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Spatial and temporal ecology of two armadillo species in Midwestern Brazil

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"... 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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Summary

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), at three sites of the Pantanal wetlands, Brazil. In the first section of this dissertation, I used direct observations and footage from camera traps placed in front of shelter locations to describe the sheltering habits of *T. matacus* and compared them to the habits of *T. tricinctus* in northeastern 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 Step Selection Functions. 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 in timing of activity and activity 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 showed that *Tolypeutes* dig their own burrows, contradicting previous belief. *Tolypeutes matacus* were active on average for 5.5±2.8 hours per day, with most of their activity concentrated in the first half of the night.

However, our models show that, as air temperature decreases, activity periods of *T. matacus* are of shorted and peak earlier in the day. Similarly, our models suggest that *E. sexcinctus* activity during the daytime decreases as air temperature increases. Relative selection strength of almost all vegetation types by *T. matacus* was related to the distance to dirt paths. *Tolypeutes matacus* selected mainly forested areas, regardless of activity status. However, *T. matacus* habitat selection can also vary across temperatures. *Euphractus sexcinctus* tends to select open vegetation areas during activity and forested areas during rest. In addition, both studied species should select forested areas when experiencing air temperatures outside their thermoneutral zones. 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. Female *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 on average 423 m apart and in only 1% of the simultaneous fixes animals were in proximity (< 50m). To my knowledge, this is the first study of free-ranging *T. matacus* in Brazil and the most comprehensive study on its ecology anywhere. The spacing and home range patterns of *T. matacus* point 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* can be characterized as a mainly nocturnal species that selects preferentially areas close to paths and forested areas, but is 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 both studied species can alter their behavior. *Tolypeutes matacus* has been classified as Data Deficient in Brazil and as Near Threatened at the international level 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, 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 explorar a ecologia espacial e temporal e a biologia social 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 passos (Step 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 uma análise 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 horários 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 mostraram que *Tolypeutes* cava suas próprias tocas, ao contrário do que se acreditava até o momento.

Tolypeutes matacus ficam ativos em média por 5.5±2.8 horas por dia, com atividade concentrada na primeira metade da noite. No entanto, nossos modelos demonstram que, à medida que a temperatura do ar diminui, seus períodos de atividade se tornam mais curtos e tem pico mais cedo. De forma similar, nossos modelos sugerem que a atividade de *E. sexcinctus* durante o período diurno diminui à medida que a temperatura do ar aumenta. A força de seleção relativa de quase todos os tipos de vegetação por *T. matacus,* está relacionada a distância aos caminhos de terra. *Tolypeutes matacus* seleciona principalmente florestas independente do status de atividade. 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. Além disso, ambas as espécies estudadas devem selecionar áreas florestais quando enfrentando temperaturas do ar fora de suas zonas de termoneutralidade. 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 (< 50m) em apenas 1% das localizações simultâneas. A 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 em qualquer lugar. O padrão de espaçamento e área de vida de *T. matacus* aponta para um comportamento geralmente associal 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 que 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 como ambas as espécies estudadas podem alterar seu comportamento. *Tolypeutes matacus* tem sido classificado como Deficiente de Dados no Brasil e como Quase Ameaçada em nível internacional 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 contained in the superorder Xenarthra (Möller-Krull et al. 2007). This superorder encompasses the orders Cingulata (armadillos) and Pilosa (sloths and anteaters), both of which have low body temperatures (32.7 to 35.5°C), low basal metabolic rates (~50% of what would be expected for a mammal of similar size), 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, for adult females, while caring for young (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 for 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 their body temperature (McNab 1985).

There is a need for factual knowledge on species biology and ecology to establish efficient conservation measures and to deal with many 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 the richest xenarthran order (20 species) with a broad distribution 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). In the relatively short time that most species spend above ground, they present a solitary and asocial behavior (McDonough 1997). These behavioral characteristics coupled 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 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 differentiation in 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 resource demands (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 fate 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 space. Ecological processes, such as inter and intra-specific interactions, variations in the landscape and their natural history, may regulate animal home ranges (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, I 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 to fill 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 Animal Behaviour. Finally, to contribute to the future study of armadillos through GPS technology, we present as Supplementary material the method developed to cope with the error pattern generated in armadillo GPS tracks due to their burrowing habits.

