

Yamil E. Di Blanco*, Karina L. Spørring and Mario S. Di Bitetti

Daily activity pattern of reintroduced giant anteaters (*Myrmecophaga tridactyla*): effects of seasonality and experience

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Abstract: We assessed the effect of seasonality and intrinsic conditions on daily activity pattern of giant anteaters reintroduced in the Iberá Reserve, Argentina. During 2007–2012 we gathered 159 24-h focal samples on 15 radio-marked individuals (11 captive-reared, four wild-reared; seven adults, eight juveniles), 216 records of beginning and end of activity bouts on 20 individuals, and 454 camera-traps records (3345 trap-days). We estimated the daily hours of activity, the percentage of diurnal and nocturnal activity, and the daily activity range and time overlap using time as a circular variable in kernel density estimations. We assessed differences between seasons, sexes, age classes, and types of rearing. The average daily hours of activity was 8:43 h. Camera-traps and radio-telemetry showed similar results. Animals exhibited both diurnal (60–65%) and nocturnal (40–35%) activity. The higher probability for being active ranged within 09:00–03:00 h. Anteaters spent more hours active and were more nocturnal during summer. Activity was highly overlapped between sexes, and wild-reared individuals were more nocturnal than captive-reared ones. Seasonal shifts in daily activity highlights the importance of thermoregulation as a selective factor in this species. The giant anteater

is a cathemeral species with flexibility to accommodate its activity pattern to local conditions or experience.

Keywords: captive-reared; cathemerality; low metabolism; seasonality; wild-reared.

Introduction

The activity pattern is an important aspect of the natural history of mammals. Globally, the majority of mammal species are nocturnal (Heesy and Hall 2010, Bennie et al. 2014), although energetic constraints may have forced some species to be active throughout hours of both light and darkness (van Schaik and Griffiths 1996). Nowadays, mammals show a diverse array of activity patterns, from diurnal, nocturnal, crepuscular or distributed fairly evenly throughout the daily 24-h cycle, a condition known as cathemerality (Curtis and Rasmussen 2006, Tattersall 2006). Additionally, mammal species vary in their flexibility in activity patterns, which is reflected in inter- and intra-population variations.

Animals distribute their time between activity periods and resting periods (Halle and Stenseth 2000). Activity periods are more expensive, representing higher energetic costs of locomotion, higher thermal stress, and higher predation risk (Dunbar 1988; Owen-Smith 1998, Suselbeek et al. 2014). Animals should optimize the amount of time that they are active in order to satisfy their basic needs while minimizing the costs (Downes 2001). There are extrinsic (environmental) and intrinsic (biological) factors and a possible interplay between them that affect activity patterns (Speakman 1997, Anderson and Jetz 2005). Extrinsic factors include ambient temperature (Donati and Borgognini-Tarli 2006), daily, moon and seasonal cycles (Hoogenboom et al. 1984, Erkert and Kappler 2004, Di Bitetti et al. 2006), habitat quality (Wauters et al. 2001), predation risk (Griffin et al. 2005), protection and poaching risk (Di Bitetti et al. 2008) and competition (Halle and Stenseth 2000, Di Bitetti et al. 2009, 2010). Intrinsic factors include sex (Zschille et al. 2010), age and body size (Mott et al. 2011), reproductive stage

*Corresponding author: Yamil E. Di Blanco, Instituto de Biología Subtropical, sede Puerto Iguazú, Universidad Nacional de Misiones (UNaM) – Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Bertoni 85, Puerto Iguazú (CPA N3370BFA), Misiones, Argentina, e-mail: yamil_db@yahoo.com.ar. <http://orcid.org/0000-0001-7428-2096>

Karina L. Spørring: The Conservation Land Trust, Argentina, Scalabrini Ortiz 3355, 4° J Ciudad Autónoma de Buenos Aires (C1425DCB), Buenos Aires, Argentina

Mario S. Di Bitetti: Instituto de Biología Subtropical, Universidad Nacional de Misiones (UNaM) – Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Facultad de Ciencias Forestales, UNaM, Bertoni 85, Puerto Iguazú (CPA N3370BFA), Misiones, Argentina

(Eriksen et al. 2011) and even individual characteristics (Wagner et al. 2001, Kaczensky et al. 2006) due to genetic differences or experience and learning of individuals. It is especially important to acknowledge these aspects of the natural history of reintroduced individuals from different rearing conditions and experiences, because they can highlight the plasticity of the specie's capacity to acclimate to a new habitat.

In the mid-20th century, the giant anteater (*Myrmecophaga tridactyla*, Linnaeus, 1758) went extinct in part of its former distribution in northeastern Argentina (Fabri et al. 2003, Pérez Gimeno and Llarín Amaya 2007, Chebez and Cirignoli 2008). The first worldwide successful reintroduction of giant anteaters was planned to restore a free-ranging population of this species in the Iberá Natural Reserve, Corrientes Province, Argentina (Jiménez Pérez 2013). This study was conducted on this reintroduced population.

