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Temperature influences the activity patterns of armadillo species in a large neotropical wetland

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Abstract In this study, we characterized the activity patterns and estimated the activity overlap between two armadillo species (*Dasypus novemcinctus* and *Euphractus sexcinctus*) in the Pantanal wetlands of Brazil. We report the effect of daily mean ambient temperature on activity onset and duration of these armadillos. We captured seven yellow armadillos and three nine-banded armadillos and fitted them with very high frequency radios and temperature loggers. By monitoring the temperature of the environment (air temperatures and burrow temperatures), we inferred when the armadillo was active (above ground) or inactive (inside the burrow). Yellow armadillos were active mainly during the daytime and in the beginning of the night, while nine-banded armadillos were active mainly during the night. However, nine-banded armadillos presented a bimodal activity pattern, becoming active for a

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short period in the middle of the morning and/or afternoon. The proportion of activity overlap was 0.28 between the species, occurring primarily at the beginning of the night. At lower temperatures, yellow armadillos tended to leave their burrows earlier and were active for longer periods. This is probably an adaptation to their physiological constraints and limited thermoregulatory capabilities. Xenarthrans could be used as models to obtain valuable information about how physiology affects mammal behavior.

Keywords Thermoregulation · *Euphractus sexcinctus* · *Dasypus novemcinctus* · Burrow · Niche partitioning · Physiological constraints

Introduction

The circadian activity period adopted by an animal is one of the most effective and generalized ways to minimize the influence of unfavorable biotic and abiotic factors (Layne and Glover 1985). Circadian activity cycles allow an animal to anticipate environmental changes and choose the appropriate moment for a specific response or activity (Aronson et al. 1993).

Most armadillos (Mammalia: Cingulata) have a strategy for avoiding unfavorable factors: they build or use burrows. Burrows can be used not only to escape from predators or for sleeping (McDonough and Loughry 2003; Desbiez and Kluyber 2013) but also for thermoregulation (González et al. 2001). Burrows work as temperature buffers (González et al. 2001); armadillos can exit them once air temperatures are favorable and return to them to maximize their energy budgets.

Mammalian circadian rhythms are responsive to environmental factors, especially light cycles (Aronson et al. 1993). However, armadillos are imperfect homeotherms and have limited thermoregulatory capabilities, low body temperatures, and low basal rates of metabolism (McNab 1985). These characteristics are probably associated with their burrowing activity and feeding habits (McNab 1979, 1980). As a result of this unique characteristic among mammals, air temperature strongly affects the activity patterns of armadillos and other xenarthrans (Layne and Glover 1985; Chiarello 1998; Mourão and Medri 2007). The influence of temperature on the activity patterns of these animals can be determined from their activity duration and timing (activity onset).

Temporal niche partitioning is a mechanism that related species adopt to avoid competition: different circadian activity patterns might result in differentiation of the use of resources or levels of predation susceptibility. It can facilitate coexistence through avoidance of direct confrontation (interference competition) or through the reduction of overlap in resource demand (resource competition; Kronfeld-Schor and Dayan 2003). Partitioning of the temporal dimension of the niche between two species implies a smaller niche overlap than expected by chance. In this phenomenon, the less competitive species, or subordinates, usually modify their activity to suboptimal periods of the circadian cycle, reducing competition with the dominant species (Gutman and Dayan 2005). However, when competition is not the most important factor, the activity periods of similar species can tolerate an overlap higher than that expected by chance. This pattern might indicate that the activity periods of both species are influenced by similar responses to external factors (e.g., external temperature or potential predators). Another hypothesis is that phylogenetic constraints of the activity period make closely related species present similar activity patterns, limiting the opportunities for temporal niche partitioning among closely related competitors (Roll et al. 2006). Even though there is no evidence to confirm this fact, this could be the case for armadillos given that their physiology makes them very sensitive to temperature variations.

The yellow armadillo, Euphractus sexcinctus (Linnaeus 1758), and the nine-banded armadillo, Dasypus novemcinctus (Linnaeus 1758), are sympatric burrowing armadillos that have overlapping dietary habits (Anacleto 2007) and may occupy the same habitat type in the Brazilian Pantanal. The former is a diurnal and conspicuous species, widely distributed throughout Brazil (except Amazonia) and South America, and is very common in the Pantanal (Eisenberg and Redford 1999). Despite these characteristics, its ecology is poorly known, and studies on its activity patterns are rare (Bonato et al. 2008). The latter is a predominantly nocturnal species (Emmons and Feer 1997; Eisenberg and Redford 1999) that is found from Argentina to the USA, which is considered as the largest geographic range among armadillos (Wetzel 1985). Even though this is the most studied species, much of the research has been done in the USA (Loughry and McDonough 2013). Hence, the available ecological information might not reflect patterns that can change from place to place, such as behavior.

