1%; Fagra; Gasparotto et al., 2017).

Activity

To define the activity status of armadillos in the GPS data, we used an adaptation of the 'residence time' method (Barraquand & Benhamou, 2008). Active periods were characterized as the time period that an individual was not inside its shelter and was moving. Each time an individual exited a shelter, moved and returned to a shelter was scored as an activity bout. We characterized the bout duration as the time elapsed between consecutive events of shelter exiting and shelter entering by the same armadillo. Thus, the total activity duration per day was the summed duration of all activity bouts during a 24 h period. Because *T. matacus* was predominantly nocturnal, we estimated the total activity duration for this species as the sum of bout durations from noon on one day until 1159 hours on the next day. Because *E. sexcinctus* is mostly diurnal/crepuscular,

total activity duration for this species was estimated as the sum of bout durations from midnight until 2359 hours on the same day. Temperature measures were taken hourly on each day of animal monitoring by automatic stations of the Brazilian National Institute of Meteorology (INMET) located in the municipality of each study site. Corumbá municipality station is located at 112 m above sea level and is the closest station to both sites 1 (100 km; 100 m above sea level) and 2 (80 km; 100–160 m above sea level). Cáceres municipality station is located at 124 m above sea level and is 50 km away from site 3 (140 m above sea level). A linear mixed-effects model (LME) was fitted to test the fixed effect of mean daily air temperature on total activity duration per day. In this analysis, we evaluate the relationship between daily average air temperature and total daily activity duration (i.e. one measure of activity per day). The model was fitted using individual identity and study site as random nested effects, and accounting for the autocorrelation structure between samples taken from the same individual on consecutive days. LME models were implemented through the function 'lme' of the R package 'nlme' (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016).

To evaluate the relationship between activity probability and hourly air temperature along the diel cycle, we first subsampled the individual trajectories to fixes matching 1 h intervals. The distance moved during each 1 h interval was estimated as the sum of all distances moved between the original (5 min) steps within that hour. Then, the square root of these distances was used as a proxy for an activity index. The square-root transformation of the distances moved was adopted to represent the activity index because it better captures the activity information associated with short steps, usually recorded when the armadillos were engaged in encamped activities. Also, this transformation facilitated normalization of the model residuals. When this distance was equal to zero, it was assumed that the animal was inactive during that 1 h period; when the values were higher than zero, it was assumed that the animal was active and outside the shelter.

LME models were also used to build this second model and evaluate variation in the activity index along the diel cycle according to hourly changes in air temperature. Time of day was included in the model using harmonics to allow a nonlinear relationship between time of day and activity index (sensu Forester, Im, & Rathouz, 2009). We included two terms ($c1 = \cosine\ 2\pi$, $s1 = \sin\ 2\pi$) that interacted with hourly air temperature for each hourly fix of each individual. These interactions allowed us to disentangle the potential confounding effects between temperature and time of day. Hence, for each species we fitted a model that included the random nested effects of individual identity and the autocorrelation structure between consecutive steps of the same individual. For this analysis, we used hourly temperature values for each day of animal monitoring, taken from the same INMET stations for each study site, as previously described. This approach allowed us to evaluate activity thermal thresholds, changes in activity probability and activity vigour, following the conceptual framework proposed by Gunderson and Leal (2016).

Habitat Selection

We used a step selection function (SSF; Fortin et al., 2005; Forester et al., 2009) to evaluate the effects of cover type, diel cycle and air temperature on habitat selection of the studied species. Following Forester et al. (2009) and Avgar, Lele, Keim, and Boyce (2017), we define 'relative selection strength' (RSS) as the effect size (i.e. exponential coefficients) of these SSFs.

First, we subsampled the individual trajectories composed of 5 min fixes to fixes with 30 min intervals. Individual trajectories were decomposed into two components: step length and turning