In comparison to other mammals, the giant anteater possesses a relatively low body temperature (27–33°C) and a low metabolic rate (McNab 1984, Stahl et al. 2012); presenting a periodic use of shallow torpor (Wislocki and Enders 1935; Fernandes and Young 2008) and prolonged periods of rest (Camilo-Alves and Mourão 2006). Most of the giant anteater's activity budget is spent searching for small prey (e.g. ants), which are consumed diluted with soil and other organic materials, resulting in the ingestion of food with a relatively low energetic content (McNab 1984, Gull et al. 2015). Therefore, giant anteaters, as other myrmecophagous mammals, should sustain their large body size by alleviating the energetic constraint through a reduction of their metabolic requirements (McNab 1984, Stahl et al. 2012). Nocturnal activity should be limited when nighttime temperatures are low, and diurnal activity when temperatures are high (Dunbar 1988, Bennie et al. 2014). To minimize metabolic costs, wild giant anteaters seem to avoid being active during times of extreme temperature (McNab 1984; Camilo-Alves and Mourão 2006, Mourão and Medri 2007). Radiotracked anteaters in the Pantanal of Brazil tended to begin their activity bouts early and reduced their total activity when the mean ambient temperature decreased, which was attributed to a strategy to prevent heat loss during low temperatures (Camilo-Alves and Mourão 2006). This pattern can be especially important in the southernmost limit of their geographic distribution, as in the Iberá Marshlands, northeastern Argentina, which are characterized by marked thermal seasonality.

Due to differences in metabolic requirements and selective pressures of males and females and of animals of different age and body size, the sex and age of individuals

are important intrinsic conditions that can affect activity patterns (Zschille et al. 2010, Eriksen et al. 2011, Mott et al. 2011). Giant anteaters do not present evident sexual dimorphism (Shaw et al. 1987), and there is no evidence suggesting marked differences in the activity pattern between sexes. On the other hand, animals adaptively trade-off their foraging efforts and their exposure to predation, but risk assessment depends on experience (Lima and Bednekoff 1999). Thus, the type of rearing may also be important for this reintroduced population of giant anteaters. Wild animals are probably more experienced in predation risk or hunting compared to animals that were reared in captivity, and animals can acquire more experience with age. Therefore, it is expected that animals of different experiences may present different activity patterns. In addition, a nocturnal habit is likely to minimize contact with humans (Bennie et al. 2014). On the other hand, it has been shown that captivity can affect the natural behavior of animals, both wild and domestic (Scott 1948, Rowell 1967, Staddon and Simmelhag 1971). For example, captive animals might have become used to forage during daylight hours, when animal caretakers typically provide the food.

Motion-sensitive radio equipment has been used extensively to study mammalian activity patterns (Beltran and Delibes 1994, Lariviere et al. 1994, Schmidt 1999), as have camera traps (van Schaik and Griffiths 1996, Azlan and Sharma 2006, Ridout and Linkie 2009, Oliveira-Santos et al. 2013). Comparisons of the results obtained with both methodologies can provide a better interpretation of time activity patterns and of potential methodological biases.

The goal of our study was to describe activity pattern of giant anteaters and assess the effect of environmental conditions (seasonality) and sex, age and rearing characteristics of individuals (if they were captive or wild-reared). Besides, we compared activity patterns estimated using two alternative methodologies, radio-telemetry and camera-traps, to highlight advantages and disadvantages of both techniques. The general hypothesis tested in this study is that environmental temperature is one of the main determinants of the activity pattern of giant anteaters, expecting shifts on their daily activity hours between seasons, resulting in more diurnal activity during the colder winter season and more nocturnal activity during the hotter summer season. Increased diurnal activity in captive reared-individuals could have been triggered by typical feeding routines during captivity. It is also expected that wild-reared animals will be active during hours of lower perceived risk of predation, being probably more nocturnal than inexperienced captive-reared

individuals. We also tested for the potential effect of sex and age of individuals.

Materials and methods

Study site

The Iberá Nature Reserve (INR), in Corrientes Province, Argentina, is a 13,000 km² multiple use protected area (Canziani et al. 2003) that includes a diverse mosaic of habitats, including flooded grasslands, grasslands, savannas and gallery forests. The climate is subtropical, with mean daily temperatures ranging from 16–17°C during the mild winter months (June and July) to 27–28°C during the relatively hot summer months (January and February). In the winter the minimum absolute temperatures can reach -2°C with low frequency of annual frosts (range: 2–10 days), and maximum absolute temperatures up to 44°C during the summer. The mean annual precipitation is 1700–1800 mm (Neiff and Poi de Neiff 2006). For this study, we divided each year in three seasons of four months based on contrasting patterns of ambient temperature at the study site: (1) “summer” (November to February), (2) “winter” (May to August) and (3) transition (March, April, September and October).

The giant anteater reintroduction area is located in the Southeastern portion of the INR (28° 39' S, 57° 23' W), in the Private Reserve Rincón del Socorro (124 km²). This land presents different habitats of different vegetation structure and composition that giant anteaters uses in different degree. There are seasonally flooded grasslands, known locally as Malezales, dominated by 1.5–2 m high *Andropogon lateralis*; savannahs, typical of the Espinal ecoregion, dominated by the caranday palm (*Copernicia alba*) and two legume trees (*Prosopis affinis* and *Acacia caven*) sparsely distributed in space or gathered in small forest patches and bushes embedded in a herbaceous layer; and hygrophilous forests, along small and temporary streams, that form a continuous canopy that reach 15–20 m in height and include a diverse array of trees typical of the Atlantic Forest (Tressens et al. 2002). These forests are highly selected by the giant anteaters, especially for resting periods (Di Blanco et al. 2015).

