



Programa de Pós Graduação em Ecologia e Conservação  
Centro de Ciências Biológicas e da Saúde  
Universidade Federal de Mato Grosso do Sul

**Spatial and temporal ecology of two armadillo species  
in a Neotropical region**

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Campo Grande  
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in a Neotropical region**

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para a obtenção do título de  
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Dr. \_\_\_\_\_

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Dr. \_\_\_\_\_

Dr. \_\_\_\_\_

"... Dou mais respeito  
às que vivem de barriga no chão  
tipo água pedra sapo.  
Entendo bem o sotaque das águas  
Dou respeito às coisas desimportantes  
e aos seres desimportantes.  
Prezo insetos mais que aviões.  
Prezo a velocidade  
das tartarugas mais que a dos mísseis.  
Tenho em mim um atraso de nascença.  
Eu fui aparelhado  
para gostar de passarinhos.  
Tenho abundância de ser feliz por isso..."  
*Manoel de Barros*

"... a importância de uma coisa não se mede com fita métrica nem com balanças nem com  
barômetros etc. Que a importância de uma coisa há que ser medida pelo encantamento que a  
coisa produza em nós..."  
*Manoel de Barros*



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## General abstract

Critical contemporary ecological problems (e.g. predicting how animals might respond to habitat alteration or climate change) require factual knowledge on species biology and ecology. Biological characteristics and ecological functions of elusive burrowing species can be inferred through the study of spatial ecology. Furthermore, even though armadillo behavior is little studied, these imperfect homeotherms provide valuable models for understanding how physiology affects mammalian behavior in response to environmental changes. Here I aim to characterize the biology of two poorly known armadillo species, understand aspects of their ecology and how they respond to environmental changes. Camera traps, VHF and GPS telemetry were used to monitor two species of armadillo (yellow armadillos, *Euphractus sexcinctus*,  $n = 17$ ; and southern three-banded armadillos, *Tolypeutes matacus*,  $n = 26$ ), in three sites of the Pantanal wetlands, Brazil. In the first section of this dissertation, I used direct observations and footages from camera traps placed in front of shelter locations to describe the sheltering habits of *T. matacus* and compared it to the habits of *T. tricinctus* in the northeast Brazil. I dedicated the second section to exploring the spatial and temporal ecology and the social biology of the little known *T. matacus*. Co-authors and I characterized its activity patterns using a non-parametric model of a conditional circular kernel function. Its habitat selection, in relation to vegetation features and distance to paths, was assessed using Resource Selection Functions. Their home range areas were estimated through Kernel probabilistic non-parametric models and Minimum Convex Polygon. The static interaction between pairs of individuals was characterized using the Utilization Distribution Overlap Index and the relationship between the movements of these pairs was explored using a Proximity analysis. In the third section, co-authors and I evaluate how variations in activity patterns and habitat selection by *T. matacus* and *E. sexcinctus* correlate with air temperature. This was done using linear mixed-effects models to evaluate the

variation of activity patterns and duration according to changes in air temperature and fitting Step Selection Functions to evaluate the effects of the cover type, circadian cycle, and air temperature on armadillo resource selection. *Tolypeutes* sp. used four types of shelter, which were used and reused with different frequencies by individuals of different sexes and age classes. Direct observations and indirect evidence proved that *Tolypeutes* dig their own burrows, contradicting previous belief. *Tolypeutes matacus* were active in average for  $5.5 \pm 2.8$  hours per day, with most of their activity concentrated in the first half of the night. However, as air temperature decreases, its activity periods became shorter and peak earlier in the day. *Euphractus sexcinctus* shows a more pronounced behavioral plasticity, shifting its activity pattern from diurnal to nocturnal, as mean daily temperature increases. The distance to dirt paths negatively affected the selection strength of *T. matacus*, regardless of the vegetation cover. *T. matacus* selected mainly forests when in proximity of dirt paths, but when relatively far from the paths the relative selection strength of pasture units increased. However, *T. matacus* habitat selection can vary across temperatures. *Euphractus sexcinctus* tends to select open vegetation areas during activity and forested areas during rest, but the strength of this habitat selection depends on temperature. Home range size of *T. matacus* males was positively related with their body mass, while female home range sizes did not scale with body mass. Adult males had larger home range areas. Females *T. matacus* did not share their home ranges and core areas with other females, regardless of age class, while ranges occupied by males overlapped with both males and females. Dyads of *T. matacus* were in average 423 m apart and in only 1% of the simultaneous fixes animals were in proximity. To my knowledge, this is the first study of free-ranging *T. matacus* in the Brazil and the most comprehensive study on its ecology everywhere. The spacing and home range patterns of *T. matacus* points out to a generally asocial behavior and a promiscuous mating system. The burrow's reduced depth suggests that the use of burrows by *Tolypeutes* is more

likely to be related to parental care and thermoregulation strategies than to defense mechanisms. *Tolypeutes matacus* could be characterized as a mainly nocturnal species that selects preferentially areas close to paths and forested areas, but also able to occupy modified landscapes. However, specific examples of the dynamic nature of activity patterns and habitat selection as functions of the air temperature illustrate how dynamically both studied species can alter their behavior. *Tolypeutes matacus* has been classified as Data Deficient and I hope that the data generated here will contribute to this species conservation. Furthermore, these results highlight the importance of habitat heterogeneity for the long-term conservation of animal species that rely on behaviour to achieve adequate thermoregulation.

## Resumo

Problemas ecológicos contemporâneos críticos (e.g. prever como animais podem responder a alteração do hábitat ou alterações climáticas), exigem o conhecimento factual sobre a biologia e ecologia de espécies. Características biológicas e funções ecológicas de espécies que utilizam tocas e são dificilmente visualizadas podem ser inferidas através do estudo de sua ecologia espacial. Além disso, mesmo que o comportamento de tatus seja pouco estudado, esses homeotermos imperfeitos podem fornecer modelos valiosos para entender como a fisiologia afeta o comportamento de mamíferos em resposta a mudanças ambientais. Aqui procuro caracterizar a biologia de duas espécies de tatus pouco conhecidas, entender aspectos de sua ecologia e como elas respondem às mudanças ambientais. Armadilhas fotográficas, VHF e GPS telemetria foram usadas para monitorar duas espécies de tatus (tatu peba, *Euphractus sexcinctus*,  $n = 17$ ; e tatu bola, *Tolypeutes matacus*,  $n = 26$ ), em três áreas do Pantanal, Brasil. Na primeira seção desta tese, junto a colaboradores, utilizei observações diretas e filmagens de armadilhas fotográficas colocadas em frente a abrigos e tocas de *T. matacus* para descrever o uso dos mesmos e comparei aos hábitos adotados por *T. tricinctus* no nordeste do Brasil. Dediquei a segunda seção a exploração da ecologia espacial e temporal e a sócio-biologia do pouco conhecido *T. matacus*. Junto a colaboradores, caracterizei o padrão de atividade usando um modelo não paramétrico de uma função circular condicional de Kernel. Caracterizei a seleção de habitat, com relação características da vegetação e distância a caminhos de terra, usando funções de seleção de recursos (Resource Selection Functions). A área de vida foi estimada através de modelos probabilísticos não paramétricos de Kernel e mínimos polígonos convexos. A interação estática entre pares de indivíduos foi caracterizada usando o índice de sobreposição de distribuição de uso (Utilization Distribution Overlap Index) e a relação entre o movimento desses pares foi explorada usando o Índice de Proximidade. Na terceira seção, eu e colaboradores avaliamos como variações em padrões de



atividade e seleção de habitat por *T. matacus* e *E. sexcinctus* estão correlacionadas com a temperatura do ar. Para avaliar a variação dos padrões de atividade e sua duração de acordo com mudanças na temperatura do ar foram usados modelos lineares de efeitos mistos. Para avaliar os efeitos do tipo de cobertura, ciclo circadiano e temperatura do ar na seleção de recursos por tatus foram usadas funções de seleção de passos (Step Selection Functions).

*Tolypeutes* sp. utilizam quatro tipos de abrigo, que são usados e reutilizados com frequências diferentes por indivíduos de sexos e classes etárias diferentes. Observações diretas e indiretas confirmam que *Tolypeutes* cava suas próprias tocas, ao contrário do que se acreditava até o momento. *Tolypeutes matacus* ficam ativos em média por  $5.5 \pm 2.8$  horas por dia, com atividade concentrada na primeira metade da noite. No entanto, à medida que a temperatura do ar diminui, seus períodos de atividade se tornam mais curtos e tem pico mais cedo.

*Euphractus sexcinctus* demonstra uma plasticidade comportamental mais pronunciada, trocando seu período de atividade de diurno para noturno, à medida que a temperatura do ar aumenta. A distância aos caminhos de terra afetou negativamente a força de seleção de habitat por *T. matacus*, independente do tipo de cobertura vegetal. *T. matacus* seleciona principalmente florestas quando próximo aos caminhos, mas quando relativamente mais distante a força de seleção relativa de áreas de pasto aumenta. No entanto, a seleção de habitat por *T. matacus* pode variar de acordo com a temperatura. *Euphractus sexcinctus* tende a selecionar áreas de vegetação aberta durante a atividade e áreas florestadas durante o descanso, mas a força de seleção do habitat depende da temperatura. O tamanho da área de vida de *T. matacus* machos foi positivamente relacionado à massa corporal, enquanto a área de vida das fêmeas não escalou com a massa. Machos adultos apresentaram áreas de vida maiores. Fêmeas de *T. matacus* não compartilharam suas áreas de vida e áreas core com outras fêmeas, independente da classe etária, enquanto áreas de vida e áreas core ocupadas por machos foram sobrepostas por outros machos e fêmeas. Díades de *T. matacus*

mantiveram distância média de 423 m e estiveram em proximidade em apenas 1% das localizações simultâneas. No meu conhecimento, este é o primeiro estudo de *T. matacus* em vida livre no Brasil e o mais abrangente estudo sobre sua ecologia até o momento. O padrão de espaçamento e área de vida de *T. matacus* aponta para um comportamento geralmente associial e um sistema reprodutivo promíscuo. A reduzida profundidade das tocas sugere que o uso de tocas por *Tolypeutes* tem mais chances de estar relacionado ao cuidado parental e estratégias de termorregulação do que a mecanismos de defesa. *Tolypeutes matacus* pode ser caracterizado como uma espécie predominantemente noturna que seleciona preferencialmente áreas próximas a caminhos de terra e áreas florestadas, mas também pode ocupar paisagens alteradas. No entanto, exemplos específicos da natureza dinâmica dos padrões de atividade e seleção do habitat em função da temperatura do ar ilustram o quão dinamicamente ambas as espécies estudadas podem alterar seu comportamento. *Tolypeutes matacus* tem sido classificado como Deficiente de Dados e espero que as informações geradas aqui possam contribuir para a conservação desta espécie. Além disso, esses resultados ressaltam a importância da heterogeneidade do habitat para a conservação em longo prazo de espécies animais que dependem de estratégias comportamentais para atingir a termorregulação adequada.

## Introduction

Some of the most specialized extant terrestrial mammals are comprised in the super order Xenarthra (Möller-Krull et al. 2007). This super order encompasses the orders Cingulata (armadillos) and Pilosa (sloths and anteaters) both of which possess low body temperatures (32.7 to 35.5°C), low basal metabolic rates (~50%), and high thermal conductance (130-200%; McNab 1985). Armadillos are fossorial animals and have the habit of excavating the soil to forage and build burrows and shelters where they rest and avoid unfavorable conditions (Eisenberg & Redford 1999, González et al. 2001). They are primarily solitary, except during the breeding season and parental care behavior (McDonough 1997, Desbiez et al. 2006).

Armadillos can be easily distinguished by the presence of a carapace, formed by ossified dermal tissue. The carapace has important consequences in the thermoregulation of armadillos (McNab 1985, Eisenberg & Redford 1999). Its high thermal conductance (McNab 1985), coupled with the low metabolism and the absence of much insulating fat or fur, maximizes heat loss and minimizes heat production in hot environments (Superina & Loughry 2012), at least in the absence of direct sunlight. Therefore, like other xenarthrans, armadillos are classified as imperfect homeotherms, i.e. even though they are able to produce body heat like other placental mammals, they have a limited capacity to regulate it (McNab 1985).

There is a need for factual knowledge on species biology and ecology to establish efficient conservation measures and to deal with most of the critical contemporary ecological problems, such as predicting how animals might respond to global climate change or to habitat modification (Greene 2005, Beyer et al. 2010). Nevertheless, even though this is a rich (21 species) and broadly distributed group throughout the Neotropics, little is known regarding armadillo ecology and biology. In a recent IUCN xenarthran assessment, Abba &

Superina (2010) highlight the lack of basic biological information for most armadillo species, such as home range measures, population sizes, natural history and types of threats.

Armadillos use burrows and shelters where they can spend long periods (McDonough & Loughry 2008) and in the relatively short time that most species spend above ground, they present a solitary and asocial behavior (McDonough 1997). These behavioral characteristics associated with the lack of an efficient and standardized methodology for capturing and monitoring armadillos hinders their study in the wild and contributes to the paucity of studies on their ecology (Loughry & McDonough 2013).

Furthermore, xenarthrans have been wrongly overlooked as a model group to answer broad ecological questions (Loughry & McDonough 2013). The question of how animals vary their behavioral patterns in response to environmental changes is central in ecology (Krebs & Davies 1993). Because temperature can strongly affect animal behavior, and because global climate change may affect organisms directly via physiological stress, understanding the relationship between environmental conditions and behavior is increasingly important (Harley 2011). As burrowing imperfect homeotherms, armadillos should present conspicuous behavioral responses to environmental changes and, as such, are valuable models for understanding how physiology affects decision-making in mammals (Maccarini et al. 2015). Mourão & Medri (2007) and Maccarini et al. (2015) began to tackle this subject and showed that giant anteaters (*Myrmecophaga tridactyla*) and yellow armadillos (*Euphractus sexcinctus* (Linnaeus, 1758)) alter their activity behavior and habitat use in response to changes in air temperature.

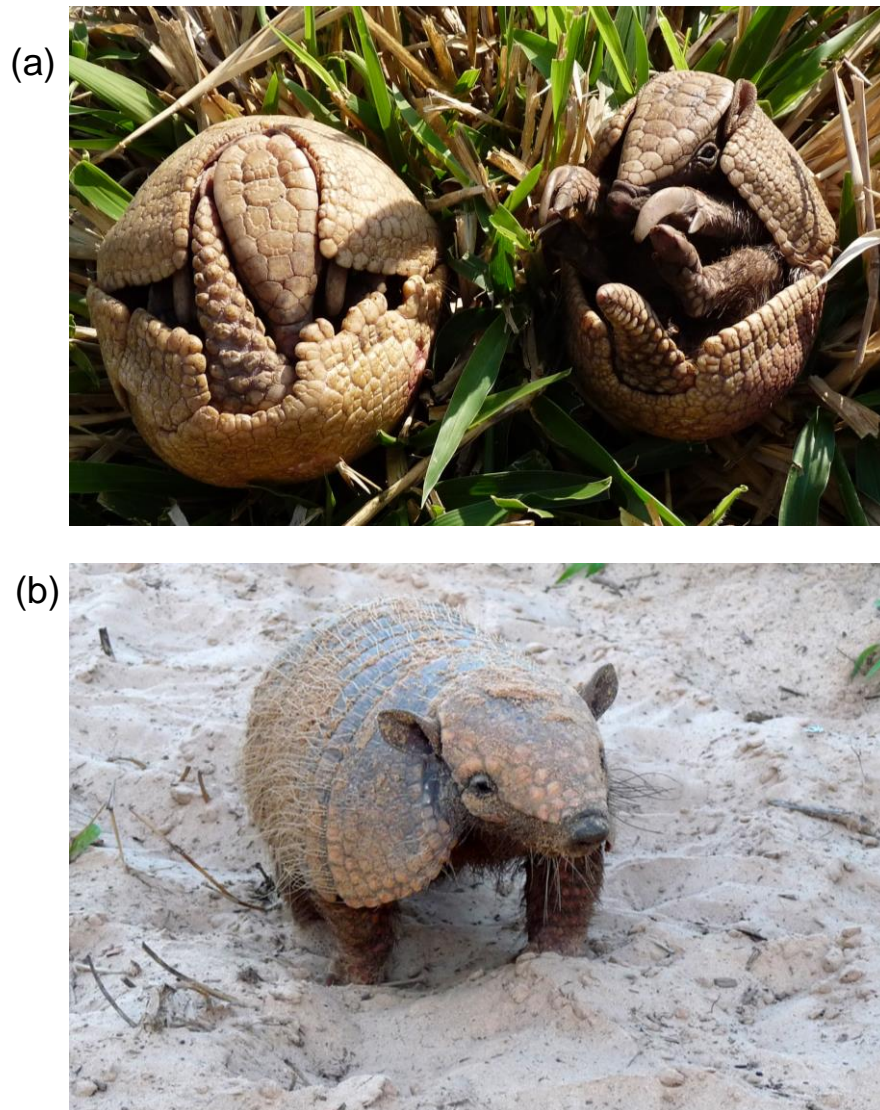
The circadian activity period adopted by an animal is one of the most effective and generalized ways to minimize the influence of unfavorable biotic and abiotic factors and to maximize the access to food and other resources (Layne & Glover 1985). It indicates how species explore the environment and is considered an important niche dimension (Pianka

1973). Different circadian activity patterns may result in the differentiation on the use of resources or in different levels of predation risk. Besides that, it may facilitate the coexistence of species through the avoidance of direct confrontation or through the reduction of the overlap in resources demand (Kronfeld-Schor & Dayan 2003). On the other hand, different behavioral responses to temperature variation may alter the relationship between species, by potentially increasing or reducing their niche overlap (Creel et al. 2016).

Animal movement plays an important role in determining the faith of individuals and in the dynamics of populations, communities and ecosystems. Spatial ecology allows us to explore the causes, mechanisms and patterns of animal movement and facilitates the understanding of the consequences of movement in the ecology and evolution of populations. Many factors can influence the way individuals use the space. Ecological processes, such as inter and intra-specific interactions, variations in the landscape and their natural history, may regulate animal's home range (Nathan et al. 2008). Hence, biological characteristics and ecological functions of species can be inferred through the study of its home range, movement patterns and habitat selection patterns (Cagnacci et al. 2010).

In this study, we explore the ecology, social biology and natural history of two armadillo species (*Tolypeutes matacus* (Desmarest, 1804) and *Euphractus sexcinctus*; Fig. 1) in the Pantanal wetlands of Brazil through the study of their behavior, activity patterns and space use patterns. Our aim was not only fulfill gaps about the ecology of poorly known armadillo species, providing tools for their long-term conservation, but also to show how these unique mammals can provide effective models on how mammal behavior can be affected by environmental changes. In the first chapter, we describe the sheltering habits of *T. matacus* and its congener *T. tricinctus*, which until the present study, were believed to be the only armadillo species not able to dig their own burrows. This chapter was published as a short-communication (Attias et al. 2016) and is presented with the format and reference style

of the journal. In the second chapter, we provide detailed information on the ecology of *T. matacus* describing its activity patterns, habitat selection patterns, spatial ecology and social biology. In the third chapter, we show how *T. matacus* and *E. sexcinctus*, as imperfect homeotherms, can provide valuable models of how habitat selection and activity patterns can be affected by environmental changes (i.e. temperature). This chapter has been submitted to Journal of Animals Behaviour. Finally, to contribute to the future study of armadillos through GPS, we present as Supplementary material the method developed to cope with the error pattern generated in armadillo GPS tracks due to their burrowing habits.



**Figure 1.** Studied armadillo species. (a) Two individuals of three-banded armadillo, *Tolypeutes matacus*, portraying the behavior of rolling into a ball, at Duas Lagos ranch, Cáceres, Mato Grosso. (b) An individual of yellow armadillo, *Euphractus sexcinctus* at Nhumirim ranch, Corumbá, Mato Grosso do Sul.

## Chapter 1 - Yes they can! Three-banded armadillos *Tolypeutes* sp.

### (Cingulata: Dasypodidae) dig their own burrows

#### Abstract

It is believed that the two species of *Tolypeutes* Illiger, 1811 are the only armadillos that do not dig their own burrows, and that these species simply re-use burrows dug by other species. Here, we show that *Tolypeutes matacus* (Desmarest, 1804) and *Tolypeutes tricinctus* (Linnaeus, 1758) dig their own burrows. We describe the burrows and three other types of shelters used by them, and provide measurements and frequency of use of the different types of shelter. We have studied free-ranging individuals of *T. matacus* in two locations in Central Brazil and individuals of *T. tricinctus* in semi-captivity in the Northeast of Brazil. Individuals of *T. matacus* were found primarily in small burrows (76%), straw nests (13%), shallow depressions covered with leaf-litter (7%) or in straw nests made on shallow depressions (4%). Adult males and females of *T. matacus* did not differ in frequency of use of different types of shelter. Sub-adults *T. matacus* used shallow depressions and nests more often (40%) than adults (22%) and nurslings (10%). Nurslings of *T. matacus* reused the shelters more frequently (66%), than sub-adults (46%) and adults (35%). Adult females reused burrows and other types of shelter more frequently than adult males. *Tolypeutes tricinctus* rested mainly in burrows and under leaf-litter, but did not dig depressions or build nests. *Tolypeutes tricinctus* occasionally used burrows dug by *Euphractus sexcinctus* (Linnaeus, 1758), but *T. matacus* never used burrows dug by other species. Nursling *T. matacus* always shared shelter with an adult female therefore, both used shelters with similar frequency. Adult females and nurslings of *T. matacus* reused shelters in higher frequency. That can be explained by the fact that adult females with offspring tend to remain for consecutive nights in the same burrow when cubs are recently born. Due to their smaller body size, sub-adult *T. matacus* used shelter strategies



that require less energetic effort more frequently than adults and nurslings. The habit of covering the burrow entrance with foliage and the burrow's reduced depth, indicates that *Tolypeutes* use of burrows is more likely to be related to parental care behavior and thermoregulation strategies than to defense mechanisms. We are confident that the burrows used for resting were indeed dug by *Tolypeutes* because, besides the direct observation of armadillos digging burrows, the measures of the burrows are very distinctive from those presented as characteristic for the co-occurring burrowing species and are congruent with *Tolypeutes* size and carapace shape. The newly acquired knowledge that species of *Tolypeutes* dig burrows can be used to increase the well-being of individuals kept in captivity by adapting enclosures to enable their digging behavior. In addition, this information contributes not only to the study of the ecology and natural history of the species, but can shed new light on the study of the anatomy of specialized diggers. *Tolypeutes* spp. can comprise the least fossorial of all living armadillo species, but they can no longer be classified as non-diggers.

**Key words:** Digging behavior, ecology, Xenarthra.

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## Resumo

Acredita-se que as duas espécies do gênero *Tolypeutes* Illiger, 1811 sejam os únicos tatus que não cavam suas próprias tocas e que estas apenas reutilizem tocas feitas por outras espécies. Neste estudo demonstramos que *Tolypeutes matacus* (Desmarest, 1804) e *Tolypeutes tricinctus* (Linnaeus, 1758) cavam suas próprias tocas. Aqui descrevemos tocas e outros três tipos de abrigo usados por eles, acompanhados de suas medidas e frequência de uso. Nós estudamos indivíduos em vida livre de *T. matacus* em duas localidades do Brasil central e indivíduos de *T. tricinctus* em semi-cativeiro no nordeste do Brasil. Indivíduos de *T. matacus* foram encontrados principalmente em pequenas tocas (76%), ninhos de palha (13%), depressões no solo cobertas por serrapilheira (7%) ou em ninhos de palha feitos em depressões no solo (4%). Machos e fêmeas adultas de *T. matacus* não diferiram com relação a frequência de uso dos diferentes tipos de abrigo. Sub-adultos de *T. matacus* usaram depressões no solo e ninhos de palha com maior frequência (40%) que adultos (22%) e juvenis (10%). Juvenis de *T. matacus* tiveram maior frequência de reutilização de abrigos (66%), em relação a sub-adultos (46%) e adultos (35%). Fêmeas adultas reutilizaram tocas e outros tipos de abrigo com maior frequência quando comparadas a machos adultos. *Tolypeutes tricinctus* foram observados descansando principalmente em tocas e debaixo de camadas de serrapilheira, mas não foram registrados cavando depressões rasas no solo em ninhos de palha. *Tolypeutes tricinctus* ocasionalmente utiliza tocas cavadas por *Euphractus sexcinctus* (Linnaeus, 1758), mas *T. matacus* nunca foi registrado usando tocas feitas por outras espécies. Juvenis de *T. matacus* sempre compartilham abrigos com uma fêmea adulta e, por isso, ambas utilizam abrigos com a mesma frequência. Fêmeas adultas e juvenis de *T. matacus* reutilizam abrigos com maior frequência. Isso pode ser explicado pelo fato de que fêmeas adultas com filhotes tendem a permanecer noites consecutivas na mesma toca quando

os filhotes são recém-nascidos. Devido ao seu menor tamanho corporal, sub-adultos de *T. matacus* utilizam estratégias de abrigo com menor requerimento energético com mais frequência que adultos e juvenis. O hábito de cobrir a entrada da toca com folhiço e a reduzida profundidade das tocas indica que o uso de tocas por *Tolypeutes* tem mais chance de estar relacionado ao comportamento de cuidado parental e estratégias de termorregulação do que a mecanismos de defesa. Temos confiança de que as tocas usadas para descanso foram de fato cavadas por *Tolypeutes* porque, além de termos feito observação direta de indivíduos cavando tocas, as medidas das tocas são muito distintas daquelas apresentadas como características à outras espécies que cavam tocas que possuem ocorrência na área e são congruentes com o tamanho e formato da carapaça de *Tolypeutes*. O recém adquirido conhecimento de que espécies de *Tolypeutes* cavam tocas pode ser utilizado para melhorar o bem-estar de indivíduos mantidos em cativeiro através da adaptação de recintos para permitir o comportamento de escavação do solo. Além disso, essa informação contribui não somente para o estudo da ecologia e história natural da espécie, como também pode lançar nova luz sobre o estudo da anatomia de cavadores especializados. *Tolypeutes* spp. pode incluir as espécies menos fossorias de todos os tatus vivos, mas não podem mais ser classificados como não cavadores.

**Palavras-chave:** Comportamento de escavação, ecologia, Xenarthra.

## Short Communication

It is believed that the two existing species of three-banded armadillos, *Tolypeutes* are the only ones among the twenty extant armadillo species that do not dig their own burrows. Even though both species have rarely been studied in the wild, the information that the species of *Tolypeutes* simply re-use burrows dug by other species is often repeated in the scientific literature (Guimarães 1997, Eisenberg & Redford 1999, Smith 2007, Wetzel et al. 2008, Medri et al. 2011).

*Tolypeutes* comprises *Tolypeutes matacus* (Desmarest, 1804) and *Tolypeutes tricinctus* (Linnaeus, 1758), both species with the unique ability to roll into an almost perfect ball as a defense mechanism (Eisenberg & Redford 1999, Wetzel et al. 2008). These armadillo species have an average head plus body length of 25 cm and an average weight of 1.1 kg (Eisenberg & Redford 1999). The southern three-banded armadillo, *T. matacus*, is found primarily in the dry forests of the central region of South America, including western Brazil, eastern and southern Bolivia, western and northern Paraguay, and northern Argentina. The Brazilian three-banded armadillo, *T. tricinctus*, occurs exclusively in the semi-arid scrub forests and savannas of the northeastern and central regions of Brazil (Wetzel et al. 2008, Feijó et al. 2015).

Unfortunately, most of the scarce information on the ecology and habits of these species is derived from captive animals (e.g., Bernier 2003), dead animals (e.g., Bolkovic et al. 1995) or occasional observations (e.g., Sanborn 1930, Marini-Filho & Guimarães 2010). Until now, only three comprehensive studies on the ecology of these species have been conducted in the wild, and only one of them has been published. Guimarães (1997) and Ilmar Bastos Santos (unpublished data) radio-tracked individuals of *T. tricinctus* in Cerrado and Caatinga areas, while Barrientos & Cuellar (2004) monitored individuals of *T. matacus* in the

Bolivian Chaco (Cuellar 2002, 2008, Barrientos & Cuellar 2004, Noss 2013). However, these studies provide only scarce and fragmented information about the use of shelters by *Tolypeutes*.

Here, we describe four types of shelters used by free-ranging *T. matacus*, including burrows, and provide evidence that both species of *Tolypeutes* are able to dig their own burrows. In addition, we provide descriptions, measurements, and information on the frequency of use of these burrows.

### ***Tolypeutes matacus***

We studied individuals of *T. matacus* in two locations. The first site is the Santa Teresa Ranch, located in the region of the Amolar Mountain Ridge, in the western limits of the Brazilian Pantanal, Corumbá, Mato Grosso do Sul state (18°17'51"S, 57°30'35"W). The second site is the Duas Lagoas Ranch, located in the Brazilian Cerrado, in Cáceres Municipality, Mato Grosso state (16°10'13"S, 58°11'12"W).

Animals were captured by hand during active searches performed by foot, horse, using ATV vehicles or using pickup trucks. From the 39 captured individuals of *T. matacus*, 13 males (12 adults and one sub-adult) and 13 females (eight adults, three sub-adults and two nurslings) were monitored. We defined adults as individuals with more than 1 kg and sub-adults as weaned individuals with less than 1 kg. Individuals were tracked by VHF (during 2 to 5 months) using the homing-in to the animal method (Samuel & Fuller 1994) and/or through GPS telemetry (during 5 to 27 days). Glue-on VHF radios and GPS tracking devices were attached to the posterior part of the pelvic carapace (using flexible cyanoacrylate super glue and/or epoxy resin), following a protocol commonly used for hard-shelled turtles (e.g., Seminoff et al. 2002). Eight individuals also had an intra-abdominal VHF radio tracking device surgically implanted in their abdominal cavity (Hernandez et al. 2010). Animals were tracked daily, at varying times between 6:00 and 22:00 h. During monitoring, camera traps

(Bushnell® Trophy Camera Brown Model 119435) were set to video mode (30 seconds duration) and placed in front of shelters ( $n = 51$ ) occupied by tracked animals ( $n = 17$ ) in different occasions.

We were able to locate and visualize the monitored individuals at 445 occasions, and on 67% of them, they were found resting. Resting records were made mainly during daytime. On these occasions, *T. matacus* were found in four types of resting-sites: small burrows (76%), straw nests (13%), shallow depressions covered with leaf litter (7%) or in straw nests made in shallow depressions (4%) (Figs. 1-5). Adult males and females showed no difference in frequency of use of the different types of shelter, both using burrows in higher frequency than any other type of shelter. Different age-classes used the types of shelter differently (Friedman  $\chi^2 = 6$ ,  $df = 2$ ,  $p = 0.05$ ). Sub-adults used shallow depressions and nests more often (40%), when compared to adults (22%) and nurslings (10%).

Burrows dug by *T. matacus* have a dome-shaped entrance,  $11 \pm 1.98$  cm high and  $12.8 \pm 2.1$  cm wide, with a depth of  $35 \pm 9.4$  cm (Table 1), ending in a nearly conical shape. Both males and females of all age classes used burrows for shelter. Burrow sharing was observed only between mothers and their single offspring. Females sharing their burrow with their nursling dug deeper burrows than did single individuals of either sexes (mean difference = 14.9 cm,  $t = 9.2$ ,  $df = 65$ ,  $p < 0.01$ ). The use of burrows was observed in both open and densely vegetated areas (i.e. all available vegetation types). Burrows were built at the base of trees, between thorny bromeliads and bushes, soil build-ups, leaf litter build-ups, and dense bushes located in the middle of open areas with tall grass.



**Figures 1-5.** (1) An individual of *Tolypeutes matacus* (arrow) resting inside its burrow at Santa Teresa Ranch, Corumbá, Mato Grosso do Sul. (2-3) Straw-nest built by *T. matacus* in a pasture area at Duas Lagoas Ranch, Cáceres, Mato Grosso: (2) upper view of the nest (circle) and (3) close-up of the same nest (arrow indicates the entrance of the nest). (4-5) (4) An almost imperceptible individual of *T. matacus* resting in a depression under leaf litter at Santa Teresa Ranch, Corumbá. The arrow points to the only visible part of the carapace. (5) The same GPS-fitted animal resting in the depression after we manually removed some of the leaf litter to expose part of its carapace (circled).

Burrows used by a single armadillo were deep enough to fit an “unrolled” adult individual, even though individuals were usually found resting on their side (half way curled) or almost completely curled into a ball. Sixty percent of the burrows where armadillos were found resting had inconspicuous entrances, covered with grass and/or tree leaves (depending upon its availability in the surroundings), and occasionally with dirt.