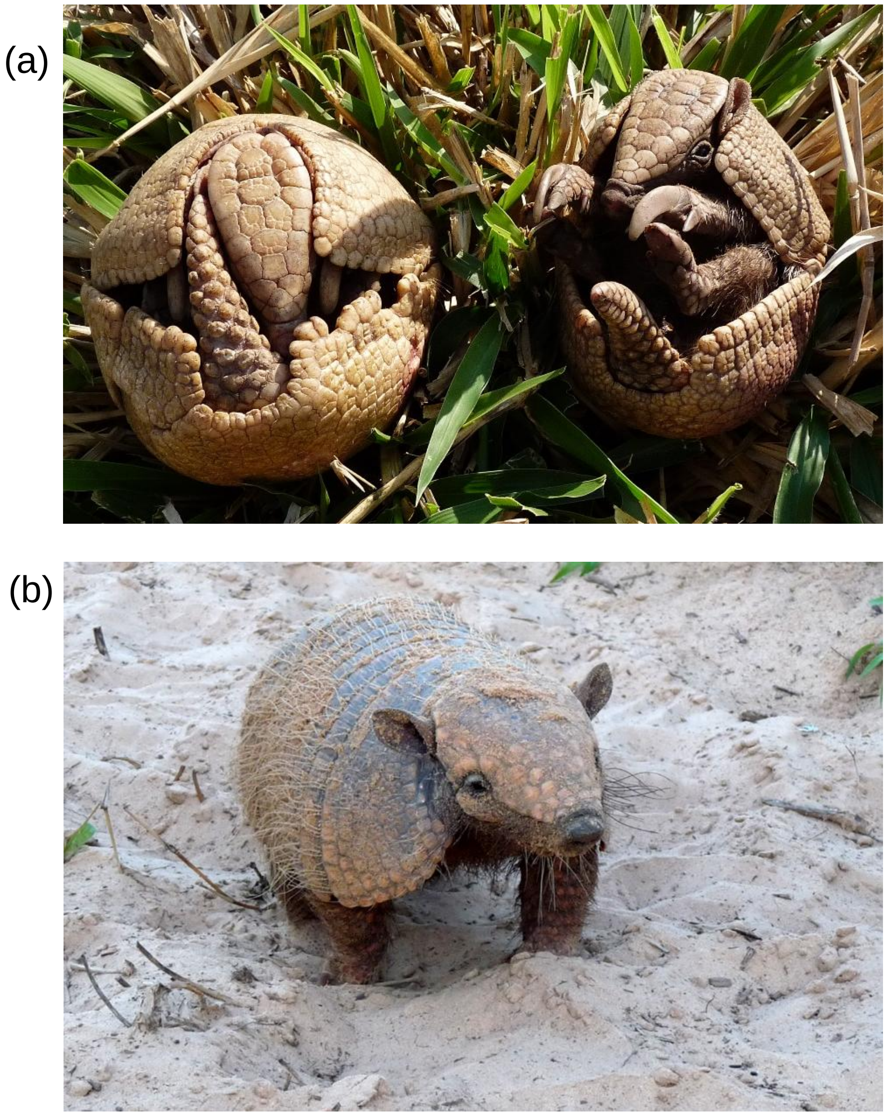

Figure 1. Studied armadillo species. (a) Two individuals of three-banded armadillo, *Tolypeutes matacus,* portraying the behavior of rolling into a ball, at Duas Lagos ranch, Cáceres, Mato Grosso. (b) An adult individual of yellow armadillo, *Euphractus sexcinctus* at Pantanal da Nhecolândia, Corumbá, 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 in shallow depressions (4%). Adult males and females of *T. matacus* did not differ in frequency of use of different types of shelter. Subadult *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 subadults (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 with higher frequency. This 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, subadult *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 indicate 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 viventes, 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 subadult) and 13 females (eight adults, three subadults and two nurslings) were monitored. We defined adults as individuals weighing more than 1 kg and subadults as weaned individuals weighing 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 on 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 with higher frequency than any other type of shelter. Different age-classes used the types of shelter differently (Friedman x2 = 6, df = 2, p = 0.05). Subadults 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 ± 1.98 cm high and 12.8 ± 2.1 cm wide, with a depth of 35 ± 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.

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.

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).

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 itself 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 (x2 = 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 subadults (46%) and then adults (35%). Adult females were recorded reusing burrows and other types of shelter more frequently than adult males (x2 = 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.