Therefore, the purpose of this study was to characterize the activity patterns of these two species of armadillo in the Brazilian Pantanal, estimate their activity overlap, and determine the influence of air temperature on their activity patterns.

Methods

Study area

The Pantanal is a large wetland region covering approximately 210,000 km² of seasonal floodplain of Rio Paraguay and includes areas of Brazil, Bolivia, and Paraguay (Mittermeier et al. 2003). The Brazilian portion of Pantanal is located in the western part of the country, near the geographic center of South America, at about 100 m in elevation. We conducted our study at the Nhumirim Ranch (18°59' S, 56°39' W), an experimental station of approximately 43 km² located in the Nhecolândia subregion in the state of Mato Grosso do Sul, Brazil. The Nhecolândia subregion is characterized by a land-scape mosaic of savannas, scrub savannas, forests, and permanent and temporary ponds (Alho et al. 1987).

The climate of the region is tropical semi-humid, and the average annual temperature is $25.5 \,^{\circ}$ C (Calheiros and Fonseca 1996). Summers are hot and rainy, averaging 1100 mm rainfall and maximum air temperatures exceeding 40 $^{\circ}$ C. Winters are warm and dry, averaging less than 300 mm rainfall and air temperatures of 20 $^{\circ}$ C, though occasional cold fronts from the south can cause air temperatures as low as 0 $^{\circ}$ C (Soriano et al. 1997).

Data collection

During September 2007 and February–May 2010, we searched for armadillos by foot or in an all-terrain vehicle, catching eight armadillos by hand and two in live traps from simultaneous studies focused on medium-sized carnivores in the area. Of these, seven were yellow armadillos (*E. sexcinctus*) and three were nine-banded armadillos (*D. novemcinctus*). We placed them in a safe and ventilated box and then transported them to the ranch laboratory. They were anesthetized there using an intramuscular dose of 4 mg/kg Zoletil[®] (1:1 tiletamine hydrochloride and zolazepam hydrochloride; Virbac S.A., Cedex, France). They were weighed, measured, and marked with numbered ear tags (model 1005-4; National Band & Tag Co., Newport, KY, USA).

With the animals under anesthesia, we attached a package (\approx 35 g) containing a StowAway Tidbit temperature data logger (Onset Computer Corporation, Bourne, MA, USA; accuracy, ± 0.4 °C at 20 °C) combined with a very high frequency radio transmitter (frequency range 164–166 MHz; model R2030; Advanced Telemetry Systems, Isanti, MN, USA) to each armadillo. Each transmitter was equipped with a mortality signal switch adjusted for 24 h.

To find the most durable and safe way to attach the packages, several techniques were used. Some devices were attached to the armadillos' tails using rubber strips covered with adhesive tape or only layers of adhesive tape. Others were attached to the edge of the carapace, at the right posterior of the body, by drilling holes in the carapace and passing cable ties through them. To perform the latter, we injected the animals with a local dose of xylocaine (Eurofarma Lab., São Paulo, Brazil). On the same day, once the anesthesia effects subsided and all procedures were completed, we released the armadillos at the same location where they were captured.

The temperature registered by the data logger attached to the armadillo was termed $T_{\text{armadillo}}$ and was affected by the instantaneous ambient temperature and the heat emitted by the armadillo's body. However, because body temperature varies according to the ambient temperature, but with less variation (Roig 1969), most of the fluctuations in $T_{\text{armadillo}}$ was attributed to the ambient temperature of the location of the armadillo at a given moment. To obtain temperatures of the burrow (T_{burrow}) and air (T_{air}) , we placed a temperature logger inside an armadillo burrow (≈ 1 m inside) and another in the meteorological station of the Nhumirim ranch. For each monitored animal, T_{burrow} was obtained by monitoring one active burrow selected in the surroundings of the capture location. We cannot ensure that the selected burrow was the one in use by the captured armadillo at that time. Nonetheless, our intention was not to record the temperature of any specific burrow as the armadillo could use more than one burrow during the monitoring period. By placing the logger inside an active burrow our intention was to verify the temperature buffering effect of burrows. All temperature loggers were set to register the temperature every 5 min. When necessary, we obtained the air temperature hourly from the automatic meteorological station.