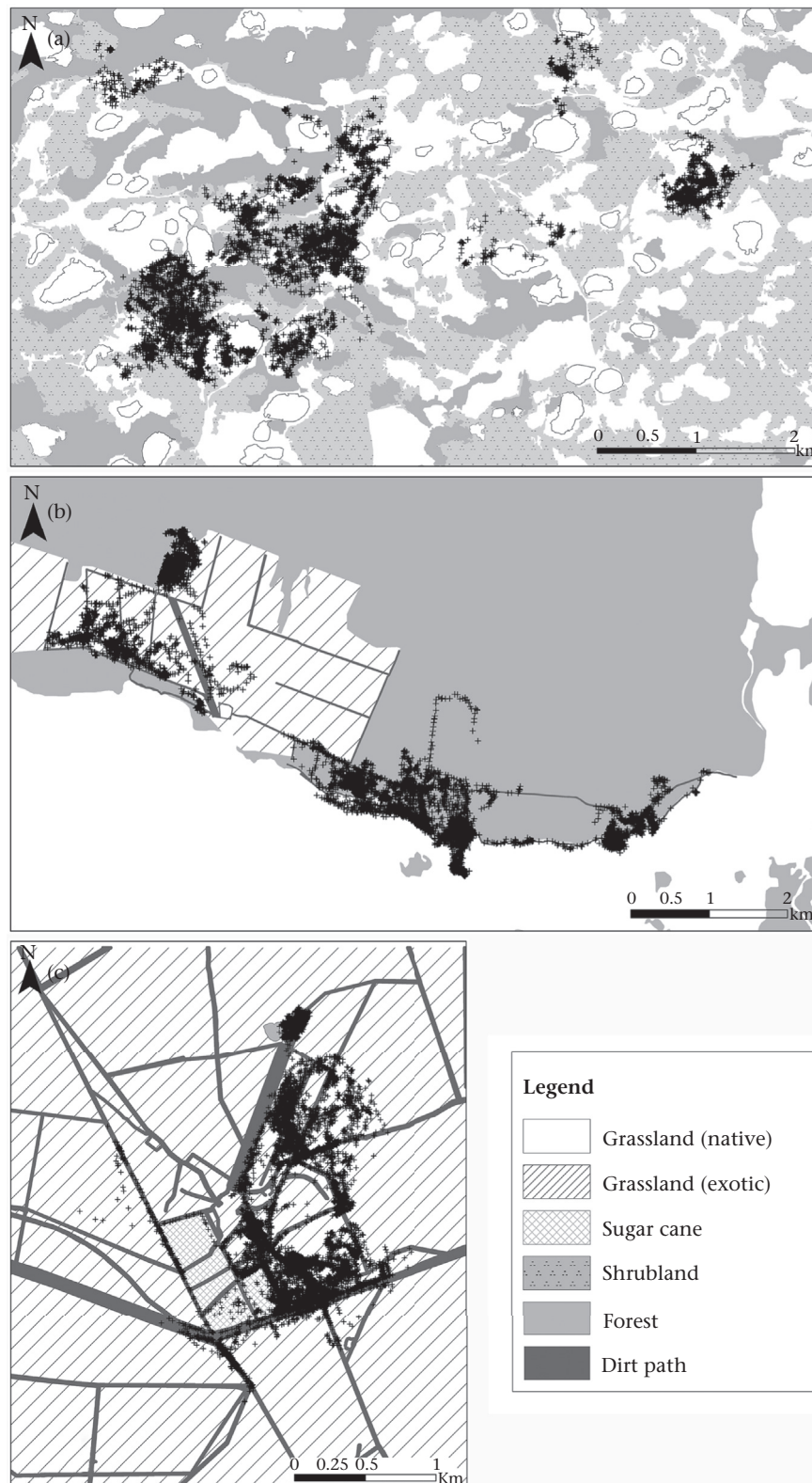


Figure 2. Locations of the monitored species (+) in different habitat categories at each study site. (a) Locations of individuals of *Euphractus sexcinctus* monitored at site 1 between March and August 2014. (b) Location of individuals of *Tolypeutes matacus* monitored at site 2 between November 2014 and April 2015. (c) Location of individuals of *T. matacus* monitored at site 3 between July and August 2015.

angle. Step length was defined as the straight-line distance between two consecutive locations, and turning angle was defined as the angular deviation between headings of two consecutive steps

(Turchin, 1991). To account for changes across space in resource availability, we generated 30 random steps originating from the starting location of each observed individual step. Random steps

were generated by sorting independent random samples from the observed distribution of step lengths and turning angles of each individual (Oliveira-Santos et al., 2016). For each observed and random step of each individual, we recorded the hour of the day, the instantaneous air temperature (hourly measures) and the habitat type at the step's ending point. The time of day was included in the SSF to allow a nonlinear relationship between time of day and selection strength. This was implemented using harmonics, which were allowed to interact with cover type and temperature for each step from each individual. These interactions allowed us to verify the effect of temperature on the selection of habitat types by armadillos.

Thus, we fitted three SSF models in increasing order of complexity: (Model 1) cover type; (Model 2) cover type + cover type*time of the day; (Model 3) cover type + cover type*time of the day*air temperature.

SSF models were fitted using a conditional logistic regression (CLR) using the function 'clogit' in the package 'survival' (Therneau, 2015) in R. CLR models were conditioned to each step within individual (where observed steps were scored as 1 and random steps were scored as 0). We used Akaike's information criterion (AIC; Burnham & Anderson, 2002) for model ranking and selection through the function 'aictab' from R package 'AICmodavg' (Mazerolle, 2016). We calculated robust standard errors for the estimated conditional logistic regression coefficients to take into account temporal autocorrelation between successive steps within individuals (Forester et al., 2009). To calculate the robust standard errors, first we fitted an LME model to the residuals of the CLR with individual identity as a random effect plus a first-order autoregressive correlation structure (Oliveira-Santos et al., 2016). Then, we fitted an autocorrelation function over the LME to identify the level of temporal autocorrelation present in the data (i.e. number of successive steps with similar values of residuals in CLR). Finally, we refitted the best CLR (based on AIC), clustering the autocorrelated successive steps, which allowed the estimation of the robust standard error of the coefficients (see Craiu, Duchesne, & Fortin, 2008). All analyses were implemented using R (R Core Team, 2017).

SSF models were plotted considering the limits of the thermoneutral zone (as defined by Eisentraut (1932) and McNab (1980) for each species) and the historic range of temperatures recorded in the study areas (-1.6°C – 43°C , from 1985 to 2013; INMET). Also, because we were interested in evaluating how these imperfect homeotherms would deal with the temperatures changes expected in a global climate change scenario, we extrapolated minimum and maximum temperatures (not frequently experienced by the animals) when plotting the models. Finally, to enable a clear visualization of how activity probability varies along the day, we fixed one of the model parameters, air temperature, and used a regular interval of 10°C between modelled temperatures.

RESULTS

Individuals of *E. sexcinctus* were monitored for an average of 11 days (range 3–27 days) and *T. matacus* for 17 days (range 4–32 days; Supplementary Material 1). With the sampling protocol of 5 min intervals between fixes, *E. sexcinctus* had an average of 816 locations per individual (range 169–2129), totalling 13 885 locations for this species. *Tolypeutes matacus* presented an average of 2919 (range 218–8248) locations per individual, totalling 61 303 locations. From these, 8067 locations were assigned as activity records of *E. sexcinctus*, with 1165 independent hourly activity records and 304 activity bouts (being 103 independent measures). From the locations gathered for *T. matacus*, 21 515 were assigned as activity records, with 4870 independent hourly activity records and 617 activity bouts (being 311 independent measures).

Activity Pattern

Individuals of *E. sexcinctus* were active during both daytime and night-time. Individuals usually had one activity bout per day (63%), but could have up to four bouts (3%). Total daily activity duration averaged 3.63 h (minimum = 0.08 h; maximum = 11.17 h). Our models suggested that variability in daily activity duration of *E. sexcinctus* was not explained by daily mean air temperature ($t_{103} = 1.44$, $P = 0.15$). However, time of day and hourly air temperature interacted to explain the activity index ($t_{1165} = 2.14$, $P = 0.03$). Thus, our second LME model indicated that *E. sexcinctus* activity during the daytime decreases as air temperature increases (Fig. 3a). At modelled air temperatures up to 30°C , *E. sexcinctus* would tend to be diurnal, with higher activity probability near noon. At intermediate temperatures (35 – 40°C), this species could be found active either at daytime or night-time (Fig. 3a). At higher air temperatures ($>40^{\circ}\text{C}$), activity could potentially switch and *E. sexcinctus* would tend to increase its nocturnal activity, especially in the first half of the night (Fig. 3a). Fig. 3b shows how temperature varied in the study area, both during the day (minimum amplitude = 1.4°C ; maximum amplitude = 11.5°C) and between days (range of mean daily temperatures = 16 – 30°C).

Tolypeutes matacus individuals usually exhibited one (53%) or two (29%) activity bouts per day, but up to seven bouts ($<1\%$) were recorded. This species was active mostly during night-time, but also at dusk and dawn. The total daily activity duration ranged from 0.18 to 14.73 h, with an average of 5.45 h. Our model indicated that the total daily activity duration of *T. matacus* would be positively related to daily mean air temperature ($t_{311} = 6.41$, $P < 0.01$). For this species also, the model indicated an interaction between air temperature and time of the day explaining the activity index ($\beta + \text{SE} = 0.54 + 0.04$, $df = 4\ 870$, $t = 14.81$, $P < 0.01$). In contrast to the responses modelled for *E. sexcinctus*, the model indicated that the activity pattern of *T. matacus* tends to change gradually as air temperature changes (Fig. 4a), and that activity probability before sunset tends to increase as air temperature decreases (Fig. 4a). Hourly measures of temperature varied from 19 to 39°C in the study areas. For a given time of the day, the amplitude varied from 11°C to a maximum of 21.8°C (Fig. 4b).