Ambient temperature was recorded by a meteorological station located in the study area since May 2008 until August 2010, and expressed as a daily mean value from 48 measurements, taken every half hour. The “winter” season was characterized by a mean daily temperature (\pm SD) of 16.2 \pm 4.5°C, ranging from 3.7°C to 28.9°C; the

“summer” by a mean of 26.5 \pm 2.8°C and a range of 18.5–33.3°C, and the transition months by a mean temperature of 20.6 \pm 4.6°C, ranging from 6.9°C to 30.6°C. We also estimated the mean hours of daylight through the `daylength()` function of the package `geosphere` (Hijmans 2014) for R environment (R Core Team 2013). Seasons defined for this study were characterized by mean photoperiod (\pm SD) of 13:58 h (\pm 0:20) during summer, 12:00 (\pm 0:33) in transition months and 10:40 h (\pm 0:19) during winter.

Study animals and activity records

During 2007–2012 we surveyed activity patterns of 20 reintroduced giant anteaters using a combination of different techniques. Most individuals were captive-reared (n=15, six males and nine females) and five of them were wild-reared (four males and a female). All animals were born at different sites of the Argentinean Chaco region, but the captive-reared animals spent an important part of their life in captivity or semi captivity since early age (<1–6 months old). Most captive-reared individuals were released as juveniles (<36 months old; we followed Redford and Eisenberg 1992 to determine these age classes), spending an average (\pm SD) of 16.3 (\pm 7.5) months in captivity. Only two captive-reared females were released as adults (\geq 36 months old) and spent 58.1 (\pm 6.6) months in captivity. Animals were reared by zoos, government facilities, or in nursery facilities belonging to The Conservation Land Trust, the institution that carried out the reintroduction project. Wild-reared animals were removed from their natural habitat at a more advanced age (one male at approximately 12 months old and four >24 months old) after being injured by hunters or in road accidents. These animals spent an average (\pm SD) of 7.2 (\pm 6.9) months in captivity where they were treated and rehabilitated for reintroduction (Jiménez Pérez 2013).

Reintroduced animals were fitted with harnesses equipped with Very High Frequency (VHF) transmitters with activity and mortality sensors (Telonics®, Mesa, AZ, USA; see Di Blanco et al. 2012). Transmitter signals are transformed in the receiving unit into a sound, which shifts depending on the pulse rhythm of the signal. Observers noted the activity state of the animal by noting the sound signal. We defined “activity” as the moments during the day period when the animals were moving, foraging or carrying out other vigil activities, while the inactivity state corresponds to the moments of resting, characterized by the complete lack of movement, when they are resting or sleeping on the ground. In previous stages of this study, we assessed the reliability of the activity sensors by

listening to the signal simultaneously with direct observations of the radio-tagged animals in captivity and in the field. Activity signal is triggered by the movement of the animal after having been active during 5–10 s, but for the radio-transmitter to change from activity to inactivity signal, the animals must have been stationary for at least 5 min. To ensure the activity state of the animal (active or inactive) during data recording, the signal was listened to during at least 1 min continuously.

We obtained 159 24-h focal samples of 15 radio-tracked individuals (eight males and seven females) recording the animals' activity within years 2007 and 2011. Eleven were captive-reared (six females and five males) and four were wild-reared animals (three males and one female). Seven were adult animals (≥ 36 months old) and the rest were juveniles and sub adults (< 36 months old). Throughout the tracking period the transmitter signal was listened at 1-h intervals (00:30, 01:30, ..., 23:30) noting whether the animals were active or inactive. The 24-h samples were taken in one continuous sampling bout ($n=29$) or in four 6-h continuous bouts (00:30–05:30, 06:30–11:30, 12:30–17:30 and 18:30–23:30; $n=130$), completing one or two 24-h samples for each individual per month. Sampling effort was evenly distributed throughout the year (n summer=40, n transition=53, n winter=66).

The signal was listened to frequently (every 10–15 min or less) while we were sampling or locating the animals. During January 2007–October 2012 we recorded *ad libitum* and opportunistically the approximate hour when a change in activity of the focal animal was detected (i.e. beginning or end of a period of activity). We only recorded changes of activity that we were certain that were not induced by the observer (e.g. when the observer was at least at 200 m and/or downwind from the animal). From 20 animals 132 records of beginning of activity and 84 of end of activity periods were detected.

After the first animals released lost their radio-harnesses, and considering the difficulty for their re-capture, we decided to deploy baited camera-traps as an alternative method of monitoring the survival and reproduction of the untagged individuals. From August 2008 to November 2012 we sat up 14 camera-trap stations at different sites previously used by giant anteaters in the study area. We used various types of camera-traps: Leaf River Trail Scan 35 mm film cameras (Model C-1, Vibra Shine, Taylorsville, MS, USA), digital Moultrie® (M40 Digital Game Camera, Alabaster, AL, USA) and Reconyx, Inc. (Model Rapidfire HC500, Holmen, WI, USA). Camera-traps were baited periodically (every 3–10 days) using the artificial food similar to the one that animals had been fed in captivity. A blended mix of cat pellets, yogurt or milk,

fruits and boiled eggs was used during captivity, and a simpler mix containing cat pellets, apple and water was used for baiting camera-trap stations.