Whenever $T_{\text{armadillo}}$ was more stable and approximately parallel to T_{burrow} , we inferred that the animal was inside the burrow and inactive. Whenever $T_{\text{armadillo}}$ presented more pronounced variations following a T_{air} variation pattern, we inferred that the animal was active and outside the burrow. It was possible to identify the activity onset by the abrupt variation in $T_{\text{armadillo}}$ values, after a sequence of similar values with smother variations (see details in Appendix 1). To verify the accuracy of our method, we visually checked the activity status of the animals (inside or outside the burrow) once or twice a day by locating the animal through radio telemetry. We performed at least nine observations per animal during their monitoring period and compared their observed activity status with the status inferred from the temperature data. To assess whether our method was reliable at inferring when the armadillos were inside or outside the burrows, we also performed an armadillo activity simulation (Appendix 1).

We tracked the transmitter/logger packages using a handheld directional antenna (RA-2AK; Telonics, Mesa, AZ, USA) and a portable receiver (Telonics TR-4). Nine out of ten packages naturally fell off the armadillos in the course of their semi-fossorial habits, after which they were recovered from the ground or burrows.

Analysis

Temperature data from all loggers were downloaded using the software Boxcar® Pro 4.0 (Onset®). To infer when the armadillos were active (above ground) or inside the burrow, we compared $T_{\text{armadillo}}$ with T_{burrow} and T_{air} simultaneously. Whenever $T_{\text{armadillo}}$ was more stable and approximately equal to T_{burrow} we inferred that the animal was inside the burrow. If instead it was approximately equal to T_{air} , we inferred that the animal was active and outside the burrow (Appendix 1). We used the values for sunrise and sunset provided by the US Department of Commerce, National Oceanic and Atmospheric Administration (http://www.esrl.noaa.gov/) to define daytime and nighttime periods for the days of monitoring. Daytime was defined as the period between sunrise and sunset and nighttime as the remaining hours of the day. To account for photoperiod variation, we corrected the time of each activity record according to the photoperiod duration of each day.

To characterize the activity period of each species and the degree of overlap in the activity periods between species, we used a continuous, non-parametric model of a conditional, circular kernel function (Oliveira-Santos et al. 2013). Kernel density functions provide a continuous measure of the density of data points throughout their distribution (Worton 1989). Much like its use to calculate home ranges, this function allows us to consider the use of time in a continuous probabilistic way, providing a clearer measure of the probability of an animal being active at a given time within its activity period.

A two-sample Kolmogorov–Smirnov test was used to test whether the distribution of activity records as a function of air temperature (1 °C interval) differed from the distribution of all temperature records registered during the study period (i.e., its "availability"). We used graphical analyses to evaluate how the armadillos' activity patterns were related to T_{air} and to verify whether activity onset and duration were affected by the mean T_{air} Activity onset was defined as the time an armadillo left its burrow each day. In cases where armadillos left their burrows more than one time per day, usually involving one or more short periods and one long activity period, we considered only the longest period as the onset time of activity. In order to avoid pseudo-replication, we calculated the average T_{air} during the monitoring period for each animal and associated it with their average activity onset and duration. Spearman correlation test was used to test if average T_{air} affected the mean time of day that yellow armadillos exited their burrows and their mean activity durations. Spearman correlation test was also used to evaluate the relation of photoperiod duration during each animal's monitoring period and the onset and duration of activity periods. Because we had data on only three nine-banded armadillos, we did not attempt to perform the correlation tests for this species, but we included the data on the graphs. All analyses were performed using R (R Development Core Team 2013).

Results

Of the seven captured yellow armadillos, two were male and five were female; of the nine-banded armadillos, one was male and two were female. Data logger packages remained on the armadillos for a period of 2 to 13 days (Supplementary material—Appendix 1). The longest duration was achieved by using rubber strips covered with adhesive tape. However, one yellow armadillo lost part of its tail after the package was attached using this technique. It could have been affixed too tight to allow normal blood circulation. Fortunately, the wound closed up well, and the armadillo was recaptured as well as photographed several times by camera traps months later. After this experience, we avoided using rubber strips and used only adhesive tape for the attachment of transmitters.

The amplitude of recorded $T_{\text{armadillo}}$ was always smaller than that of T_{air} (Fig. 1). T_{burrow} was far more stable (range= 23.6–30.9 °C; CV=0.07) than T_{air} (range=5.7–40 °C; CV= 0.29), and the differences between them (T_{burrow} – T_{air}) ranged from –11.6 °C to +18.3 °C. This pattern allowed a confident estimate of the activity period of the monitored animals and the efficiency of the proposed method (for method details, see Supplementary material—Appendix 2). Nine-banded armadillos were active in a narrower and milder range of T_{air} (range=13.4–29.3 °C; CV=0.14) compared to yellow armadillos (range=13.2–36.2 °C; CV=0.20; Fig. 1). The distribution of activity records as a function of air temperature differed from the distribution of all temperature records registered during the study period (for *D. novemcinctus*, *D*=0.2678, *p*<0.001; for *E. sexcinctus*, *D*=0.1587; *p*<0.001).