Despite the occurrence of three other armadillo species – *Euphractus sexcinctus* (Linnaeus, 1758), *Cabassous unicinctus* (Linnaeus, 1758) and *Dasypus novemcinctus* (Linnaeus, 1758) – and at least four other burrowing animals (iguanas, agoutis, pacas and the spiny rat) at our study sites, *T. matacus* was never found using burrows resembling those belonging to other species.

Nests and depressions were also used as shelters by *T. matacus*. The “nest” nomenclature has already been used by Barrientos & Cuellar (2004), for *T. matacus*, due to the resemblance of the structure to a bird nest. In the present study, nests were composed of a structured assemblage of dry grass and straw. Using camera traps set to video mode, we recorded individuals of *T. matacus* actively assembling dry grass and straw to repair their nests (Appendix S1\*). Nests were usually conspicuous, being built at soil level (76%) or in depressions (24%), in the pasture, under fences and occasionally inside dense bushes (Figs. 2-3).

The main difference between nests and depressions is that the nest is a structured assemblage of grass and straw, while when resting in depressions armadillos simply cover themselves with any type of vegetation available in the surroundings, with no structured arrangement. In addition, nests are structured in a tri-dimensional way standing above ground, while the foliage assembled over depressions tends to lay flat over the animal and becomes inconspicuous among the rest of leaf litter on the landscape.



When using depressions, *T. matacus* were completely covered with leaf litter at the soil level, leaving almost no visible evidence of their presence (Figs. 4-5). Occasionally, the armadillos were resting within the leaf litter in places of difficult access, such as areas with dense coverage of thorny lianas, dense bushes, and near roots of trees or fallen logs. However, it was not uncommon to observe the use of depressions in grasslands. It was not always possible to determine if the depressions used were natural to the relief of the landscape or dug by the animals. However, the depressions were always deep enough so that the animal could lay down on its side, cover himself with leaf litter and those leaves would be at similar level to the soil compared to the leaf litter in the surroundings. Armadillos were observed using nests and depressions on both open and densely vegetated areas (i.e., all available vegetation types). Both males and females of all age classes used nests and depressions as shelters.

Individuals were observed changing resting places on consecutive nights, using the same burrow or nest for consecutive nights, and reusing the resting place after long periods of no use (up to 36 days). Our radio-tracking and camera trap data shows that no individual was ever recorded using burrows or nests previously used by another monitored individual. The reuse of shelters varied among age classes ( $\chi^2 = 8.7$ ,  $df = 2$ ,  $p = 0.01$ ), being more commonly observed in nurslings (66% of the inactivity records of the individuals were made in shelters previously used), followed by sub-adults (46%) and then adults (35%). Adult females were recorded reusing burrows and other types of shelter more frequently than adult males ( $\chi^2 = 3.4$ ,  $df = 1$ ,  $p = 0.06$ ).

**Table 1.** Measurements of *Tolypeutes matacus* burrows at Santa Teresa ranch, Corumbá, Mato Grosso do Sul, and Duas Lagoas ranch, Cáceres, Mato Grosso.

	N	Height (cm)	Width (cm)	Depth (cm)
Male	59	$10.9 \pm 1.8$	$12.8 \pm 1.7$	$30.3 \pm 4.7$
Female	52	$11.1 \pm 2.1$	$12.7 \pm 2.4$	$38.7 \pm 10.5$
Female with nurslings	26	$11.6 \pm 2.8$	$13.3 \pm 2.9$	$45 \pm 8.5$
Female without nurslings	26	$10.6 \pm 1$	$12.2 \pm 1.7$	$29.6 \pm 4.9$
Male and Female	111	$11 \pm 2$	$12.8 \pm 2.1$	$35 \pm 9.4$

We were able to record other animals visiting the burrows built by *T. matacus*. We have recorded small rodents, small lizards and teju lizards entering and/or exiting the burrow. Hence, three-banded armadillos burrowing habits could be potentially benefiting other species.

### ***Tolypeutes tricinctus***

Two individuals of *T. tricinctus*, a male and a female, were encountered in the backyard of a private property at Buriti dos Montes Municipality, Piauí state, Brazil (5°18'33"S, 41°5'52"W). They had been kept in that property for a period between one to two years. At this locality, it was possible to record burrows covered by leaf litter, built near trees and in open areas (Figs. 6-7). Additionally, we were able to observe an individual actively digging a burrow, when we approached it during capture procedures (Fig. 8).

Both individuals were captured and relocated to a reserve, Reserva Natural Serra das Almas, Crateús, Ceará state, Brazil (5°8'30"S, 40°54'58"W), where they were kept for six months (July 2014 to January 2015). When the animals were taken to Serra das Almas, they were initially placed in a temporary enclosure. The animals were placed inside burrows that had been dug by the staff. However, the animals did not use these structures and immediately began digging their own burrows. After seven days, the animals were relocated to their permanent semi-captive enclosure. The enclosure was established inside the reserve, in an area of 93 m<sup>2</sup> of deciduous forest typical to the Caatinga eco-region, where the species naturally occurs. The animals were enclosed in a fine meshed-wire fence to prevent the access or outlet of small mammals and any other burrowing animal known to occur in the area. Two burrows, probably dug by yellow-armadillos (*E. sexcinctus*) prior to the establishment of the facility and the arrival of the three-banded armadillos were present in the enclosure. Despite the fact that the pre-existing burrows were initially used by the three-banded armadillos, they built and used four new burrows during the period in which the

armadillos were kept in the enclosure (Fig. 9). The enclosure was monitored with camera traps and it was possible to record the animals digging and using the new structures. Nevertheless, the animals continued to use the yellow-armadillo burrows occasionally.

The burrows dug by *T. tricinatus* in semi-captivity ( $n = 4$ ) were  $10.5 \pm 1.4$  cm high,  $14 \pm 2.9$  cm wide, with depth of  $43.5 \pm 12.8$  cm (Table 2). These animals also rested under leaf-litter, but did not dig depressions or build nests. They rested in open areas and under leaf-litter amongst thorny bromeliads and lianas.

Predictably, nursing *T. matacus* used shelters with similar frequency of *T. matacus* adults, since nurslings always shared shelter with an adult female. Sub-adults have a smaller body weight, when compared with adults, and were not seen accompanied by any adult individual. Their smaller body size might make the burrow building activity even more challenging, making it more likely for these individuals to use shelter strategies that require less energetic effort, such as nests and depressions covered with leaves.

Six, out of the eight adult females of *T. matacus* monitored, had nurslings (of varied sizes/ages) with them. The higher rate of reuse of shelter by females and the nurslings can be explained by the fact that adult females with offspring tend to remain for consecutive nights in the same burrow when the cubs are recently born.

The reduced depth of the burrow of *Tolypeutes* compared to other armadillo species burrows (e.g., Abba et al. 2005) and the habit of covering its entrance indicates that the use of burrows by these species is more likely to be related to parental care behavior and thermoregulation strategies (Maccarini et al. 2015) than to defense mechanisms. The cover of burrow entrances could contribute to buffer the burrow temperature, as observed to be an important thermoregulation strategy to other armadillo species (Maccarini et al. 2015).



**Figure 6-9.** (6) Burrow of *Tolypeutes tricinctus* with entrance covered by leaves at Buriti dos Montes, Piauí. (7) Animal leaving the burrow after removal of the leaf litter cover. (8) An individual of *T. tricinctus* actively digging as an escape behavior at Buriti dos Montes. (9) Burrow dug by *T. tricinctus* in semi-captive conditions at Reserva Natural Serra das Almas, Ceará.

Unlike other armadillo species, which have carapaces that can easily be perforated by predators (Carter & Encarnação 1983), *Tolypeutes* can roll into an almost perfect ball (Eisenberg & Redford 1999, Wetzel et al. 2008) and is likely to be predated only by top predators that have the strength to punch the carapace and/or a mouth big enough to fit the entire animal (e.g., jaguars, pumas and maned wolves, Hannibal et al. 2015). Hence, *Tolypeutes* may not rely as strongly on burrows as a protection against predators as other armadillo species do (Carter & Encarnação 1983). Alternatively, the reduced depth of *Tolypeutes* burrow compared to other armadillo species burrows (e.g., Abba et al. 2005), could be related to the very hard soil types of our study areas, that could make the burrowing activity for this small species even harder.

Usually, the shape of the cross section of a burrow entrance is in accordance with the shape of the cross section of the body of the burrower. Hence, besides the direct observation of animals digging, the width and the shape of the entrance of a burrow can allow the identification of a burrowing species (Krieg 1929 apud Abba et al. 2007). As shown in Table 1 and 2, the dimensions and the dome-shape of the burrows where the individuals of *Tolypeutes* were found are congruent with the animal size and carapace shape. When observing animals entering and exiting the small burrows, the perfect congruence of the shape of the carapace and that of the burrow is evident (Appendices S2\* and S3\*).

In addition, the observed measures of burrows of *T. matacus* are very distinctive from those presented as characteristic for the co-occurring armadillo species that dig dome-shaped burrows, such as *E. sexcinctus* (W = 24 cm, H = 20 cm) and *D. novemcinctus* (W = 20 cm, H = 21 cm, Borges & Tomás 2008). The remaining co-

**Table 2.** Measurements of burrows of *Tolypeutes tricinctus* kept in semi-captivity at Reserva Natural Serra das Almas, Crateús, Ceará state, Brazil.

Burrow	Height (cm)	Width (cm)	Depth (cm)
#1	9.4	11.1	47
#2	10	13	60
#3	12.5	18	32
#4	10	14	35
Mean $\pm$ SD	10.5 $\pm$ 1.4	14 $\pm$ 2.9	43.5 $\pm$ 12.8

occurring species of armadillo, *C. unicinctus*, is known to dig perfectly round burrows oriented vertically to the ground (Borges & Tomás 2008), presenting a very distinct pattern from the burrows where the *Tolypeutes* individuals were found resting. Finally, the spiny rat is known to dig long and complex tunnels and iguanas only dig burrows in close proximity of water bodies, during the breeding season (Z. Campos, pers. comm.). There is no reason to believe that *T. matacus* would be using or modifying other species burrows, since it is the smallest armadillo species occurring in the studied areas, using the shortest burrows found there. A species that uses another species' burrows could change its shape, but would not be able to make a burrow smaller than its original size. Finally, we were able to record free-ranging individuals actively digging burrows at Duas Lagoas ranch (Appendix S4\*), leaving no further doubt on the ability of *T. matacus* to build the structures in which they had been recorded resting.

Vizcaíno & Milne (2002), based on anatomical features and the lack of direct behavioral observations in the field, misclassified *Tolypeutes* as a non-digger species. However, our direct observations demonstrate that, like all other armadillo species, *Tolypeutes* do dig their own burrows. These animals possess such long claws on the toes of their forefeet that they actually have to walk on their claws (Figs. 10-11, Eisenberg & Redford 1999). Such a remarkable apparatus is suitable for digging, and it is comparable with the same structure observed in other well-known, burrow-digging armadillo species. Yellow armadillos, for example, usually present body sizes two to three times larger than the three-banded armadillos, and their longest fore-claw is similar in size to that of the average *Tolypeutes* (N. Attias pers. obs.). Hence, three-banded armadillos do not seem to have any anatomical constraint that would impair them to be efficient diggers. Evolutionarily, it would be unexpected that such an apparatus evolved for foraging purposes alone, as opposed to serving a dual function, as is evident in all the other armadillos.



Eisenberg & Redford (1999) only recognized that “*Tolypeutes* can occasionally dig shallow foraging holes”. Indeed, we have recorded *Tolypeutes* digging shallow foraging holes using their fore claws. Nevertheless, we have also seen those animals digging burrows up to 54 cm deep and using them as shelters. The individuals of *Tolypeutes* used their front claws to dig and their hind legs to push away the accumulated dirt, just like other armadillo species do when digging their burrows (Appendix S4\*). Borges & Tomás (2008) previously described a specific pattern for *T. matacus* burrows. They were not able to record animals actively digging or using the assigned burrows, but relied on tracks in and out of burrows to state that *T. matacus* constructs burrows with almost circular entrances of 13 to 14 cm in diameter, which is similar to the pattern we documented at our study sites.

The newly acquired knowledge that these species dig burrows, might help to clarify some incongruence between anatomical aspects of the limbs of armadillos and their digging behavior, found by Vizcaíno & Milne (2002). It can also be used to increase the well-being of individuals kept in captivity by adapting enclosures to enable their digging behavior, especially during the breeding season. This new information on the behavior of *Tolypeutes* species contributes not only to the study of the ecology and natural history of the species, but can shed new light on the study of the anatomy of specialized diggers. *Tolypeutes* spp. can comprise the least fossorial of all living armadillo species, but they can no longer be classified as non-diggers.

## Appendices

Online Supplementary Material available with the HTML version of the article at <http://www.scielo.br/zool>:

*Appendix S1.* An individual of *Tolypeutes matacus* gathers straw to repair the nest it is currently using. The video is a compilation of several (30 sec.) videos captured by a camera trap set in front of the nest. The activity of gathering straw and bringing it to the nest was recorded for a period of one hour on July 21st, 2015 at Duas Lagoas Ranch, Cáceres, Mato Grosso. To enable the visualization of the complete behavior in a shorter time, the video was edited and its speed is four times the speed of the actual behavior.

(<http://www.scielo.br/img/revistas/zool/v33n4/1984-4689-zool-33-04-e20160035-sS1.mp4>)

*Appendix S2.* An individual of *Tolypeutes matacus* enters its burrow at Santa Teresa Ranch, Corumbá, Mato Grosso do Sul. In this video it is possible to observe the perfect congruence between the shape of the carapace of the animal and the burrow it builds.

(<http://www.scielo.br/img/revistas/zool/v33n4/1984-4689-zool-33-04-e20160035-sS2.mp4>)

*Appendix S3.* An individual of *Tolypeutes matacus* exits its burrow that had the entrance covered by leaf litter, at Santa Teresa Ranch, Corumbá, Mato Grosso do Sul. Again, in this video it is possible to observe the perfect congruence between the shape of the carapace of the animal and the burrow it builds.

(<http://www.scielo.br/img/revistas/zool/v33n4/1984-4689-zool-33-04-e20160035-sS3.mp4>)

*Appendix S4.* An individual of *Tolypeutes matacus* actively digging a burrow from scratch at Duas Lagoas Ranch, Cáceres, Mato Grosso. The recording of the digging behavior

began at 21:14 h and ended at 21:18 h. The mid-section of the video had its speed doubled to enable the visualization of the behavior in a shorter time.

(<http://www.scielo.br/img/revistas/zool/v33n4/1984-4689-zool-33-04-e20160035-sS4.mpg>)

## **Chapter 2 - Ecology and social biology of the poorly known southern three-banded armadillo (*Tolypeutes matacus*)**

### **Abstract**

Critical contemporary ecological problems (e.g. predicting how animals might respond to habitat alteration and loss), require factual knowledge on species biology and ecology. Biological characteristics and ecological functions of elusive burrowing species can be inferred through the study of their home range, movement and habitat use patterns. Here we aim to characterize and understand the ecology and social biology of the poorly known southern three-banded armadillo (*Tolypeutes matacus*) through its movement behavior. We used VHF and GPS telemetry to monitor 26 individuals from two sites in the Pantanal wetlands of Brazil. We characterized their activity patterns using a non-parametric model of a conditional circular kernel function. We used Resource Selection Functions to characterize habitat selection in relation to vegetation features and distance to paths. To estimate home range areas we used Kernel probabilistic non-parametric models (KUD) and the Minimum Convex Polygon. We evaluated the relationship between sex and body mass with home range size, how the mean daily distance traveled varied between sexes and how it was related to home range size. We estimated the joint distribution probability of pairs of individuals using the Utilization Distribution Overlap Index and used a Proximity analysis to explore how the movement of these pairs were related. Our results indicate that three-banded armadillos were active in average for  $5.5 \pm 2.8$  hours per day, with most of their activity concentrated in the first half of the night. The distance to dirt paths negatively affected the selection strength of active and sheltering armadillos in both sites, regardless of the vegetation cover. Armadillos selected mainly forests when in proximity of dirt paths, but when relatively far from the paths the relative selection strength of pasture units increased. Home range size of males was positively

related with their body mass, while female home range sizes did not scale with body mass. Adult males were heavier than adult females and the home range area (KUD 95%) of adult males were, in average, about 2.8 times larger than those of adult females. On a daily basis, adult males moved more than adult females. The relationship between mean daily displacement and the square root of home range area shows an asymptotic tendency. The probability of space use sharing was higher when animals were active and at home range level (12%), when compared to inactive periods (6%) and core area level (1%). Females did not share their home ranges and core areas with other females (<1%), regardless of age class, while the ranges occupied by males overlapped with both males (12%) and females (18%). Dyads were in average 423 m apart and in only 1% of the simultaneous fixes animals were in proximity to each other, indicating tolerance behavior. To our knowledge, this is the first study of *T. matacus* in the wild in the Brazilian territory and the most comprehensive study on its ecology in situ. We characterize three-banded armadillos as a mainly nocturnal species that selects preferentially forested areas but is able to occupy modified landscapes. Their home range and spacing patterns points out to a generally asocial behavior and a promiscuous mating system, but some of our behavioral observations point out the need of further field observations to explore its potentially richer social behavior. This species has been classified as Data Deficient until now by the Brazilian authorities and we hope that the data generated here will contribute to this species conservation in Brazil and guide future research efforts to support the conservation of this globally near threatened species.

## Resumo

Problemas ecológicos contemporâneos críticos (e.g. prever como animais podem responder a alteração e perda do hábitat), exigem o conhecimento factual sobre a biologia e ecologia de espécies. Características biológicas e funções ecológicas de espécies que utilizam tocas e são dificilmente visualizadas podem ser inferidas através do estudo de sua área de vida, padrões de movimentação e uso do habitat. Neste estudo temos por objetivos caracterizar e entender a ecologia e sociobiologia do desconhecido tatu-bola (*Tolypeutes matacus*) através dos seus padrões de movimento. Nós utilizamos rádio e GPS telemetria para monitorar 26 indivíduos em duas localidades do Pantanal brasileiro. Nós caracterizamos o padrão de atividade da espécie usando um modelo não paramétrico de uma função Kernel circular. Utilizamos funções de "Resource Selection" para caracterizar a seleção de habitat com relação aos tipos de vegetação e sua distância a trilhas e estradas de terra. Para estimar áreas de vida nós usamos modelos não paramétrico probabilísticos de Kernel (KUD) e Mínimos Polígonos Convexos. Nós avaliamos a relação entre sexo e massa corporal com tamanho da área de vida, como o deslocamento médio diário varia entre sexos e como este está relacionado ao tamanho da área de vida. Estimamos a probabilidade de distribuição conjunta de pares de indivíduos utilizando o índice de sobreposição "Utilization Distribution Overlap Index" e utilizamos uma análise de proximidade para explorar como o movimento desses pares de indivíduos está relacionado. Nossos resultados indicam que tatus-bola estão ativos em média por  $5.5 \pm 2.8$  horas por dia, com maior parte de sua atividade concentrada na primeira metade da noite. A distância das trilhas e estradas afetou negativamente a força de seleção do habitat dos tatus quando ativos e quando dentro de seus abrigos em ambas as áreas de estudo, independente do tipo de cobertura vegetal. Tatus selecionaram principalmente florestas quando em proximidade a trilhas e estradas de terra, mas em áreas relativamente mais afastadas das trilhas a força relativa de seleção de áreas com pasto aumenta. O tamanho da área de vida de machos foi positivamente relacionado a sua

massa corporal, enquanto a área de fêmeas não escalou com sua massa corporal. Machos adultos foram mais pesados que fêmeas adultas e a área de vida (KUD95%) de machos adultos foram, em média, 2.8 vezes maiores que àquelas de fêmeas adultas. Machos adultos tiveram maior deslocamento médio diário do que fêmeas. A relação entre deslocamento médio diário e a raiz quadrada da área de vida demonstrou uma tendência assintótica. A probabilidade de compartilhamento do espaço entre pares de animais foi maior quando estes estavam ativos e em nível de área de vida (12%), quando comparada a períodos de inatividade (6%) e áreas core (1%). Fêmeas não compartilharam suas áreas de vida e áreas core com outras fêmeas (<1%), independente da classe etária, enquanto que as áreas ocupadas por machos sobrepuseram com ambos machos (12%) e fêmeas (18%). Pares de indivíduos mativeram em média 423 m de distância e em apenas 1% de suas localizações simultâneas estes foram encontrados em proximidade um ao outro, indicando um comportamento de tolerância. Até onde sabemos, este é o primeiro estudo de *T. matacus* em vida livre no Brasil e o mais abrangente estudo sobre sua ecologia in situ. Nós caracterizamos tatus-bola como uma espécie primariamente noturna que seleciona preferencialmente áreas florestadas, mas é capaz de ocupar paisagens degradadas. Sua área de vida e padrão de sobreposição apontam para um comportamento em geral não-social e um sistema reprodutivo promíscuo. No entanto, algumas de nossas observações comportamentais apontam a necessidade de observações adicionais em campo para explorar este comportamento social potencialmente mais rico. Até o momento esta espécie foi classificada como Deficiente de Dados pelas autoridades brasileiras. Nós esperamos que as informações geradas aqui contribuam para a conservação desta espécie no Brasil e possam guiar futuros esforços de pesquisa para auxiliar na conservação desta espécie que é considerada Quase Ameaçada globalmente.

## Introduction

The way animals move and use the space is a fundamental component of almost any ecological process (Nathan et al. 2008). Hence, biological characteristics and ecological functions of species can be inferred through the study of their home range, movement and habitat use patterns (Cagnacci et al. 2010). Home ranges are descriptive models of space use that reflect not only species energetic requirements but also their interactions with the different components of the environment (e.g. conspecifics, predators, resource abundance and distribution; Harestad & Bunnell 1979, Beyer et al. 2010). Another, short-term, measure of space use that reflects species energetic requirements and constraints is the daily distance traveled. This measure, however, should be related not only to the species ecology (e.g. dietary habits) but also to individual body mass (Garland 1983, Carbone et al. 2005).

Animals do not establish home ranges at random locations and multiple competing demands may shape their use of heterogeneous landscapes (Beyer et al. 2010). When there is a disproportional use of resources, in comparison to its availability, use is said to be selective (Manly et al. 2002). Habitat selection involves both innate and behavioral decisions (Hutto 1985) and provides information on species strategies to meet their requirements for survival, ultimately reflecting fitness in the different habitats (Boyce & McDonald 1999, Manly et al. 2002). At the same time, complementary behavioral strategies, such as circadian activity patterns, also indicate how species explore the environment (Pianka 1973) and is one of the most effective and generalized ways to minimize the influence of unfavorable biotic and abiotic factors and to maximize the access to food and other resources (Layne & Glover 1985).

When studying elusive burrowing mammals, such as armadillos, data on space use by conspecifics can help us understand their mating system and spatial organization (Clutton-Brock 1989). Mating systems can be inferred through the evaluation of home range sizes and



the degree of home range overlap between individuals of the same sex and of opposite sexes (i.e. static interaction; Clutton-Brock 1989, McDonough & Loughry 2008). Further social behavior information can be obtained when accounting for the temporal component of interactions. Dynamic interactions can provide information on simultaneous joint space use and contact rates, showing how the movement of pairs of individuals is related (Macdonald et al. 1980, Long et al. 2014).

Critical contemporary ecological problems (e.g. predicting how animals might respond to habitat alteration and loss), require factual knowledge on species biology and ecology (Greene 2005, Beyer et al. 2010). However, despite Cingulata's (armadillos) richness (21 species) and broad distribution throughout the Neotropics, most of its species are still poorly known, regarding their biology and ecology. Information on home range measures, population size, natural history, and types of threats are scarce or inexistent for some species (Abba & Superina 2010). Armadillos are terrestrial and fossorial animals and have the habit of excavating the soil to build burrows, where they can spend long periods (McDonough & Loughry 2008). They are known to be primarily solitary and asocial, with exception of the breeding season and parental care behavior (McDonough 1997, Desbiez et al. 2006). The combination of these characteristics hinders the study of armadillos in the wild and contributes to the paucity of studies on their ecology (Loughry & McDonough 2013).

The southern three-banded armadillo (*Tolypeutes matacus* Desmarest, 1804; here on three-banded armadillo) is found primarily in the dry forests of the central region of South America (Feijó et al. 2015) and is distributed along western Brazil, Bolivia, Paraguay and Argentina (Wetzel et al. 2007). Species of this genus are classified as opportunistic insectivores (Bolkovic et al. 1995) and weight between 1.1 - 1.5kg (Eisenberg & Redford 1999). *Tolypeutes* species are believed to be active throughout the day and night (Eisenberg

& Redford 1999) and can use burrows and other types of shallow shelters for resting (Attias et al. 2016).

Some may state that there is a relative abundance of information on *T. matacus*, when compared to its congener, *T. tricinatus* (Linnaeus, 1758), and some other armadillo species. However, most of this information is derived from captive animals (e.g. Bernier 2003), dead animals (e.g. Bolkovic et al. 1995), occasional observations (e.g. Sanborn 1930) and field excursions not necessarily focused on the study of the species (e.g. Barrientos & Cuellar 2004). Most studies that address the species ecology in the wild are derived from the same region in the Bolivian Chaco (Cuellar 2002, Barrientos & Cuellar 2004, Cuellar 2008, Noss 2013). In addition, these were not designed to acquire species-specific information and were based on census techniques destined to evaluate the impact of traditional hunting on the local fauna.

*Tolypeutes matacus*, along with its congener, are the only armadillos that can roll into a ball as a defense mechanism (Eisenberg & Redford 1999). This behavior however, facilitates its capture by humans and increases the vulnerability of both species to hunting pressure. That, associated with habitat loss, has contributed to population decline in recent years (Abba & Superina 2010). The three-banded armadillo is classified as Near Threatened by IUCN (A2cd; Abba & Superina 2010) and as Data Deficient in Brazil (Reis et al. 2015). Until now, no studies on its biology had been performed in the wild in Brazil. The creation of a National Action Plan for the conservation of three-banded armadillos (PAN Tatu-bola) further highlights the priority of conservation efforts towards this species. The action plan has as a specific goal to broaden the knowledge on the biology and ecology of the species to guide species-specific conservation strategies at a national level.

Hence, given its uniqueness and current conservation status, here we aim to characterize and understand the ecology and social biology of the poorly known southern

three-banded armadillo. More specifically, we aim to: (1) characterize the species activity pattern; (2) estimate measures of space use by different sexes, such as home range areas and daily distance traveled; (3) characterize habitat selection and evaluate how it can be related to the availability of natural and anthropic habitat features; and (4) characterize their social biology, through the association of all information gathered and measures of static and dynamic interaction.

## **Methods**

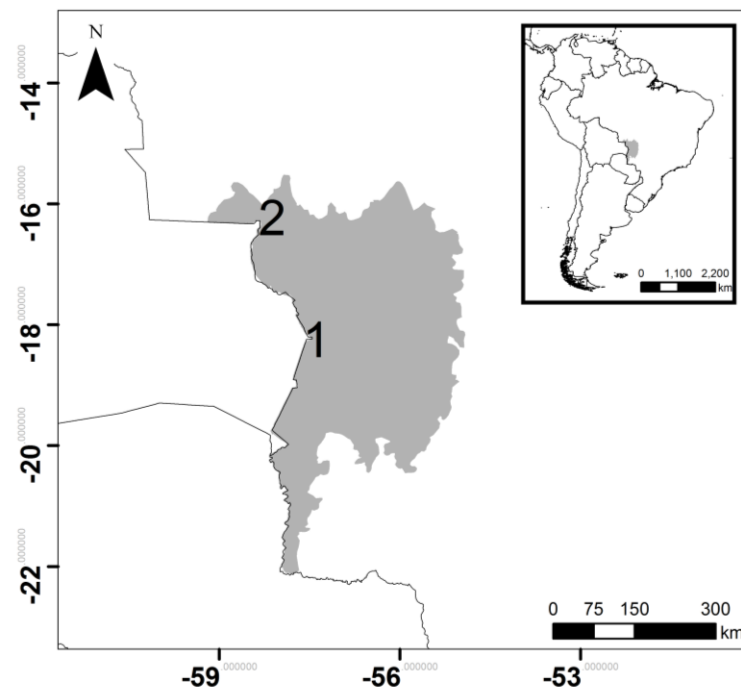
### *Study area*

This study was carried out in the Pantanal wetlands of Western Brazil (Fig. 1). The Pantanal is one of the largest continuous Neotropical wetlands and is located in a lowland floodplain of the upper Paraguay River (Mittermeier et al. 2003). The region is classified by Köppen's system as tropical sub humid (Aw), with average annual rainfall of 1100 mm and mean annual temperature of 25°C. We worked in two sites (250 km apart; Fig. 1) which presented different management strategies, either prioritizing the maintenance of the natural landscape (Site 1) or their economic activities (Site 2; Fig. 2).

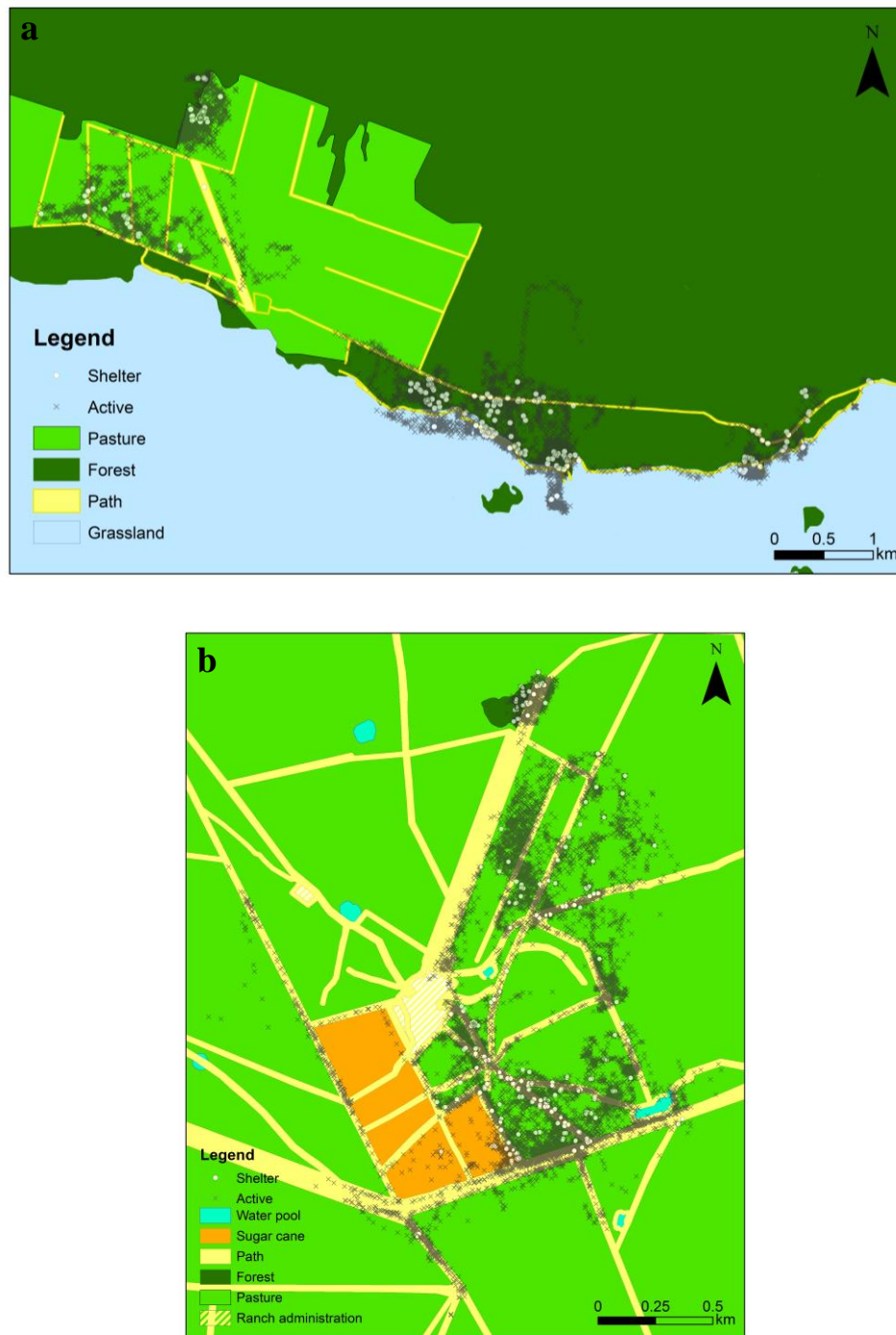
The Site 1 (Santa Teresa Ranch) is located in the region of the Amolar Mountain Ridge, in the western limits of the Brazilian Pantanal, Corumbá municipality, Mato Grosso do Sul state (Fig. 1). The variable relief (90 to 1,000 m of altitude) of this mountainous region defines the vegetation structure. Pastures and humid and dry savannas occupy the lowland areas, which remain flooded during the flood season. The higher areas are dominated by deciduous and semi-deciduous forests (Tortato et al. 2015). This 63,000 ha private property is part of the Network for the Protection and Conservation of Serra do Amolar and only 3% of its area have been modified into exotic pasture, dedicated to cattle grazing (Fig. 2a). Even

though most part of this site is of preserved forest, individuals were captured and monitored in both altered and non-altered habitats.