The sample stations consisted of one camera-trap attached to a trunk in a shady location 25–50 cm above ground. Vegetation between the camera and the bait was cleared. Cameras were set to be active throughout the 24-h cycle, triggering one to three photographs per detection with a 5 min delay between successive detections. Each camera-trap station was active for variable periods of time (with a mean \pm SD of 239 \pm 336 trap-days), totaling 3345 trap-days of effort. Baited stations tend to produce successive photographs of the same individual at short time intervals. We considered as an independent record photographs obtained at least 1 h apart, or within this period only if we were able to unambiguously identify different individuals (e.g. radio-tagged or not). During this survey we recorded 454 independent photographs of giant anteaters.

Data analysis

We used the total number of activity hours in a 24-h sample only to estimate the amount of hours of activity within a day period. We used a one-way ANOVA and a Tukey's test to assess the existence of differences in the number of hours of activity among seasons.

To account for independence of continuous data and describe, analyze and compare other aspects of activity patterns (i.e. activity range, concentration and overlap) we used: (1) one randomly selected record of activity within a 24-h period per individual, (2) *ad libitum* records of beginning and end of activity and (3) independent records from camera-traps. To randomly select an activity record within a 24-h period we use the `RANDBETWEEN` function in Excel.

From 24-h samples and camera-trap data we estimated the proportion of records occurring during daylight or at night. We used the `sunrise()` function of the `maptools` package (Bivand and Lewin-Koh 2015) to calculate, for the study site, the time of sunrise and sunset for the date of each record and determine if the record occurred within daylight hours or during nighttime. We tested for seasonal and intra-population differences between sex, age (adults vs. juveniles) and rearing (captive or wild-reared) categories. All wild-reared animals were adults, and all juvenile animals were captive-reared. To avoid possible biases we only used adult captive-reared individuals (three females) to assess differences between adults and juveniles and between captive-reared and wild-reared individuals.

We used kernel density functions (Worton 1989), performed with the `modal.region()` function from the circular R-package (Agostinelli and Lund, 2013) to identify the periods when animals are usually active by the isopleths of 95% (“activity range”) and the time periods where activity is concentrated by the isopleths of 50% (“core activity range”). The bandwidth was fixed to five, following recommendations from Oliveira-Santos et al. (2013). The precision was estimated by the 95% confidence intervals (CIs) as percentile intervals from 1000 bootstrap samples (Ridout and Linkie 2009).

We also used kernel density estimates to compute overlap analysis (Ridout and Linkie 2009). We estimated the coefficient of overlap (Δ), which varies from 0 (no overlap) to 1 (complete overlap), to assess and plot the relationship between different data sets of giant anteater activity patterns using the R-package `overlap` (Meredith and Ridout 2013). To calculate the coefficient of overlap we used the estimator Δ_1 for small sample sizes (<75 records) and Δ_4 for samples with more than 75 records. The precision of the estimator of overlap was estimated by the 95% CIs for Δ as percentile intervals from 1000 bootstrap samples (Ridout and Linkie 2009).

We also tested for differences between sex, age and rearing condition of the animals on time activity patterns using Mardia-Watson-Wheeler tests (Batschelet 1981, Mardia and Jupp 2000), a non-parametric test that evaluates if two or more circular samples (angles) possess the same distribution, where the p value is estimated assuming that the statistic value (W) follows a chi squared distribution. All statistical analyses were implemented in the software R 3.0.2 (R Core Team 2013).

Results

The average hours of activity (\pm SE) in a 24-h period for all individuals and seasons combined was 8:43 h (\pm 0:11; range 1–18, $n=159$ 24-h bouts). Anteaters were often active almost continuously during one main activity bout each day: we collected 29 continuous 24-h periods, of which 25 (82.76%) had only one bout of activity and one or two inactivity periods. Active bouts could be interrupted by brief resting periods of an hour or less. The amount of hours of activity (mean \pm SE) was higher during summer (9:38 \pm 0:21 h, $n=40$ 24-h bouts) than during winter (8:16 \pm 0:19 h, $n=66$ 24-h bouts), with intermediate values during transition (8:36 \pm 0:17 h, $n=53$ 24-h bouts; $F_{2,156}=4.381$, $p=0.0141$; Tukey’s test: summer-winter, $p=0.011$; summer-transition, $p=0.0906$; winter-transition, $p=0.7173$; Figure 1).

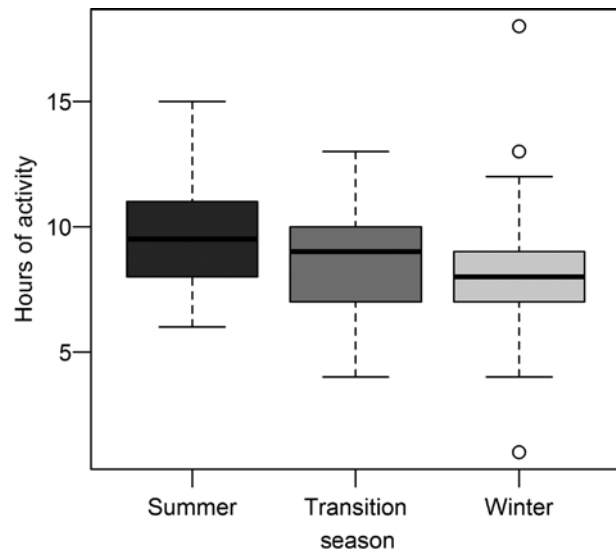


Figure 1: Box-plots depicting the number of hours of activity of radio-tracked individuals in 24-h periods in three different seasons. There is an evident reduction on the amount of time of activity from summer to winter. Whiskers extend to the further observation within a step, or 1.5 times the interquartile rank beyond the box (first and third quartiles). Hollow points indicate outliers or observations beyond this step.