Habitat Selection

Individuals of *T. matacus* and *E. sexcinctus* used all available habitat types in their study areas. There was almost 100% evidence (AICc weight = 1) that the best model to explain habitat selection for both *E. sexcinctus* and *T. matacus* was the model that accounted for habitat type, and its interactions with time of the day and hourly air temperature (Tables 1 and 2, respectively; see Supplementary Material 2 and 3 for model coefficients).

The best model suggested that at air temperatures of 25°C , close to the lower limit of its thermoneutral zone, *E. sexcinctus* would use forests according to availability, irrespective of time of day (Fig. 3c). If experiencing air temperatures close to the upper limit of its thermoneutrality (35°C) or higher (45°C) during the warmest hours of the afternoon, *E. sexcinctus* would be expected to select the buffered forest areas and avoid them during the remaining hours of the day. If temperatures below its thermoneutral zone (15°C) were to be experienced during the night-time, when activity probability is low (Fig. 3a), or in the early morning, *E. sexcinctus* would select the buffered forest areas (Fig. 3c), and it should also be sheltering in its burrows. The model suggested that the pattern of selection of shrubland areas would be similar to that observed for forests. However, when compared to forests, there would be less variability at different air temperatures and at different times of day (Fig. 3d). Finally, the model suggested that when *E. sexcinctus* experiences air

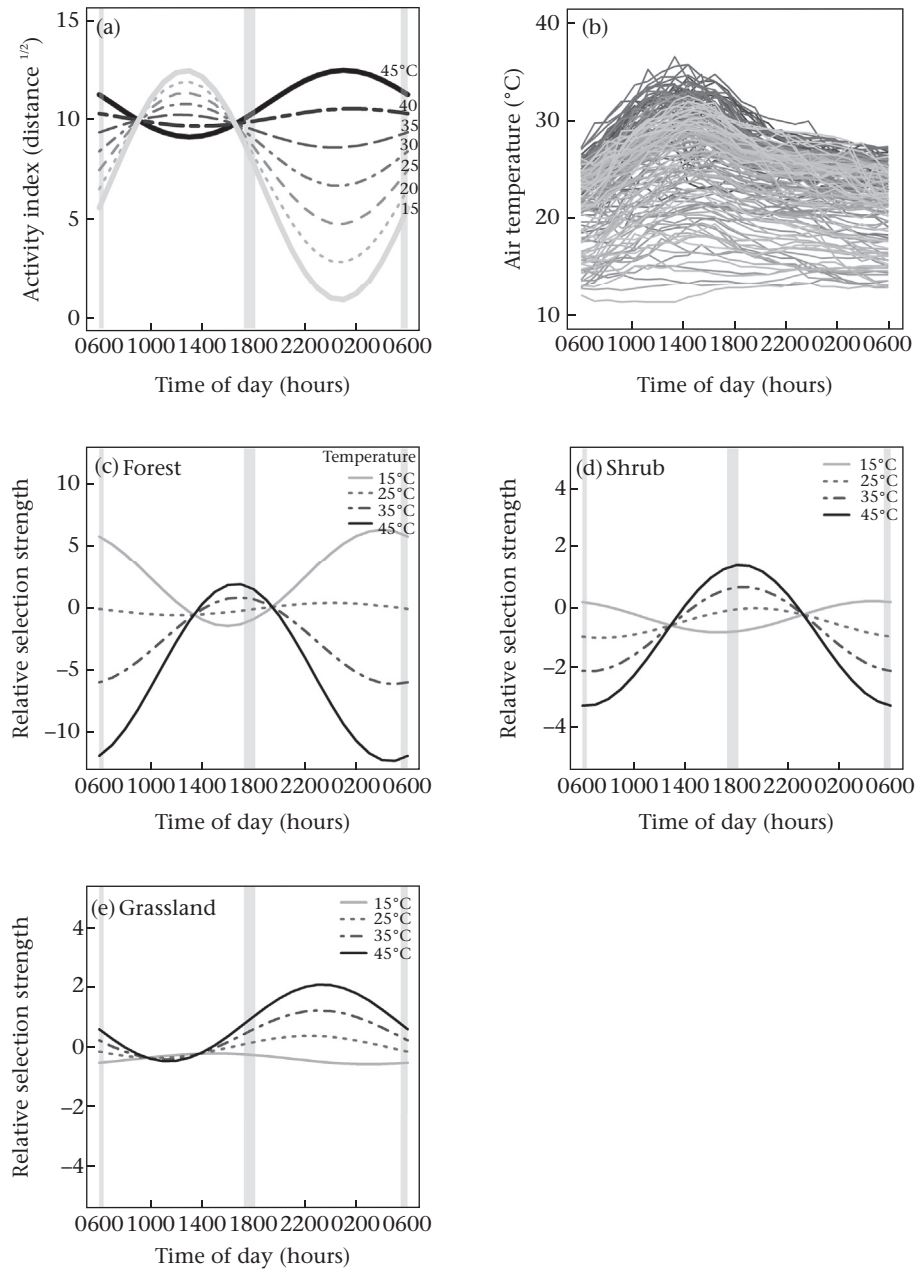


Figure 3. Models of activity pattern and relative habitat selection strength by *Euphractus sexcinctus* throughout the day, at different air temperatures. (a) Activity probability estimates throughout the day at varying instant air temperatures according to an LME model. (b) Daily variation of air temperature at the study site during the study period. Selection strength of (c) forests, (d) shrublands and (e) grasslands at four air temperature scenarios according to the best fit model (see Table 1, Supplementary material 2). Vertical light grey bars represent the range of sunset and sunrise times during the study period. Data from 17 armadillos tracked at site 1 (see Fig. 1) from March to August 2014.

temperatures within its thermoneutrality (25 °C and 35 °C) and above (45 °C) during daytime, grassland areas would be used according to availability (Fig. 3e). However, if the same range of air temperatures were to be experienced after the sunset, grassland areas would be positively selected. In contrast, the model suggested that, at chilly temperatures (15 °C), grassland areas would be slightly avoided by *E. sexcinctus* at all times of day (Fig. 3e).