The Site 2 (Duas Lagoas Ranch) is located in Cáceres Municipality, Mato Grosso state in a transition zone between the Pantanal and Cerrado eco-regions. A company dedicated to teak plantation (*Tectona grandis*) owns this ranch and has converted 4,155 ha (of its 7,378 ha) to this activity. A portion of the property still holds native vegetation (1,630 ha), consisting of cerrado woodland ("cerradão"), bush savanna ("cerrado"), grassland and gallery forest. The remaining area is dedicated to cattle ranching and is occupied by exotic pasture (*Brachiaria* sp.; 1,209 ha) and sugarcane plantation (24 ha; Fig. 2b). At this site, monitored individuals occupied mostly altered areas.



**Figure 1.** Location of both study sites in the Brazilian Pantanal Wetlands. Site 1: Santa Teresa Ranch ( $18^{\circ}17'51''\text{S}$ ,  $57^{\circ}30'35''\text{W}$ ). Site 2: Duas Lagoas Ranch ( $16^{\circ}10'13''\text{S}$ ,  $58^{\circ}11'12''\text{W}$ ).



**Figure 2.** Thematic habitat maps classified according to vegetation features with locations of shelters (white circles) and of activity records (x). Data from 26 individuals of *Tolypeutes matacus* monitored at (a) Santa Teresa ranch (site 1) and (b) Duas Lagoas Ranch (site 2), between November 2014 and August 2015.

### *Capture and tracking methods*

From November 2014 until August 2015, we captured 39 individuals of *T. matacus*, 12 at Site 1 and 27 at Site 2. We performed active searches by foot, horse, using ATV vehicles or pickup trucks, and captured animals by hand. From the captured individuals we were able to monitor 11 individuals at site 1 (7F; 4M) and 15 individuals at site 2 (7F; 8M). From the 26 monitored animals, there were 14 females (8 adults, 3 sub-adults and 3 nurslings) and 12 males (10 adults and 2 sub-adults). We defined adults as individuals with more than 1 kg and sub-adults as weaned individuals with less than 1 kg.

For each monitored animal, we took information on age, sex, reproductive condition, body mass and body measures. To enable their monitoring, we equipped animals ( $n = 21$ ) with a package containing a glue-on VHF radio (model R1920, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) and a GPS tracking device (non-commercial prototype used in other studies of the Wildlife Laboratory of the Brazilian Agricultural Research Corporation of Pantanal, e.g. Oliveira-Santos et al. 2015). Total package weight was ~50g and corresponded to up to 4% of animals' weight. Four juveniles and one pregnant female were equipped only with VHF radios, which weighted 14g and corresponded to up to 1% of their weight. Due to the unique behavior and anatomy of this species, we used a protocol commonly used for hard-shelled turtles (e.g. Seminoff et al. 2002) that did not prevent the animals from rolling into a ball and attached the tracking devices to the posterior part of the pelvic carapace (using flexible cyanoacrylate super glue and/or epoxy resin). Individuals were monitored through GPS telemetry, using five-minute interval fixes, and through VHF telemetry, using the homing-in to the animal method (Samuel & Fuller 1994). We tracked animals daily, at varying times between 6:00 and 22:00 h, to ensure GPS functioning and record individual behavior.

Even though all the procedures described could be accomplished through physical restraint, some of the animals ( $n = 19$ ) were anaesthetized through an intramuscular injection on the hinder limbs to enable the collection of biological samples used in other studies. The anesthetic protocol was composed of Ketamine 25mg/kg (Quetamina® 10% - Vetnil), Xilazine 0.5mg/kg (Rompun® 2% - Bayer), Midazolam 0.5mg/kg (Dormire® 0.5% - Cristalia) and Atropine 0.02mg/kg (Atropina® 1% - Fagra). All the procedures described follow the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011) and were approved by the ethics committee of the Federal University of Mato Grosso do Sul (process 570/2013).

### *Activity*

The raw locations were submitted to a protocol described elsewhere (Supplementary Material), in order to account for the GPS inaccuracies, and then improve the detection of the shelter locations. The animals were classified as active when they were not inside shelters and were moving. We identified 21,515 activity records from the 61,303 GPS locations of three-banded armadillos (Fig. 2). To characterize activity patterns 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 1987). 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. We used 95 and 50% probabilities to characterize the activity pattern and core activity period, respectively.



### *Habitat selection*

We evaluated habitat selection during active and resting periods, separately. Habitat selection during activity indicates the selection of areas where animals can find suitable conditions to perform activities such as foraging and finding mating partners, while selection during resting periods indicates where animals find suitable places to establish their shelters. To characterize third-order habitat selection (i.e. within their home range), first we sub sampled the animal's trajectories of each activity data set to fixes with one-hour intervals. For each location of the trajectory, we generated 30 random locations that represent plausible next step locations. This was done by adding the easting (x) and northing (y) UTM coordinate of the actual location to 30 values taken from a normally random distribution with zero mean and the estimated standard deviation from the observed distribution of x and y coordinates of each individual's track, respectively. This approach allowed us to evaluate resource selection at a finer spatial scale, accounting for changes in resource availability along an individual's track, instead of using the overall average habitats within the study area to characterize availability (Fortin et al. 2005, Boyce 2006).

We then extracted information on habitat type and distance to paths for each of the observed and random steps. Habitat type values were extracted from maps classified in categories according to vegetation features of the landscape of each study site (Fig. 2). Using RapidEye satellite imagery, habitat types were classified into: forest, pasture (both encountered in both study areas), natural grasslands (encountered only at Site 1), sugar cane plantation and water pools (encountered only at Site 2). Values of distance to paths were extracted from a second thematic map, which had its pixels classified with continuous values according to their Euclidean distance to the nearest path. We classified as paths features of the landscape that promoted a linear clearing, such as unpaved dirt roads, cattle tracks and fences. Using this data, we fitted a model to evaluate the effect of habitat type and distance to

paths on the resource selection of three-banded armadillos, considering that there is an interaction between these two factors. Resource Selection Function models (RSF; one for each study site) were fitted using the function `rsf` of the package 'ResourceSelection' in R (Lele et al. 2017, R Core Team 2017). RSF's allow us to understand the differential selection of resources by comparing the proportion of use and availability of each resource type, according to a biologically relevant a priori classification (Lele & Keim 2006). During data analysis, one out of our ten monitored individuals at Site 1, a sub adult female (tm4), presented a habitat use behavior very distinct from all other individuals, hence we decided to exclude it from the final model presented for this Site. To improve the visualization of the results, we standardized the values of selection strength of the plots dividing it by the maximum value obtained for each model.

### *Home range*

To estimate the home range of the armadillos we used Kernel probabilistic non-parametric models (Worton 1987). Besides emphasizing more stable central tendencies, the final function of the Kernel model identifies peaks of use and less used areas during the monitored period (Powell 2000). This method is considered more appropriate to Kernohan's et al. (2001) definition of home range, given that it considers the use of space in a probabilistic and continuous manner (Millspaugh et al. 2006). Kernel Use Density (KUD) were estimated using the same grid for all individuals (grid = 400) and bivariate normal distribution for each kernel. The fixed smoothing parameter ( $h = 70.97$ ) was estimated as the mean value of the normal reference rule values ( $h$ -ref; Worton 1995) obtained for each individual. In addition, to allow the comparison of our results with those of previous studies, we generated home range area estimates through the Minimum Convex Polygon (MCP), a simple estimator that consists on connecting the most external records forming the smallest polygon without

concavities (Mohr 1947). All analysis were performed using the R package 'AdehabitatHR' (Calenge 2006).

To assess if armadillos body mass and home range size estimates differed between study areas, we used a Student's t-test. We used the same approach to evaluate differences in home range size estimates and body mass between sexes. To evaluate the relationship between home range size (KUD 95%) with sex and body mass, we fitted an ANCOVA model. Since body mass and sex interacted to explain home range size, we performed linear regressions for each sex to assess how home range area estimates vary according to armadillo's body mass.

#### *Daily distance traveled*

The daily distance traveled by individuals was estimated as the cumulative sum of all step lengths during each day of monitoring. The mean distance traveled was estimated for each individual considering its entire monitoring period. We used Student's t-test to assess if daily displacement varied between sexes. To describe the relationship between mean daily displacement and the square root of home range area (KUD 95%), we used a non-linear model.

#### *Static interaction*

To estimate the static interaction between individuals, first we divided our data into activity and inactivity records. Animals were classified as inactive when they were inside their shelters (e.g. burrows and nests). Then, we estimated core (KUD 50%) and home range areas (KUD 95%) of each individual during these two states, active and inactive. Finally, we estimated the static interaction of individuals at each activity state and home range level separately using the R package 'AdehabitatHR' (Calenge 2006). To evaluate the static

interaction between pairs of individuals of different sexes and age classes in the four above-described occasions, we used the Utilization Distribution Overlap Index (UDOI). The UDOI is a symmetric index that measures the amount of overlap relative to two individuals using the same space uniformly, i.e. the joint distribution probability of two individuals. This index equals zero for two home ranges that do not overlap and equals 1 if both UD's are uniformly distributed and have 100% overlap. However, UDOI can be  $>1$  if the two UD's are non-uniformly distributed and have a high degree of overlap. UDOI is a function of the product of two UD's and assumes that the evaluated animals use the space independently (Fieberg & Kochanny 2005).

#### *Dynamic interaction*

While the static interaction indices give us information on the potential contact and interaction between animals, the dynamic interaction analysis incorporates the temporal dimension of this interaction and explores how the movements of pairs of individuals are related (Macdonald et al. 1980). We explored the dynamic interaction of nine dyads of armadillos that presented high static interaction (i.e. spatial overlap  $> 0.5$ ) and had at least 24 hours of temporal overlap on monitoring periods. Through a proximity analysis (Bertrand et al. 1996, Long et al. 2014) we estimated the proportion of simultaneous fixes at which the individuals of a dyad were less than 50 meters apart and used this as an indicator of attraction between individuals. Since our GPS devices were programmed to record locations with five minutes intervals, we defined a temporal threshold of 2.5 minutes to define simultaneous fixes. When locations of proximity of a dyad were identified, they were plotted over the map of the study area for visual inspection. The analysis were implemented through 'WildlifeDI' R package (Long 2014) and QGIS (QGIS Development Team, 2016).

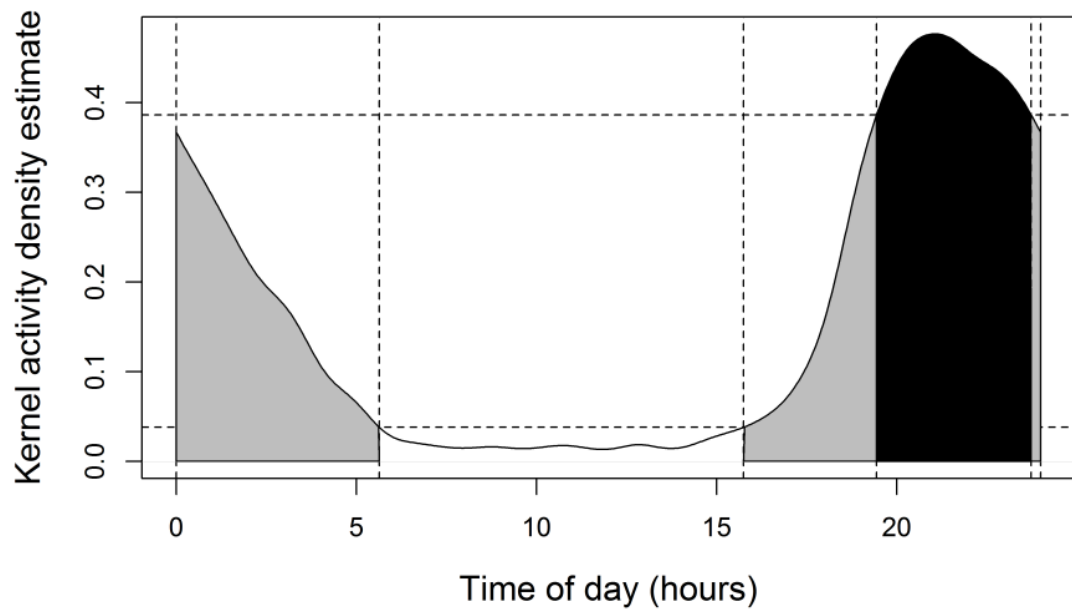
## Results

Animals were monitored with GPS devices for an average of 17 days (min = 4, max = 32). This generated an average of 2,919 locations per individual (min = 218, max 8,248) and a total of 61,303 locations. VHF tracking generated an average of 39 locations per individual (min = 16, max = 62) and a total of 157 locations (Appendix 1).

### *Activity*

Three-banded armadillos were in general nocturnal, with most of their activity concentrated in the first half of the night (Fig. 1). Usually, activity onset occurred between the late afternoon and the beginning of the night (17:00-20:30h), and activity termination occurred in the second half of the night (Supplementary Material). Activity patterns of males and females were similar, with 88% overlap. Juveniles tended to leave shelters earlier (~18:00h) and return earlier (~22:15h) than adults.

Three-banded armadillos had up to seven activity bouts per day (<1%), but most commonly exited their shelters once (53%) or twice (29%) a day. Activity bouts lasted from one minute to 14 hours (mean =  $3.3 \pm 2.9$  hours) and summed to an average daily activity duration of  $5.5 \pm 2.8$  hours. Armadillos stayed inside their shelters for long periods, with an average of  $14 \pm 6.7$  hours/day and a maximum of 19.7 hours/day.



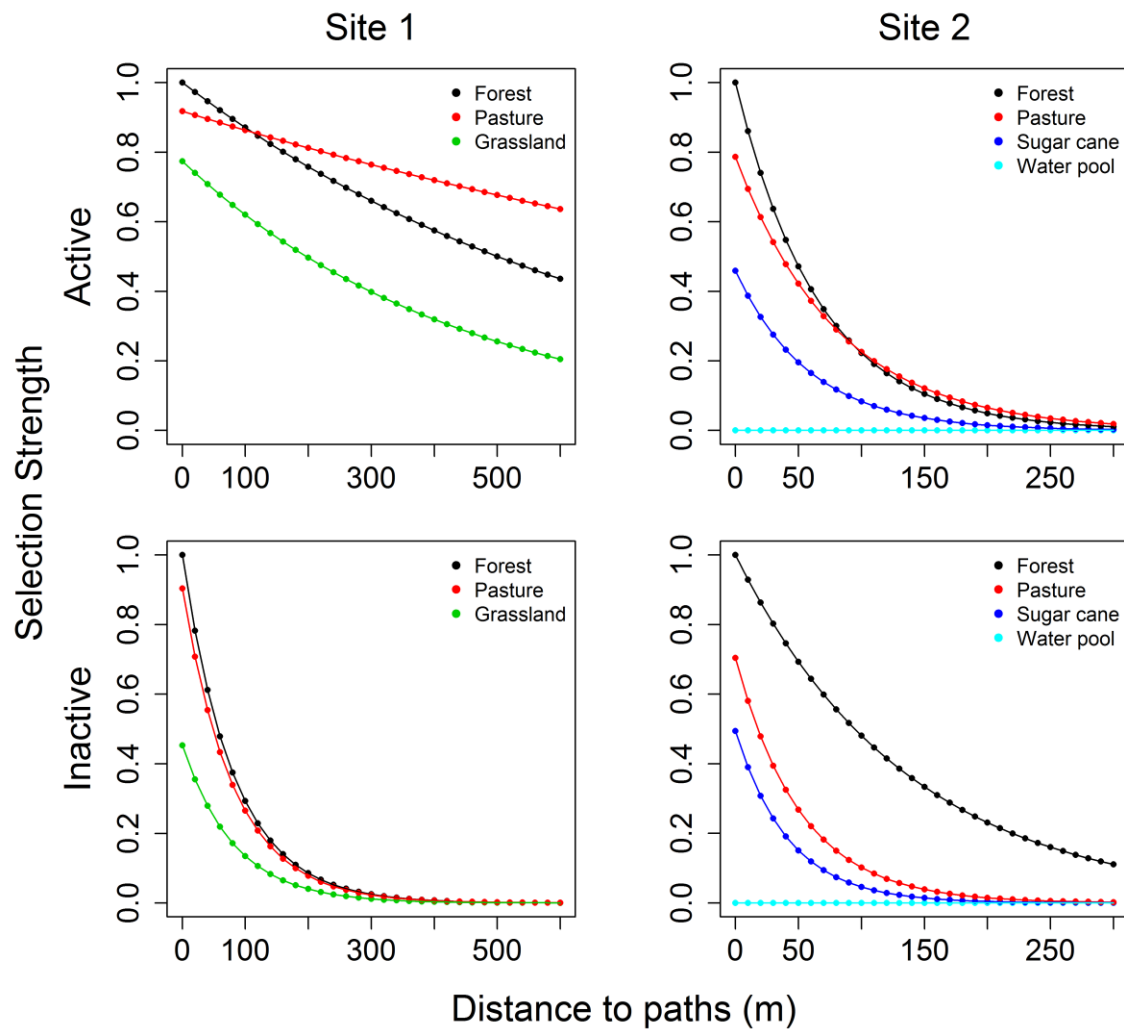
**Figure 3.** Kernel density estimates for the activity of *Tolypeutes matacus*. Gray areas represent the activity range (95% Kernel activity density estimates), while black area represents activity core (50% Kernel activity density estimates) during a 24-h period. Data derived from 21,515 GPS activity records from 21 armadillos tracked in two sites in the Pantanal of Brazil, from November 2014 until August 2015.

### *Habitat selection*

The selection strength of active and sheltering armadillos in both sites were negatively affected by the distance to the dirt paths, regardless of their vegetation cover (Appendix 2). The only exception was the water pools of Site 2, which were not selected, irrespective of distance to the dirt paths (Fig. 2). When active, armadillos of Site 1 selected mainly forests when in the proximity of the dirt paths, but selected with more strength units with pasture when relatively far from the paths (i.e. >110 m). In Site 2, active armadillos also selected mainly forests when close to the dirt paths, but the selection strength becomes almost the same for forest and pasture units far from the paths (i.e. >90 m). For sheltering, forest and pastures were almost equally selected by armadillos of Site 1, but forest was the most strongly selected habitat in Site 2 (Fig. 2).

### *Home range*

Neither the body mass ( $t = -1.45$ ,  $df = 10.97$ ,  $p = 0.15$ ), nor the home range size of adult individuals differed between the two study sites ( $t = -1.371$ ,  $df = 15$ ,  $p = 0.19$ ). Therefore, we pooled together the data from the two sites to exam the relationship between home range size, body mass and sex of all tracked individuals. Since body mass and sex of the armadillos interacted to explain their home range size (Fig. 3;  $F_{(1,17)} = 7.32$ ,  $p_{\text{interaction}} = 0.05$ ), we examined the effect of body mass on home range sizes separately for each sex. Home range size of male *T. matacus* was positively related with their body mass ( $r^2 = 0.35$ ,  $F_{(1,9)} = 4.95$ ,  $p = 0.05$ ), while female home range sizes did not scale with their body mass ( $F_{(1,8)} = 0.008$ ,  $p = 0.93$ ; Fig. 2). Adult males were heavier than adult females (Tab. 1; Appendix 1) and the home range area (KUD 95%) of adult males *T. matacus* were, in average, about 2.8 times larger than the home range area of adult females (Tab. 1). To allow comparisons with previous



**Figure 4.** Relative selection strength of vegetation types according to distance to paths. Results of Resource Selection Function models for active periods (top) and when in shelters (bottom) at Site 1 (left) and Site 2 (right). Data from twenty-one *Tolypeutes matacus* monitored from November 2014 until August 2015.



studies, we also included the MCP 100% estimates in Table 1, since mean KUD 95% home range estimates differs from mean MCP estimates ( $t = 2.14$ ,  $df = 20$ ,  $p = 0.04$ ).

#### *Daily distance traveled*

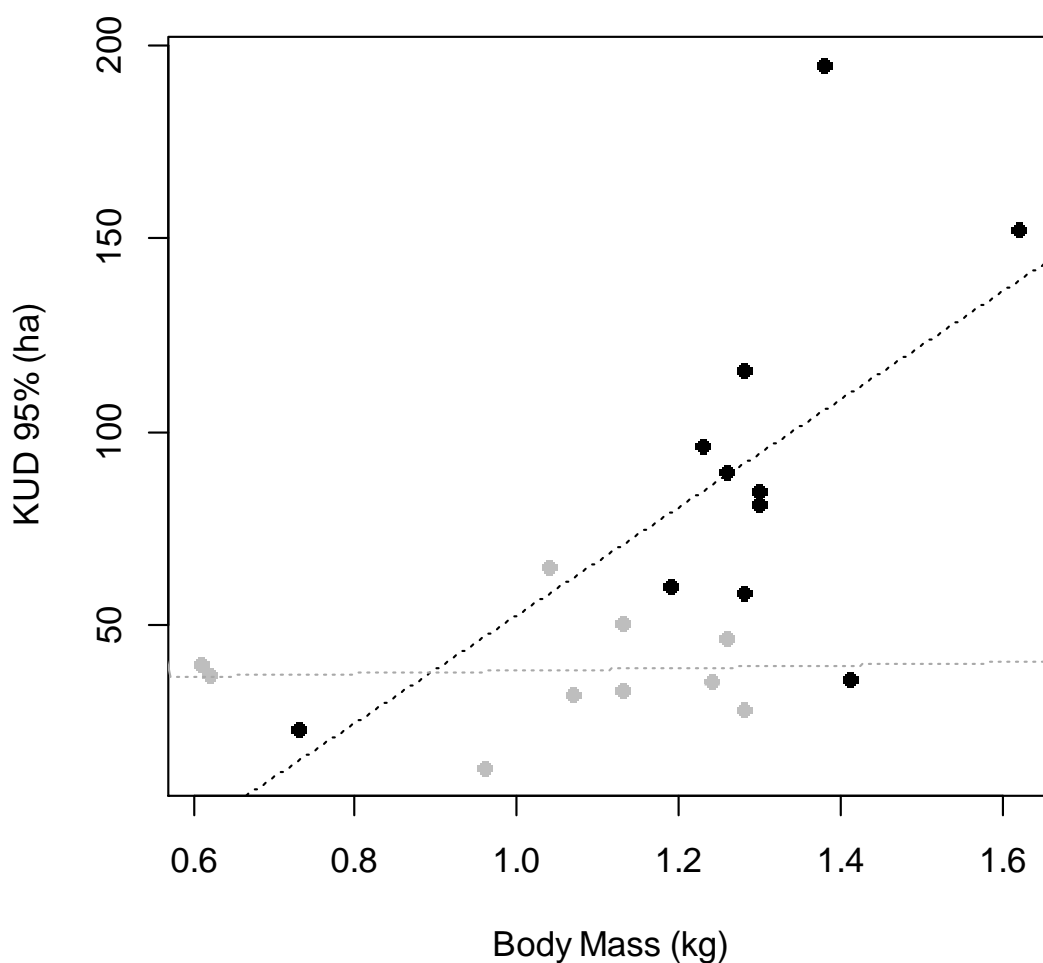
In a daily basis, adult males moved more than adult females (Tab. 3). The relationship between mean daily displacement and the square root of home range area shows an asymptotic tendency (Fig. 4). The estimated non-linear model indicates an asymptote at 3,536 m ( $SE = 1,331$ ,  $p = 0.01$ ) and a curvature value (b) of 5,269 ( $SE = 2,113$ ,  $p = 0.02$ ). However, it was not possible to estimate the intercept of the curve ( $c = 0.18$ ) with confidence ( $SE = 0.18$ ,  $p = 0.32$ ).

#### *Static interaction*

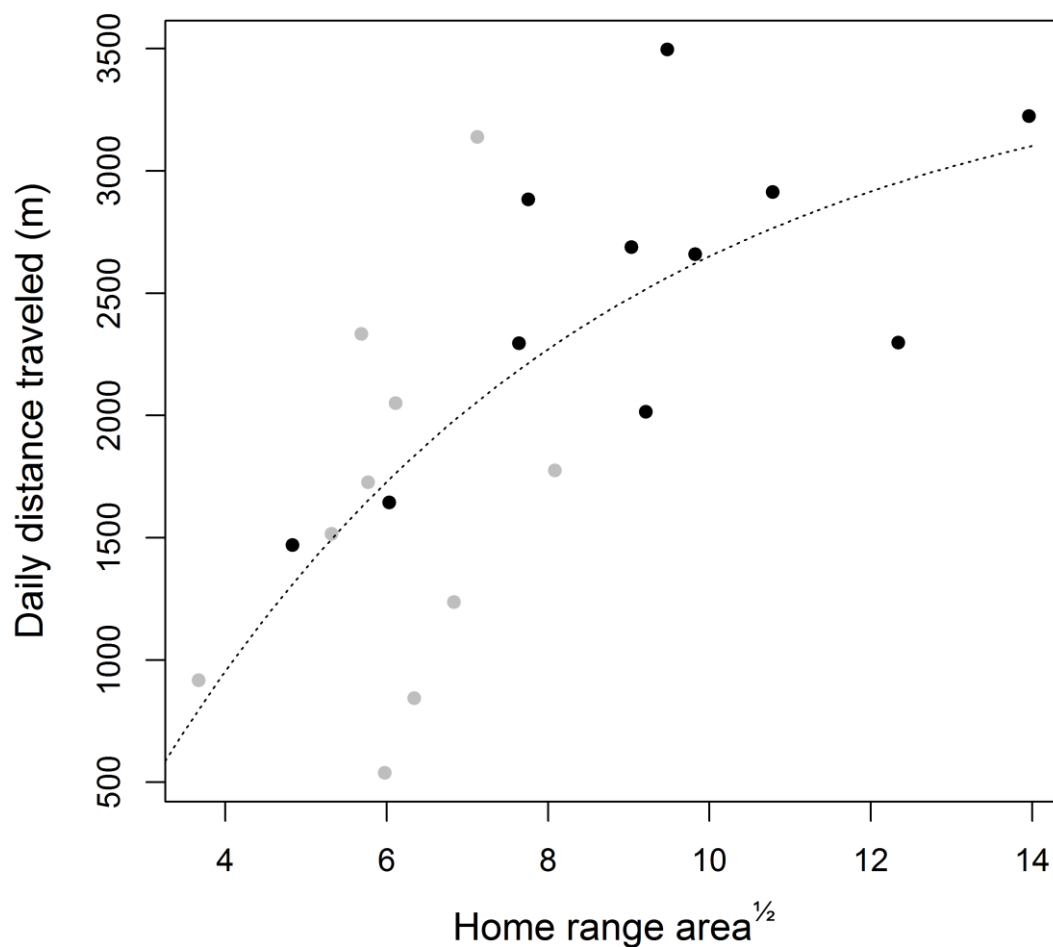
Sex and age class of armadillos influenced the probability of space use sharing between pairs of individuals (UDOI; Appendix 3). The probability of space use sharing (UDOI) is higher when animals are active and at home range level (12%), when compared to inactive periods (6%) and core area level (1%), respectively. During inactive periods, the probability of space use sharing between animals of different age classes was higher (9%) than that of animals of the same age class (5% for adults and 0 for juveniles). The probability of space use sharing of two adults during inactive periods is close to zero, regardless of their sex (Appendix 3).

**Table 1.** Comparison of mean and standard deviation of body mass, Kernel Use Density (KUD) home range size, Minimum Convex Polygon (MCP) home range size, and mean daily distance traveled for adult males and females of *Tolypeutes matacus*. Data from 21 armadillos tracked in two sites in the Pantanal of Brazil, from November 2014 until August 2015.

	Female	Male	t	df	p
Body mass (kg)	1.17 (0.12)	1.32 (0.12)	-2.65	16	0.02
KUD 95% (ha)	34.4 (12.25)	97.12 (47.11)	-3.41	15	< 0.01
MCP 100% (ha)	27.89 (18.69)	134.20 (82.62)	-3.31	15	< 0.01
Daily distance traveled (km)	1.63 (0.88)	2.61 (0.56)	-2.82	15	0.01



**Figure 5.** Relationship between body mass (kg) and Kernel Use Density home range size (KUD 95%) of twenty-one *Tolypeutes matacus* tracked in two sites in the Pantanal of Brazil, from November 2014 until August 2015. Dotted lines indicated the slope of the linear regressions for each sex. Males (black) scaled their home range with increasing body mass ( $KUD_{95\%} = -86.6 + 139.2 \times \text{Body Mass}$ ,  $F_{(1,9)} = 4.95$ ,  $r^2 = 0.35$ ,  $p = 0.05$ ). The home range size of females (grey) was not related to their body weight ( $F_{(1,8)} = 0.008$ ,  $p = 0.93$ ).



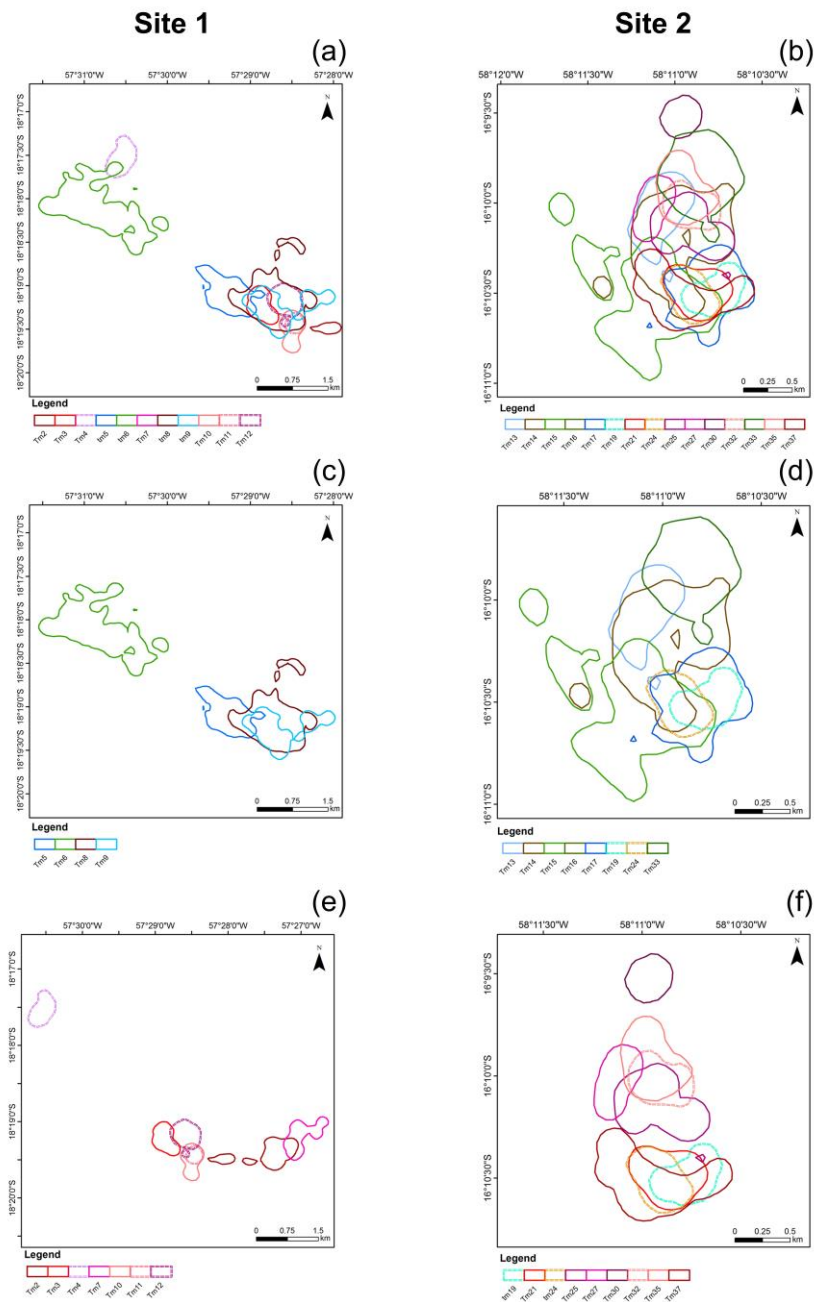
**Figure 6.** Relationship between mean daily distance traveled and the square root of the home range area of twenty-one *Tolypeutes matacus* tracked in two sites in the Pantanal of Brazil, from November 2014 until August 2015. Home range was estimated by the Kernel method (95%). Gray points represent females and black points represent males. The dotted line represents the estimated non-linear model.