Giant anteaters were active during both day and night, from 60–65% of activity during daylight and 40–35% during nighttime, based on camera-trap or radio-telemetry data, respectively. This pattern changed between seasons. During summer, 52% of activity records occurred at nighttime for both sample methodologies. During winter most activity records occurred during daylight (76% for camera-trap data and 62% for radio-telemetry data). Adult animals, only captive-reared ones (three females), presented a balanced nocturnal and diurnal activity (57% and 43% of diurnal and nocturnal activity, respectively). Juveniles (all captive-reared) were highly diurnal (82% of activity records during daylight). Wild-reared animals were more nocturnal (around 70% of records; Table 1).

Giant anteaters concentrated most of their activity in a wide range of time throughout the year. This range was estimated to have a duration of 16:41 h (95% CI=15:40–17:32 h) from radio-telemetry data and of 18:37 h (95% CI=16:58–19:46 h) based on camera-trap data, with a higher chance of being active between approximately 09:00 and 03:00 h. Core activity ranges (kernel 50%) were similar between different methodologies: 5:56 h (95% CI=5:08–6:48 h) and 5:32 h (95% CI=5:09–5:56 h) based on 24-h following of radio-tagged animals and camera-trap data, respectively, with most activity concentrated in the afternoon and the evening (between 13:00 and 20:00 h). Camera-trap data showed a wider activity range during

Table 1: Percentage of diurnal and nocturnal activity, activity range (95% kernel) and core activity range (50% kernel) estimates through camera-trap and radio-telemetry data.

Methodology	Data set	n Individuals/ n records	Diurnal activity (%)	Nocturnal activity (%)	Activity range length [h (CIs)] ^a	Approx. activity range (h) ^b	Core activity range length [h (CIs)] ^a	Approx. activity range (h) ^b
Camera-traps	All	-/454	64.95	35.05	18:37 (16:58–19:46)	09:00–03:30	5:32 (5:09–5:56)	14:30–20:00
	Summer	-/123	47.73	52.27	19:15 (17:22–20:26)	12:00–07:00	5:43 (4:52–6:39)	17:00–23:00
	Winter	-/221	76.47	23.53	13:35 (12:19–14:54)	09:00–22:30	4:26 (4:03–4:47)	14:30–19:00
24-h	All	15/159	59.75	40.25	16:41 (15:40–17:32)	11:00–03:00	5:56 (5:08–6:48)	13:00–18:00
	Summer	15/40	47.50	52.50	17:28 (14:28–19:14)	12:30–06:00	5:49 (4:30–7:22)	16:00–22:00
	Winter	13/66	62.12	37.88	20:19 (17:14–21:15)	09:00–05:00	6:12 (4:59–7:32)	13:00–19:00
	Captive-reared adults ^c	3/54	57.41	42.59	19:28 (16:46–20:26)	09:00–04:00	7:04 (5:35–8:20)	14:00–21:30
	Juveniles ^d	8/62	82.26	17.74	18:49 (15:44–20:52)	05:00–00:00	5:20 (4:18–6:39)	14:00–19:00
	Wild-reared ^e	4/43	30.23	69.77	18:53 (16:27–20:57)	11:00–06:00	7:32 (5:56–8:42)	16:30–00:00

Ranges are estimated for different seasons, age and rearing conditions of individuals. ^aValues represent the amount of hours (and its 95% CI). ^bApproximate values obtained from visual observation of plots. ^cThe three captive-reared adult individuals were females. ^dAll juveniles were captive-reared. ^eThe four wild-reared animals were adults.

summer (19:15 h) than during winter (13:35 h), while radio-telemetry data showed the opposite pattern (17:28 h during summer and 20:02 h during winter), although with wide and highly overlapping CIs (Table 1).

In general, giant anteaters increased their activity to a peak around 18:00 h (Figure 2). Radio-telemetry data showed that the activity pattern differed among seasons, with summer and winter overlapping least, owing to the displacement of the activity curve towards night-time hours during summer. The transition season overlapped highly with winter (Figure 2A–C). Camera-trap data showed the same overall results among seasons as the 24-h data, but overlap was similar between winter-transition and summer-transition contrasts (Figure 2D–F). Giant anteaters started and finished their activity following a similar pattern as described above, but with more evident peaks and variations. During summer animals had a higher probability of beginning their activity at dusk, and in winter and transition at noon (Figure 3A–C). End of activity was concentrated at dusk during the transition and the winter seasons and was less concentrated but with a peak at dawn during the summer (Figure 3D–F). There was high overlap in the periods of activity of males and females (Figure 4A). Captive-reared juveniles tended to be more diurnal than captive-reared adults, with a strong peak of activity in the late afternoon (Figure 4B). Wild-reared animals (all adults) were more nocturnal than captive-reared adult animals, showing less overlap (Figure 4C). Activity patterns did not differ between sexes or age classes, but in general were significantly different among seasons, and between rearing conditions (Table 2).