Air temperature in the study areas of *T. matacus* reached its daily peak in the mid-afternoon and its lowest values right before sunrise. The best model suggested that, in most cases, the selection strength of different habitats by *T. matacus* tends to vary with the time of day and instant air temperature (Fig. 4). The model suggested that buffered forest areas would tend to be

selected by *T. matacus* at the most extreme temperature scenarios, i.e. if air temperatures of 45 °C were to be experienced during the daytime or if temperatures of 15 °C were experienced during the night-time (Fig. 4c). If temperatures of 15 °C or 25 °C were to be experienced by *T. matacus* at any time of day, it would tend to avoid sugarcane plantations (Fig. 4c). However, a positive selection of sugarcane plantations would be expected if warmer temperatures (35 °C or 45 °C) were experienced during the night-time, when animals are expected to be active and out of their shelters. Finally, the model suggested an almost inverse pattern of selection for grasslands when compared to that for forest areas (Fig. 4e). *Tolypeutes matacus* should select grassland areas either during the daytime, when experiencing low

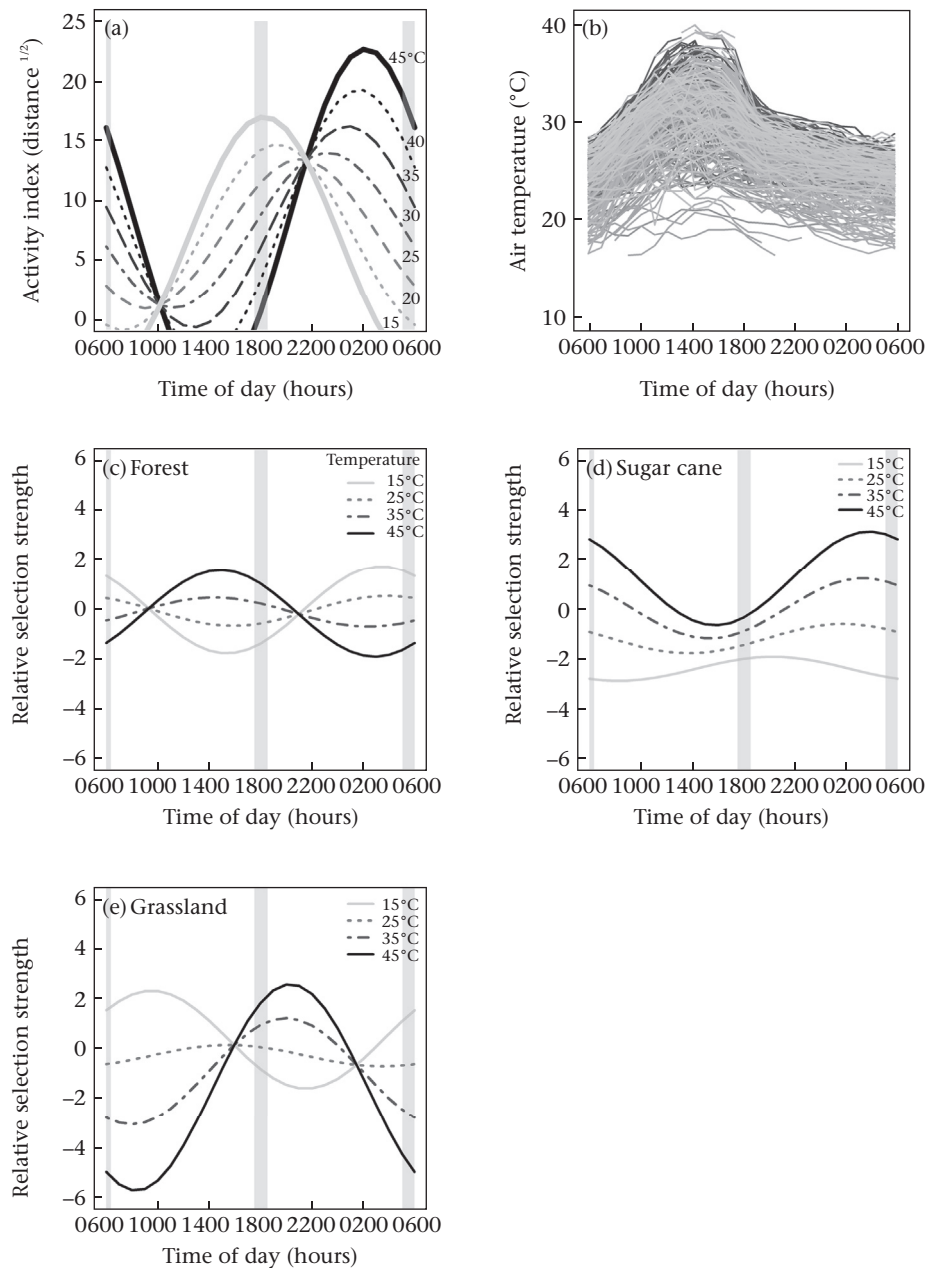


Figure 4. Models of activity pattern and relative habitat selection strength by *Tolypeutes matacus* throughout the day, at different air temperatures. (a) Activity probability estimates throughout the day at varying instant air temperatures according to an LME model. (b) Daily variation of air temperature at both study sites during the study period. Selection strength of (c) forests, (d) grasslands and (e) sugarcane plantations at four air temperature scenarios according to the best fit model (see Table 2, Supplementary material 3). Vertical light grey bars represent the range of sunset and sunrise times during the study period. Data from 21 armadillos tracked at sites 2 and 3 (see Fig. 1) from November 2014 to August 2015.

temperatures (15 °C) or, after sunset, when experiencing warmer temperatures (35 °C or 45 °C). At intermediate temperatures of about 25 °C, which are likely to fall within its thermoneutral zone, the model suggested that grassland areas would be used according to their availability.

DISCUSSION

Although *E. sexcinctus* and *T. matacus* have been generally classified, respectively, as diurnal and cathemeral species (Cuéllar, 2008; Eisenberg & Redford, 1999; Medri, 2008), our results

Table 1
Ranking of the three competing step selection function models fitted to characterize habitat selection of *E. sexcinctus*

| Model | K | ΔAIC | AICc Wt | Cum. Wt | LL |
|---|----|-----------|---------|---------|------------|
| Cover type+cover type*time of day*air temperature | 23 | 0 | 1 | 1 | −14 743.96 |
| Cover type+cover type*time of day | 11 | 17 160.49 | 0 | 1 | −23 336.21 |
| Cover type | 3 | 17 213.13 | 0 | 1 | −23 370.54 |

Models account for the effects of vegetation cover type, diel cycle variation (time of day) and hourly air temperature. Number of parameters (K), relative difference between models (ΔAIC), weight of the model (AICc Wt), cumulative weight (Cum. Wt) and log likelihood (LL). Data from 17 armadillos tracked at site 1 (see Fig. 1) from March to August 2014.

Table 2Ranking of the three competing step selection function models fitted to characterize habitat selection of *T. matacus*

| Model | K | ΔAIC | AICc Wt | Cum. Wt | LL |
|---|----|-------|---------|---------|------------|
| Cover type+cover type*time of day*air temperature | 29 | 0 | 1 | 1 | –87 108.41 |
| Cover type+cover type*time of day | 14 | 32.27 | 0 | 1 | –87 139.54 |
| Cover type | 4 | 52.64 | 0 | 1 | –87 158.73 |

Models account for the effects of vegetation cover type, diel cycle variation (time of day) and hourly air temperature. Number of parameters (K), relative difference between models (ΔAIC), weight of the model (AICc Wt), cumulative weight (Cum. Wt) and log likelihood (LL). Data from 21 armadillos tracked at sites 2 and 3 (see Fig. 1) from November 2014 to August 2015.

highlight the major importance of temperature in modulating both diel activity and habitat selection for these species.