Females did not share their home ranges and core areas with other females, regardless of age class (Fig. 5). The highest probability of space use sharing between females is 1%, during active periods, at home range level (Appendix 3). Nevertheless, nursing juvenile females tended to have home ranges almost completely encompassed by their mother's home range (Fig. 5). When compared to all others, pairs of females show a lower overlap probability at both home range (1%) and core area levels (<1%). On the other hand, the ranges occupied by males overlapped with both males (12%) and females (18%). In general, the probability of adult inter-sexual (M-F) space use sharing is higher (19%) than the intra-sexual probability (M-M 11%; F-F 3%). The probability of encountering an adult male inside an adult female home range is about 45% (Appendix 3). Each male overlapped the home range of at least two females and one of the tracked males overlapped the home range of six females, almost all the monitored females in an area (Fig. 5).

#### *Dynamic interaction*

Dyads were in average 423 m apart and in only 1%, of the 3,129 simultaneous fixes, animals were in proximity (i.e. < 50 m) to each other. Most of the proximity situations indicated tolerance behavior, occurring during short periods in foraging locations and areas used as displacement paths, such as dirt roads and trails.

The analysis of proximity dynamics of different dyads can provide us information about the social dynamics of the three-banded armadillo. For example, a dyad composed by an adult male and an adult female (TM33-TM35; Appendix 4) had overlapping adjacent home ranges. The proximity analysis showed that in five out of 10 days of simultaneous monitoring, the animals were in close proximity. The female of the dyad was lactating, although her cub (TM32; Appendix 1) was almost her size. At that time, mother and cub no



**Figure 7.** Home range contour (Kernel 95%) of twenty-one *Tolypeutes matacus* tracked in two sites in the Pantanal of Brazil, from November 2014 until August 2015. Spatial organization and home range overlap between (a, b) males and females, (c, d) between males and (e, f) between females. Dashed lines represent juvenile individuals. Juvenile males were also plotted into female range to illustrate the spatial relationship between mother and offspring.

longer shared a shelter every night, indicating that the cub should soon be weaned. This, and the fact that the two other inter-sexual dyads evaluated had zero or just one encounter during their simultaneous monitoring period (3-10 days), indicates that some type of social interaction could be taking place in this dyad (TM33-TM35).

Despite the high home range overlap between males, proximity patterns provided evidence of tolerance but not of any other type of interaction between individuals. Even though we have captured dyads of adult males together in two occasions (TM13-TM14; TM8-TM9; Appendix 4), these same animals were rarely in proximity during monitoring. The moments of proximity between males were the result of the common use of displacement routes and foraging places, shared over the highly overlapping home ranges.

Even though most females maintained almost exclusive territories, one dyad of adult females (TM21-TM37) presented higher static and dynamic interaction than any other. This dyad was in proximity in five occasions, during the 15 simultaneous days of monitoring, representing 2% of their fixes in that period. Unlike the dynamic interactions recorded in the other dyads, their proximity took place not only in displacement routes, but also in foraging areas and near resting shelters, portraying a higher tolerance than any other intra-sexual pair.

## **Discussion**

### *Activity*

Three-banded armadillos were mainly nocturnal. Even though Eisenberg & Redford (1999) have reported both diurnal and nocturnal activity for *T. matacus* and we have captured some individuals during daytime, we estimated a low probability of one to find them active during the daytime. Studies conducted in the Paraguayan and Bolivian Chaco also have characterized *T. matacus* as being mainly nocturnal (Barrientos & Cuellar 2004, Smith 2007, Cuéllar 2008). In contrast, hunters in the Bolivian Chaco report a diurnal activity pattern for the species, but

this pattern may be biased by an unequal hunting effort along the hours of the day (Barrientos & Cuellar 2004, Cuéllar 2008). The activity pattern observed in the present study is also similar to that reported for the congener *T. tricinatus*, which also seems to be active in the end of the afternoon and in the first half of the night (Bocchiglieri 2010).

Juvenile three-banded armadillos tended to leave shelters earlier than adults did. Juveniles of this species have been reported to have a diurnal activity on warm winter days in Paraguay (Merritt 2008). In the United States, young nine-banded armadillos (*Dasypus novemcinctus*) also tend to be more diurnal when compared to adults, which have a more crepuscular and nocturnal behavior (Layne & Glover 1985, McDonough & Loughry 1997). Differences in activity behavior between age classes can be related to predation risk, (McDonough & Loughry 1997) and/or variation in body mass between age classes and its consequences for thermoregulation (McNab 1980).

Armadillos are known to spend most of the day inside their burrows and shelters, being active and above ground for only a few hours per day (McDonough & Loughry 1997, Maccarini et al. 2015). When inside shelters, armadillos can be either inactive or performing activities such as nesting, sheltering or thermoregulating (McDonough & Loughry 1997, González et al. 2001, Maccarini et al. 2015). In the same wetland region, larger armadillo species such as the omnivorous *Euphractus sexcinctus* and the more insectivorous *D. novemcinctus* both presented slightly shorter periods of daily activity (4.4 hours and 4.9 hours, respectively; Maccarini et al. 2015), when compared to *T. matacus* (5.45 hours). The short activity period duration of armadillos is commonly attributed to their low metabolic rates and poor body temperature regulation mechanisms (González et al. 2001, Maccarini et al. 2015). Burrows can work as thermal shelters and are used for behavioral thermoregulation by these imperfect homeotherms (González et al. 2001, Maccarini et al. 2015).



### *Habitat Selection*

Three-banded armadillos have been reported to rest in forested areas but often leaving this vegetation type to forage in open habitats (Smith 2007). In the present study, armadillos presented higher selection strength for forested areas, regardless of activity status. The use of forested areas has been reported in the Bolivian Chaco, where most studies with this species have been performed (Cuellar 2008, Merritt 2008). However, Cuellar (2008) points out that the species only selects forested areas with well-drained soils. At Site 1, armadillos occupied forested areas adjacent to temporarily flooded areas with (shrubby) grassland vegetation. However, they were only recorded using the grassland areas (with medium-drained soil) during the dry season, with low overall selection strength. In Central Chaco, Merritt (2008) reports the occurrence of this species in natural grassland patches and in open thorn bush habitat. Besides natural grasslands, in the present study, armadillos also selected other habitats with more open vegetation types, such as pastureland and sugar cane plantation, and used these vegetation types for foraging and resting.

Even though animals selected natural areas (e.g. forests and grasslands), they also selected (with relatively lower strength) some modified elements of the landscape, such as sugar cane plantations and pastureland composed of exotic grasses (*Brachiaria* sp.). In fact, exotic pastures were selected with high selection strength, being only deferred over forest areas. At Site 2, two individuals (which were not tracked) were captured in an area of teak (*Tectona grandis*) plantation. In Central Chaco, this species is also found in agricultural lands and around rural dwellings, if patches of scrubby forest vegetation are present nearby (Smith 2007). Its congener, *T. tricinatus*, has also been recorded in landscapes composed by a mosaic of natural (e.g. cerrado strictu sensu) and modified elements (e.g. *Pinus* sp. plantation, deforested areas and soy plantation; Bocchiglieri 2010) in Northeast Brazil. Hence, even though three-banded armadillos show a strong selection of natural forest areas, they can also

use altered habitats. Smith (2007) states that this species can tolerate moderate habitat conversion, especially to agricultural activities, but that more accentuated habitat modification should have a negative effect on populations. Our results also indicate that three-banded armadillos can tolerate some disturbed habitats but we still need to understand the degree of habitat modification and distance from natural areas tolerated by this species. The use of agricultural areas has its inherent downsides. During a couple of few weeks of sugar cane plowing, we saw at least three armadillos being trampled and killed by tractors. In addition, the selection of specific resource units (e.g. habitat types) is always assumed to bring fitness advantages for a species, but in modified landscapes with a source-sink dynamics that may not always be true (Manly et al. 2002, Vynne et al. 2011). To assess the consequences of resource selection in modified landscapes, further studies on health aspects of three-banded armadillos could be performed in areas with different degrees of alteration.

One remarkable aspect of three-banded armadillo resource selection is that all selected habitat types presented higher selection strength in units closer to paths. Indeed, sightings and captures of this species and its congener in dirt roads have been repeatedly reported for other areas (e.g. Merritt 2008, Bocchiglieri 2010). Other species of armadillos, such as the giant armadillo *Priodontes maximus*, also showed a tendency to occupy units closer to roads when occupying areas of croplands in central Brazil. The authors state that this selection is likely due to the greater stability of these areas when compared to inner part of plantations, which are subject to bi-annual plowing (Vynne et al. 2011).

Landscape features derived from human activity, such as roads and fences, can be of particular interest for conservation, since they have become a conspicuous and abundant element in many landscapes (Beyer et al. 2014). The selection of human-build linear features, such as unpaved roads, has been recorded mostly for large carnivores (e.g. African wild dogs *Lycaon pictus* and wolves *Canis lupus*; Latham et al. 2011, Abrahms et al. 2015).

Nevertheless, small mammals (e.g. black-eared opossum *Didelphis aurita*) have been recorded to use plantation rows guidelines as dispersal venues in heterogeneous landscapes (Prevedello et al. 2010). Linear paths can provide references, such as visual marks and other sensory cues (e.g. scent marks) that can facilitate animal displacement. For marsupials, the selection of paths is related to the use of environmental cues and the increase in perceptual range (Prevedello et al. 2010). Armadillos, however, are not visually oriented, and should not have their perceptual range benefitted in the same manner by the use of paths. Since moving through a landscape has a cost, in terms of energy, time and exposure to risk (Fahrig 2007), the selection of dirt paths and areas near it by three-banded armadillos could be related to landscape permeability. This linear feature should provide less resistance to animal movement in comparison to surrounding landscape features, being selected as the most cost-effective route of displacement.

The ability to move through different landscape features can be affected by morphological, behavioral and locomotory adaptations of a species (Prevedello et al. 2010). Vegetation obstruction, such as dense undercover of forested areas and tall grasses, could limit, to some extent, the displacement of the morphologically specialized three-banded armadillo. This plantigrade species has short legs and is heavily armored, with a hard and inflexible carapace (with just three movable bands) that extends almost to its feet (Smith 2007, Superina & Loughry 2012). When being chased, three-banded armadillos move in a tortuous manner ('zig-zag') avoiding vegetation, with its legs moving rapidly “like a clockwork toy” (Smith 2007). Like other armadillo species, it can be very loud when moving through vegetation, due to the displacement of foliage that is pushed by its carapace and tail (pers. Obs.). Hence, moving through tall grass or dense vegetation could be a demanding task for this small-bodied species with limited flexibility. When using areas of dense vegetation, even the large sized African wild dogs presented increasing selection strength of unpaved

roads (Abrahms et al. 2015). At Site 1, which has 66% of its area covered by forest vegetation with dense undercover, and only a few dirt paths, distance to paths alone was able to predict resource selection by three-banded armadillos. Relative landscape permeability could also explain the high selection strength of pasture areas, especially because its selection does not scale with distance to paths in the same manner as other more covered habitats, like forests and taller grasslands. Since the areas of the Pantanal and Midwest Brazil are largely dedicated to farming activities, this information on habitat use is critical for the conservation of the species outside protected areas (i.e. in landscapes composed by a mosaic of natural and modified habitats).

#### *Home range and Static interaction*

Home range size is related to the energetic requirement of a species, intra and inter-specific interactions, habitat productivity, and resource patchiness (Harestad & Bunnell 1979).

Comparison of *T. matacus* home range estimates obtained in this study ( $90.4 \pm 82.9$  ha) with those reported by Barrientos & Cuéllar (2004) for *T. matacus* inhabiting areas of the Bolivian Chaco are useless, as these authors used a modified MCP estimate where they considered only non-overlapping areas as an animal's home range. On the other hand, the MCP estimates for *T. matacus* obtained here did not differ from those obtained for its only congener,

*T. tricinctus* ( $122 \pm 121$  ha; Guimarães 1997) in Mideast Brazil ( $t = 1.01$ ,  $df = 7.90$ ,  $p = 0.34$ ).

Thus, for such a small body mass (1.1 - 1.5kg), *Tolypeutes* presents a relatively large home range area when compared to heavier armadillos from other subfamilies and more generalist habits, such as *E. sexcinctus* (4.4kg,  $17 \pm 23$ ha; Medri 2008) and *D. novemcinctus* (3.2 to 4.4kg, 2 to 20ha; Loughry & McDonough 1998, Eisenberg & Redford 1999). McDonough & Loughry (2008) suggested that species that rely heavily on ants and termites, such as those

from the Tolypeutinae subfamily (i.e. *Tolypeutes* sp., *Cabassous* sp., *Priodontes* sp.), tend to have large, dispersed home ranges and few social interactions.

Although little is known about the mating behavior of this genus, our results point out to a promiscuous or polygynous mating system. In this type of mating system, males may mate with any receptive female, with no long-term bond between the mating individuals (Clutton-Brock 1989). The sexual dimorphism observed in *T. matacus* (with larger males) is one indication of this mating system, since different selection pressures on males and females can generate more pronounced sexual dimorphism in the body size of polygynous species (Clutton-Brock et al. 1989). The non-territorial roving behavior observed for male three-banded armadillo can occur when females are solitary and unpredictably distributed. Instead of guarding a territory, dominant promiscuous males tend to increase their chances of reproductive success by actively searching for females (Clutton-Brock 1989). Since receptive females are distributed in an unpredictable manner across space and time, males can try to increase their chance of encountering receptive females by covering areas larger than those defined strictly by their energetic requirements (Sandell 1989). In our study, each male overlapped the home range of at least two females and one of the tracked males was able to overlap the home range of six females, almost all the monitored females in an area. In addition, daily distance traveled scaled with home range size and male home range size scaled with body mass, granting higher daily ranges for larger males. Hence, larger males can afford, energetically, to rove over larger areas and increase their chances of encountering females in oestrous. In a long-term monitoring project with *D. novemcinctus*, McDonough (2000) reports that females tend to pair with males with high overlap over their home range. Thus, dominance in males of three-banded armadillo could be associated with body mass, since these individuals have larger home ranges and higher daily distances traveled, potentially encountering more females. In addition, chasing behavior, like that described for

*E. sexcinctus* (Desbiez et al. 2006, Tomas et al. 2013), where several males pursue a single female presumably in oestrous, has been reported for *T. matacus* congener, *T. tricinctus* (Bernier 2003, Bocchiglieri 2010, Marini-Filho & Guimarães 2010). This behavior suggests that larger males are more successful in keeping smaller distances from receptive females during the chase, reinforcing the importance of body mass on breeding success of males.

Differently from males, female spacing is mainly dictated by resource abundance and distribution (Sandell 1989). The smaller and almost exclusive ranges occupied by the studied females should guarantee enough resources for them and their offspring. This spacing pattern also corroborates with the proposed mating system and indicates a relatively stable and evenly distributed resource supply (Sandell 1989). Females of *T. matacus* are uniparous and are solely responsible for the care of the young (Eisenberg & Redford 1999). This is an opportunistic insectivorous species that can also feed on plant matter (Bolkovic et al. 1995). Since these resources are relatively abundant and evenly distributed in the tropical areas that they inhabit, female spacing patterns should not be strongly shaped by food resource availability. The observed spacing patterns were also related to age class and activity status of individuals and reinforce the socio-biological aspects found for other armadillos which are characterized as solitary, asocial mammals, with rare social interaction, mostly related to breeding behavior (Loughry & McDonough 2013; Loughry et al. 2015). Individuals of different age classes presented higher probabilities of space use sharing, regardless of their activity status, when compared to same age pairs. This can be at least partially explained by the fact that females tend to share their shelters, and consequently their home range, with their young (Attias et al. 2016). Interestingly, with the exception of nursing females, which had their home range almost completely encompassed by their mother's home range, adult females do not tend to tolerate any overlap of other females, regardless of age class. Even dispersing sub-adult females seem to avoid extensive overlap with other females. The lower

probability of core area sharing can be related to the fact that burrow sharing between adult *T. matacus* is not common and has only been recorded in rare occasions of extreme cold and in a temporary manner (Merritt 2008). The higher inter-sexual probability of overlap, when compared to the intra-sexual, reinforces the breeding related aspects of the rare social interactions between *T. matacus* individuals.

Like in *T. matacus*, males of *T. tricinctus* also present home range areas larger ( $238 \pm 103$  ha) than those of adult females ( $24 \pm 12$  ha; Guimarães 1997). The similarities with the spatial patterns encountered by Guimarães (1997) for *T. tricinctus*, where males are heavier, home ranges scale with body mass, and males present larger home ranges than females, indicate that both species of the genus *Tolypeutes* might share a similar mating strategy.

#### *Dynamic interaction*

Even though the simultaneously monitored animals were in close proximity only in 1% of the fixes, we were able to identify some interactions worth further exploration. The repeated encounters between adult individuals of opposite sexes could indicate some type of long-term social relationship (e.g. kin-related or breeding), or simply high sharing rates of foraging patches. The repeated encounter between two adult females is conflicting with the idea of territorial solitary females, inferred from the static interaction. The fact that one of the females was pregnant, and thus not receptive, could be related to this increased mutual tolerance. Even though armadillos are generally classified as solitary and asocial, these long-lived mammals can present high home range overlap and some species have been reported to occupy the same area throughout years, granting them opportunity for the establishment of short and long-term social relationships (Loughry & McDonough 2001, McDonough & Loughry 2008). However, kinship analysis and/or longer-term behavioral studies should be

conducted to elucidate three-banded armadillo social relationships, which could be more complex than previously reported.

Besides the information obtained through animal tracking, our direct field observations also suggests the maintenance of types of social interactions not previously reported for this species. In one situation, we found one of our monitored lactating females (TM25) foraging in close proximity (~1m) to two males (TM33 and TM34), one of which with evident testicles. The animals did not seem to be disturbed by each other's presence, characterizing a tolerance behavior, but when the female and one of the males almost touched each other, the female walked away rapidly. On another occasion, the same lactating female was seen foraging near another pair of individuals on a fallen tree log. However, an adult male and female composed this pair of individuals. The intra-sexual pair was foraging in close proximity, sharing the same foraging holes, and constantly touching each other (nose to nose, smelling each other's genital areas and putting their forefeet over each others back). All three individuals were aware of each other's presence, and the individuals that composed the pair, at different moments, tried to get closer to the female and smell her, however, the female walked away every time, but kept foraging a few meters away. The set of interactions between this intra-sexual pair is similar to the reproductive pairing behavior described for *D. novemcinctus* (McDonough & Loughry 2008). Even though Silva & Oren (1993) have recorded adult pairs of *T. tricinctus* foraging together in multiple occasions, the previously described reproductive behavior for this genus was composed only by chasing behavior, presumably followed by coitus, with no mate guarding reported. The other species that presents reproductive chasing behavior, *E. sexcinctus*, has also never been seen presenting a pairing behavior, pre or post coitus (Desbiez et al. 2006, Tomas et al. 2013). We did not record any events of reproductive chasing behavior during our study, even though we captured many females at different gestational stages, which indicate reproductive activity



during our study period. Nevertheless, pairs of adult males were seen displacing close to each other on three different occasions, and in two of the pairs, one individual presented evident testicles but no sign of aggressive behavior was recorded, as reported by Marini-Filho & Guimarães (2010) in their observation of chasing behavior.

Even though this study was not designed to compare preserved and altered areas, we did not find differences in the basic ecological patterns evaluated for this species. Home range size, overlap patterns between individuals, habitat selection and activity patterns encountered were similar between areas. Nevertheless, future studies should address more directly how this species can be affected by habitat modification to enable proper species-specific conservation planning.

## **Conclusion**

To our knowledge, this is the first study of *T. matacus* in the wild in the Brazilian territory and the most comprehensive study on its ecology in situ. We were able to characterize the basic aspects of this species ecology and make valuable inferences on its social biology. We characterize three-banded armadillos as a mainly nocturnal species that selects preferentially forested areas but is able to occupy modified landscapes. Their home range and spacing patterns point out to a generally asocial behavior and a promiscuous mating system, but some of our behavioral observations point out the need of further field observations to explore its potentially richer social behavior. This species has been classified as Data Deficient until now by the Brazilian authorities and we hope that the data generated here will be able to contribute to this species conservation in Brazil and guide future research efforts to support the conservation of this globally near threatened species.

## Appendix 1.

Detailed information on the individuals of *Tolypeutes matacus* monitored in two sites in the Pantanal of Brazil, from November 2014 until August 2015.

**Table 2.** Individuals of *Tolypeutes matacus* monitored in two sites in the Pantanal of Brazil, from November 2014 until August 2015. Here we present information on: Study site - 1 (Santa Tereza ranch), 2 (Duas Lagoas ranch); Sex - male (M), female (F); Age class - adult (A), sub-Adult (S) and juvenile (J); Body mass (kg); Number of locations obtained through GPS telemetry (N Locations (GPS)); Number of locations obtained through conventional VHF telemetry (N Locations (VHF)); Total monitoring time span (with VHF and/or GPS); Number of days that the animal was tracked with GPS telemetry; and two estimates of home range - Kernel Use Density (KUD 95%) and Minimum Convex Polygon (MCP 100%). KUD 95% home range areas were estimated based only on GPS data. MCP 100% home range area was estimated with all locations, i.e. GPS and VHF radio data.

Id	Site	Sex	Age class	Body mass (kg)	N Locations (GPS)	N Locations (VHF)	Monitoring time span (days)	GPS Tracking period (days)	Mean daily distance traveled (m)	MCP100% (rad + gps)	KUD95%
TM2	1	F	S	1.04	3,256	12	131	19.9	1,774.8	123.84	65.38
TM3	1	F	A	1.24	895	10	127.5	28.6	538.4	24.06	35.73
TM4	1	F	S	0.62	3,040	7	74	25.2	2,049.5	40.1	37.36
TM5	1	M	A	1.3	1,799	5	87.1	19.2	2,688	99.27	81.62
TM6	1	M	A	1.38	2,556	5	69.6	17	3,223.2	289.14	194.91
TM7	1	F	A	1.26	351	11	20.5	9	1,236.7	40.62	46.7
TM8	1	M	A	1.62	1,664	13	122.3	23.9	2,297.2	240.18	152.27
TM9	1	M	A	1.3	263	5	54.9	6.3	2,015.3	82.59	84.87
TM10	1	F	A	1.13	1,616	7	30.6	18.5	1,727.1	24.05	33.3
TM11	1	F	J	0.72	0	5	27.9	0	-	0.77	-
TM12	1	F	J	0.61	218	1	6.1	5.1	843.9	24.78	40.2
TM13	2	M	A	1.41	1,078	4	12	4.18	1,644.2	24.07	36.37
TM14	2	M	A	1.23	5,396	27	36.6	26.4	2,658.6	133.74	96.55
TM15	2	M	A	1.28	8,248	23	39.5	32.9	2,913.2	191.68	116.3
TM16	2	M	A	1.26	1,197	4	7.7	5.15	3,496.3	143.46	89.81
TM17	2	M	A	1.28	4,420	19	35.53	17.9	2,294.9	34.56	58.38
TM19	2	M	S	0.94	0	16	27.6	0	-	6.31	-
TM21	2	F	A	1.28	4,664	41	51	21.9	1,515.7	24.3	28.29
TM24	2	M	S	0.73	3,705	20	20.4	17.6	1,470.2	13.91	23.35
TM25	2	F	A	1.31	0	62	47.1	0	-	21.99	-
TM27	2	F	S	0.68	0	49	44	0	-	2.35	-
TM30	2	F	A	0.96	5,056	22	34.8	20.1	917.4	3.27	13.47
TM32	2	F	J	0.7	0	30	25.7	0	-	6.73	-
TM33	2	M	A	1.19	2,632	12	27.5	10.7	2,883.6	61.45	60.17
TM35	2	F	A	1.07	4,841	22	19.3	18.8	2,332.4	23.97	32.33
TM37	2	F	A	1.13	4,408	17	17.6	17.6	3,138.5	64.65	50.74
<b>Mean</b>		-	-		<b>2,919</b>		-	<b>17.4</b>	<b>2,079</b>	<b>64.09</b>	<b>65.62</b>

## Appendix 2.

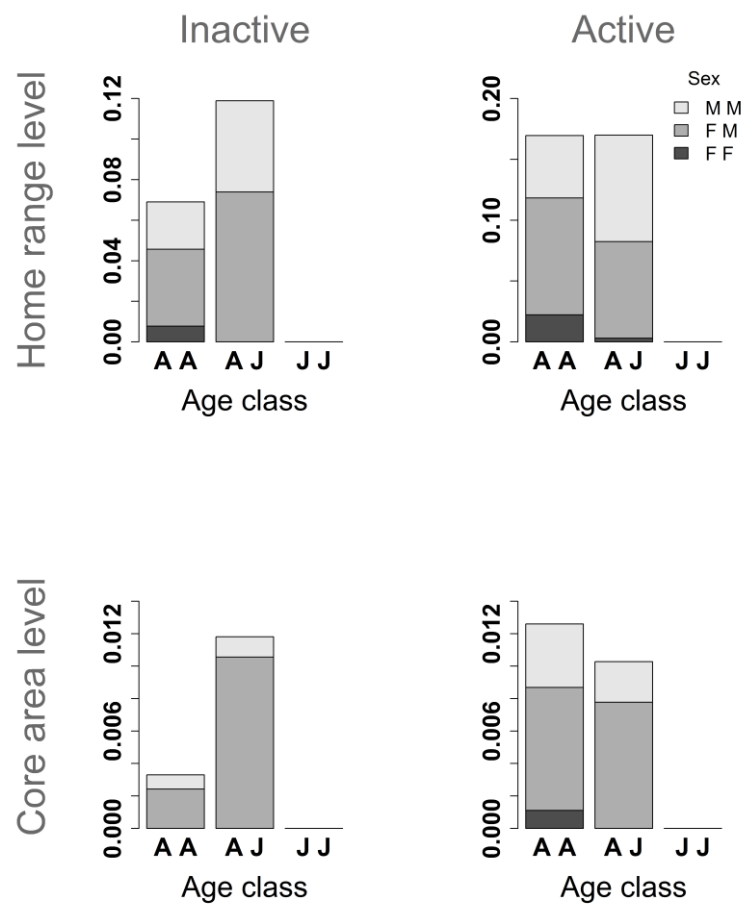
**Table 3.** Estimates of the Resource Selection Function of ten individuals of *Tolypeutes matacus* tracked at Santa Tereza ranch (Site 1), between November 2014 and March 2015.

	Status	Estimate	Standard Error	z	p
<b>Distance to paths</b>	Active	-0.002	<0.01	-3.17	<0.01*
	Inactive	-0.012	<0.01	-2.93	<0.01*
<b>Forest</b>	Active	0.256	0.05	5.05	<0.01*
	Inactive	0.791	0.24	3.26	<0.01*
<b>Pasture</b>	Active	0.170	0.06	2.96	<0.01*
	Inactive	0.691	0.36	1.91	0.05*
<b>Distance to paths * Forest</b>	Active	0.001	<0.01	1.12	0.26
	Inactive	-0.001	<0.01	-0.04	0.96
<b>Distance to paths * Pasture</b>	Active	0.002	<0.01	1.94	0.05*
	Inactive	-0.001	<0.01	-0.03	0.98

**Table 4.** Estimates of the Resource Selection Function of eleven individuals of *Tolypeutes matacus* tracked at Duas Lagoas ranch (Site 2), from July to August 2015.

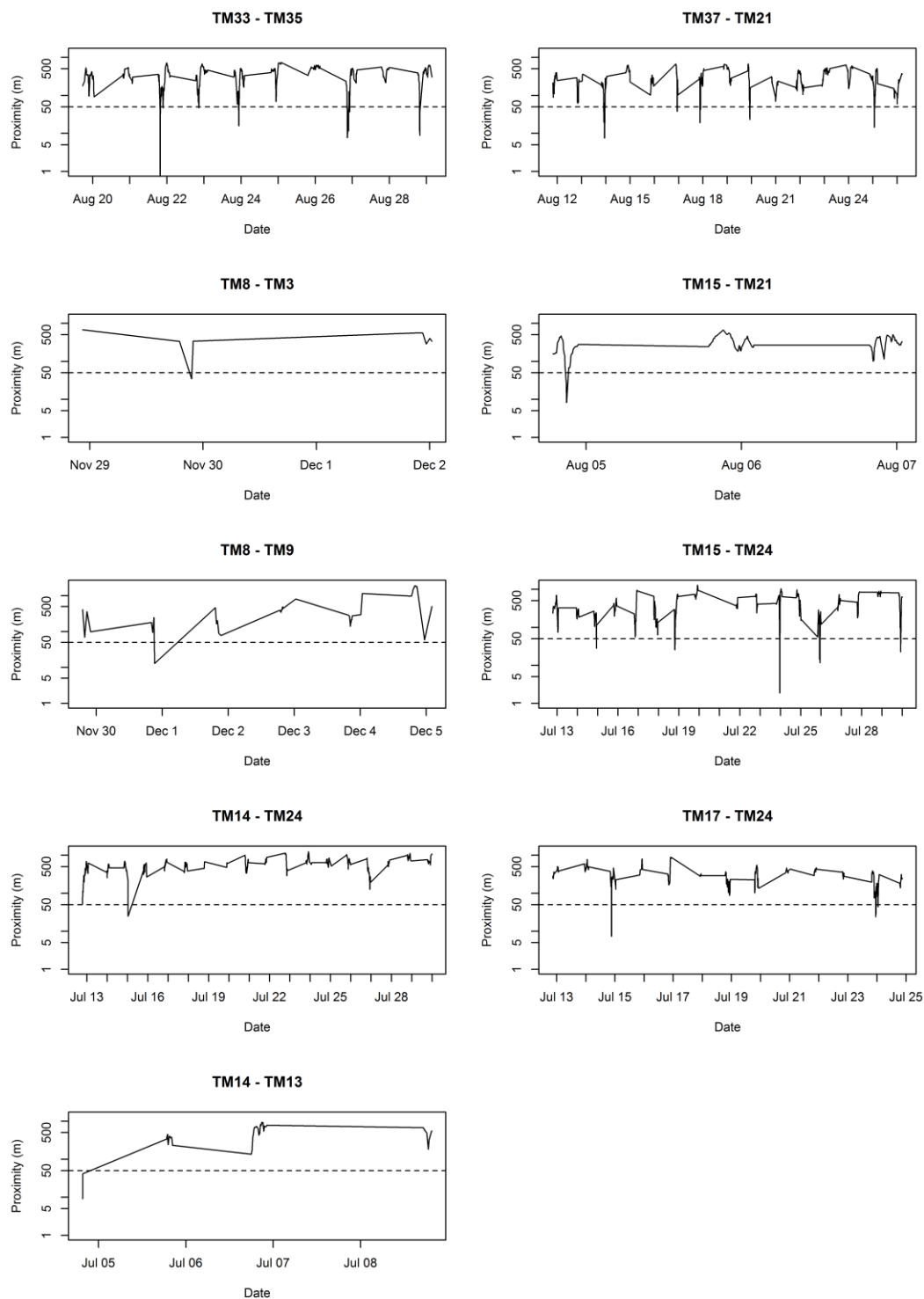
	<b>Status</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>z</b>	<b>p</b>
<b>Distance to paths</b>	Active	-0.001	<0.01	-0.32	0.75
	Inactive	-0.001	<0.01	-0.03	0.97
<b>Sugar cane</b>	Active	12.99	0.25	52.48	<0.01*
	Inactive	13.33	0.41	32.44	<0.01*
<b>Forest</b>	Active	13.77	0.12	112.33	<0.01*
	Inactive	14.04	0.25	56.63	<0.01*
<b>Pasture</b>	Active	13.53	0.14	98.21	<0.01*
	Inactive	13.69	0.24	57.87	<0.01*
<b>Water pool</b>	Active	0.57	0.94	0.61	0.54
	Inactive	-0.05	1.13	-0.05	0.96
<b>Distance to paths * Sugar cane</b>	Active	-0.02	<0.01	-3.78	<0.01*
	Inactive	-0.02	0.01	-1.81	0.07
<b>Distance to paths * Forest</b>	Active	-0.01	<0.01	-4.30	<0.01*
	Inactive	-0.007	<0.01	-1.12	0.26
<b>Distance to paths * Pasture</b>	Active	-0.01	<0.01	-7.18	<0.01*
	Inactive	-0.02	<0.01	-4.22	<0.01*
<b>Distance to paths * Water pool</b>	Active	-0.001	<0.01	-0.01	0.99
	Inactive	0.001	0.01	0.02	0.98

### Appendix 3.



**Figure 8.** Joint distribution probability of pairs of *Tolypeutes matacus* of different sex and age classes, according to the UDOI index. We divided our dataset according to the activity status of the individuals ("Active" or "Inactive") and estimated the probability of space use sharing at the home range level (KUD 95%) and at the core area level (KUD 50%) for each subset of locations. Individuals were tracked in two sites in the Pantanal of Brazil from November 2014 until August 2015

## Appendix 4.



**Figure 9.** Proximity and encounters (distances below 50 m) between nine dyads of simultaneously monitored *Tolypeutes matacus* in two sites in the Pantanal of Brazil, from November 2014 until August 2015.