Table 1. Measurements of adult *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

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 m2 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 ± 1.4 cm high, 14 ± 2.9 cm wide, with depth of 43.5 ± 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, nursling *T. matacus* used shelters with similar frequency of *T. matacus* adults, since nurslings always shared shelter with an adult female. Subadults 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 & 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*).

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.

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 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.

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 ± SD	10.5 ± 1.4	14 ± 2.9	43.5 ± 12.8

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. may be 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 Step 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 on average for 5.5±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 relative selection strength of active and sheltering armadillos at both sites, regardless of vegetation cover. *Tolypeutes matacus* selected mainly forested areas, regardless of activity status. Relative selection strength was higher in habitat units closer to dirt paths, regardless of vegetation cover type. 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 areas (KUD 95%) of adult males was, on average, about 2.8 times larger than that 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 on average 423 m apart and in only 1% of the simultaneous fixes animals were in proximity (< 50m) 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 point 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 their 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 "Step 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±2.8 horas por dia, com maior parte de sua atividade concentrada na primeira metade da noite. *Tolypeutes matacus* Tatus selecionaram principalmente florestas quando em proximidade a trilhas e estradas de terra. A força de seleção relativa foi maior em unidades de habitat mais próximas a trilhas e estradas de terra, independente do tipo de cobertura vegetal. 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 um 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 mantiveram em média 423 m de distância e em apenas 1% de suas localizações simultâneas estes foram encontrados em proximidade (< 50m) 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 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 the energetic requirements of species 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 their 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 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 exploit the environment (Pianka 1973) and are 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).

Factual knowledge on species biology and ecology is essential to develop efficient strategies to deal with the most critical contemporary ecological problems (Greene 2005, Beyer et al. 2010). However, despite its richness (20 species) and broad distribution throughout the Neotropics, the ecology and biology of most Cingulata (armadillo) species is poorly known. Information on home range measures, population size, natural history, and types of threats are scarce or nonexistent 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; hereon 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. 2008). Species of this genus are classified as opportunistic insectivores (Bolkovic et al.1995) and weigh 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. tricinctus* (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 fieldwork 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 a single region in the Bolivian Chaco (Cuellar 2002, Barrientos & Cuellar 2004, Cuellar 2008). 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. This, associated with habitat loss, has contributed to population declines in recent years (Abba & Superina 2010). The three-banded armadillo is classified as Near Threatened by the IUCN Red List of Threatened Species under criterion 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; ICMBio 2017) further highlights the priority of conservation efforts towards this species. One of the specific goals of the action plan is 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 each sex, 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, such as dirt paths; 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 at two sites (250 km apart; Fig. 1) that presented different management strategies, either prioritizing the maintenance of the natural landscape (Site 1) or economic activities (Site 2; Fig. 2).

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 may remain flooded during the flood season (November to April). Natural grasslands remained flooded for most of our study period, except for the short period of late January and early February 2015. 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 has been modified into exotic pasture, dedicated to cattle grazing (Fig. 2a). Even though most of this site is preserved forest, individuals were captured and monitored in both altered and non-altered habitats.

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.

Capture and tracking methods

We captured 39 individuals of *T. matacus*, 12 at Site 1 (November 2014 to March 2015) and 27 at Site 2 (July to August 2015). 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). Of the 26 monitored animals, 14 were females (8 adults, 3 subadults and 3 nurslings) and 12 males (10 adults and 2 subadults). We defined adults as individuals weighing more than 1 kg and subadults as weaned individuals weighing less than 1 kg.

For each monitored animal, we collected information on age, sex, reproductive condition and body mass. 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. 2016). 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 weighed 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). During the short period the devices were allowed to remain attached to the individuals (maximum 32 days), we did not record any significant ulcerations in its carapaces.

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 to ensure GPS functioning, animal welfare and record individual behavior. Each animal was tracked at varying times across the days, between 6:00 and 22:00 h.

Even though all the procedures described could be accomplished through physical restraint, some of the animals (n = 19) were anaesthetized through an intramuscular injection in the hind limbs to enable the collection of biological samples used in other studies. The anesthetic protocol was composed of Ketamine 25mg/kg (Quetamina® 10% - Vetnil), Xylazine 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 followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016) and were approved by the ethics committee of the Federal University of Mato Grosso do Sul (process 570/2013).