Discussion and conclusion

The results of this study are consistent with those conducted on wild populations of giant anteaters, showing a peak of activity around 18:00 h and seasonal variations probably related to ambient temperature (Shaw et al. 1987, Camilo-Alves and Mourão 2006, Mourão and Medri 2007). The total amount of active hours of reintroduced giant anteaters at Iberá was similar to those found in wild populations. They also decreased their total activity or spent a great amount of time resting during the winter, suggesting a reduction of total activity to prevent heat loss when temperatures are low (Camilo-Alves and Mourão 2006). The amount of time spent being active can also be affected by food abundance (Dunbar 1988). Mammals may optimize their energetic balance using two alternative strategies: 1) increasing foraging effort when food intake per unit

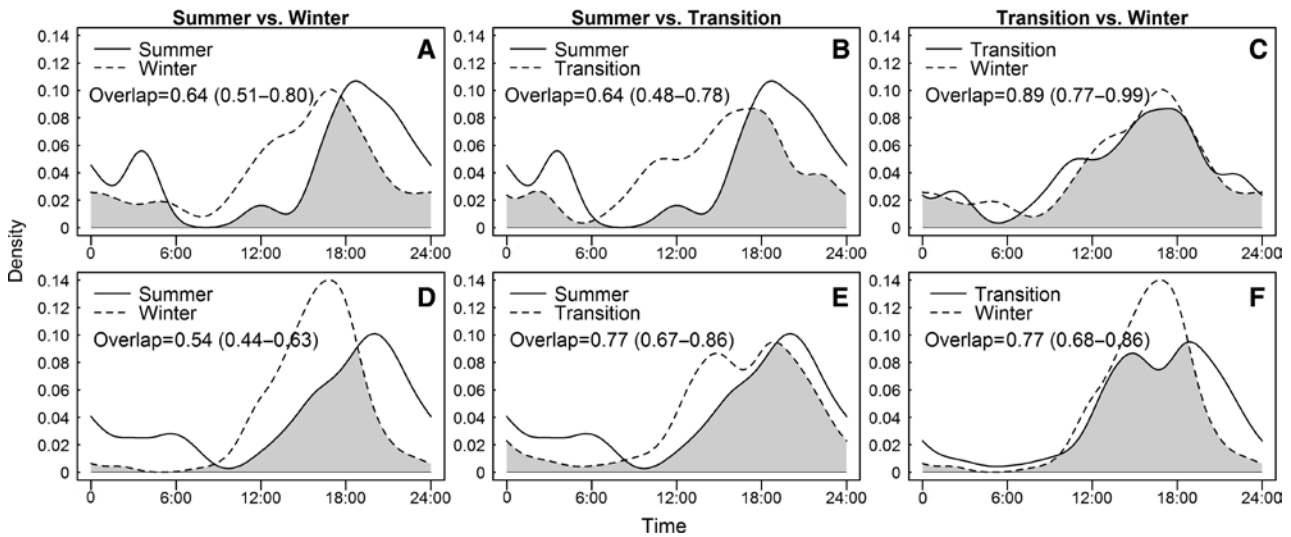


Figure 2: Kernel density estimates of the activity pattern overlap between seasons based on one random selected record of activity in a 24-h period from telemetry data (A–C) and camera-trap data (D–F). (A and D) summer vs. winter, (B and E) summer vs. transition and (C and F) transition vs. winter. Overlap coefficients and 95% CIs are indicated within plots.

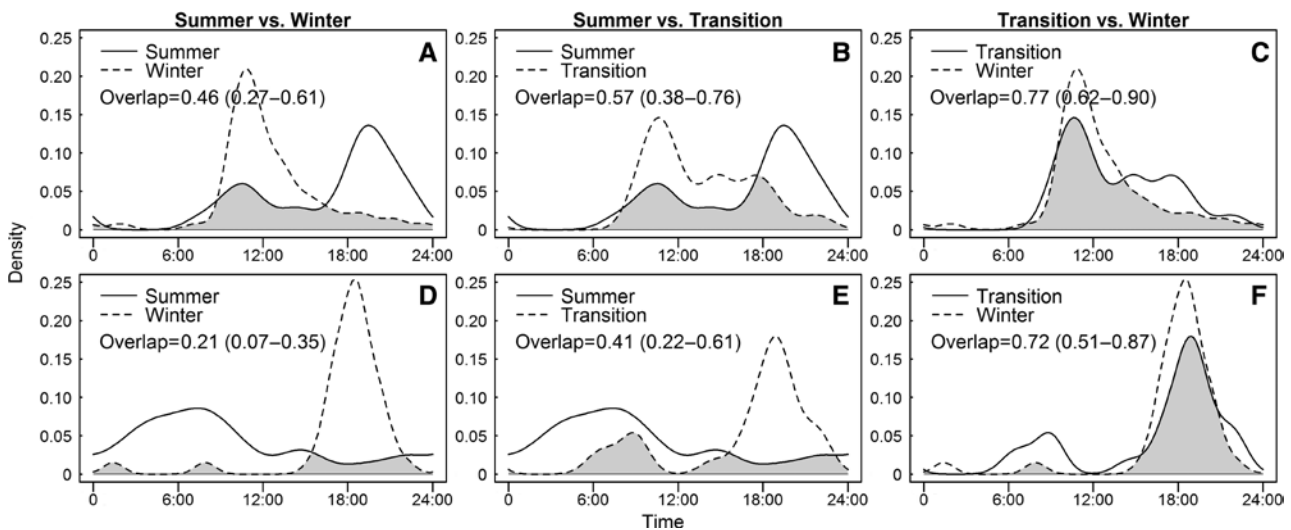


Figure 3: Kernel density estimates of the activity pattern overlap between seasons based on records of the beginning (A–C) and end (D–F) of an activity period from telemetry data. (A and D) summer vs. winter, (B and E) summer vs. transition and (C and F) transition vs. winter. Overlap coefficients and 95% CIs are indicated within plots.