**Table 5.** Details about the dynamic interaction between nine dyads of *Tolypeutes matacus* monitored in two sites in the Pantanal of Brazil, from November 2014 until August 2015. Identification of the individuals of each dyad, sex, number of days of simultaneous monitoring, number of encounters (distance < 50m) within that period, and proportion of simultaneous fixes at which the individuals of the dyad were less than 50 meters (proximity index as defined by Bertrand et al. 1996, Long et al. 2014).

Dyad	Sex	N Days	Encounters	Proximity index
TM33-TM35	M-F	10	5	0.01
TM9-TM3	M-F	4	0	0
TM15-TM21	M-F	3	1	0.01
TM37-TM21	F-F	15	5	0.02
TM17-TM24	M-M	12	2	0.02
TM15-TM24	M-M	17	5	0.03
TM14-TM24	M-M	17	2	0.002
TM13-TM14	M-M	4	1	0.02
TM8-TM9	M-M	8	2	0.01



## **Chapter 3 - Effects of air temperature on habitat selection and activity patterns of two tropical imperfect homeotherms**

### **Abstract**

In this study, we aim to evaluate how air temperature is related to variations in activity patterns and habitat selection by two tropical armadillos, which are imperfect homeotherms. Although their behavior is little studied, armadillos provide valuable models for understanding how physiology affects mammalian behavior in response to environmental changes. We used GPS devices to track two species of armadillo (yellow armadillos, *Euphractus sexcinctus* and southern three-banded armadillos, *Tolypeutes matacus*) in three sites of the Pantanal wetlands, Brazil. We used linear mixed-effects models to evaluate the variation of activity patterns and duration according to changes in air temperature. We fitted Step Selection Functions to evaluate the effects of the cover type, circadian cycle, and air temperature on armadillo resource selection. *Euphractus sexcinctus* shifts its activity pattern from diurnal to nocturnal as mean daily temperature increases. This species tends to select open vegetation areas during activity and forested areas during rest, but the strength of this habitat selection depends on temperature. In contrast, *T. matacus* shows less variation on its activity pattern at different air temperatures, maintaining a predominantly nocturnal activity pattern. However, as air temperature decreases, its activity periods are of shorter duration and peak earlier in the day. This species also shows higher variation in habitat selection across temperatures. 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 behavior. Our results highlight the importance of habitat heterogeneity for the long-term conservation of animal species that rely on behaviour to achieve adequate thermoregulation.

**Key-words:** armadillo, GPS telemetry, Pantanal wetlands, spatial ecology, step selection functions, Xenarthra

## Resumo

Neste estudo temos como objetivo avaliar como a temperatura do ar está relacionada à variação nos padrões de atividade e seleção do habitat por duas espécies tropicais de tatus, que são homeotermos imperfeitos. Apesar de terem seu comportamento pouco estudado, tatus podem fornecer valiosos modelos para compreender como a fisiologia afeta o comportamento de mamíferos em resposta a mudanças no ambiente. Nós utilizamos equipamentos de GPS para monitorar duas espécies de tatus (tatu peba, *Euphractus sexcinctus* e tatu bola, *Tolypeutes matacus*) em três áreas do Pantanal, Brasil. Nós utilizamos modelos lineares de efeitos mistos para avaliar a variação nos padrões de atividade e sua duração total de acordo com mudanças na temperatura do ar. Nós ajustamos "Step Selection Functions" para avaliar os efeitos do tipo de cobertura vegetal, ciclo circadiano e temperatura do ar na seleção de recursos pelos tatus. *Euphractus sexcinctus* muda seu padrão de atividade de diurno para noturno a medida que a temperatura média diária aumenta. Esta espécie tende a selecionar vegetações abertas durante o período de atividade e áreas florestadas para descanso, mas a força de seleção é dependente da temperatura. Em contraste, *T. matacus* apresenta menor variação em seu padrão de atividade em diferentes temperaturas do ar, mantendo um padrão de atividade predominantemente noturno. No entanto, à medida que a temperatura do ar diminui, seus períodos de atividade são mais curtos e tem seu pico mais cedo. Esta espécie também apresenta maior variação na seleção do habitat de acordo com variações na temperatura. Este estudo apresenta exemplos específicos da natureza dinâmica dos padrões de atividade e seleção do habitat e ilustra como limitações térmicas, que variam dinamicamente ao longo dos ciclos circadianos e ao longo dos dias, podem afetar o comportamento. Nossos resultados destacam a importância da heterogeneidade do habitat para a conservação em longo prazo de espécies animais que dependem de estratégias comportamentais para alcançar termorregulação adequada.

**Palavras-chave:** tatus, GPS telemetria, Pantanal, ecologia espacial, step selection function, Xenarthra

## Introduction

Animals use a combination of physiological, physical and behavioral processes to achieve thermal balance (Tattersall & Cadena 2010). The question of how animals vary their behavioral patterns in response to environmental changes is central in ecology (Krebs & Davies 1993). Because temperature can strongly affect animal behavior, and because global climate change may affect organisms directly via physiological stress, understanding the relationship between environmental conditions and behavior is increasingly important (Harley 2011).

Animal activity, behavior, 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; Rietveld et al. 1993, Nathan et al. 2008). Behavioral decisions are guided by trade-offs between gaining access to resources and minimizing negative effects (e.g., physiological stress), ultimately maximizing individual fitness. Such behavioral decisions may involve both timing of activity and selection of habitats (Fortin et al. 2008, Tattersall & Cadena 2010).

Habitat selection is a dynamic process that is likely to be influenced by a variety of temporally variable factors, such as temperature (Sunde et al. 2014). Furthermore, circadian cycles of activity allow animals to anticipate 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 their shape (Rietveld et al. 1993).

The super order 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). Xenarthrans possess low body temperatures (32.7 to 35.5°C), low basal metabolic rates (~50%), and high thermal conductance (130-200%).

They are considered imperfect homeotherms. That is, even though xenarthrans are able to generate body heat like other placental mammals, they have a limited capacity to regulate it (McNab 1985). Armadillos build burrows used to rest, to avoid adverse environmental conditions, and to shelter from predators (McDonough & Loughry 2008). As burrowing imperfect homeotherms, armadillos and other xenarthrans should present conspicuous behavioral responses to environmental changes and, as such, are valuable models for understanding how physiology affects decision-making in mammals (Maccarini et al. 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 (Tattersall & Cadena 2010, Superina & Loughry 2012). The association between the low basal metabolic rate and high thermal conductance causes armadillos to maintain temperature differential with ambient temperature at their lower limit of thermoneutrality, regardless of their body mass (McNab 1985). The thermoneutral zone is defined as the ambient temperature interval where the animal's metabolic rate is independent of temperature (McNab 2002). The carapace increases the lower limit of thermoneutrality for armadillos by defining its minimal thermal conductance and allowing small differences between body temperature and environment (McNab 1985, 2002). A higher lower limit of thermoneutrality means that, even in the tropics, armadillos frequently face environmental temperatures that require an increased metabolic expenditure to maintain their body temperature (McNab 1985).

Metabolic thermoregulation is especially costly from an energetic standpoint (Liwanag 2010), especially for imperfect homeotherms. To reduce such energetic costs, xenarthrans can adopt behavioral strategies to overcome unfavorable environmental conditions and mitigate thermal limitations. Variations in habitat use and activity patterns have been recorded for xenarthrans such as giant anteaters (*Myrmecophaga tridactyla*) and

yellow armadillos (*Euphractus sexcinctus*) as responses to temperature variation (e.g., Mourão & Medri 2007, Maccarini et al. 2015).

Here, we aim to test how air temperature drives shifts in activity patterns and habitat selection by two species of imperfect homeotherms (*E. sexcinctus* and *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 et al. 2011). It is found in open areas, savannas, shrublands, dry and semi-deciduous forests (Eisenberg & Redford 1999). The species' optimal ambient temperature is close to 30°C (Roig 1969), and it has only been recorded active in the Pantanal at air temperatures between 13.2 and 36.2°C (Maccarini et al. 2015).

In contrast, the southern three-banded armadillo (*T. matacus*) is restricted to western Brazil, Bolivia, Paraguay and Argentina (Wetzel et al. 2007). Like its congener, this species can roll into a ball as a defense mechanism. *Tolypeutes matacus* weighs ca. 1.1kg and is classified as an opportunistic insectivore (Bolkovic et al. 1995, Eisenberg & Redford 1999). When resting, it can use burrows and other types of shallow shelters (Attias et al. 2016). This species can be active throughout the day and night, though its activity pattern may be primarily influenced by temperature and rainfall (Eisenberg & Redford 1999, Cuellar 2008).

Because the circadian activity pattern adopted by an animal is one of the most effective and generalized ways to minimize the influence of unfavorable biotic and abiotic factors (Layne & Glover 1985), we expect armadillos to alter their periods of activity to avoid physiologically unfavorable ambient temperatures. For example, we hypothesize that, on days with low temperatures, armadillos should increase their activity during the warmest hours of the day. Moreover, we hypothesize that armadillos may select different habitats as a function of temperature, allowing them to control their temperatures by spending more time

in cooler or warmer habitats as conditions dictate. We expect this because thermoregulation appears to be most important proximate factor influencing habitat selection by terrestrial heterotherms (Reinert 1993), and is thus likely to affect behavior 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 on those days featuring extreme air temperatures (either unusually hot or unusually cold) in comparison to typical conditions in the Pantanal. This behavior should facilitate armadillo thermoregulation without the increased cost of metabolic changes imposed on animals with low basal metabolic rates.

Furthermore, even though both species face similar thermoregulatory constraints, they present subtle physical (e.g. body mass, carapace shape), physiological (e.g. thermal conductance of the carapace) and ecological (e.g. diet specialization) differences. Hence, the species can present distinct behavioral responses to temperature variation, potentially increasing or reducing their niche overlap, exacerbating or offsetting ecological interactions (e.g. predator-prey, intra-guild competition; Creel et al. 2016). Thus, we hypothesize that *E. sexcinctus* might present a comparatively higher activity behavior plasticity due to its higher thermal conductance and tendency to forage in open habitats, being more vulnerable to temperature variations. This could potentially alter the degree of overlap of the temporal niche dimension between species.

## **Materials and methods**

### *Study area*

This study was carried out in three sites, 120 to 350 km apart, located in the Pantanal wetlands, Midwest of Brazil (Fig. 1). The Pantanal is a large Neotropical wetland, with an



extension of 210,000 km<sup>2</sup> over Brazil, Bolivia and Paraguay (Mittermeier et al. 2003). Its climate is classified by Köppen's system as tropical sub humid (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).

The Nhumirim 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 km<sup>2</sup> and altitude of 98 m.a.s.l. (Fig. 2a). The landscape comprises a mosaic of environments, consisting of large grassland areas, permanent and temporary ponds surrounded by grassland vegetation, savanna and woodland areas (Abdon et al. 1998). At this site, we captured and monitored *E. sexcinctus* in undisturbed areas.

The Santa Teresa Ranch (Site 2) is located in the Serra do Amolar Mountain Ridge, in the western limits of the Brazilian Pantanal (18°17'51''S, 57°30'35''W; Fig. 2b). The variable relief in the area (90 to 1,000 m of altitude) influences the vegetation structure. The non-flooded areas are dominated by deciduous and semi-deciduous forests, while pastures and humid and dry savannas occupy the areas subjected to flooding (Tortato et al. 2015). This private property is part of the Network for the Protection and Conservation of Serra do Amolar and only 3%, of its 630 km<sup>2</sup>, were converted into exotic pasture for cattle ranching. At this site, we captured and monitored *T. matacus* in both disturbed and undisturbed habitats.



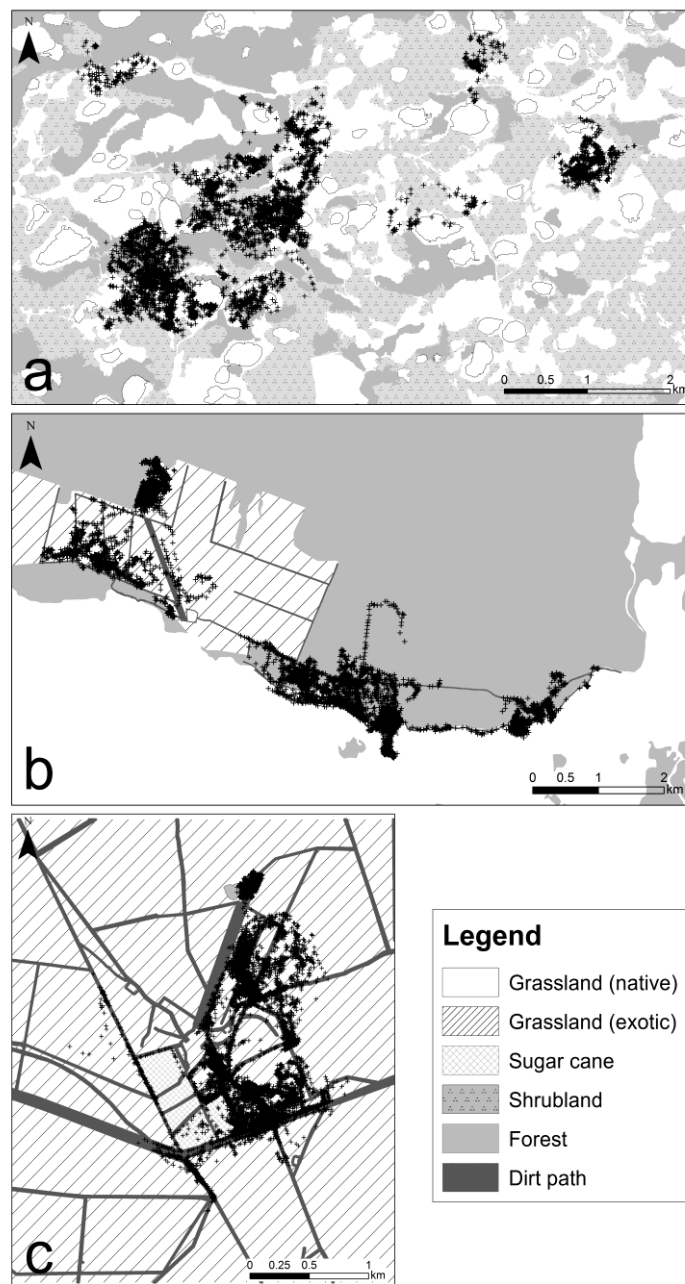
**Figure 1.** Location of the Pantanal Wetlands in South America, and location of the three study sites: (1) Nhumirim Ranch; (2) Santa Teresa Ranch; and (3) Duas Lagoas Ranch.

The Duas Lagoas Ranch (Site 3; 16°10'13"S, 58°11'12"W) is located the transition zone between the Pantanal and Cerrado eco-regions (Fig. 2c). This 74 km<sup>2</sup> ranch is owned by the private company Floresteca. Their main economic activity is the teak plantation (*Tectona grandis*; 42 km<sup>2</sup>), but there are also areas of exotic pasture (*Brachiaria* sp.) dedicated to cattle ranching (12 km<sup>2</sup>) and a small sugarcane plantation (0.24 km<sup>2</sup>). Besides these areas, the ranch encompasses 16.3 km<sup>2</sup> of native remnants of cerrado woodland, scrub savanna, grassland and gallery forest. At this ranch, we captured and monitored *T. matacus* almost exclusively at disturbed areas.

Using RapidEye satellite imagery (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, dirt paths and sugar cane 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 sugar cane plantations only at Site 3.

#### *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 March to August 2014, we captured and tracked 17 *E. sexcinctus*. From these, 10 were male (nine adults; one cub) and seven female (all adults). From November 2014 until August 2015, we captured and monitored 21 *T. matacus*, 10 at Site 2 and 11 at Site 3, including three sub-adults and one cub. Age class was determined based on body mass. *Euphractus sexcinctus* with less than 2 kg were classified as cubs (Medri 2008). For *T. matacus*, we defined adults as individuals with more than 1 kg and sub-adults as weaned individuals with less than 1 kg.



**Figure 2.** Locations of the monitored species (+) at 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.

Captured animals were temporarily contained in ventilated plastic boxes or cloth bags until processing. Information on age, sex, reproductive condition, body mass and body measures 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, Minnesota, USA) and a GPS tracking device (non-commercial prototype used in other studies of the Wildlife Laboratory of Embrapa Pantanal, e.g. Oliveira-Santos et al. 2016). The package mass (~50g) 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 carapace of *T. matacus*, using flexible cyanoacrylate super glue and/or epoxy resin, following a protocol commonly used for hard-shelled turtles (e.g., Seminoff et al. 2002). This procedure did not prevent *T. matacus* from rolling into a ball. All individuals were monitored through GPS telemetry, using a five-minute interval between fixes. We tracked animals daily, at varying times between 6:00 and 22:00 h, to ensure GPS functioning and to locate resting sites.

Even though all the procedures described above could be accomplished through physical restraint, some of the animals were anaesthetized through an intramuscular injection on the hind limbs to enable the collection of biological samples not used in this study. Eleven individuals of *E. sexcinctus* and nineteen of *T. matacus* were anaesthetized with a combination of Ketamine (Quetamina® 10% - Vetnil), 30 mg/kg for *E. sexcinctus* and 25 mg/kg for *T. matacus*, Xilazine 0.5 mg/kg (Rompun® 2% - Bayer), Midazolam 0.5 mg/kg (Dormire® 0.5% - Cristalia) and Atropine 0.02 mg/kg (Atropina® 1% - Fagra).

### *Activity*

Active periods were characterized as the time-period an individual spent outside its shelter. 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-hour period. Because *T. matacus* are predominantly nocturnal, total activity duration for this species was estimated as the sum of bout durations from noon of one day, until 11:59 am of the next day.

A linear mixed-effects model (LME) was fitted to test the fixed effect of mean daily air temperature on the total activity duration. The model was fitted using individual identity and study sites as random nested effects, and accounting for the autocorrelation structure between samples taken from the same individual on consecutive days. To characterize the air temperature, we estimated daily means of the hourly measures provided by the Brazilian National Institute of Meteorology (INMET) for each study site. LME models were implemented through the function 'lme' of the R package 'nlme' (Pinheiro et al. 2016).

To evaluate the relationship between activity and air temperature, we first sub-sampled the individual trajectories to fixes matching one-hour intervals. The distance moved at each one-hour interval was estimated as the sum of all distances moved between the original (five-minute) steps within that hour. Then, the square root of these distances was used as a proxy for an activity index. When this distance was equal to zero, it was assumed that the animal was inactive during that one-hour period; when the values were higher than zero, it was assumed that the animal was active and outside the shelter.

LME models were used to model activity along the circadian cycle according to changes in air temperature. 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. Time of the day was included in the model using harmonics to allow a nonlinear relationship between time of day

and activity index (sensu Forester et al. 2009). We included two terms ( $c1 = \cosine 2\pi$ ,  $s1 = \sin 2\pi$ ) that interacted with air temperature for each 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, which included the random nested effects of individual identity, and the auto-correlation structure between consecutive steps of the same individual.

### *Habitat selection*

We used Step Selection Function (SSF; Fortin et al. 2005, Forester et al. 2009) to evaluate the effects of the cover type, circadian cycle, and air temperatures on the resource selection of the studied species. First, we subsampled the individual trajectories composed of fixes with 5 min to fixes with 30 minutes intervals. Individual trajectories were decomposed into two components: step length and turning angle. Step length was defined as the straight-line distance between two consecutive relocations and turning angles as the angular deviations between headings of two consecutive steps (Turchin et al. 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 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 determined 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 Information Criteria (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 a LME model to the residuals of the CLR with the 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 auto-correlated successive steps, which allowed the estimation of the robust standard error of the coefficients (see Craiu et al. 2008). SSF models were plotted considering the limits of the thermoneutral zone of each species (Eisentraut 1931, Roig 1969).

## Results

### *Activity pattern*

Individuals of *E. sexcinctus* were active during both daytime and nighttime. Individuals usually had one activity bout per day (63%), but could have up to four bouts (3%). Total daily activity duration averaged 3.63 hours (min = 0.08; max = 11.17 hours). Activity duration variation was



not explained by air temperature ( $t = 1.44$ ,  $df = 103$ ,  $p = 0.15$ ). However, there was a relationship between the distance moved and the interaction between time of day and air temperature ( $t = 2.14$ ,  $df = 1165$ ,  $p = 0.03$ ). The LME model indicates that the activity pattern of *E. sexcinctus* varied according to air temperature, with a shift, from diurnal to nocturnal activity, as air temperature increases (Fig. 3a). At modeled air temperatures up to 35 °C, *E. sexcinctus* is diurnal, with higher activity probability near noon. At intermediate temperatures, this species can be found active during either daytime or nighttime (Fig. 3a). At the higher air temperatures, there is a switch on activity behavior, and *E. sexcinctus* tends to increase its nocturnal activity, especially in the first half of the night (Fig. 3a). In figure 3b, it is possible to see 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 = 16–30°C).

*Tolypeutes matacus* individuals usually exhibited one (53%) or two (29%) activity bouts per day, but up to seven activity bouts (<1%) were recorded in a day. This species was active mostly during nighttime, but also during dusk and dawn. Total daily activity duration was positively related to air temperature ( $t = 6.41$ ,  $df = 311$ ,  $p < 0.01$ ), and ranged from 0.18 to 14.73 hours, with an average of 5.45 hours. The interaction between air temperature and time of the day explained the activity index pattern (value = 0.54,  $se = 0.04$ ,  $df = 4870$ ,  $t = 14.81$ ,  $p < 0.01$ ). In contrast with the responses modeled for *E. sexcinctus*, the activity pattern of *T. matacus* changes gradually as air temperature changes (Fig. 4a). The probability of higher activity before sunset increases as air temperature decreases (Fig. 4a). The 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 ( $w = 1$ ) that the best model to explain habitat selection for both *E. sexcinctus* and *T. matacus* is the model that accounts for habitat type, and its interactions with time of the day and instant air temperature (Tables 1 and 2, respectively). The best model suggested that on warm days (45°C), *E. sexcinctus* tends to select forested areas during the warmest hours of the afternoon, and avoid forests during the rest of the day (Fig. 3c). On chilly days (15°C), *E. sexcinctus* tends to show an almost inverse pattern, selecting forested areas during the coldest hours of the night. At air temperatures close to the armadillos' thermoneutrality (30°C), *E. sexcinctus* show slight avoidance of forested areas during nighttime. Shrubs are used in a similar way to forests but the influence of temperature and time of the day seems weaker, in comparison to the pattern observed for forested areas selection (Fig. 3d). Grasslands were used according to their availability, with a slightly positive selection at night on warm days (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. In most cases, the strength of selection of different habitats by *T. matacus* varied with the time of the day and instant air temperature (Fig. 4). On chilly days (15°C), *T. matacus* selected forested areas in the nocturnal period, while on warm days (45°C) they selected forests during the daytime. The selection strength for grasslands followed an almost inverse pattern (Fig. 4d). On chilly days, *T. matacus* avoided grasslands in the end of the afternoon and in the first half of the night while on warm days, armadillos avoided open vegetation areas during the daytime, and selected them in the first half of the night. At milder temperatures (30°C), close to their thermo-neutral zone, *T. matacus* used forests according to their availability and slightly avoided grasslands from midnight until the early morning. Despite its relatively low availability in both study sites, *T. matacus* positively selected dirt paths, especially at warm temperatures (Fig. 4e). On chilly days, sugar cane

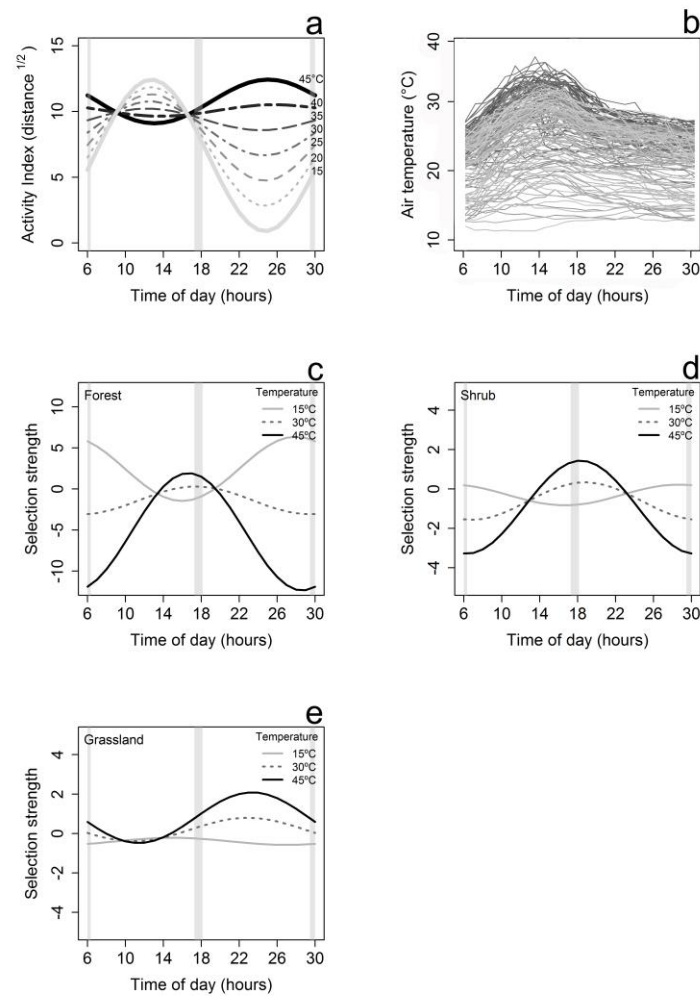
plantations were avoided, while on warm days, *T. matacus* disproportionately used plantation habitat, markedly so during nighttime (Fig. 4f).

**Table 1.** Step selection function model selection for *Euphractus sexcinctus*. Number of parameters (K), relative difference between models ( $\Delta AIC$ ), weight of the model (AICcWt), cumulative weight (Cum. Wt), and Log Likelihood (LL). Data from 17 armadillos tracked at Site 1 (see. Fig. 1) from March to August 2014.

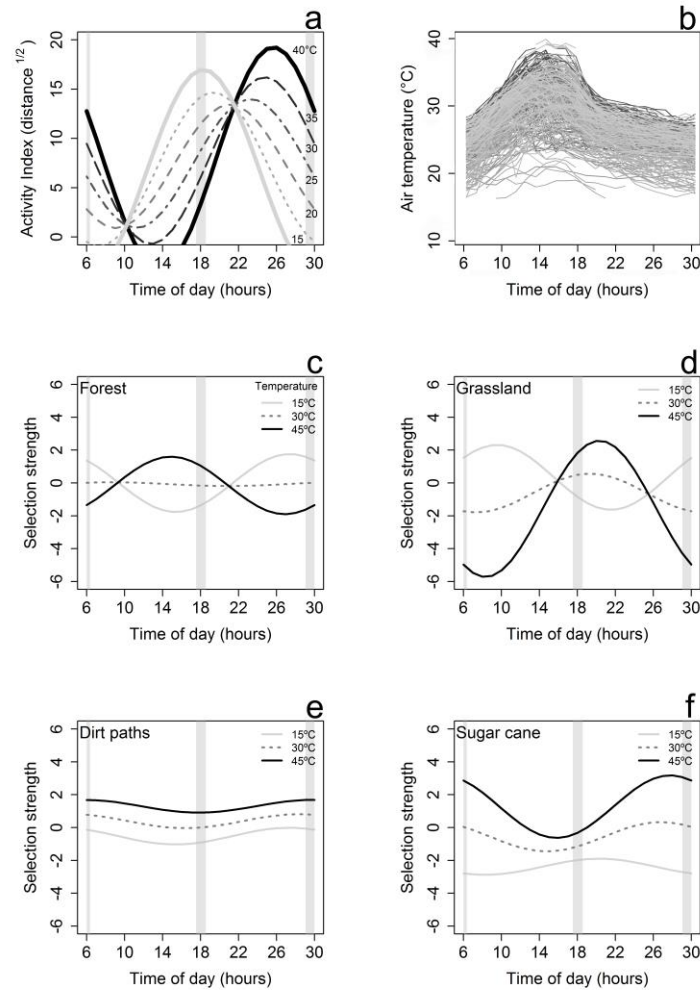
<b>Model</b>	<b>K</b>	<b><math>\Delta AIC</math></b>	<b>AICc Wt</b>	<b>Cum Wt</b>	<b>LL</b>
<b>Cover type + Cover type : Time of day : Air temperature</b>	23	0	1	1	-14743.96
<b>Cover type + Cover type : Time of day</b>	11	17160.49	0	1	-23336.21
<b>Cover type</b>	3	17213.13	0	1	-23370.54

**Table 2.** Step selection function model selection for *Tolypeutes matacus*. Number of parameters (K), relative difference between models ( $\Delta AIC$ ), weight of the model (AICcWt), cumulative weight (Cum. Wt), and Log Likelihood (LL). Data from 21 armadillos tracked at Sites 2 and 3 (see Fig. 1) from November 2014 until August 2015.

<b>Model</b>	<b>K</b>	<b><math>\Delta AIC</math></b>	<b>AICc Wt</b>	<b>Cum Wt</b>	<b>LL</b>
<b>Cover type + Cover type : Time of day : Air temperature</b>	29	0	1	1	-87108.41
<b>Cover type + Cover type : Time of day</b>	14	32.27	0	1	-87139.54
<b>Cover type</b>	4	52.64	0	1	-87158.73



**Figure 3.** Models of activity pattern and relative habitat selection strength by *Euphractus sexcinctus* through the day, at different air temperature. (a) Activity index probability estimates throughout the day at varied instant air temperatures according to 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 three different daily mean air temperature scenarios according to the best fit model (see Table 1). For clarity, time of the day is represented from six to 30 hours, *i.e.* 24 hours were added to times between midnight and 6:00 a.m., allowing a continuous visualization of the nighttime period. 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.



**Figure 4.** Models of activity pattern and relative habitat selection strength by *Tolypeutes matacus* through the day, at different air temperature. (a) Activity index probability estimates throughout the day at varied instant air temperatures according to LME model. (b) Daily variation of air temperature at our study sites during the study period. Selection strength of (c) forests, (d) grasslands, (e) dirt paths, and (f) sugar cane plantations at three different daily mean air temperature scenarios according to the best fit model (see Table 2). For clarity, time of the day is represented from six to 30 hours, *i.e.* 24 hours were added to times between midnight and 6:00 a.m., allowing a continuous visualization of the nighttime period. 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 until August 2015.

## Discussion

Although *E. sexcinctus* and *T. matacus* have been generally classified, respectively, as diurnal and cathemeral species (Eisenberg & Redford 1999, Cuellar 2008, Medri 2008), our results highlight the major importance of temperature in modulating both circadian activity and habitat selection for these imperfect homeotherms.