The influence of air temperature on activity has been reported for other imperfect homeotherms, such as anteaters, sloths, echidnas, pangolins and other armadillos (Brice, Grigg, Beard, & Donovan, 2002; Camilo-Alves & Mourão, 2006; Giné, Cassano, Almeida, & Faria, 2015; Greigor, 1985; Maccarini et al., 2015; McNab, 1980; Pietersen, McKechnie, & Jansen, 2014). Small-bodied species of imperfect homeotherms that occur in regions with extreme temperatures, such as the pichi, *Zaedyus pichii*, and the short-beaked echidna, *Tachyglossus aculeatus*, can enter daily torpor and even hibernate to compensate for their thermoregulatory limitations (Brice et al., 2002; Superina & Boily, 2007). Animals that occupy areas with subtropical and temperate climates, such as the nine-banded armadillo, *Dasypus novemcinctus*, the screaming hairy armadillo, *C. vellerosus*, and Temminck's ground pangolin, *Smutsia temminckii*, tend to be more diurnal (i.e. at warmer hours of the day) in cold winters and more nocturnal in summers (Greigor, 1985; Layne & Glover, 1985; Pietersen et al., 2014). *Tolypeutes matacus* and *E. sexcinctus* have a mainly tropical distribution (Feijó et al., 2015) and are physiologically adapted to relatively warm air temperatures (Eisenbraut, 1932; McNab, 1980; Roig, 1969). Our study species also tend to adjust their activity as a function of air temperature and seem to vary their activity on a scale of days. Because temperature may drop suddenly in the Pantanal due to cold fronts, this short-term behavioural response provides activity pattern plasticity and can be an efficient energetic strategy for these species.

Because armadillo burrows can buffer the external air temperature and work as thermal shelters (Maccarini et al., 2015), the decision to remain inside or leave a burrow constitutes a behavioural thermoregulation strategy for armadillos. Temperatures inside burrows tend to decrease with burrow depth and are correlated with the characteristics of the regional soil and ground cover (Bennett, Jarvis, & Davies, 1988). In general, the daily amplitude of temperature fluctuation is smaller with increasing depth. At a burrow depth of about 30 cm, daily temperature fluctuations are relatively small and, at depths greater than 60 cm, temperatures inside a burrow oscillate minimally throughout the day (Bennett et al., 1988; Reichman & Smith, 1990). Hence, the shallower burrows of *T. matacus* (length = 35 ± 9.4 cm; Attias et al., 2016) should be less effective as thermal shelters than those of *E. sexcinctus* (>1 m; Maccarini et al., 2015), and the shelter location should be more important for the former species. Furthermore, as in other armadillo species, the short activity duration of the studied species, and the tendency to have even a shorter duration of activity at lower air temperatures, could be attributed to their limited capability to physiologically regulate body temperature and their reliance on the burrows as a thermal shelter (Maccarini et al., 2015). However, the increase in hours of restriction inside burrows limits the time available for foraging activities, constraining costly metabolic functions such as mating, ultimately decreasing individual fitness and increasing the risk of population extinction (Sinervo et al., 2010).

Once an animal makes a decision to leave its thermal shelter (i.e. timing of activity), it can engage in different types of activity and adopt additional strategies of behavioural thermoregulation, like choosing the most appropriate habitat feature to perform its activities (Gunderson & Leal, 2016). Our models indicate that, besides the variation in activity patterns, temperature can also be related to changes in habitat selection by armadillos. Similarly to ectotherms, armadillos can move between open habitats and shaded areas to help regulate body temperature (Huey, 1974). The influence of temperature on the activity and relative habitat selection of xenarthrans seems to be related mainly to internal factors, i.e. the group's peculiar combination of morphophysiological adaptations (Layne & Glover, 1985; Maccarini et al., 2015). Compared to a nonxenarthran placental mammal of its size, *E. sexcinctus* has a lower metabolic rate (42%) and a much higher thermal conductance (172%; McNab, 1985). These traits, together with its low body temperature of 34.2 °C, increase the susceptibility of *E. sexcinctus* to changes in air temperature (Maccarini et al., 2015). Furthermore, the tendency to be active in areas of open vegetation makes this species especially susceptible to gain heat through direct exposure to solar radiation or to radiative heat loss on cold nights. Hence, the reliance on burrow use for thermoregulation should be especially conspicuous for *E. sexcinctus*. This would result in more variability in diel activity patterns when compared with *T. matacus*, as indicated by our models.

The different behavioural responses of the studied species to temperature variation could be due to differences in physiology, anatomy, body mass and behaviour. *Tolypeutes* stand out for having one of the lowest body temperatures (33 °C) and metabolic rates (31% of what would be expected for a nonxenarthran mammal of its size) among armadillos (i.e. lower than *E. sexcinctus*), probably due to their low energy myrmecophagous diet (McNab, 1980). Noticeably, other ant-eating species, such as short-beaked echidnas, *T. aculeatus*, can have basal metabolic rates as low as *Tolypeutes* (McNab, 1985) and also have their behaviour strongly influenced by air temperature (Brice et al., 2002). Even though the thermal conductance of *T. matacus* is 133% of what would be expected for other mammals of its size, it is one of the lowest thermal conductances among armadillos (McNab, 1980). This is probably due to its unique anatomy and habit of rolling into a ball. Besides being thicker, the carapace of *Tolypeutes* covers a much larger proportion of the body (leaving only the distal extremities of its limbs exposed to environmental conditions) when compared to other armadillo species (M. Superina, personal communication, August 2017). In addition, when the carapace is closed or partially closed, the air trapped between the body and the carapace can further reduce thermal conductance (McNab, 1985). However, this also means that their thermal conductance is related, to some extent, to their activity status. That is, inactive ('rolled up') armadillos will have lower thermal conductance than active ('unrolled') ones. Nevertheless, this assumption should be further explored for *T. matacus* by evaluating the variation in body and shelter temperature as functions of air temperature variation (e.g. Camilo-Alves & Mourão, 2006; Maccarini et al., 2015). Furthermore, the small body mass

of *T. matacus* provides it less thermal inertia, when compared to the larger *E. sexcinctus*, with a comparatively higher rate of heat loss in cold environments. The association of these factors could also explain *T. matacus* shorter activity duration on colder days. Finally, if the limits of thermoneutrality of *T. matacus* proposed by Eisentraut (1932; 16–28 °C) represented the species' physiology at our study sites, this could also explain the comparatively smaller variability in the diel activity patterns of *T. matacus* and the predominantly nocturnal activity suggested by the models.