of time decreases, which will require more investment in time dedicated to foraging or, 2) when the intake energy rate per unit of foraging time drops below a critical level, animals can reduce the energy expenditure by reducing activity, a common pattern found in animals that feed on food of low energy content (Milton 1998; Rezende and Bozinovic 2001). Considering that in the study site the abundance of ants greatly diminishes during the cold season (Calcaterra et al. 2008, 2014), it is likely that the reduction of time invested on activity during the winter

is the results of giant anteaters using the “energy saving” strategy when faced with less food availability.

The wider activity range during winter estimated from radio-telemetry may suggest the opposite pattern, but the sample size during summer was reduced (40 records, when the minimum suggested for this analysis is 50, C. Zucco pers. comm.) to produce a reliable estimate. In addition, the CIs were wide and highly overlapping between seasons, whereas this did not occur with estimations based on camera-trap data. Sample sizes of camera-trap data

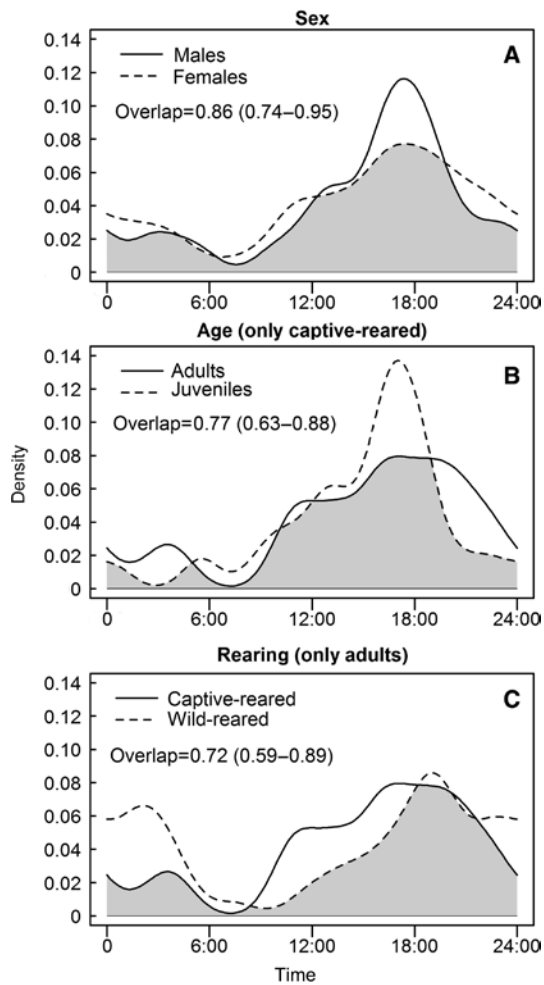


Figure 4: Kernel density estimates of the activity pattern overlap between sexes, age classes (adult vs. juveniles) and rearing condition (wild-reared vs. captive-reared) based on one random selected record of activity in a 24-h period from telemetry data. Overlap coefficients and 95% CIs are indicated within plots.

were more appropriate, and CIs did not overlapped. With these data giant anteaters showed the expected pattern of a more limited activity range during winter (Table 2).

Radio-telemetry and camera-trap data gave similar results, so both sampling methods prove to be thorough, efficient and little (or similarly) biased methodologies to describe activity patterns, at least when using sample protocols similar to this study. Although radio-telemetry needs more time and effort investment, it allows for the assessment of intrinsic factors such as sex, age (Rowcliffe et al. 2014, Suselbeek et al. 2014) and other conditions of the study animals, such as the rearing differences of the individuals. The records of beginning-end of activity periods give different information to describe and compare activity patterns and are relatively easy to obtain using radio-telemetry but not available with camera-trap data. This also depends on the data collection protocols, which should be rigorous to avoid disturbance that can cause changes in the activity state of the animal observed, and the effort should evenly cover the entire 24-h cycle in a balanced manner.

Giant anteaters showed a cathemeral pattern of daily activity, which gave them the capacity to modify their activity according to shifting environmental conditions – in this case, seasonally – to avoid being active during hours of extreme temperatures: cold winter nights and very hot summer days (Camilo-Alves and Mourão 2006, Mourão and Medri 2007). Strictly diurnal animals cannot overcome the *circa* 12 h of activity during a diel cycle, which is why it has been proposed that cathemerality is a behavioral (adaptive) response that enables animals to take advantage of additional foraging time (van Schaik and Griffiths 1996, Merritt and Vessey 2000).

Table 2: Mardia-Watson-Wheeler tests between different data sets.