The influence of air temperature on activity behavior has been reported for other imperfect homeotherms, such as anteaters, sloths, echidnas, pangolins and other armadillos (McNab 1980, Brice et al. 2002, Camilo-Alves & Mourão 2006, Pietersen et al. 2014; Giné et al. 2015; Maccarini et al. 2015). Small-bodied species of imperfect homeotherms that occur in regions with extreme temperatures, such as the pichi (*Zaedyus pichiy*) 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 sub-tropical and temperate climates, such as the nine-banded armadillo (*Dasypus novemcinctus*), the screaming hairy armadillo (*Chaetophractus vellerosus*), and Temminck's ground pangolin (*Smutsia temminckii*) tend to be more diurnal in cold winters and more nocturnal in higher summer temperatures (Gregor 1985, Layne & Glover 1985, Pietersen et al. 2014). *Tolypeutes matacus* and *E. sexcinctus* have a tropical distribution (Feijó et al. 2015) and are physiologically adapted to warm air temperatures (~28°C and ~30°C respectively, Eisentraut 1932, Roig 1969). Armadillo species with sub-tropical distribution, such as *D. novemcinctus* and *C. vellerosus*, adjust their activity patterns by being active earlier (i.e., at warmer hours of the day) as the mean daily temperature decreases along the year (Gregor 1985, Layne & Glover 1985). The studied species also adjust their activity behavior as a function of air temperature, but vary their activity on a scale of days instead of the seasonal patterns reported for sub-tropical armadillos. Because temperature may drop suddenly in the



Pantanal due to cold fronts, this short-term behavioral response provides activity pattern plasticity and can be an efficient energetic strategy for these imperfect homeotherms.

Our results indicate that, besides the activity behavior plasticity, temperature was also related to changes in habitat selection by armadillos. Our best-fit models indicate that on warm days, both armadillo species tended to select forests at the hottest hours of the day but avoid forests during nighttime. On chilly days, both species tended to show the reverse pattern, avoiding forests during daytime and selecting forests at the coldest hours of the night. Because *E. sexcinctus* tends to become nocturnal when mean air temperature increases, it tends to avoid forests while active but select them while inactive (as suggested by Medri 2008). On the other hand, *T. matacus* shows less variation in its nocturnal activity behavior at different air temperatures. Hence, *T. matacus* can select forests for both activity and resting, depending on daily mean air temperature. At air temperatures close to their thermoneutrality, *T. matacus* uses forest habitat according to its availability, whereas *E. sexcinctus* slightly avoids these areas during nighttime (i.e., for resting). The avoidance of forests could indicate that *E. sexcinctus* are handling air temperature variation mostly through activity behavior plasticity and/or it could be related to predator avoidance, since their main predators in the area are large and mid-sized cats, which tend to occupy forests (Astete et al. 2008, Bianchi et al. 2016).

The selection strength of areas with intermediate cover density varied between species. *Tolypeutes matacus* selected sugar cane plantations at the coldest hours of warm days and avoided them all day long on chilly days. *Euphractus sexcinctus* used shrubs in a similar way to forests, but the influence of temperature and time of the day were comparatively weaker. The selection of open vegetation areas, such as natural and exotic grasslands, also varied between species. On warm days, *T. matacus* selected grasslands when air temperature started to drop (e.g., near sunset) and avoided them during daytime (i.e., during resting periods). On chilly days, *T. matacus* avoided grasslands at sunset and shortly thereafter (i.e., during activity)

but selected such habitats during daytime resting periods. *Euphractus sexcinctus* used natural grasslands according to their availability, with increased selection strength at night on warm days, when there is an increased probability of nocturnal activity.

Niche switches, such as changes in time of activity or habitat use, can be limited by internal factors (e.g., sensory and thermoregulatory capabilities), and by external factors (e.g., biotic and abiotic environmental conditions; Hut et al. 2012). As imperfect homeotherms, armadillos are likely to have their behavior influenced by ambient temperature. Moreover, because armadillos are primarily guided by odor and tactile stimuli rather than vision (Emerling & Springer 2015), other prominent environmental variations, such as light availability, should not constrain their behavioral plasticity.

The influence of temperature on the activity behavior and habitat selection of xenarthrans seems to be related mainly to internal factors, *i.e.* the group's peculiar combination of morpho-physiological adaptations (Layne & Glover 1985, Maccarini et al. 2015). Compared to a homeothermic 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 body temperature of 34.2°C, mean that *E. sexcinctus* can be very susceptible to air temperature changes (Maccarini et al. 2015). *Tolypeutes* stand out for having one of the lowest body temperatures (33°C) and metabolic rates (31%) amongst armadillos, probably due to its low energy myrmecophagous diet (McNab 1980). Noticeably, other ant-eating species, such as short-beaked echidnas (*Tachyglossus aculeatus*), can have basal metabolic rates as low as *Tolypeutes* (McNab 1985) and also have their behavior 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. When the carapace is closed or partially closed, the air trapped between the body and

the carapace can reduce thermal conductance (McNab 1985). However, that 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.

The aforementioned ecological and morpho-physiological characteristics could shed light onto the armadillos' habitat selection and activity patterns that we observed. 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 constitutes an additional behavioral thermoregulation strategy for armadillos. Hence, as in other armadillo species, the short activity duration of the studied species, and the even 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 temperature buffer (Maccarini et al. 2015).

The reliance on burrow use for thermoregulation should be especially conspicuous on *E. sexcinctus*, because they present a high thermal conductance (McNab 1985) and tend to forage in open habitats, potentially gaining and losing heat fast, depending on air temperature. Likewise, *T. matacus* may enter and emerge from shelters for thermoregulation even though they possess a comparatively lower thermal conductance. This is because their defensive behavior of rolling into a ball interacts with their thermal conductance: at lower temperatures, animals could lose heat faster while active and 'unrolled', when compared to resting animals. Such an effect could explain the comparatively shorter activity duration for this species on colder days. Nevertheless, this assumption should be further explored for *T. matacus* by evaluating the variation in body and shelter temperature according to air temperature variation (e.g. Camilo-Alves & Mourão 2006, Maccarini et al. 2015).

As mean temperatures change, different behavioral responses of different species could affect their interactions (e.g. predator-prey, intra-guild competition; Creel et al. 2016). Our models show that these two sympatric species adopt different behavioral responses to

temperature variation. As daily temperature increases *E. sexcinctus* adopts a nocturnal behavior (like *T. matacus* already has) whereas *T. matacus* tends to forage in open vegetation areas (like *E. sexcinctus* already does), increasing the overlap of the temporal and spatial niche dimensions between the two species, and setting the stage for a potential increase in intra-guild competition.

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 & Medri (2007) recorded temperatures up to 5°C higher in forests than those recorded in the grasslands on cold days, and 8°C lower in hot days. Hence, imperfect homeotherms are selecting the different elements of the landscape to cope with their physiological constraints. Such behavioral 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 it occurs in many other parts of South America, currently one of the main threats to the conservation of the Pantanal is habitat conversion. More than 40% of the forest and savanna habitats have been altered for cattle ranching through the introduction of exotic grasses in the Pantanal (Harris et al. 2005). Hence, even though we have recorded the studied species using altered habitats, such as sugar cane 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 imperfect homeotherms. The importance of landscape heterogeneity should be even higher in the future, since the estimated mean warming for the Pantanal ranges from 2.5–3.5°C in the period of 2011-2040 and 5–7°C in 2071-2100 (Marengo et al. 2016).

As imperfect homeotherms, armadillos should present a conspicuous response to temperature variation. This study shows a specific example of the dynamic nature of activity patterns and habitat selection and illustrates how thermal constraints vary dynamically over the

daily cycle and among days. More generally, models like those presented here can be used to understand better the consequences of climate change on animals inhabiting Neotropical savannas, highlighting the importance of habitat heterogeneity for the long-term conservation of animal species in a scenario of global climate change.

## General Conclusion

The lack of in situ studies hinders basic discoveries on species ecology and biology. To my knowledge, this was the first study of *T. matacus* in the wild in the Brazilian territory and the most comprehensive study on its ecology in situ. This study contributes to the ecology and natural history knowledge framework of *T. matacus* reporting never documented behaviour in a systematic manner (e.g. sheltering habits). Through this study, it was possible to characterize *T. matacus* as a nocturnal, promiscuous, generally asocial species that selects forested and pasture areas and has its habitat selection influenced by the presence of dirt paths. Like in *E. sexcinctus*, temperature affects both activity patterns and habitat selection strength of this species. As air temperature decreases, *T. matacus* activity periods are of shorter duration and peak earlier in the day. As daily temperatures increase, activity peaks later and it tends to forage in open vegetation areas. Hence, we are a step further away from the Data Deficient status reported for this species in Brazil and a step closer to defining effective measures for its conservation.

Common species such as armadillos may be taken for granted as study subjects and as model species. Nevertheless, *E. sexcinctus* and *T. matacus* physiology and habits coupled with their behavioral plasticity and adaptations have made these into interesting model species to answer ecological questions that concern most terrestrial mammals. By modeling the behavioral responses of these imperfect homeotherms to temperature variation, we get closer to understanding the consequences of global climate change and habitat degradation on the conservation of animals inhabiting Neotropical savannas. Here, it is provided a specific example of how thermal constraints can vary dynamically over the daily cycle and among days. This study also highlights the dynamic nature of activity patterns and habitat selection, commonly reported as static characteristics of species. For example, *Euphractus sexcinctus* is commonly reported as a diurnal species in the literature, however here we see that this

species shifts its activity pattern from diurnal to nocturnal as mean daily temperature increases. In addition, it tends to select open vegetation areas during activity and forested areas during rest, but the strength of this habitat selection depends on temperature. Its habitat selection changes according to activity status, selecting open vegetation areas during activity and forested areas during rest, but the selection strength is dependent of air temperature. The conspicuous behavioral responses of armadillos and other xenarthrans, coupled with armadillo species richness (21 species) and body mass range (from 100 g up to 60 kg), highlights their potential as model species for future studies on how external drivers and habitat heterogeneity may shape animal behavior.

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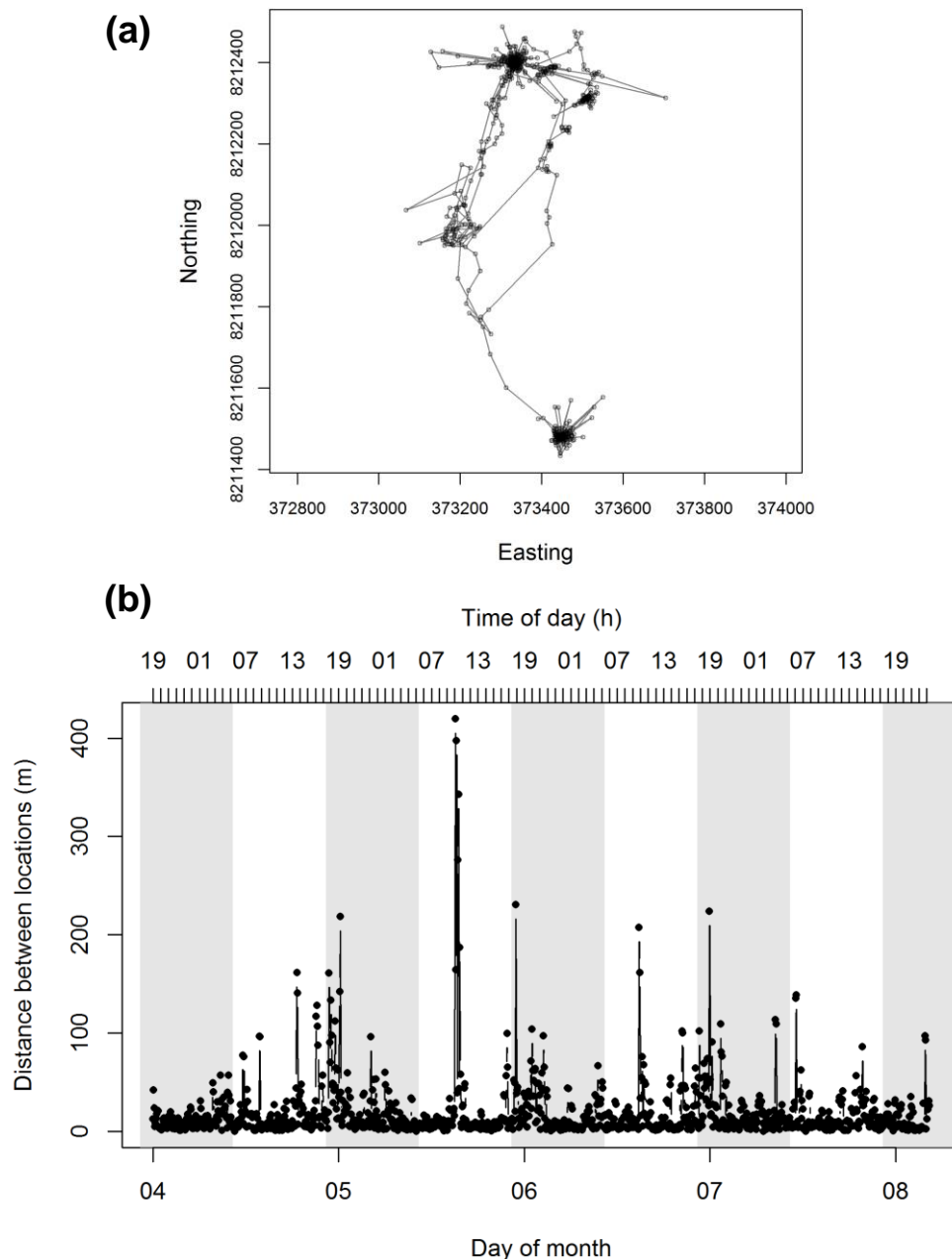
## Supplementary Material

### *GPS track cleaning methodology*

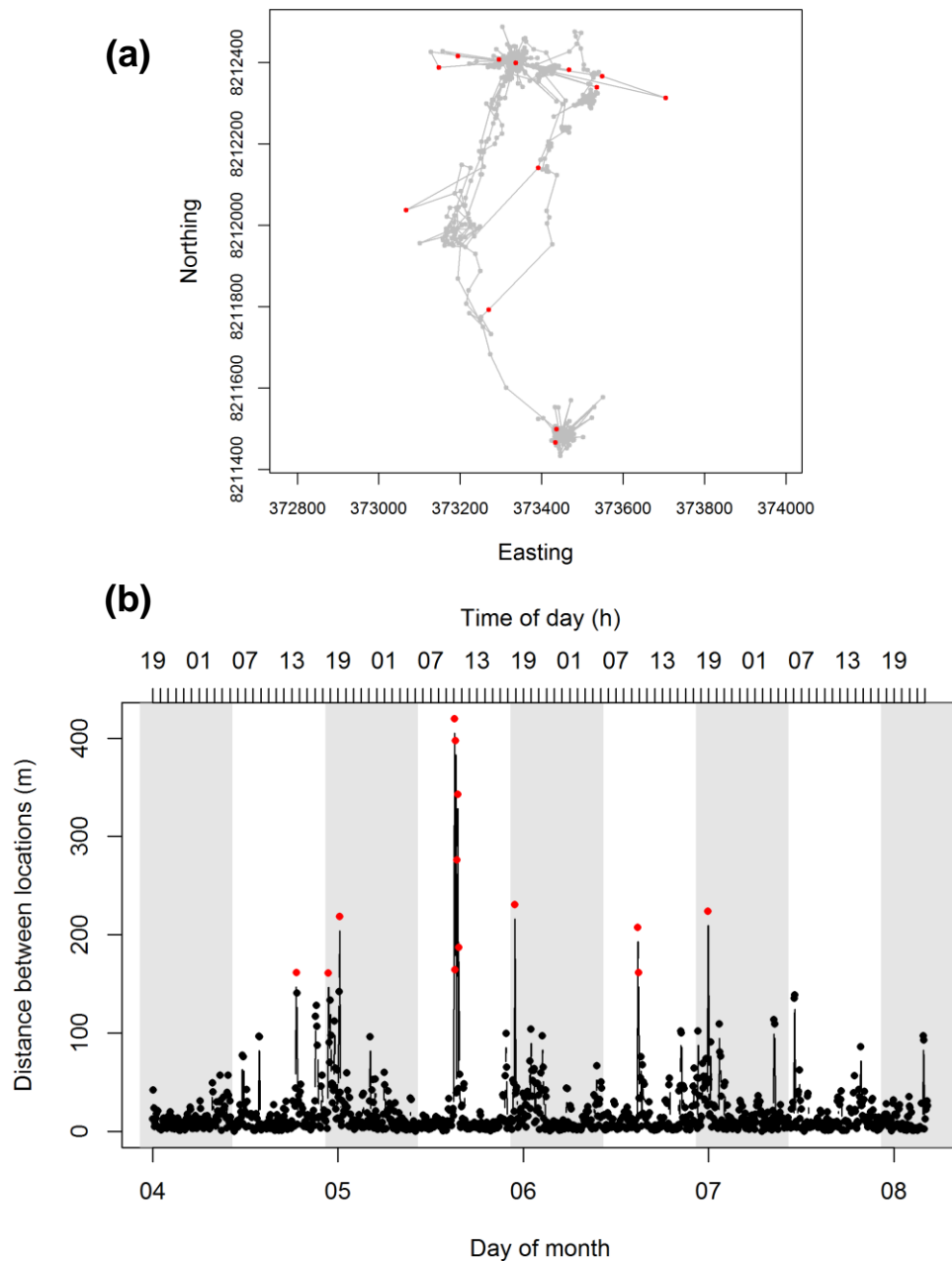
Due to the burrowing habits of armadillos, whenever they entered their shelters GPS signal reception was either reduced, creating a temporal concentration of points with large errors, or lost completely, generating long gaps in the tracking data (Fig. 1). Here, we applied several criteria to make sure that no spurious movements resulting from GPS errors were incorporated to the movement track. We also used this error patterns to identify when animals were inside shelters or not (characterizing periods of activity and inactivity), and define shelter locations. Each animal track was evaluated individually and the R script used to perform all described procedures is presented in the end of this section.

As a first step, we excluded locations that had unlikely speeds associated with them and were probably resulting from GPS errors instead of actual animal movement. Hence, we excluded locations with speeds higher than the estimated 99% quantile (Fig. 2).

During field activities, we placed a GPS device in a known location. This allowed us to identify location errors and allowed us to notice that coordinate errors were correlated with altitude errors. This was noticeable because the study area where the test was performed has a flat relief, with altitudes between 195 and 230 m.a.s.l.. Any higher deviation from this altitude value can be easily detected (Fig. 3). For this reason, we also excluded the locations with altitudes lower than the estimated 5% quantile and higher than the 95% quantile (Fig. 4). This first approach eliminated almost all of the most spurious locations in the track. Following this, we applied a rolling mean of three to the track coordinates (x and y).

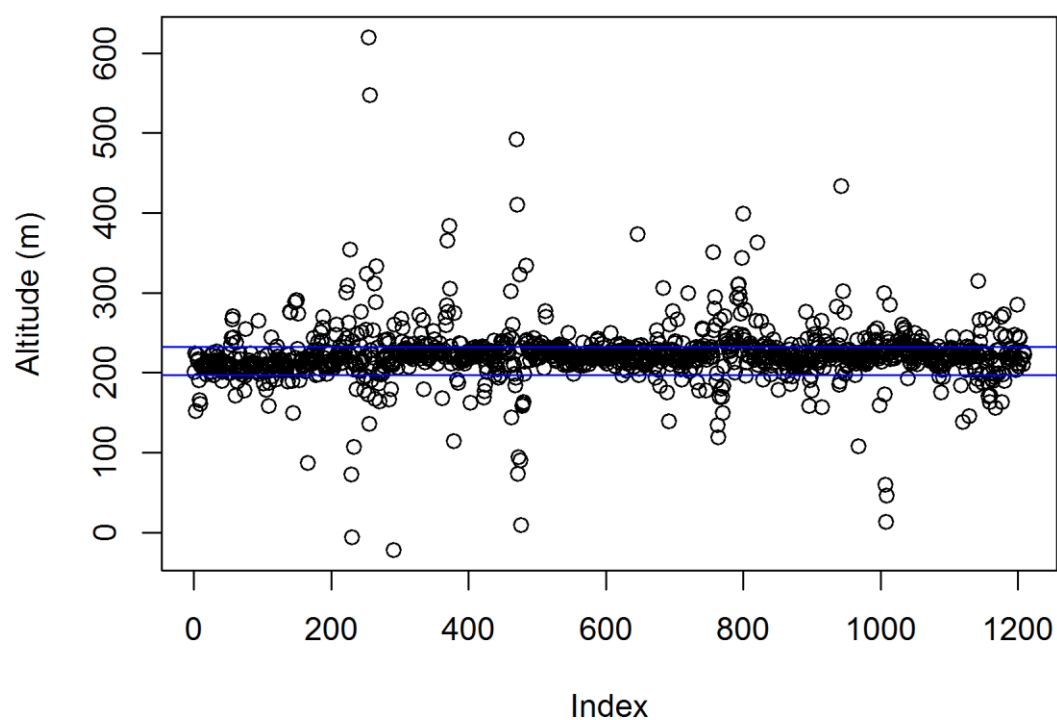


**Figure 1.** Original track (a) and distances moved between locations (b) by an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. . Coordinates are in Universal Transverse Mercator coordinate system (UTM, zone 21K). The errors created when the animal enters its shelter are characterized by a "star shaped" cluster of points and large steps. Shaded areas in figure **b** indicate nighttime periods.

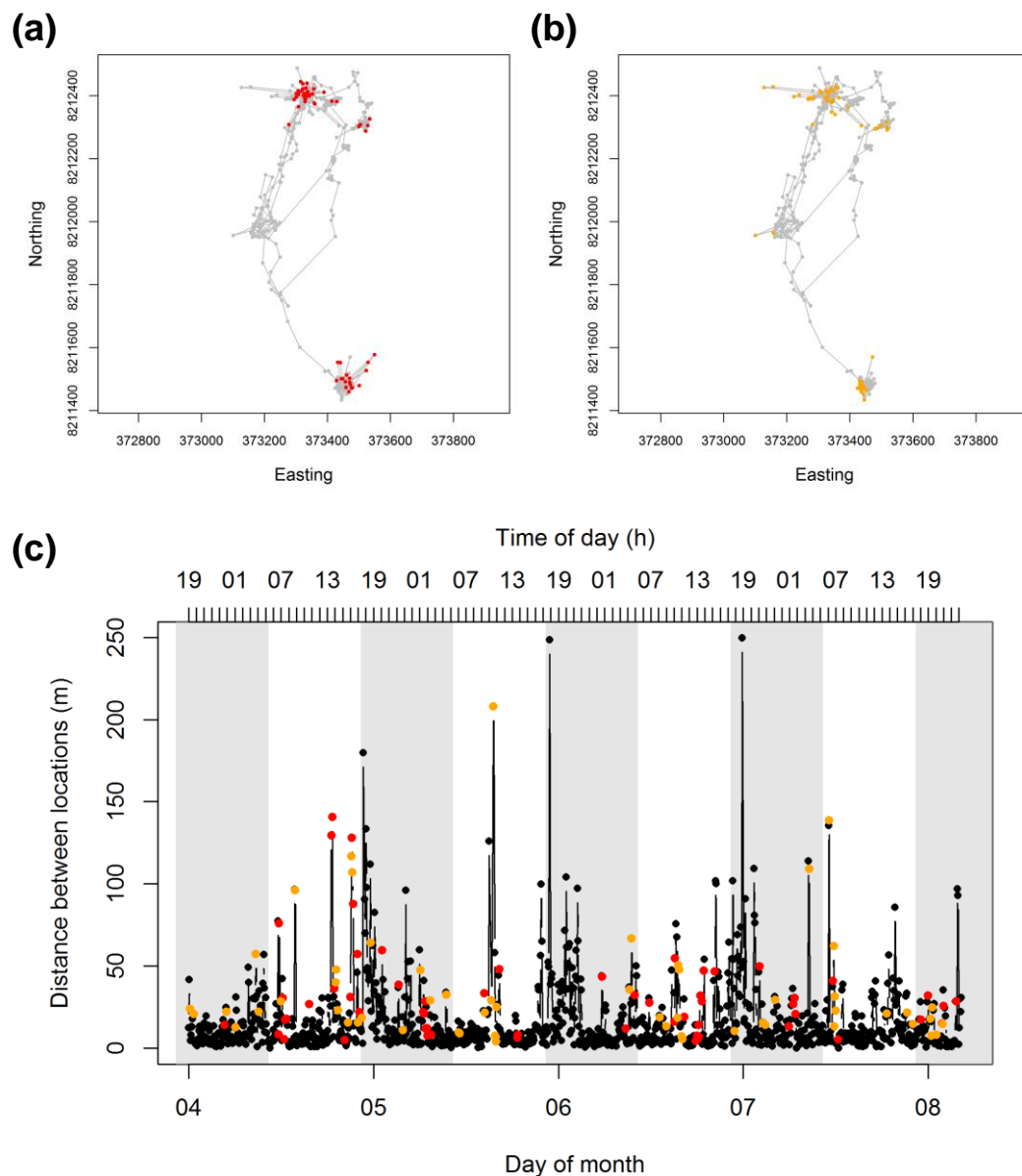


**Figure 2.** GPS track (a) and distances moved between locations (b) by an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. Locations with speeds higher than the 99% quantile are marked in red. Coordinates are in Universal Transverse Mercator coordinate system (UTM, zone 21K). Shaded areas in figure **b** indicate nighttime periods.





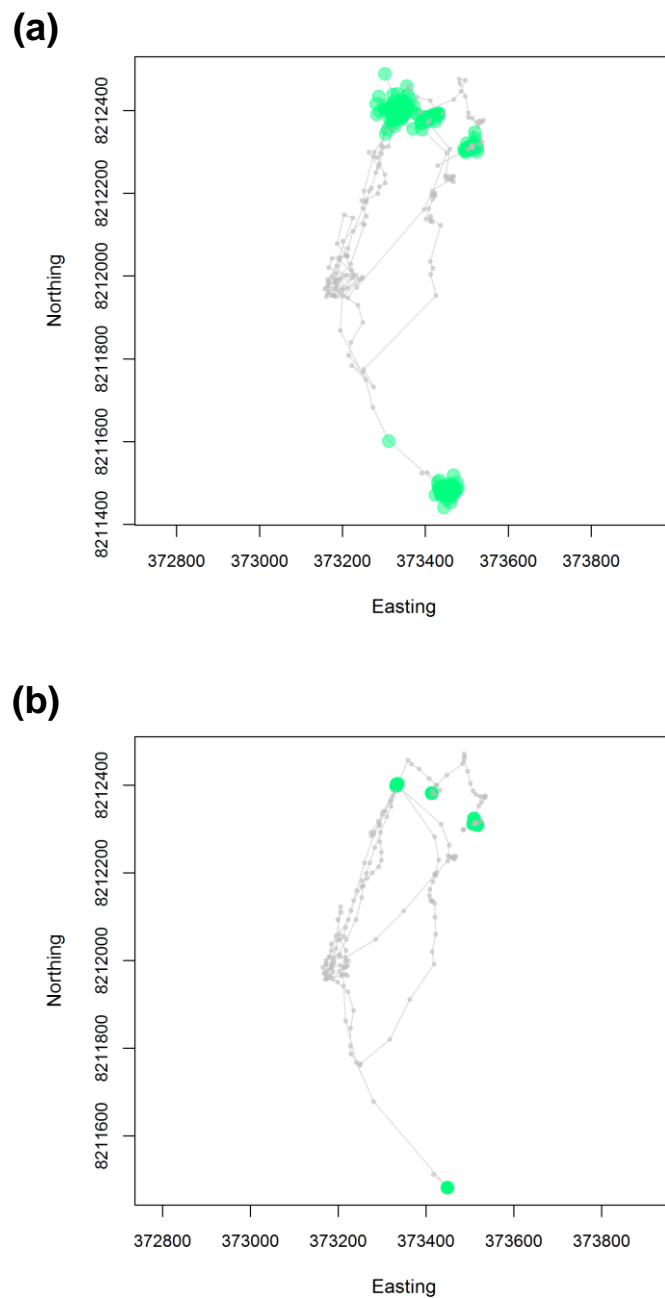
**Figure 3.** Altitudes associated with each location of the original track of an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. Blue lines indicate the range of altitude of the study area.



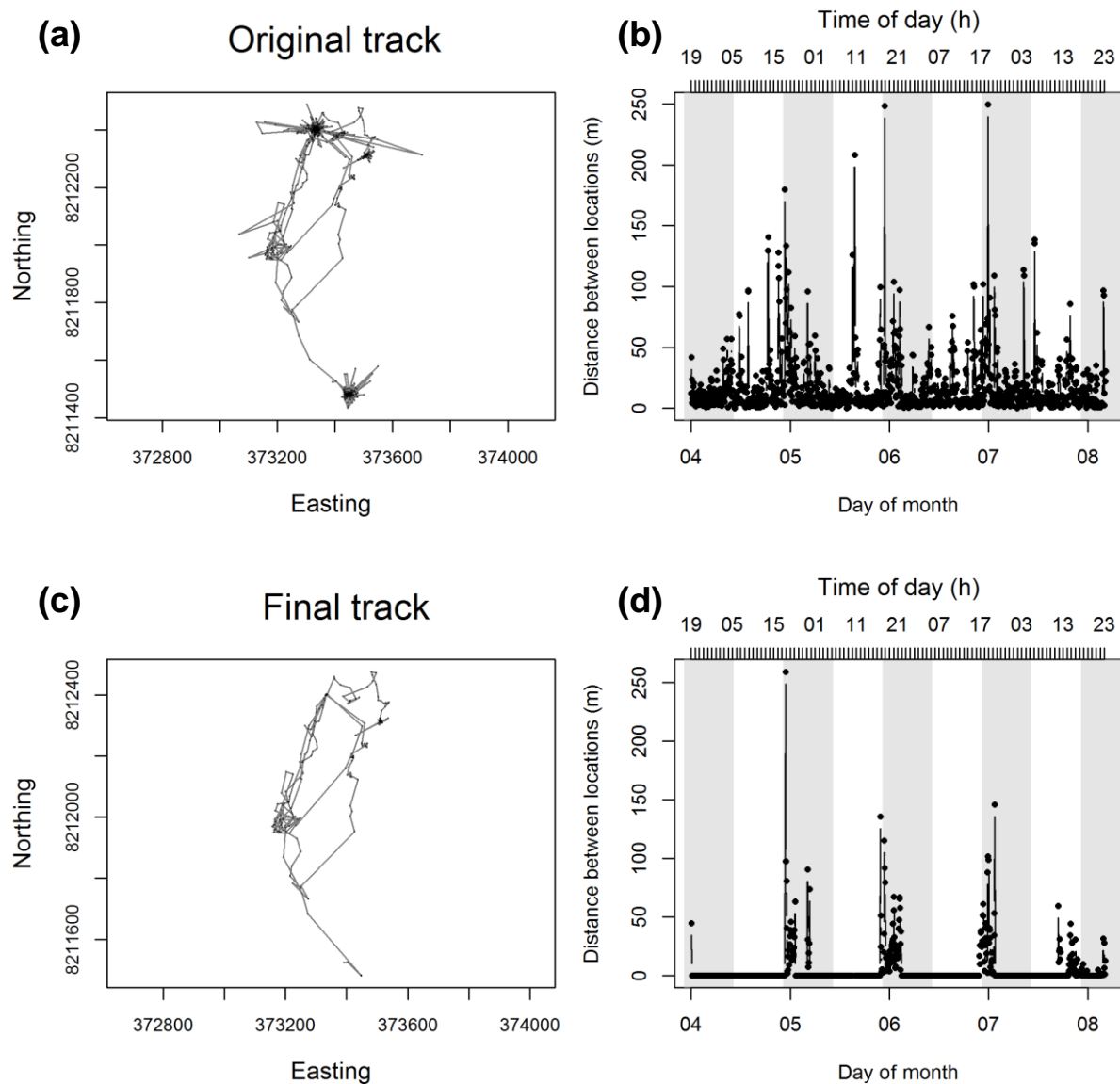
**Figure 4.** GPS track and distances moved between locations by an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. In red, locations with altitudes higher than the 95% quantile and, in orange, location with altitudes lower than the estimated 5% quantile. Coordinates are in Universal Transverse Mercator coordinate system (UTM, zone 21K). Shaded areas in figure **c** indicate nighttime periods.

To define which locations corresponded to activity or inactivity records we used a Residence Time approach (Barranquand & Benhamou 2008). A residence time series can be obtained by considering the movement portions encompassed within virtual circles of constant radius centered at successive locations in an individual's trajectory. This method yields particularly clear signals for resting behavior, when an animal spends long periods within a small spatial range (Barranquand & Benhamou 2008). To define the size of the radius and time period threshold spent inside that radius that characterized inactivity we used the control track data to test the efficiency of the residence time method in predicting previously known records of activity and inactivity. The control data was generated through our field simulation, where we manually placed a GPS device inside and outside a shelter during known periods. Using this data, we evaluated the efficiency of 10 radii values, between 10 and 100 meters, and 20 values of time threshold, from one to 20 hours, in correctly assigning both records of activity and inactivity of our control track data. We obtained the best congruence rate using a radius of 20 meters and a time threshold of one hour.