Regardless of their timing of activity, our models indicate that *E. sexcinctus* tends to avoid forests while active, but it tends to select them while inactive (as suggested by Medri, 2008). The tendency to avoid forests during activity could indicate that *E. sexcinctus* tends to handle air temperature variation mostly through activity variation. Alternatively, it could be related to predator avoidance, because their main predators in the region are large and mid-sized cats, which tend to occupy forests (Astete, Sollmann, & Silveira, 2008; Bianchi, Olifiers, Gompper, & Mourão, 2016). In contrast, the models for *T. matacus* indicate that they could select forests for both activity and resting, depending on air temperature. Its relatively shallower burrows and above-ground straw nests (Attias et al., 2016) should provide less effective thermal shelters, when compared to the deeper *E. sexcinctus* burrows, making habitat selection during resting an additional thermoregulation strategy. The relatively higher flexibility of *T. matacus* in habitat selection, when compared to *E. sexcinctus*, could also be due to its comparatively thicker carapace and its defensive behaviour of rolling into a ball, which grants *T. matacus* fewer natural predators. It is likely that only large carnivores, such as jaguars, *Panthera onca*, and maned wolves, *Chrysocyon brachyurus*, can overcome *Tolypeutes*'s defences.

As air temperatures change, different behavioural responses of different species could affect their interactions (e.g. predator–prey, intraguild competition; Creel et al., 2016). Our models show that these two sympatric species could adopt different behavioural responses to air temperature variation. As daily temperature increases, *E. sexcinctus* tends to adopt a more nocturnal behaviour (like *T. matacus* already has) whereas *T. matacus* tends to forage in open vegetation areas (like *E. sexcinctus* already does). These changes potentially increase the overlap of the temporal and spatial niche dimensions between the two species, setting the stage for a potential increase in intraguild competition. Differential responses of species to temperature variation can lead to a cascade of changing biotic interactions, potentially leading to changes in community dynamics, ultimately affecting ecosystem functions (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010; Harley, 2011; Traill, Lim, Sodhi, & Bradshaw, 2010). Hence, the different responses to temperature variation by two closely related species can help inform our understanding of the potential for changes in biotic interactions in a climate change scenario.

In the Pantanal, forests work as temperature buffers, being cooler than open vegetation areas during the hottest hours of the day and warmer during the coldest hours (Mourão & Medri, 2007). At site 1, Mourão and Medri (2007) recorded temperatures up to 5 °C higher in forests than those recorded in the grasslands on cold days, and 8 °C lower on hot days. The buffering effect should be proportional to arboreal vegetation cover, granting shrubland and sugarcane areas an intermediate level of temperature buffering, when compared to forest and grassland areas. Hence, the species could select the different elements of the landscape to cope with their physiological constraints. Such behavioural reliance on different habitats as a function of temperature shows the importance of the maintenance of the natural heterogeneity of the Pantanal wetland landscape. As in many other parts of South America, one of the main threats to the conservation of the Pantanal is

habitat conversion. More than 40% of the forest and savannah habitats have been altered for cattle ranching through the introduction of exotic grasses in the Pantanal (Harris et al., 2005), and if conversion rates continue to follow the historic trend, a complete loss of native vegetation can be expected by 2045 (Silva, Abdon, Silva, & Moraes, 2011). Hence, even though we have recorded the studied species using altered habitats, such as sugarcane plantations and exotic pasturelands, areas with denser forest cover are shown to have an important and strategic role in the ecology and thermoregulation strategies of these species.

The importance of landscape heterogeneity and forest cover maintenance should be even higher in the future, because the mean warming for the Pantanal is expected to range from 2.5 °C to 3.5 °C during 2011–2040 and from 5 °C to 7 °C during 2071–2100 (Marengo et al., 2016). In a climate change scenario, with increased frequency of extreme climatic events (Marengo et al., 2016), other homeothermic species might have to rely on behavioural thermoregulation to reduce physiological stress (e.g. van Beest, Van Moorter, & Milner, 2012). However, as portrayed by the different behavioural responses of our study species, the environmental characteristics that will define a landscape patch as adequate for thermoregulatory behaviour are species specific. This highlights even further the importance of landscape heterogeneity for biodiversity conservation in tropical savannahs in this scenario (Hannah et al., 2014). Furthermore, the maintenance of the natural landscape heterogeneity can benefit multiple species through the increased probability of the establishment of stepping-stones or microrefugia (i.e. unusual microclimates, in relation to its surrounding landscape), that enable isolated populations of a species to endure periods of unfavourable climate (Mosblech, Bush, & van Woesik, 2011).

As burrowing, imperfect homeotherms, armadillos present a conspicuous response to temperature variation. Here, we provide a specific example of the dynamic nature of activity patterns and habitat selection and illustrate how thermal constraints vary over the diel cycle and among days. More generally, models like those presented here can be used to better understand the consequences of climate change on animals inhabiting Neotropical savannahs, highlighting the importance of habitat heterogeneity for the long-term conservation of animal species in a scenario of global climate change.

Acknowledgments

We are grateful to Acaia Pantanal, Embrapa Pantanal, Teresa Bracher, Fazenda Santa Teresa, Floresteca and Instituto Homem Pantaneiro for logistic support. We thank the Rufford Foundation, Embrapa Pantanal (Project SEG 02.10.06.007.00.02) and Fundect (Project Pronex - 006/2015) for financial support and Idea Wild and Neotropical Grassland Conservancy for equipment donation. We are grateful to CNPq for the fellowship awarded to G. Mourão (process 308631/2011-0), to Capes for the scholarship awarded to N. Attias (number 1575316), Fundect for the scholarship awarded to N. Attias (process 23/200.715/2013) and the fellowship awarded to L.G.R. Oliveira-Santos and the National Science Foundation for the grant awarded to W. Fagan (ABI 1458748). We thank the PAPOS-MS program (Fundect/Capes number 44/2014, process 23/2000.638/2014) for travel assistance granted to N. Attias. We thank A. Canena, A. C. Vasques, R. Sepúlveda and S. Pimentel for the field assistance and V. Gasparotto, G. Soresini and Projeto Tamandua Brasil for their help with veterinary procedures. We are thankful to E. Gurarie for his help on initial data processing and A. C. R. Lacerda, M. Oliveira, R. Pellegrin and A. Coelho for their help with map classification. Finally, we thank M. Leal and two anonymous referees for their valuable comments to the original version of this manuscript.

Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.anbehav.2018.04.011>.