The yellow armadillos were active for an average of 4.42 h/ day, mainly during the day and at the beginning of the night. The nine-banded armadillos were active for an average of 4.97 h/day and had primarily nocturnal activity. However, they presented a bimodal activity pattern, leaving the burrows for short periods in the middle of the morning and/or in the middle of the afternoon (Fig. 2). The proportion of activity overlap between the two species was 0.28 (smoothing parameter=37.4; isopleth=0.95), which is considered as a low overlap (Oliveira-Santos et al. 2013). The overlap occurred at the



Fig. 1 Distribution of temperatures registered during the monitoring period at the Nhumirim ranch, Nhecolândia Pantanal, Mato Grosso do Sul state, Brazil (September 2007 and February–May 2010). *Solid bars* indicate the relative frequency at which each air temperature was registered during the monitoring period (n_{dn} =12,473; n_{es} =14,541). *Dashed bars* indicate the relative frequency of each air temperature during active periods of **a** nine-banded armadillo (*D. novemcinctus*, *n*= 2813) and **b** yellow armadillo (*E. sexcinctus*, *n*=1822)

beginning of the night (1806 to 0048 hours), before sunrise (0324 to 0515 hours), and in the middle of the morning (0830 to 0900 hours). Among the yellow armadillos, mean T_{air} affected the mean activity onset positively (rho=0.82, p=0.03; Fig. 3) and mean activity duration negatively (rho=-0.96, p<0.01; Fig. 4). There was no correlation between



Fig. 2 Kernel activity density estimates for nine-banded armadillo (*D. novemcinctus*, n=3; *solid line*) and yellow armadillo (*E. sexcinctus*, n=7; *dashed line*) during a 24-h period. *Gray areas* represent periods of higher activity overlap (95 % kernel) between the species



Fig. 3 Response of the armadillos' mean activity onset to the mean air temperature. *Black dots* represent yellow armadillos (*E. sexcinctus*, n=7). *Gray dots* represent the nine-banded armadillo (*D. novemcinctus*, n=3)

photoperiod duration and activity onset (rho=0.32, p=0.40) or duration (rho=-0.64, p=0.1).

Discussion

Despite our small sample size, it was possible to conclude that air temperature affected the activity onset and duration of the studied yellow armadillos. We did not have enough data to perform this analysis with nine-banded armadillos, but the three monitored individuals generally exited their burrows



Fig. 4 Response of the armadillos' mean activity duration to mean air temperature. *Black dots* represent yellow armadillos (*E. sexcinctus*, n=7). *Gray dots* represent nine-banded armadillos (*D. novemcinctus*, n=3)

during the first half of the night, irrespective of air temperature.

Our data show that, as daily mean temperature decreases, yellow armadillos tend to leave their burrows earlier and be active for longer periods, maximizing their diurnal activity (Figs. 3 and 4). The zone of thermal comfort for yellow armadillos is in air temperatures of around 30 ° C. When subjected to ambient temperatures lower or higher than 30 ° C, the yellow armadillos show signs of excitation and more variable body temperatures (Roig 1969). Hence, yellow armadillos seem to be physiologically adapted to warm air temperatures (\sim 30 ° C).

Yellow armadillos presented a relatively higher proportion of activity records at a certain air temperature range (Fig. 1) and changes in activity behavior according to air temperature variation (Figs. 3 and 4). These could be evidences that the monitored animals are able, to a certain point, to adjust their behavior to deal with their physiological constraints that requires them to be active at relatively warm air temperatures. This is also supported by empirical observations in the Pantanal wetlands, where yellow armadillos are commonly seen active during the hottest periods of the day when most animals are sheltered.

It is well established that some species of armadillo can adapt their activity patterns in response to changes in temperature (McNab 1980; Breece and Dusi 1985; McDonough and Loughry 2003; Superina and Boily 2007). For example, the nine-banded armadillo and the little hairy armadillo (*Chaetophractus vellerosus*) tend to be more diurnal in cold winters and more nocturnal in the summers at higher temperatures (Layne and Glover 1985; Greegor 1985). In tropical areas, the yellow armadillo is generally classified as diurnal (Emmons and Feer 1997; Eisenberg and Redford 1999; Trolle 2003; Cuéllar 2008), while the nine-banded armadillo is reported as nocturnal (Eisenberg and Redford 1999; Trolle 2003).