Hence, we estimated the residence time of each individual in a 20 m radius, and applied a rolling mean of five to the residence time estimates to remove any spurious departures from the supposed shelter area. We considered animals as inactive if they spend more than one hour inside this 20 meters radius and active in all other occasions (Fig. 5). Finally, we estimated the mean value of the x and y coordinates for each inactivity bout (i.e. each shelter location), and replaced the original inaccurate coordinates values by these ones (Fig. 5). All locations where the animals were classified as active by the residence time method had their previous coordinates maintained in the final track (Fig. 6). All analyses were implemented through the R package *adehabitatLT* (Calenge 2006).



**Figure 5.** Shelter locations (green) as identified by the Residence time method (where the animal spent more than one hour inside a 20 meters radius). Identification of shelter location prior (a) and after (b) the estimation of the average shelter coordinates. Data from an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. Coordinates are in Universal Transverse Mercator coordinate system (UTM, zone 21K).



**Figure 6.** GPS track and distance moved between locations by the same individual (a and b) before and (c and d) after being subjected to our protocol for identification and correction of GPS errors. Data from an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. Coordinates are in Universal Transverse Mercator coordinate system (UTM, zone 21K). Shaded areas indicate nighttime periods.

Bellow follows and R markdown script created in collaboration with Dr. Eliezer Gurarie from the University of Maryland. Here you can find the script and its outputs for an individual of *T. matacus* used as an example. This script was used to ensure no spurious movements resulting from GPS errors were incorporated to the movement track of each individual, to identify periods of activity and inactivity and to identify burrow locations.

Required packages

```
library(adehabitatLT)
```

```
require(zoo)
```

```
require(scales)
```

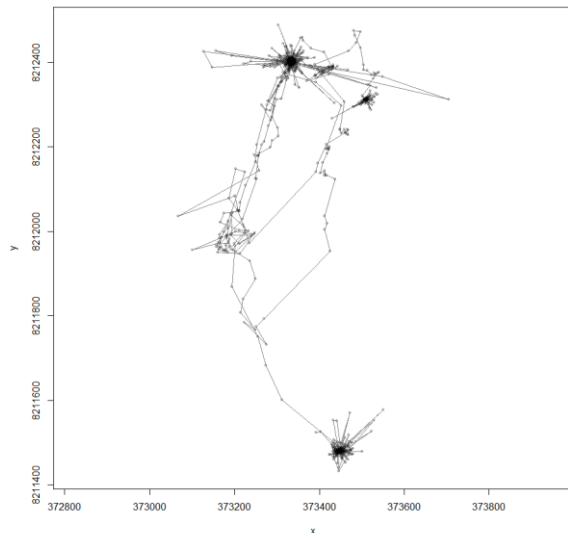
Load data:

```
Tm13<- read.csv("~/Doutorado_UFMS/GPSdata/TM13/Tm131.txt", h=T)
armadillo <- Tm13
head(armadillo)
```

##	t	utm	zona	x	y	data	hora	alt	nada
## 1	t	utm	21K	373391.7	8211524	07-04-2015	23:38:23	201.13	1
## 2	t	utm	21K	373403.9	8211526	07-04-2015	23:43:15	224.34	0
## 3	t	utm	21K	373430.6	8211494	07-04-2015	23:48:06	152.38	0
## 4	t	utm	21K	373453.1	8211486	07-04-2015	23:53:01	222.49	0
## 5	t	utm	21K	373454.7	8211482	07-04-2015	23:57:58	214.56	0
## 6	t	utm	21K	373446.6	8211481	07-05-2015	00:03:37	217.24	0

Plot original armadillo track:

```
with(armadillo, plot(x,y, asp=1, type="o", cex=.5,
col=rgb(0,0,0,.5)))
```



Convert date to format POSIX:

```
armadillo$date<-strptime(paste(armadillo$data,armadillo$hora),"%m-%d-%Y %H:%M:%S") - 4*3600;head(armadillo) #study area located at UTC -4
```

Convert to ltraj

```
armadillo.traj <- with(armadillo, as.ltraj(xy = data.frame(x,y), date = date, infolocs = data.frame(alt), id = "Tm13"))
```

Pre-filter track by velocity and altitude

Analyze velocities:

```
V <- armadillo.traj[[1]]$dist/armadillo.traj[[1]]$dt
v.max<-quantile(V, 0.99, na.rm=TRUE)
v.max<-as.numeric(v.max)
```

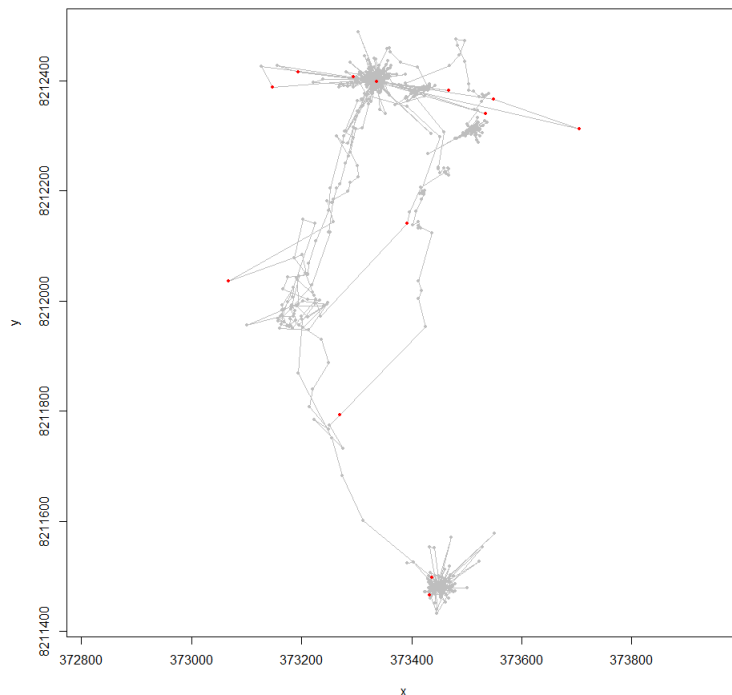
Filtering away points from the raw data where velocity > 99% (m/sec)

```
which(V>v.max)
```

```
## [1] 223 273 291 469 470 471 473 474 476 563 755 756 864
```

```
with(armadillo, plot(x,y, asp=1, pch=19, cex=0.5, col="grey", type="o"))
```

```
with(subset(armadillo, V > v.max), points(x,y, asp=1, pch=19, cex=0.5, col="red"))
```



*Temporary subset of the track data filtered by velocity*

```
armadillo.temp <- subset(armadillo, V < v.max, na.rm=T)
```

Apply an altitude filter

```
alt.max<- quantile(armadillo.temp$alt, 0.95, na.rm=TRUE)
```

```
alt.max<- as.numeric(alt.max)
```

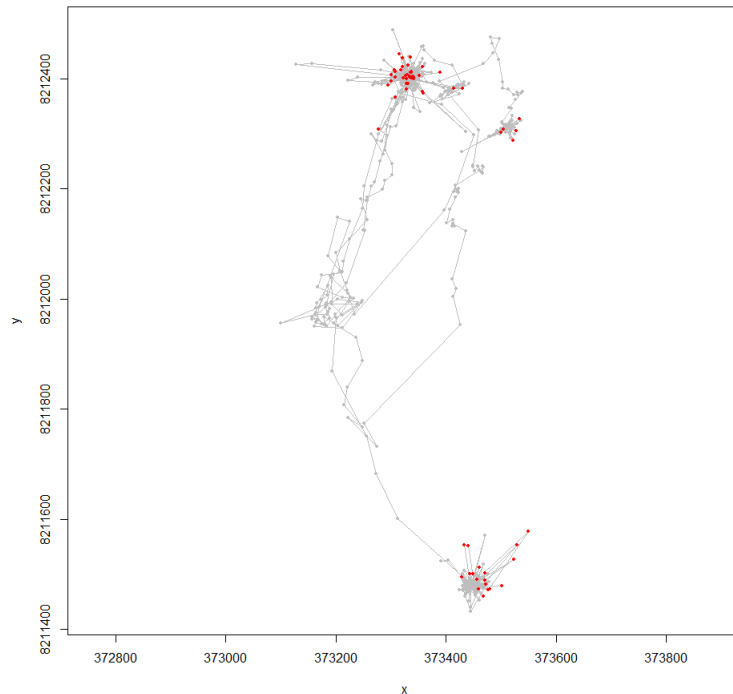
```
which(armadillo.temp$alt > alt.max)
```

```
## [1] 57 140 141 147 149 150 152 188 222 223 226 242
251 253
## [15] 255 262 264 265 299 325 363 365 366 367 369 370
376 458
## [29] 475 503 504 636 673 687 710 746 747 761 779 780
781 782
## [43] 783 784 786 788 791 808 878 923 930 932 934 992
1000 1129
## [57] 1140 1163 1166 1186
```

```
with(armadillo.temp, plot(x,y, asp=1, pch=19, cex=0.5, col="grey",
type="o"))
```



```
with(subset(armadillo.temp, armadillo.temp$alt > alt.max),
points(x,y, asp=1, pch=19, cex=0.5, col="red"))
```



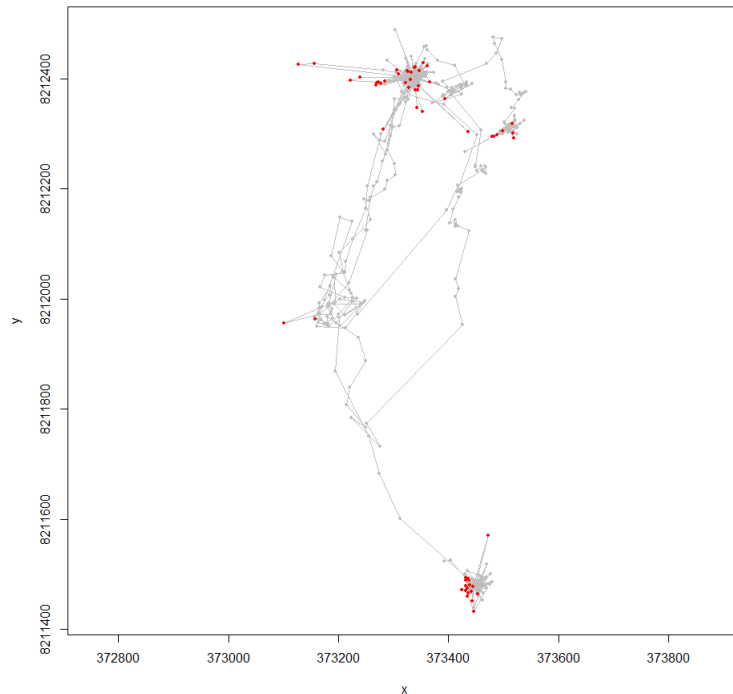
```
armadillo.temp2 <- subset(armadillo.temp,armadillo.temp$alt <
alt.max, na.rm=T)
```

```
alt.min<-quantile(armadillo.temp2$alt, 0.05, na.rm=TRUE)
alt.min<- as.numeric(alt.min)
which(armadillo.temp2$alt < alt.min)
```

```
## [1] 3 8 9 59 72 104 108 141 159 217 218 221
235 239
## [15] 240 247 251 264 312 339 349 373 392 393 431 438
439 441
## [29] 442 443 646 649 691 701 714 715 716 720 721 791
834 838
## [43] 853 902 933 939 940 941 942 1020 1052 1061 1087 1089
1090 1097
## [57] 1106
```

```
with(armadillo.temp2, plot(x,y, asp=1, pch=19, cex=0.5, col="grey",
type="o"))
```

```
with(subset(armadillo.temp2, armadillo.temp2$alt < alt.min),
points(x,y, asp=1, pch=19, cex=0.5, col="red"))
```

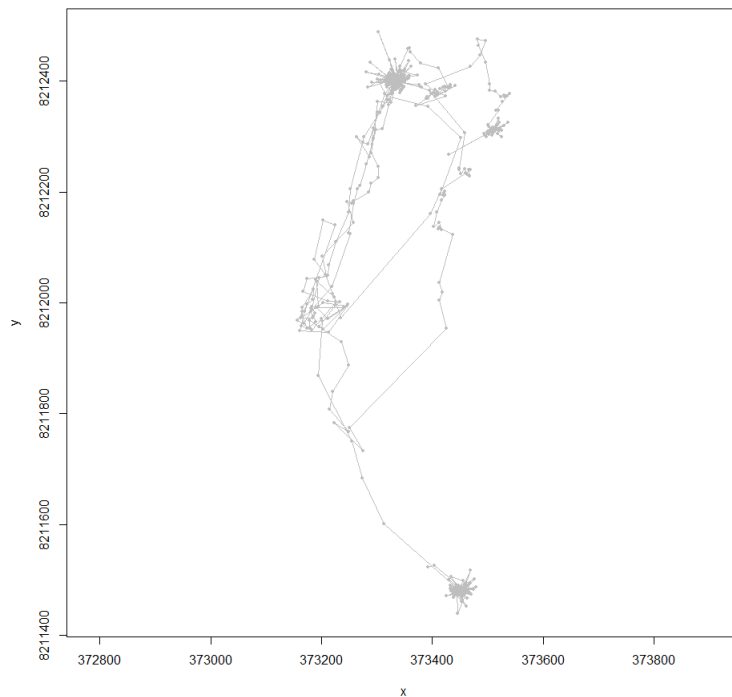


*#Filtered by velocity and altitude*

```
armadillo2 <- subset(armadillo.temp2, armadillo.temp2$alt > alt.min,
na.rm=T)
```

Creating the filtered track objects

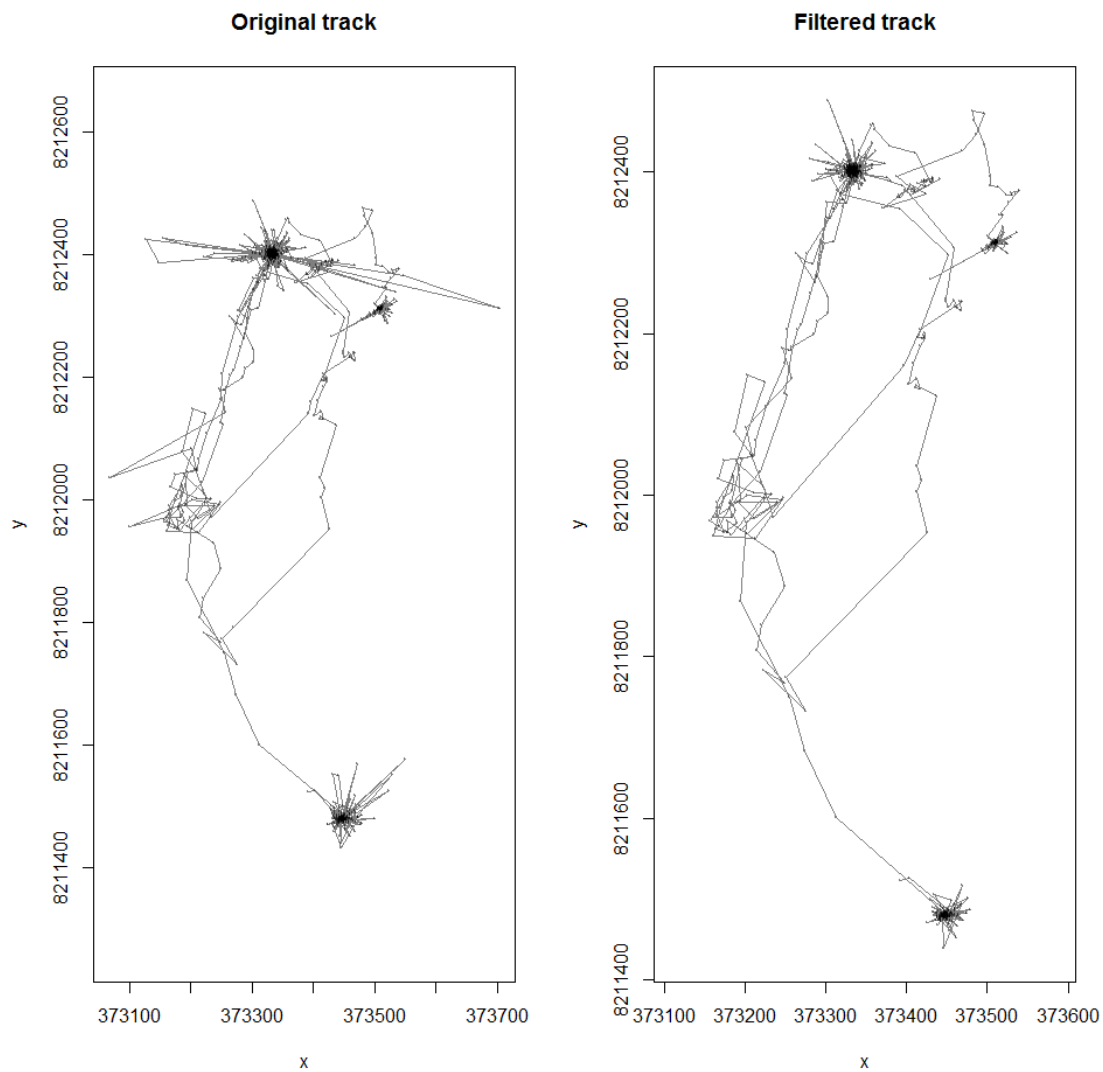
```
armadillo2$id <- 'tm13'
with(armadillo2, plot(x,y, asp=1, pch=19, cex=0.5, col="grey",
type="o"))
```



```
armadillo.traj <- with(armadillo2, as.ltraj(xy = data.frame(x,y),
date = date, infolocs = data.frame(alt), id = "tm13"))
```

Comparing the filtered and original tracks

```
par(mfrow=c(1,2))
with(armadillo, plot(x,y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Original track"))
with(armadillo2, plot(x,y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = 'Filtered track')) #track filtered by
velocity and altitude
```



Apply a rolling mean of 3 to the filtered track 'armadillo2'

```
require(zoo)
```

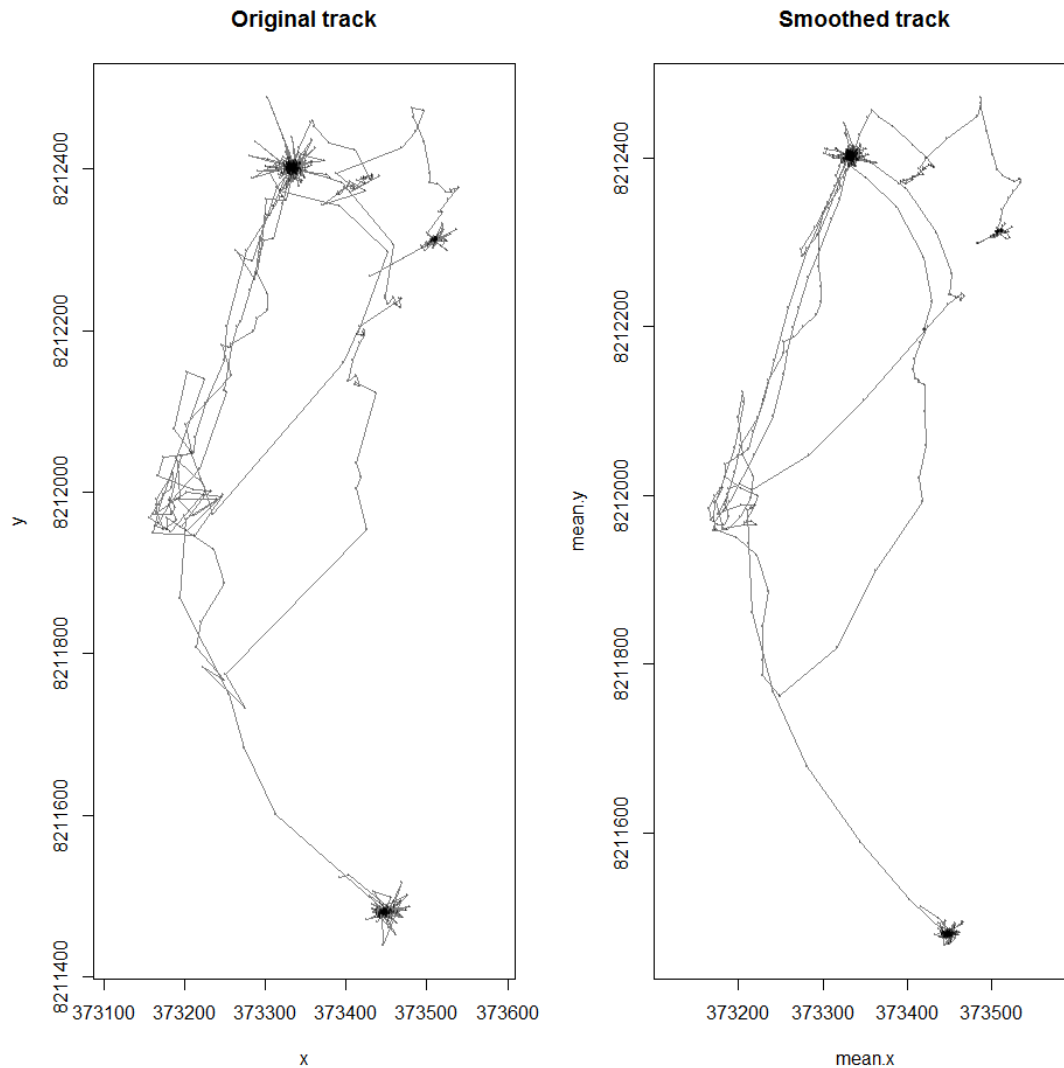
```
armadillo2$mean.x = rollapply(armadillo2[,4], 3, mean, na.rm = TRUE,
fill=NA)
armadillo2$mean.y = rollapply(armadillo2[,5], 3, mean, na.rm = TRUE,
fill=NA)
```

Plot armadillo smoothed by the rolling mean and compare to original track:

```

par(mfrow=c(1,2))
with(armadillo2, plot(x,y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Original track"))
with(armadillo2, plot(mean.x,mean.y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Smoothed track"))

```



*#Redefining the 'ltraj' object*

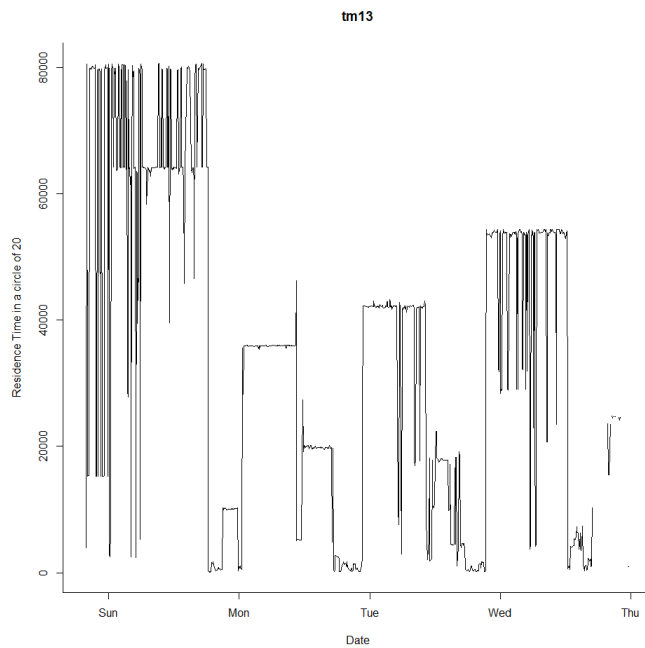
```

armadillo.traj.s <- with(armadillo2, as.ltraj(xy =
data.frame(mean.x,mean.y), date = date, infolocs = data.frame(alt),
id = "tm13"))

```

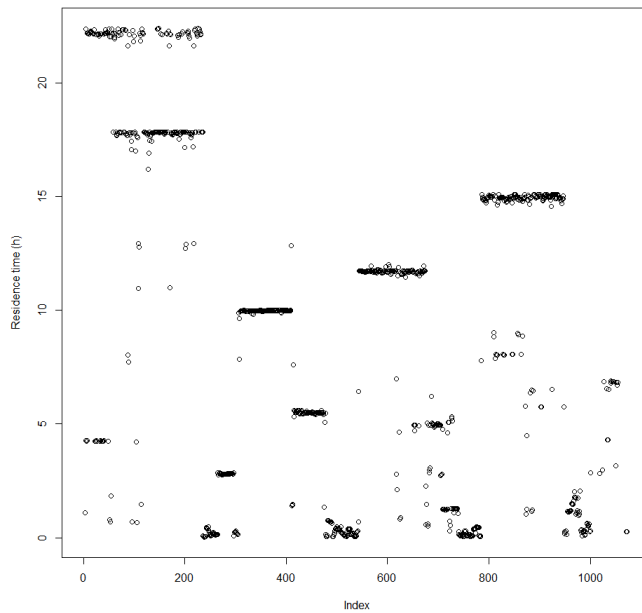
Residence time

```
par(bty="l")
a.rt <- residenceTime(armadillo.traj.s, radius = 20,
                     maxt = 0.25,
                     units = "hours")
plot(a.rt)
```



Extract the residence time vector and convert to hours:

```
myrt <- a.rt[[1]]$RT.20/3600
plot(myrt, ylab = 'Residence time (h)')
```



Apply a rolling mean to remove "spurious" departures (i.e. flatten the cycles)

```
require(zoo)
```

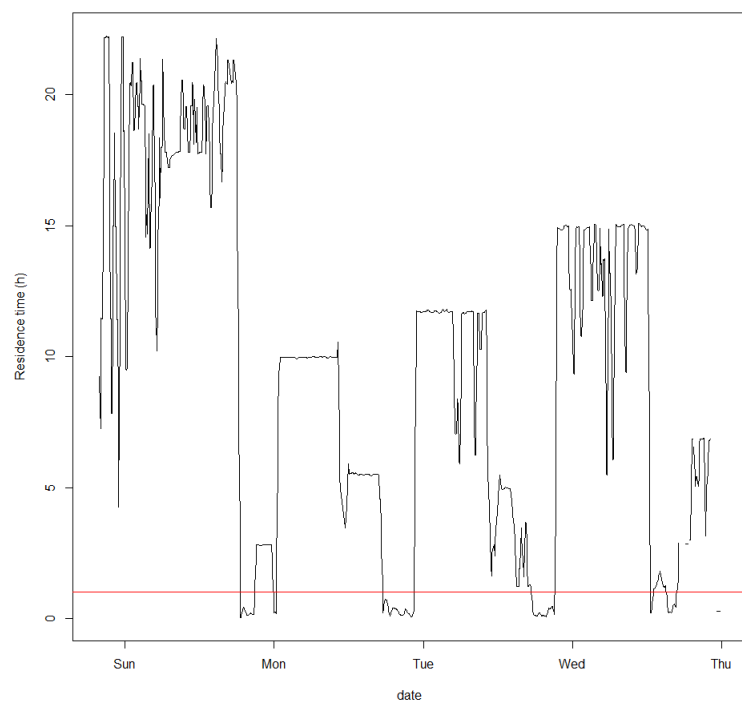
```
date <- armadillo2$date
```

```
threshold <- 1 # 1 hour threshold
```

```
myrt.smoothed <- rollapply(myrt, 5, mean, main = "5 step smoothing",  
na.rm = TRUE, fill=NA)
```

```
plot(date, myrt.smoothed, type="l", ylab = "Residence time (h)")
```

```
abline(h = threshold, col=2) # time threshold that defines active  
and inactive moments
```





Assigning points to "In Burrow" (i.e. inactivity periods) based on the window-of-five smoothing + time threshold of 1 hour + radius of 20m

```
threshold <- 1 #time threshold
```

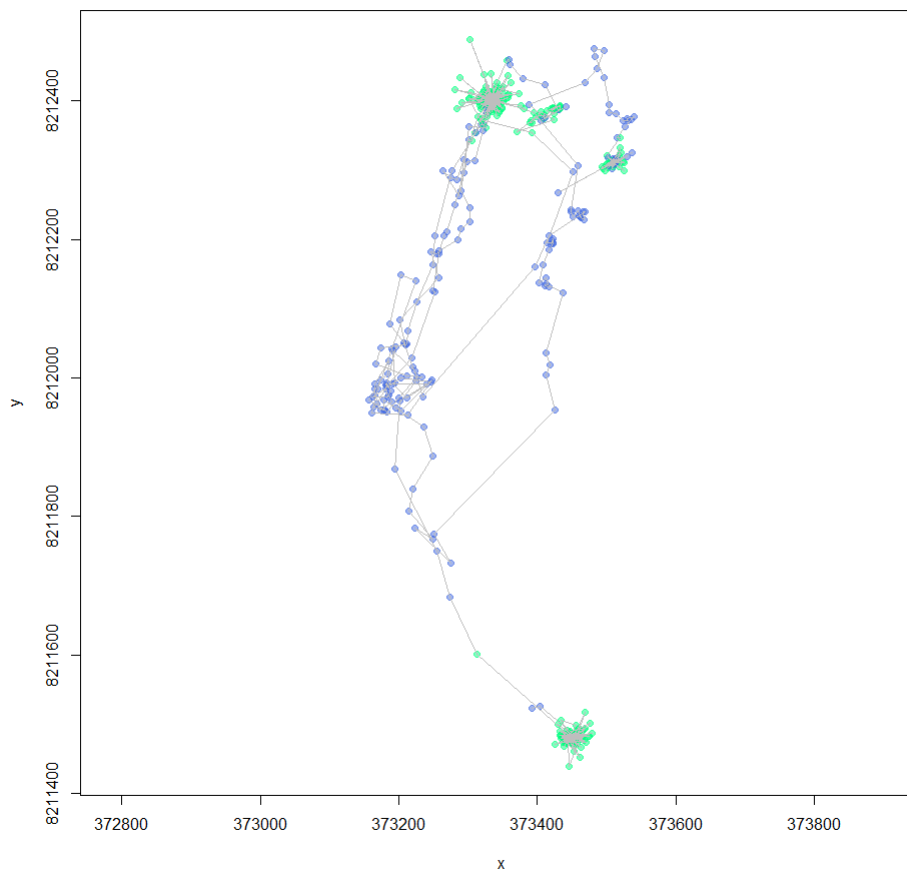
```
armadillo2$InBurrow <- myrt.smoothed > threshold  
armadillo2$InBurrow[is.na(armadillo2$InBurrow)] <- 0
```

```
require(scales)
```

```
cols <- alpha(c("royalblue", "springgreen"),.5)
```

```
#Visualize what has been assigned as shelter (green)
```

```
with(armadillo2, {  
plot(x,y, col = cols[InBurrow+1], asp=1, pch=19)  
  lines(x,y, col="grey")})
```



Define shelter locations by averaging the points assigned as 'In Burrow':

```
armadillo2$BurrowBout <- c(0,cumsum(diff(armadillo2$InBurrow)==1)) *  
(armadillo2$InBurrow == 1)
```