Methodology	Comparison	n	W	df	p-Value
Camera-traps 24-h	Summer-transition-winter	132–111–221	63.6316	4	<0.0001
	Summer-transition-winter	40–53–66	16.849	2	0.0032
	Males-females	72–87	3.756	2	0.1739
	Captive-reared adults ^a -juveniles ^b	54–62	4.901	2	0.08625
	Captive-reared adults ^a -wild-reared ^c	54–43	16.7153	2	0.0005
Beginning of activity	Summer-transition-winter	65–38–29	25.593	4	<0.0001
	Males-females	59–73	3.0423	2	0.2361
	Captive-reared adults ^a -juveniles ^b	46–46	0.1963	2	0.9065
	Captive-reared adults ^a -wild-reared ^c	46–38	12.124	2	0.0023
End of activity	Summer-transition-winter	24–24–36	33.2697	4	<0.0001
	Males-females	40–44	3.8674	2	0.1453
	Captive-reared adults ^a -juveniles ^b	25–41	1.4627	2	0.4813
	Captive-reared adults ^a -wild-reared ^c	25–18	14.848	2	0.0006

W is the statistic of the test, equivalent to a χ^2 -value. ^aThe three captive-reared adult individuals were females. ^bAll juveniles were captive-reared. ^cWild-reared animals were adults.

The flexibility of cathemerality also allows animals to locally-seasonally schedule their time activity patterns to reduce encounters with predators and competitors or to reduce the energetic costs of thermoregulation (Donati and Borgognini-Tarli 2006). In our study site, where there are no important competitors or predators, and where the range of daily activity of giant anteaters is lower than 12 h, thermal stress seems to be the most important determinant of the observed time activity patterns. This suggests that thermoregulation is the main factor determining the observed activity patterns and may explain the cathemerality of this species.

A cathemeral activity pattern represents a more generalized behavior and is less expected for species with morphological or physiological specializations to exploit a particular niche or having a specific diet (Schoener 1974). Nonetheless, the giant anteater, a highly specialized mammal in terms of its diet, presents marked seasonal shifts in their time activity pattern, with more diurnal activity during winter. In addition, the hour of activity termination seems to be less predictable during the summer, but highly concentrated at dusk during the coldest season, suggesting that animals avoid being active after the sudden drop of ambient temperature following sunset during winter. Giant anteaters can gain heat through exposure to sunlight (Camilo-Alves and Mourão 2006, Mourão and Medri 2007), being less capable to regulate their body temperature during nighttime. This can explain differences in the pattern of ending of activity between summer and winter.

Giant anteater activity pattern did not vary between sexes and is not markedly different between juveniles and adults, although it seems to differ according to the rearing characteristics of the individuals. Juvenile animals (all captive-reared) were highly diurnal. Juvenile animals may have different selection pressures than adults (predators, diet, temperature) which can affect their optimal time of activity. On the other hand, the performance of young animals may not be as efficient as that of the adults due to lack of experience (and should adjust the pattern as they grow). The four wild-reared animals were consistently more nocturnal than captive-reared ones, presenting the opposite proportion of day-night activity. In spite of the reduced sample size, these results suggest that the experience and learning of animals can affect time activity pattern of giant anteater. Daily activity pattern may also be affected by captivity (Scott 1948, Rowell 1967, Staddon and Simmelhag 1971). Captive animals are usually fed at a specific time and place with similar food items during daytime working hours of their caretakers, which might have made animals used to forage during daylight.

Wild-reared animals spent a considerable amount of time in captivity and had a similar feeding routine to the captive-reared individuals. However, wild-reared individuals were older than captive-reared ones when they were captured. Before they were captured, wild-reared individuals may have faced dogs (*Canis lupus familiaris*, Linnaeus, 1758) and experienced predation attempts. In addition, adult wild-reared animals were captured in the wild by humans and suffered traumatic incidents (wounded by poachers, road accidents) that might have induced their avoidance of humans. Anti-predatory behaviors, including a more nocturnal activity pattern, may have become entrenched in them before their reintroduction into a new site and may explain the difference observed between captive-reared and wild-reared animals.

The activity levels of most animals reflect a tradeoff between energy intake requirements and avoidance of predation where, in general, animals reduce their foraging activity level when predation pressure increases (Lima and Dill 1990, Bednekoff 2007). Animals can concentrate their diel activity during hours of the day when encounters with predators are minimized (Lima and Bednekoff 1999, Whitham and Mathis 2000, Van Buskirk et al. 2002, Higginson et al. 2012). This kind of behavior has been reported for a great diversity of mammals, especially for those cathemeral and with high behavioral plasticity (Di Bitetti et al. 2009). In addition, a nocturnal habit is likely to minimize contact with humans (Bennie et al. 2014).

The giant anteater is a cathemeral species that shows seasonal variations in its activity, but also has the capability of modifying its time activity pattern according to the individual experience of animals. The habitat characteristics may also influence behavior, using habitats with more vegetation cover to rest, and more open habitats for activity periods (Camilo-Alves and Mourão 2006, Mourão and Medri 2007, Di Blanco et al. 2015), which suggests that the species has the plasticity to adjust their time activity patterns and other behaviors according to environmental conditions. The ability of reintroduced individuals to acclimate to a new area is frequently uncertain, especially those sourced from captive populations (Kleiman 1989, Converse et al. 2013). The plasticity of giant anteater may play an important role that facilitates the management of the species with conservation purposes and may partly explain the success of this reintroduction project even though based on animals that came from captivity.

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