Our data suggest that, in similar air temperatures, the ninebanded armadillo tends to leave its burrow later than the yellow armadillo (Fig. 3). Nonetheless, the yellow armadillo was both diurnal and nocturnal, as previously reported by Bonato et al. (2008). The nine-banded armadillo tended to be nocturnal, but there were short periods of diurnal activity that confirm an earlier report by Layne and Glover (1985). These activity patterns indicated a low activity overlap (0.28) between these armadillo species. This could be considered as a preliminary evidence of separation in the temporal niches of the two species. However, this separation could be due to a variety of causes, and further studies should be performed to clarify this matter.

Several studies focused on thermoregulation strategies of anteaters (Montgomery and Lubin 1977; Shaw et al. 1987; Medri and Mourão 2005; Mourão and Medri 2007), sloths (Chiarello 1998; Urbani and Bosque 2007) and armadillos (Roig 1969; McNab 1980; Superina and Boily 2007). However, we could not find studies that focused on the activity onset of xenarthrans, with the exception of Camilo-Alves and Mourão (2006). Their results indicated that the air temperature linearly and positively affected the activity onset of giant anteaters. The activity onset of the yellow armadillos seems to be even more affected by air temperature than that of the giant anteater (Camilo-Alves and Mourão 2006).

Factors limiting temporal niche switches may be divided into internal (i.e., anatomic or physiological, such as sensory and thermoregulatory capabilities) and external (i.e., biotic and abiotic environmental conditions; Hut et al. 2012). Because armadillos are imperfect homeotherms (McNab 1985) and are primarily guided by odor and tactile stimuli, with very poor eyesight (Emerling and Springer 2014), it is not at all surprising that their activity pattern is mainly regulated by temperature rather than light. Their foraging activity does not seem to be harmed by this adaptive behavior, and they must gain physiological benefits.

Although the variability of the activity period durations of both armadillo species was high, the mean activity durations of the yellow armadillo and the nine-banded armadillo were similar and short. Armadillos are known to be active above-ground a few hours per day (McDonough and Loughry 1997) and spend the rest of their time inside the burrow, either inactive or performing activities such as nesting, sheltering, or thermoregulating (González et al. 2001; McDonough and Loughry 2003; McDonough and Loughry 2008). Such a short period of activity is frequently associated with body temperature regulation (González et al. 2001). Since xenarthrans have a low basal metabolic rate, about 40–60 % of what would be expected for a placental mammal of similar weight (McNab 1985), they have a limited capability to control body temperature and use burrows as thermal shelters.

McDonough and Loughry (1997) hypothesized that the levels of activity of nine-banded armadillos might increase on nights with higher soil temperatures and lower humidity. In these conditions, insects and other invertebrates, some of the main food sources for armadillos (Breece and Dusi 1985; McDonough and Loughry 2008), would be less available, and thus armadillos would have to spend more time active aboveground to be able to find sufficient food. We were not able to determine if the activity period of nine-banded armadillos was affected by the air temperature in the Pantanal because our sample size was small. However, the periods of activity of vellow armadillos tended to be negatively related to average daily temperature, disagreeing with what was expected by the McDonough and Loughry (1997) hypothesis. Such results might be related to the fact that, in contrast to the ninebanded armadillo, the yellow armadillo spends most of its time in open areas, such as grasslands and forest edges (Eisenberg and Redford 1999; Trolle 2003). Forested habitats work as temperature buffers (Camilo-Alves and Mourão 2006; Mourão and Medri 2007); thus, the nine-banded armadillo is somewhat sheltered from large temperature variations and extremes. Conversely, the yellow armadillo needs to avoid extreme air temperatures, frequently experienced in open habitats, by returning to its burrow to "regulate" its body temperature. Additionally, yellow armadillos are omnivorous and have a broader diet compared to the more insectivorous diet of nine-banded armadillos (Anacleto 2007); hence, they are not as influenced by the availability of invertebrate prey.

Studies concerning the activity budgets of armadillos are important because they may be conspicuously affected by their physiological constraints, such as low metabolic rate and high thermal conductance of the carapace, interacting with large-scale environmental conditions, such as the climate or landscape. In addition, physiological aspects may be more influential, affecting their behavior and activity more than other ecological traits, such as food availability. Armadillos and other xenarthrans could be used as models to obtain valuable information about how physiology affects decision making in mammals.

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