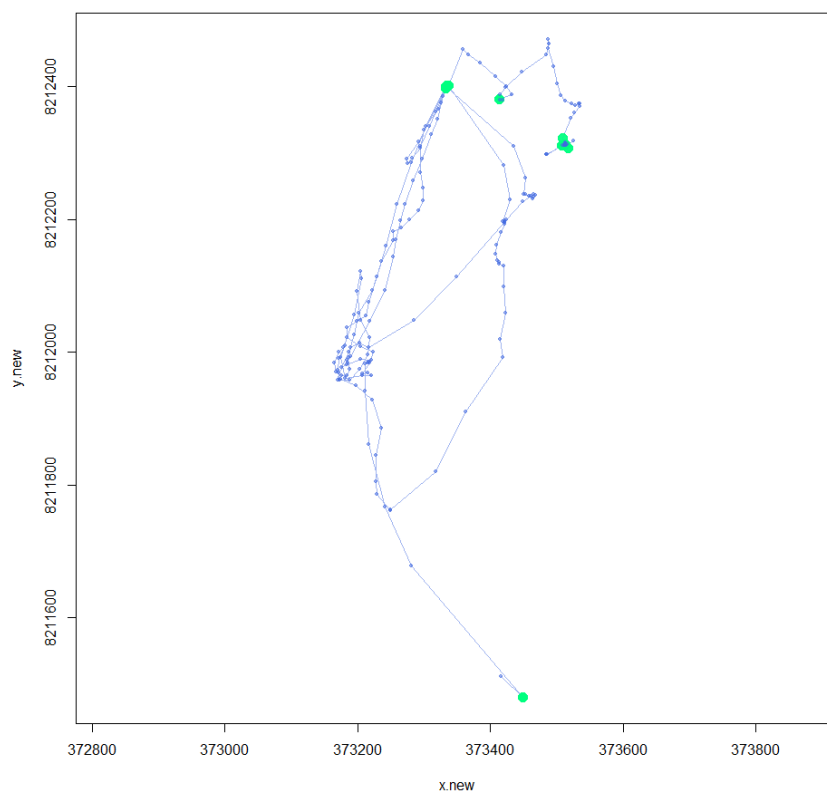
```
n.bouts <- max(armadillo2$BurrowBout, na.rm=TRUE)
```

```
armadillo2$x.new <- armadillo2$mean.x  
armadillo2$y.new <- armadillo2$mean.y
```

```
for(i in 1:n.bouts){  
  armadillo2$x.new[armadillo2$BurrowBout == i] <-  
mean(armadillo2$mean.x[armadillo2$BurrowBout == i])  
  armadillo2$y.new[armadillo2$BurrowBout == i] <-  
mean(armadillo2$mean.y[armadillo2$BurrowBout == i])  
}
```

*#Plotting averaged shelter locations*

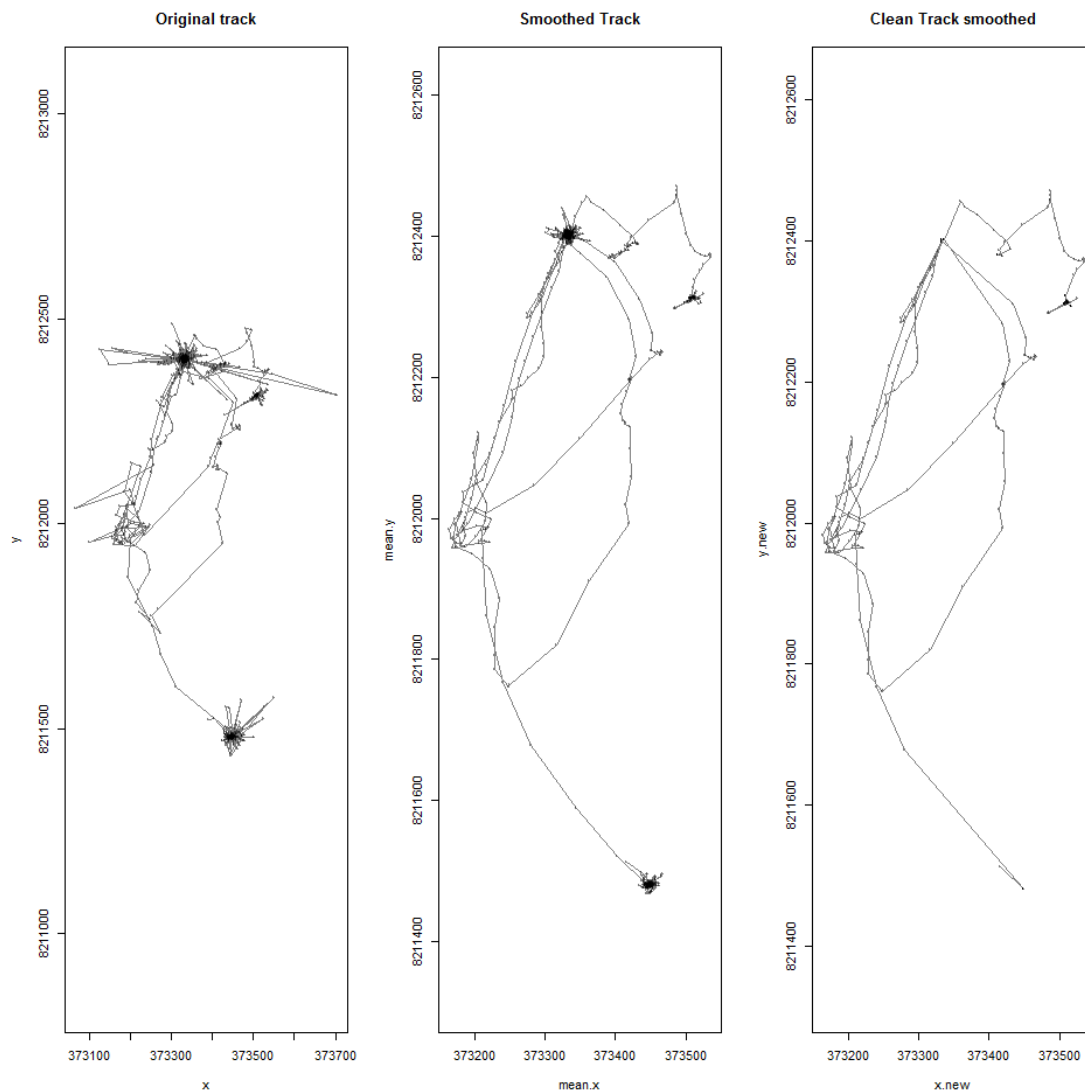
```
with(armadillo2, plot(x.new, y.new, asp=1, type="o",  
cex=(BurrowBout>0)*1+.5, col=cols[(BurrowBout>0)+1], pch=19))  
#burrows in green, and 'active' locations in blue
```





Comparing tracks through the different steps of data cleaning

```
par(mfrow=c(1,3))
with(armadillo, plot(x,y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Original track"))
with(armadillo2, plot(mean.x,mean.y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Smoothed Track"))
with(armadillo2, plot(x.new,y.new, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5),main = "Clean Track smoothed"))
```



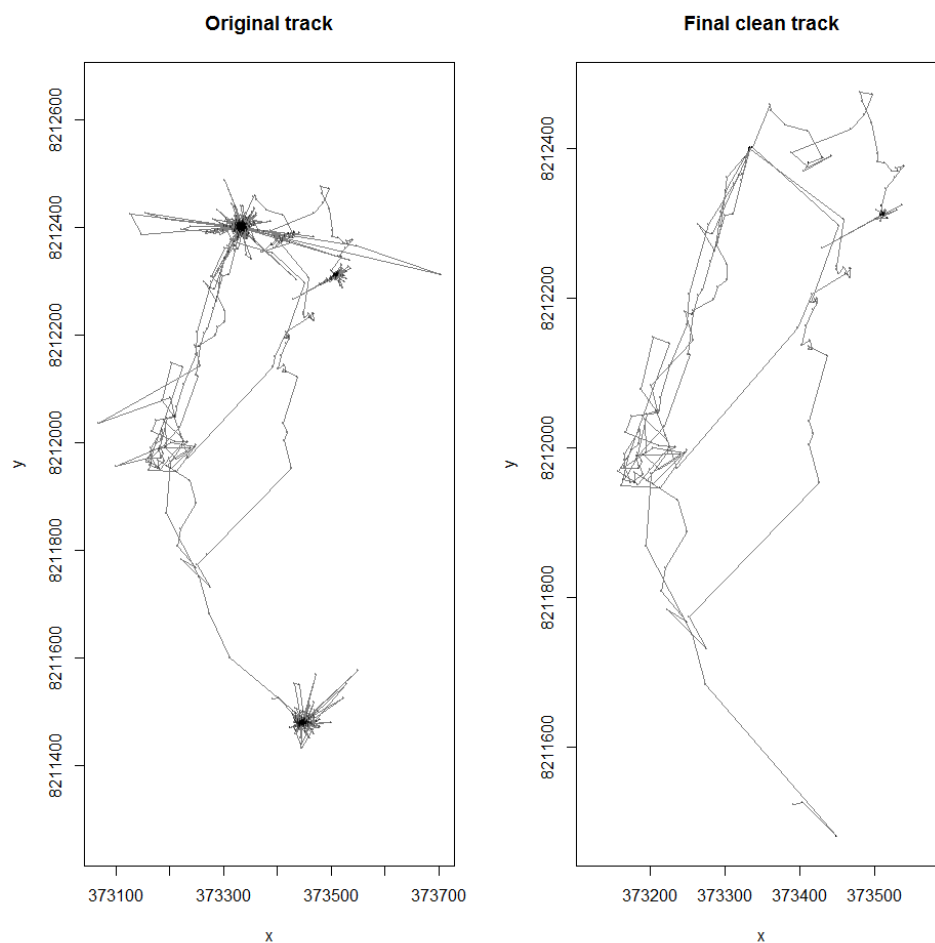
Creating a new track without the errors

Maintaining the original coordinates when the animal is outside the shelter (i.e. active) and using the new averaged coordinates when the animal is inside the shelter

```
armadillo2$x.new2 = ifelse(armadillo2$InBurrow==1, armadillo2$x.new,
armadillo2$x)
armadillo2$y.new2 = ifelse(armadillo2$InBurrow==1, armadillo2$y.new,
armadillo2$y)
```

*#Comparing tracks*

```
par(mfrow=c(1,2))
with(armadillo, plot(x,y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Original track"))
with(armadillo2, plot(x.new2,y.new2, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Final clean track", xlab = 'x',
ylab='y'))
```



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# SHORT COMMUNICATION

## Yes, they can! Three-banded armadillos *Tolypeutes* sp. (Cingulata: Dasypodidae) dig their own burrows

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**ABSTRACT.** It is believed that the two species of *Tolypeutes* Illiger, 1811 are the only armadillos that do not dig their own burrows, and that these species simply re-use burrows dug by other species. Here, we show that *Tolypeutes matacus* (Desmarest, 1804) and *Tolypeutes tricinctus* (Linnaeus, 1758) dig their own burrows. We describe the burrows and three other types of shelters used by them, and provide measurements and frequency of use of the different types of shelter. We have studied free-ranging individuals of *T. matacus* in two locations in Central Brazil and individuals of *T. tricinctus* in semi-captivity in the Northeast of Brazil. Individuals of *T. matacus* were found primarily in small burrows (76%), straw nests (13%), shallow depressions covered with leaf-litter (7%) or in straw nests made on shallow depressions (4%). Adult males and females of *T. matacus* did not differ in frequency of use of different types of shelter. Sub-adults *T. matacus* used shallow depressions and nests more often (40%) than adults (22%) and nurslings (10%). Nurslings of *T. matacus* reused the shelters more frequently (66%), than sub-adults (46%) and adults (35%). Adult females reused burrows and other types of shelter more frequently than adult males. *Tolypeutes tricinctus* rested mainly in burrows and under leaf-litter, but did not dig depressions or build nests. *Tolypeutes tricinctus* occasionally used burrows dug by *Euphractus sexcinctus* (Linnaeus, 1758), but *T. matacus* never used burrows dug by other species. Nursling *T. matacus* always shared shelter with an adult female therefore, both used shelters with similar frequency. Adult females and nurslings of *T. matacus* reused shelters in higher frequency. That can be explained by the fact that adult females with offspring tend to remain for consecutive nights in the same burrow when cubs are recently born. Due to their smaller body size, sub-adult *T. matacus* used shelter strategies that require less energetic effort more frequently than adults and nurslings. The habit of covering the burrow entrance with foliage and the burrow's reduced depth, indicates that *Tolypeutes* use of burrows is more likely to be related to parental care behavior and thermoregulation strategies than to defense mechanisms. We are confident that the burrows used for resting were indeed dug by *Tolypeutes* because, besides the direct observation of armadillos digging burrows, the measures of the burrows are very distinctive from those presented as characteristic for the co-occurring burrowing species and are congruent with *Tolypeutes* size and carapace shape. The newly acquired knowledge that species of *Tolypeutes* dig burrows can be used to increase the well-being of individuals kept in captivity by adapting enclosures to enable their digging behavior. In addition, this information contributes not only to the study of the ecology and natural history of the species, but can shed new light on the study of the anatomy of specialized diggers. *Tolypeutes* spp. can comprise the least fossorial of all living armadillo species, but they can no longer be classified as non-diggers.

**KEY WORDS.** Digging behavior, ecology, Xenarthra.

It is believed that the two existing species of three-banded armadillos, *Tolypeutes* are the only ones among the twenty extant armadillo species that do not dig their own burrows. Even though both species have rarely been studied in the wild, the

information that the species of *Tolypeutes* simply re-use burrows dug by other species is often repeated in the scientific literature (GUIMARÃES 1997, EISENBERG & REDFORD 1999, SMITH 2007, WETZEL et al. 2008, MEDRI et al. 2011).

*Tolypeutes* comprises *Tolypeutes matacus* (Desmarest, 1804) and *Tolypeutes tricinctus* (Linnaeus, 1758), both species with the unique ability to roll into an almost perfect ball as a defense mechanism (EISENBERG & REDFORD 1999, WETZEL et al. 2008). These armadillo species have an average head plus body length of 25 cm and an average weight of 1.1 kg (EISENBERG & REDFORD 1999). The southern three-banded armadillo, *T. matacus*, is found primarily in the dry forests of the central region of South America, including western Brazil, eastern and southern Bolivia, western and northern Paraguay, and northern Argentina. The Brazilian three-banded armadillo, *T. tricinctus*, occurs exclusively in the semi-arid scrub forests and savannas of the northeastern and central regions of Brazil (WETZEL et al. 2008, FEIJÓ et al. 2015).

Unfortunately, most of the scarce information on the ecology and habits of these species is derived from captive animals (e.g., BERNIER 2003), dead animals (e.g., BOLKOVIC et al. 1995) or occasional observations (e.g., SANBORN 1930, MARINI-FILHO & GUIMARÃES 2010). Until now, only three comprehensive studies on the ecology of these species have been conducted in the wild, and only one of them has been published. GUIMARÃES (1997) and Ilmar Bastos Santos (unpublished data) radio-tracked individuals of *T. tricinctus* in Cerrado and Caatinga areas, while BARRIENTOS & CUELLAR (2004) monitored individuals of *T. matacus* in the Bolivian Chaco (CUELLAR 2002, 2008, BARRIENTOS & CUELLAR 2004, NOSS 2013). However, these studies provide only scarce and fragmented information about the use of shelters by *Tolypeutes*.

Here, we describe four types of shelters used by free-ranging *T. matacus*, including burrows, and provide evidence that both species of *Tolypeutes* are able to dig their own burrows. In addition, we provide descriptions, measurements, and information on the frequency of use of these burrows.

### *Tolypeutes matacus*

We studied individuals of *T. matacus* in two locations. The first site is the Santa Teresa Ranch, located in the region of the Amolar Mountain Ridge, in the western limits of the Brazilian Pantanal, Corumbá, Mato Grosso do Sul state (18°17'51"S, 57°30'35"W). The second site is the Duas Lagoas Ranch, located in the Brazilian Cerrado, in Cáceres Municipality, Mato Grosso state (16°10'13"S, 58°11'12"W).

Animals were captured by hand during active searches performed by foot, horse, using ATV vehicles or using pickup trucks. From the 39 captured individuals of *T. matacus*, 13 males (12 adults and one sub-adult) and 13 females (eight adults, three sub-adults and two nurslings) were monitored. We defined adults as individuals with more than 1 kg and sub-adults as weaned individuals with less than 1 kg. Individuals were tracked by VHF (during 2 to 5 months) using the homing-in to the animal method (SAMUEL & FULLER 1994) and/or through GPS telemetry (during 5 to 27 days). Glue-on VHF radios and GPS tracking devices were attached to the posterior part of the pelvic carapace (using flexible cyanoacrylate super glue and/or epoxy resin), following a protocol commonly used for hard-shelled turtles (e.g., SEMINOFF

et al. 2002). Eight individuals also had an intra-abdominal VHF radio tracking device surgically implanted in their abdominal cavity (HERNANDEZ et al. 2010). Animals were tracked daily, at varying times between 6:00 and 22:00 h. During monitoring, camera traps (Bushnell® Trophy Camera Brown Model 119435) were set to video mode (30 seconds duration) and placed in front of shelters (n = 51) occupied by tracked animals (n = 17) in different occasions.

We were able to locate and visualize the monitored individuals at 445 occasions, and on 67% of them, they were found resting. Resting records were made mainly during daytime. On these occasions, *T. matacus* were found in four types of resting-sites: small burrows (76%), straw nests (13%), shallow depressions covered with leaf litter (7%) or in straw nests made in shallow depressions (4%) (Figs. 1-5). Adult males and females showed no difference in frequency of use of the different types of shelter, both using burrows in higher frequency than any other type of shelter. Different age-classes used the types of shelter differently (Friedman  $\chi^2 = 6$ , df = 2, p = 0.05). Sub-adults used shallow depressions and nests more often (40%), when compared to adults (22%) and nurslings (10%).

Burrows dug by *T. matacus* have a dome-shaped entrance,  $11 \pm 1.98$  cm high and  $12.8 \pm 2.1$  cm wide, with a depth of  $35 \pm 9.4$  cm (Table 1), ending in a nearly conical shape. Both males and females of all age classes used burrows for shelter. Burrow sharing was observed only between mothers and their single offspring. Females sharing their burrow with their nursling dug deeper burrows than did single individuals of either sexes (mean difference = 14.9 cm, t = 9.2, df = 65, p < 0.01). The use of burrows was observed in both open and densely vegetated areas (i.e. all available vegetation types). Burrows were built at the base of trees, between thorny bromeliads and bushes, soil build-ups, leaf litter build-ups, and dense bushes located in the middle of open areas with tall grass.

Table 1. Measurements of *Tolypeutes matacus* burrows at Santa Teresa ranch, Corumbá, Mato Grosso do Sul, and Duas Lagoas ranch, Cáceres, Mato Grosso.

	N	Height (cm)	Width (cm)	Depth (cm)
Male	59	10.9 ± 1.8	12.8 ± 1.7	30.3 ± 4.7
Female	52	11.1 ± 2.1	12.7 ± 2.4	38.7 ± 10.5
Female with nurslings	26	11.6 ± 2.8	13.3 ± 2.9	45 ± 8.5
Female without nurslings	26	10.6 ± 1	12.2 ± 1.7	29.6 ± 4.9
Male and Female	111	11 ± 2	12.8 ± 2.1	35 ± 9.4

Burrows used by a single armadillo were deep enough to fit an "unrolled" adult individual, even though individuals were usually found resting on their side (half way curled) or almost completely curled into a ball. Sixty percent of the burrows where armadillos were found resting had inconspicuous entrances, covered with grass and/or tree leaves (depending upon its availability in the surroundings), and occasionally with dirt.





Figures 1-5. (1) An individual of *Tolypeutes matacus* (arrow) resting inside its burrow at Santa Teresa Ranch, Corumbá, Mato Grosso do Sul. (2-3) Straw-nest built by *T. matacus* in a pasture area at Duas Lagoas Ranch, Cáceres, Mato Grosso: (2) upper view of the nest (circle) and (3) close-up of the same nest (arrow indicates the entrance of the nest). (4-5) (4) An almost imperceptible individual of *T. matacus* resting in a depression under leaf litter at Santa Teresa Ranch, Corumbá. The arrow points to the only visible part of the carapace. (5) The same GPS-fitted animal resting in the depression after we manually removed some of the leaf litter to expose part of its carapace (circled).

Despite the occurrence of three other armadillo species – *Euphractus sexcinctus* (Linnaeus, 1758), *Cabassous unicinctus* (Linnaeus, 1758) and *Dasypus novemcinctus* Linnaeus, 1758) – and at least four other burrowing animals (iguanas, agoutis, pacas and the spiny rat) at our study sites, *T. matacus* was never found using burrows resembling those belonging to other species.

Nests and depressions were also used as shelters by *T. matacus*. The “nest” nomenclature has already been used by BARRIENTOS & CUELLAR (2004), for *T. matacus*, due to the resemblance of the structure to a bird nest. In the present study, nests were composed of a structured assemblage of dry grass and straw. Using camera traps set to video mode, we recorded individuals of *T. matacus* actively assembling dry grass and straw to repair their nests (Appendix S1\*). Nests were usually conspicuous, being built at soil level (76%) or in depressions (24%), in the pasture, under fences and occasionally inside dense bushes (Figs. 2-3).

The main difference between nests and depressions is that the nest is a structured assemblage of grass and straw, while when resting in depressions armadillos simply cover themselves with any type of vegetation available in the surroundings, with no structured arrangement. In addition, nests are structured in a tri-dimensional way standing above ground, while the foliage

assembled over depressions tends to lay flat over the animal and becomes inconspicuous among the rest of leaf litter on the landscape.

When using depressions, *T. matacus* were completely covered with leaf litter at the soil level, leaving almost no visible evidence of their presence (Figs. 4-5). Occasionally, the armadillos were resting within the leaf litter in places of difficult access, such as areas with dense coverage of thorny lianas, dense bushes, and near roots of trees or fallen logs. However, it was not uncommon to observe the use of depressions in grasslands. It was not always possible to determine if the depressions used were natural to the relief of the landscape or dug by the animals. However, the depressions were always deep enough so that the animal could lay down on its side, cover himself with leaf litter and those leaves would be at similar level to the soil compared to the leaf litter in the surroundings. Armadillos were observed using nests and depressions on both open and densely vegetated areas (i.e., all available vegetation types). Both males and females of all age classes used nests and depressions as shelters.

Individuals were observed changing resting places on consecutive nights, using the same burrow or nest for consecutive nights, and reusing the resting place after long periods of no use (up to 36 days). Our radio-tracking and camera trap data shows

\*Available as Online Supplementary Material with the HTML version of the article at <http://www.scielo.br/zool>

that no individual was ever recorded using burrows or nests previously used by another monitored individual. The reuse of shelters varied among age classes ( $\chi^2 = 8.7$ ,  $df = 2$ ,  $p = 0.01$ ), being more commonly observed in nurslings (66% of the inactivity records of the individuals were made in shelters previously used), followed by sub-adults (46%) and then adults (35%). Adult females were recorded reusing burrows and other types of shelter more frequently than adult males ( $\chi^2 = 3.4$ ,  $df = 1$ ,  $p = 0.06$ ).

We were able to record other animals visiting the burrows built by *T. matacus*. We have recorded small rodents, small lizards and teju lizards entering and/or exiting the burrow. Hence, three-banded armadillos burrowing habits could be potentially benefiting other species.

### *Tolypeutes tricinctus*

Two individuals of *T. tricinctus*, a male and a female, were encountered in the backyard of a private property at Buriti dos Montes Municipality, Piauí state, Brazil (5°18'33"S, 41°5'52"W). They had been kept in that property for a period between one to two years. At this locality, it was possible to record burrows covered by leaf litter, built near trees and in open areas (Figs. 6-7). Additionally, we were able to observe an individual actively digging a burrow, when we approached it during capture procedures (Fig. 8).

Both individuals were captured and relocated to a reserve, Reserva Natural Serra das Almas, Crateús, Ceará state, Brazil (5°8'30"S, 40°54'58"W), where they were kept for six months (July 2014 to January 2015). When the animals were taken to Serra das Almas, they were initially placed in a temporary enclosure. The animals were placed inside burrows that had been dug by the staff. However, the animals did not use these structures and immediately began digging their own burrows. After seven days, the animals were relocated to their permanent semi-captive enclosure. The enclosure was established inside the reserve, in an area of 93 m<sup>2</sup> of deciduous forest typical to the Caatinga eco-region, where the species naturally occurs. The animals were enclosed in a fine meshed-wire fence to prevent the access or outlet of small mammals and any other burrowing animal known to occur in the area. Two burrows, probably dug by yellow-armadillos (*E. sexcinctus*) prior to the establishment of the facility and the arrival of the three-banded armadillos were present in the enclosure. Despite the fact that the pre-existing burrows were initially used by the three-banded armadillos, they built and used four new burrows during the period in which the armadillos were kept in the enclosure (Fig. 9). The enclosure was monitored with camera traps and it was possible to record the animals digging and using the new structures. Nevertheless, the animals continued to use the yellow-armadillo burrows occasionally.

The burrows dug by *T. tricinctus* in semi-captivity ( $n = 4$ ) were  $10.5 \pm 1.4$  cm high,  $14 \pm 2.9$  cm wide, with depth of  $43.5 \pm 12.8$  cm (Table 2). These animals also rested under leaf-litter, but did not dig depressions or build nests. They rested in open areas and under leaf-litter amongst thorny bromeliads and lianas.

Table 2. Measurements of burrows of *Tolypeutes tricinctus* kept in semi-captivity at Reserva Natural Serra das Almas, Crateús, Ceará.

Burrow	Height (cm)	Width (cm)	Depth (cm)
#1	9.4	11.1	47.0
#2	10.0	13.0	60.0
#3	12.5	18.0	32.0
#4	10.0	14.0	35.0
Mean $\pm$ SD	$10.5 \pm 1.4$	$14 \pm 2.9$	$43.5 \pm 12.8$

Predictably, nursling *T. matacus* used shelters with similar frequency of *T. matacus* adults, since nurslings always shared shelter with an adult female. Sub-adults have a smaller body weight, when compared with adults, and were not seen accompanied by any adult individual. Their smaller body size might make the burrow building activity even more challenging, making it more likely for these individuals to use shelter strategies that require less energetic effort, such as nests and depressions covered with leaves.

Six, out of the eight adult females of *T. matacus* monitored, had nurslings (of varied sizes/ages) with them. The higher rate of reuse of shelter by females and the nurslings can be explained by the fact that adult females with offspring tend to remain for consecutive nights in the same burrow when the cubs are recently born.

The reduced depth of the burrow of *Tolypeutes* compared to other armadillo species burrows (e.g., ABBA et al. 2005) and the habit of covering its entrance indicates that the use of burrows by these species is more likely to be related to parental care behavior and thermoregulation strategies (MACCARINI et al. 2015) than to defense mechanisms. The cover of burrow entrances could contribute to buffer the burrow temperature, as observed to be an important thermoregulation strategy to other armadillo species (MACCARINI et al. 2015). Unlike other armadillo species, which have carapaces that can easily be perforated by predators (CARTER & ENCARNÇÃO 1983), *Tolypeutes* can roll into an almost perfect ball (EISENBERG & REDFORD 1999, WETZEL et al. 2008) and is likely to be predated only by top predators that have the strength to punch the carapace and/or a mouth big enough to fit the entire animal (e.g., jaguars, pumas and manned wolves, HANNIBAL et al. 2015). Hence, *Tolypeutes* may not rely as strongly on burrows as a protection against predators as other armadillo species do (CARTER & ENCARNÇÃO 1983). Alternatively, the reduced depth of *Tolypeutes* burrow compared to other armadillo species burrows (e.g., ABBA et al. 2005), could be related to the very hard soil types of our study areas, that could make the burrowing activity for this small species even harder.

Usually, the shape of the cross section of a burrow entrance is in accordance with the shape of the cross section of the body of the burrower. Hence, besides the direct observation of animals digging, the width and the shape of the entrance of a burrow can allow the identification of a burrowing species (KRIEG 1929 apud ABBA et al. 2007). As shown in Table 1 and 2, the dimensions and the dome-shape of the burrows where





Figures 6-9. (6) Burrow of *Tolypeutes tricinctus* with entrance covered by leaves at Buriti dos Montes, Piauí. (7) Animal leaving the burrow after removal of the leaf litter cover. (8) An individual of *T. tricinctus* actively digging as an escape behavior at Buriti dos Montes. (9) Burrow dug by *T. tricinctus* in semi-captive conditions at Reserva Natural Serra das Almas, Ceará.

the individuals of *Tolypeutes* were found are congruent with the animal size and carapace shape. When observing animals entering and exiting the small burrows, the perfect congruence of the shape of the carapace and that of the burrow is evident (Appendices S2\* and S3\*).

In addition, the observed measures of burrows of *T. matacus* are very distinctive from those presented as characteristic for the co-occurring armadillo species that dig dome-shaped burrows, such as *E. sexcinctus* (W = 24 cm, H = 20 cm) and *D. novemcinctus* (W = 20 cm, H = 21 cm, BORGES & TOMÁS 2008). The remaining co-occurring species of armadillo, *C. unicinctus*, is known to dig perfectly round burrows oriented vertically to the ground (BORGES & TOMÁS 2008), presenting a very distinct pattern from the burrows where the *Tolypeutes* individuals were found resting. Finally, the spiny rat is known to dig long and complex tunnels and iguanas only dig burrows in close proximity of water bodies, during the breeding season (Z. Campos, pers. comm.). There is no reason to believe that *T. matacus* would be using or modifying other species burrows, since it is the smallest armadillo species occurring in the studied areas, using the shortest burrows found there. A species that uses another

species' burrows could change its shape, but would not be able to make a burrow smaller than its original size. Finally, we were able to record free-ranging individuals actively digging burrows at Duas Lagoas ranch (Appendix S4\*), leaving no further doubt on the ability of *T. matacus* to build the structures in which they had been recorded resting.

VIZCAÍNO & MILNE (2002), based on anatomical features and the lack of direct behavioral observations in the field, misclassified *Tolypeutes* as a non-digger species. However, our direct observations demonstrate that, like all other armadillo species, *Tolypeutes* do dig their own burrows. These animals possess such long claws on the toes of their forefeet that they actually have to walk on their claws (Figs. 10-11, EISENBERG & REDFORD 1999). Such a remarkable apparatus is suitable for digging, and it is comparable with the same structure observed in other well-known, burrow-digging armadillo species. Yellow armadillos, for example, usually present body sizes two to three times larger than the three-banded armadillos, and their longest fore-claw is similar in size to that of the average *Tolypeutes* (N. Attias pers. obs.). Hence, three-banded armadillos do not seem to have any anatomical constraint that would impair them to be efficient

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Figures 10-11. (10) Lateral and (11) frontal view of *Tolypeutes matacus* front claws.

diggers. Evolutionarily, it would be unexpected that such an apparatus evolved for foraging purposes alone, as opposed to serving a dual function, as is evident in all the other armadillos.

EISENBERG & REDFORD (1999) only recognized that “*Tolypeutes* can occasionally dig shallow foraging holes”. Indeed, we have recorded *Tolypeutes* digging shallow foraging holes using their fore claws. Nevertheless, we have also seen those animals digging burrows up to 54 cm deep and using them as shelters. The individuals of *Tolypeutes* used their front claws to dig and their hind legs to push away the accumulated dirt, just like other armadillo species do when digging their burrows (Appendix S4\*). BORGES & TOMÁS (2008) previously described a specific pattern for *T. matacus* burrows. They were not able to record animals actively digging or using the assigned burrows, but relied on tracks in and out of burrows to state that *T. matacus* constructs burrows with almost circular entrances of 13 to 14 cm in diameter, which is similar to the pattern we documented at our study sites.

The newly acquired knowledge that these species dig burrows, might help to clarify some incongruence between anatomical aspects of the limbs of armadillos and their digging behavior, found by VIZCAÍNO & MILNE (2002). It can also be used to increase the well-being of individuals kept in captivity by adapting enclosures to enable their digging behavior, especially during the breeding season. This new information on the behavior of *Tolypeutes* species contributes not only to the study of the ecology and natural history of the species, but can shed new light on the study of the anatomy of specialized diggers. *Tolypeutes* spp. can comprise the least fossorial of all living armadillo species, but they can no longer be classified as non-diggers.

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## APPENDICES

About the Online Supplementary Material (available with the HTML version of the article at <http://www.scielo.br/zool>):

Appendix S1. An individual of *Tolypeutes matacus* gathers straw to repair the nest it is currently using. The video is a compilation of several (30 sec.) videos captured by a camera trap set in front of the nest. The activity of gathering straw and bringing it to the nest was recorded for a period of one hour on July 21<sup>st</sup>, 2015 at Duas Lagoas Ranch, Cáceres, Mato Grosso. To enable the visualization of the complete behavior in a shorter time, the video was edited and its speed is four times the speed of the actual behavior.



Appendix S2. An individual of *Tolypeutes matacus* enters its burrow at Santa Teresa Ranch, Corumbá, Mato Grosso do Sul. In this video it is possible to observe the perfect congruence between the shape of the carapace of the animal and the burrow it builds.

Appendix S3. An individual of *Tolypeutes matacus* exits its burrow that had the entrance covered by leaf litter, at Santa Teresa Ranch, Corumbá, Mato Grosso do Sul. Again, in this video it is possible to observe the perfect congruence between the shape of the carapace of the animal and the burrow it builds.

Appendix S4. An individual of *Tolypeutes matacus* actively digging a burrow from scratch at Duas Lagoas Ranch, Cáceres, Mato Grosso. The recording of the digging behavior began at 21:14 h and ended at 21:18 h. The mid-section of the video had its speed doubled to enable the visualization of the behavior in a shorter time.