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

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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.

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

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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. Greegor, 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 nonxenarthran 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.