References

- Abdon, M. M., Silva, J. S. V., Pott, V. J., Pott, A., & Silva, M. P. (1998). Utilização de dados analógicos do Landsat-TM na discriminação da vegetação de parte da sub-região da Nhecolândia no Pantanal. *Pesquisa Agropecuária Brasileira*, 33, 1799–1813.
- Aronson, B. D., Bell-Pedersen, D., Block, G. D., Bos, N. P., Dunlap, J. C., Eskin, A., et al. (1993). Circadian rhythms. *Brain Research Reviews*, 18, 315–333.
- Astete, S., Sollmann, R., & Silveira, L. (2008). Comparative ecology of jaguars in Brazil. *Cat News Special Issue*, 4, 9–14.
- Attias, N. (2017). *Spatial and temporal ecology of two armadillo species in a Neotropical region (Doctoral dissertation)*. Campo Grande, MS, Brazil: Federal University of Mato Grosso do Sul.
- Attias, N., Miranda, F. R., Sena, L. M. M., Tomas, W. M., & Mourão, G. M. (2016). Yes, they can! Three-banded armadillos *Tolypeutes* sp. (Cingulata: Dasypodidae) dig their own burrows. *Zoologia*, 33, e20160035.
- Avgar, T., Lele, S. R., Keim, J. L., & Boyce, M. S. (2017). Relative selection strength: Quantifying effect size in habitat and step selection inference. *Ecology and Evolution*, 7(14), 5322–5330.
- Barraquand, F., & Benhamou, S. (2008). Animal movement in heterogeneous landscapes: Identifying profitable places and homogeneous movement bouts. *Ecology*, 89(12), 3336–3348.
- van Beest, F. M., Van Moorter, B., & Milner, J. M. (2012). Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour*, 84, 723–735.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377.
- Bennett, N. C., Jarvis, J. U. M., & Davies, K. C. (1988). Daily and seasonal temperatures in the burrows of African rodent moles. *South African Journal of Zoology*, 23(3), 189–195.
- Bianchi, R. C., Olifiers, N., Gompper, M. E., & Mourão, G. M. (2016). Niche partitioning among mesocarnivores in a Brazilian wetland. *PLoS One*, 11, e0162893.
- Bolkovic, M. L., Cazziani, S. M., & Protomastro, J. J. (1995). Food habits of the three-banded armadillo (*Xenarthra*: Dasypodidae) in the dry Chaco of Argentina. *Journal of Mammalogy*, 76, 1199–1204.
- Brice, P. H., Grigg, G. C., Beard, L. A., & Donovan, J. A. (2002). Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: Correlates with ambient temperature, time to the day and season. *Australian Journal of Zoology*, 50, 461–475.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach*. London, U.K.: Springer-Verlag.
- Calheiros, D. F., & Fonseca, W. C. (1996). *Perspectivas de estudos ecológicos sobre o Pantanal*. Corumbá, MS, Brazil: Embrapa CPAP.
- Camilo-Alves, C. S. P., & Mourão, G. M. (2006). Responses of a specialized insectivorous mammal (*Myrmecophaga tridactyla*) to variation in ambient temperature. *Biotropica*, 38, 52–56.
- Craiu, R. V., Duchesne, T., & Fortin, D. (2008). Inference methods for the conditional logistic regression model with longitudinal data. *Biometrical Journal*, 50, 97–109.
- Creel, S., Creel, N. M., Creel, A. M., & Creel, B. M. (2016). Hunting on a hot day: Effects of temperature on interactions between African wild dogs and their prey. *Ecology*, 97, 2910–2916.
- Cuéllar, E. (2008). Biology and ecology of armadillos in the Bolivian Chaco. In S. F. Vizcaino, & W. J. Loughry (Eds.), *The biology of the Xenarthra* (1st ed., pp. 306–312). Gainesville, FL: University Press of Florida.
- Eisenberg, J. F., & Redford, K. H. (1999). *Mammals of the Neotropics: The central Neotropics: Ecuador, Peru, Bolivia, Brazil*. Chicago, IL: University of Chicago Press.
- Eisentraut, M. (1932). Biologische Studien im bolivianischen Chaco. IV. Die Wärmeregulation beim Kugeltier (*Tolypeutes conurus* Js. Geoff.). *Zeitschrift für vergleichende Physiologie*, 18, 174–185.
- Feijó, A., Garbino, G. S. T., Campos, B. A. T. P., Rocha, P. A., Ferrari, S., & Langguth, A. (2015). Distribution of *Tolypeutes* Illiger, 1811 (*Xenarthra*: Cingulata) with comments on its biogeography and conservation. *Zoological Science*, 32, 77–87.
- Forester, J. D., Im, H. K., & Rathouz, P. J. (2009). Accounting for animal movement in estimation of resource selection functions: Sampling and data analysis. *Ecology*, 90, 3554–3565.
- Fortin, D., Hawthorne, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320–1330.
- Gasparotto, V. P. O., Attias, N., Miranda, F. R., Soaresini, G. C. G., Canena, A. C., & Mourão, G. (2017). Chemical immobilization of free-ranging yellow armadillos (*Euphractus sexcinctus*) for implantation of intra-abdominal transmitters. *Journal of Wildlife Diseases*, 53(4), 896–900.
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, 25, 325–331.
- Giné, A. F., Cassano, C. R., Almeida, S. S., & Faria, D. (2015). Activity budget, pattern and rhythm of maned sloths (*Bradypus torquatus*): Responses to variations in ambient temperature. *Mammalian Biology*, 80, 459–467.
- Gregeor, D. H. (1985). Ecology of the little hairy armadillo *Chaetophractus vellerosus*. In G. G. Montgomery (Ed.), *The evolution and ecology of armadillos, sloths and vermilinguas* (pp. 397–405). Washington, D.C.: Smithsonian Institution Press.
- Gunderson, A. R., & Leal, M. (2016). A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global climate change. *Ecology Letters*, 19, 111–120.
- Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and micro-refugia. *Trends in Ecology & Evolution*, 29(7), 390–397.
- Harley, C. D. G. (2011). Climate change, keystone predation, and biodiversity loss. *Science*, 334, 1124–1127.
- Harris, M., Tomas, W., Mourão, G. M., Silva, C. J., Guimarães, E., Sonoda, F., et al. (2005). Safeguarding the Pantanal wetlands: Threats and conservation initiatives. *Conservation Biology*, 19, 714–720.
- Huey, R. B. (1974). Behavioral thermoregulation in lizards: Importance of associated costs. *Science*, 184, 1001–1003.
- Krebs, J. R., & Davies, N. B. (1993). *An introduction to behavioural ecology* (3rd ed.). Oxford, U.K.: Wiley-Blackwell.
- Layne, J. N., & Glover, D. (1985). Activity patterns of the common long-nosed armadillo *Dasypus novemcinctus* in south-central Florida. In G. G. Montgomery (Ed.), *The evolution and ecology of armadillos, sloths and vermilinguas* (pp. 407–417). Washington, D.C.: Smithsonian Institution Press.
- Leadley, P., Pereira, H. M., Alkemade, R., Fernandez-Manjarres, J. F., Proenca, V., Scharlemann, J. P. W., et al. (2010). *Biodiversity scenarios: Projections of 21st century change in biodiversity and associated ecosystem services (Technical Series No. 50)*. Montreal, QC: Secretariat of the Convention on Biological Diversity.
- Liwanag, H. E. M. (2010). Energetic costs and thermoregulation in northern fur seal (*Callorhinus ursinus*) pups: The importance of behavioral strategies for thermal balance in furred marine mammals. *Physiological and Biochemical Zoology*, 83(6), 898–910.
- Maccarini, T. B., Attias, N., Medri, I. M., Marinho-Filho, J., & Mourão, G. M. (2015). Temperature influences the activity patterns of armadillo species in a large neotropical wetland. *Mammal Research*, 60, 403–409.
- Marengo, J. A., Alves, L. M., & Torres, R. R. (2016). Regional climate change scenarios in the Brazilian Pantanal watershed. *Climate Research*, 68, 201–213.
- Mazerolle, M. J. (2016). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)* (R package version 2.1-0). <https://cran.r-project.org/package=AICcmodavg>.
- McDonough, C. M., & Loughry, W. J. (2008). Behavioral ecology of armadillos. In S. F. Vizcaino, & W. J. Loughry (Eds.), *The biology of the Xenarthra* (pp. 281–293). Gainesville, FL: University Press of Florida.
- McNab, B. K. (1980). Energetics and the limits to a temperate distribution in armadillos. *Journal of Mammalogy*, 61, 606–627.
- McNab, B. K. (1985). Energetics, population biology, and distribution of xenarthrans, living and extinct. In G. G. Montgomery (Ed.), *The evolution and ecology of armadillos, sloths and vermilinguas* (pp. 219–232). Washington, D.C.: Smithsonian Institution Press.
- McNab, B. K. (2002). Short-term energy conservation in endotherms in relation to body mass, habitats, and environment. *Journal of Thermal Biology*, 27, 459–466.
- Medri, I. M. (2008). *Ecologia e história natural do tatu-peba, Euphractus sexcinctus (Linnaeus, 1758), no Pantanal da Nhecolândia, Mato Grosso do Sul* (Ph.D. thesis). Brasília, Brazil: University of Brasília.
- Medri, I. M., Mourão, G. M., & Rodrigues, F. H. G. (2011). Ordem Cingulata. In N. R. Reis, A. L. Peracchi, W. A. Pedro, & I. P. Lima (Eds.), *Mamíferos do Brasil* (2nd ed., pp. 76–90). Londrina, Brazil: Nélro R. dos Reis.
- Mittermeier, R. A., Mittermeier, C. G., Brooks, T. M., Pilgrim, J. D., Konstant, W. R., da Fonseca, G. A. B., et al. (2003). Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 10309–10313.
- Möller-Krull, M., Delsuc, F., Churakov, G., Marker, C., Superina, M., Brosius, J., et al. (2007). Retrosposed elements and their flanking regions resolve the evolutionary history of xenarthran mammals (armadillos, anteaters, and sloths). *Molecular Biology and Evolution*, 24, 2573–2582.
- Mosblech, N. A. S., Bush, M. B., & van Woesik, R. (2011). On metapopulations and microrefugia: Palaeoecological insights. *Journal of Biogeography*, 38(3), 419–429.
- Mourão, G. M., & Medri, I. M. (2007). Activity of a specialized insectivorous mammal (*Myrmecophaga tridactyla*) in the Pantanal of Brazil. *Journal of Zoology*, 271, 187–192.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., et al. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19052–19059.
- Oliveira-Santos, L. G. R., Forester, J. D., Piovezan, U., Tomas, W. M., & Fernandez, F. A. S. (2016). Incorporating animal spatial memory in step selection functions. *Journal of Animal Ecology*, 85, 516–524.
- Pietersen, D. W., McKechnie, A. E., & Jansen, R. (2014). Home range, habitat selection and activity patterns of an arid-zone population of Temminck's ground pangolin *Smutsia temminckii*. *African Zoology*, 49, 265–276.

- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2016). *nlme: Linear and nonlinear mixed effects models (R package version 3.1-126)*. <http://CRAN.R-project.org/package=nlme>.
- R Development Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reichman, O. J., & Smith, S. C. (1990). Burrows and burrowing behavior by mammals. In H. H. Genoways (Ed.), *Current mammalogy* (pp. 197–244). New York, NY: Plenum Press.
- Reinert, H. K. (1993). Habitat selection in snakes. In R. A. Seigel, & J. T. Collins (Eds.), *Snakes: Ecology and behavior* (pp. 201–240). New York, NY: McGraw-Hill.
- Rietveld, W. J., Minors, D. S., & Waterhouse, J. M. (1993). Circadian rhythms and masking: An overview. *Chronobiology International*, 10, 306–312.
- Roig, V. G. (1969). Termorregulación en *Euphractus sexcinctus* (Mammalia: Dasypodidae). *Physis*, 29, 27–32.
- Seminoff, J. A., Resendiz, A., & Nichols, W. J. (2002). Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series*, 242, 253–265.
- Silva, J. S. V., Abdon, M. M., Silva, S. M. A., & Moraes, J. A. (2011). Evolution of deforestation in the Brazilian Pantanal and surroundings in the timeframe 1976–2008. *Geografia*, 36, 35–55.
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., et al. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899.
- Sunde, P., Thorup, K., Jacobsen, L. B., & Rahbek, C. (2014). Weather conditions drive dynamic habitat selection in a generalist predator. *PLoS One*, 9, e88221.
- Superina, M., & Boily, P. (2007). Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). *Comparative Biochemistry and Physiology A*, 148, 893–898.
- Superina, M., & Loughry, W. J. (2012). Life on the half-shell: Consequences of a carapace in the evolution of armadillos (Xenarthra: Cingulata). *Journal of Mammalian Evolution*, 19, 217–224.
- Tattersall, G. J., & Cadena, V. (2010). Insights into animal temperature adaptations revealed through thermal imaging. *Imaging Science Journal*, 58, 261–268.
- Therneau, T. (2015). *A package for survival analysis in S (Version 2.38)*. <http://CRAN.R-project.org/package=survival>.
- Tortato, F. R., Layme, V. M. G., Crawshaw, P. G., Jr., & Izzo, T. J. (2015). The impact of herd composition and foraging area on livestock predation by big cats in the Pantanal of Brazil. *Animal Conservation*, 18, 539–547.
- Traill, L. W., Lim, M. L. M., Sodhi, N. S., & Bradshaw, C. J. A. (2010). Mechanisms driving change: Altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology*, 79, 937–947.
- Turchin, P. (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology*, 72, 1253–1266.
- Wetzel, R. M., Gardner, A. L., Redford, K. H., & Eisenberg, J. F. (2008). Order Cingulata. In A. L. Gardner (Ed.), *Mammals of South America: Marsupials, xenarthrans, shrews and bats* (Vol. 1, pp. 128–156). Chicago, IL: University of Chicago Press.