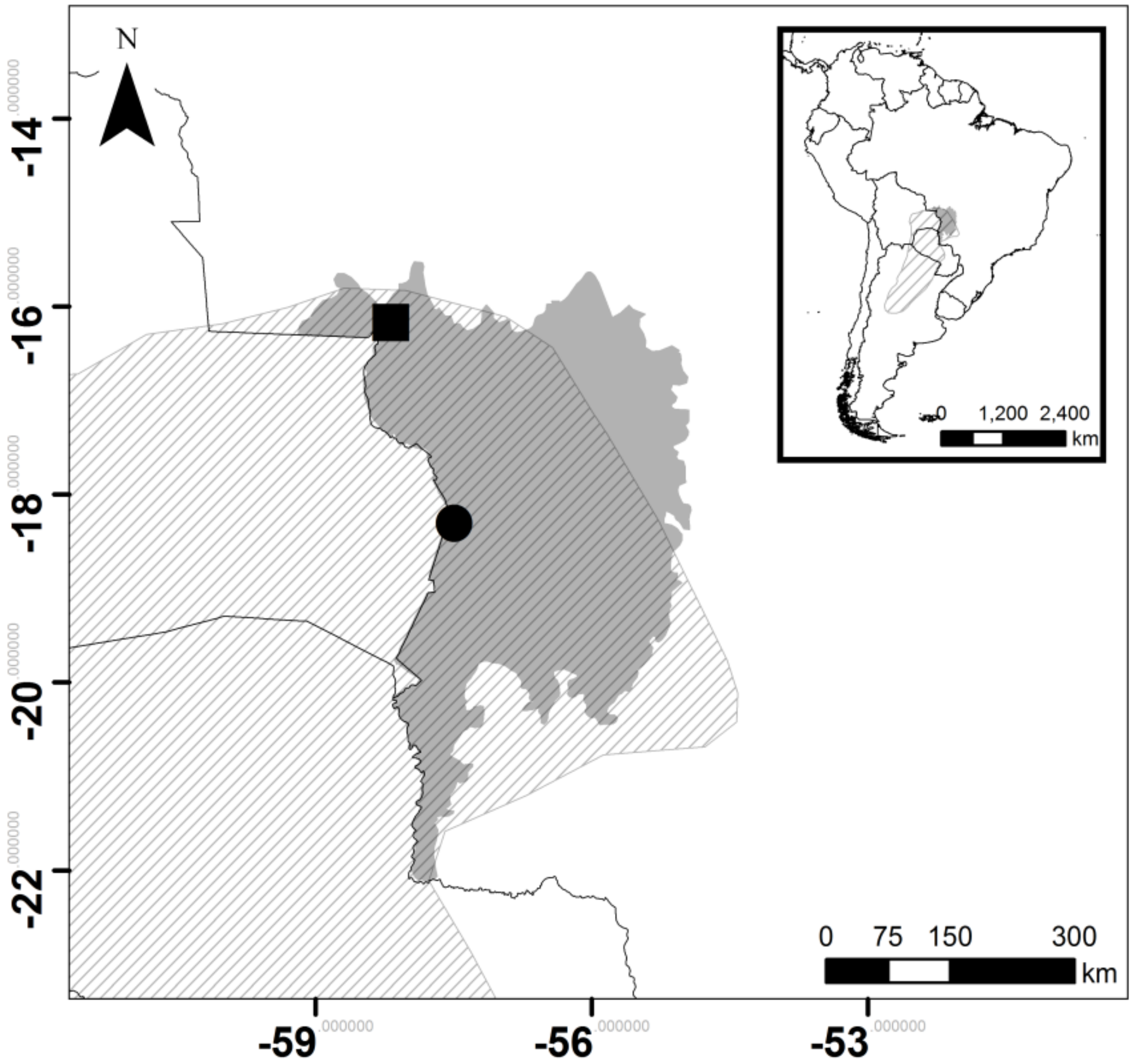


Figure 1. Location of the study Site 1 (circle, 18°17’51” S, 57°30’35” W) and study Site 2 (square, 16°10’13” S, 58°11’12” W) in the Pantanal (grey area), on the border of Brazil, Bolivia and Paraguay. The inset figure shows the location of the Brazilian Pantanal (grey area) in South America. In both images, the dashed area indicates the known distribution of *Tolypeutes matacus* according to IUCN.

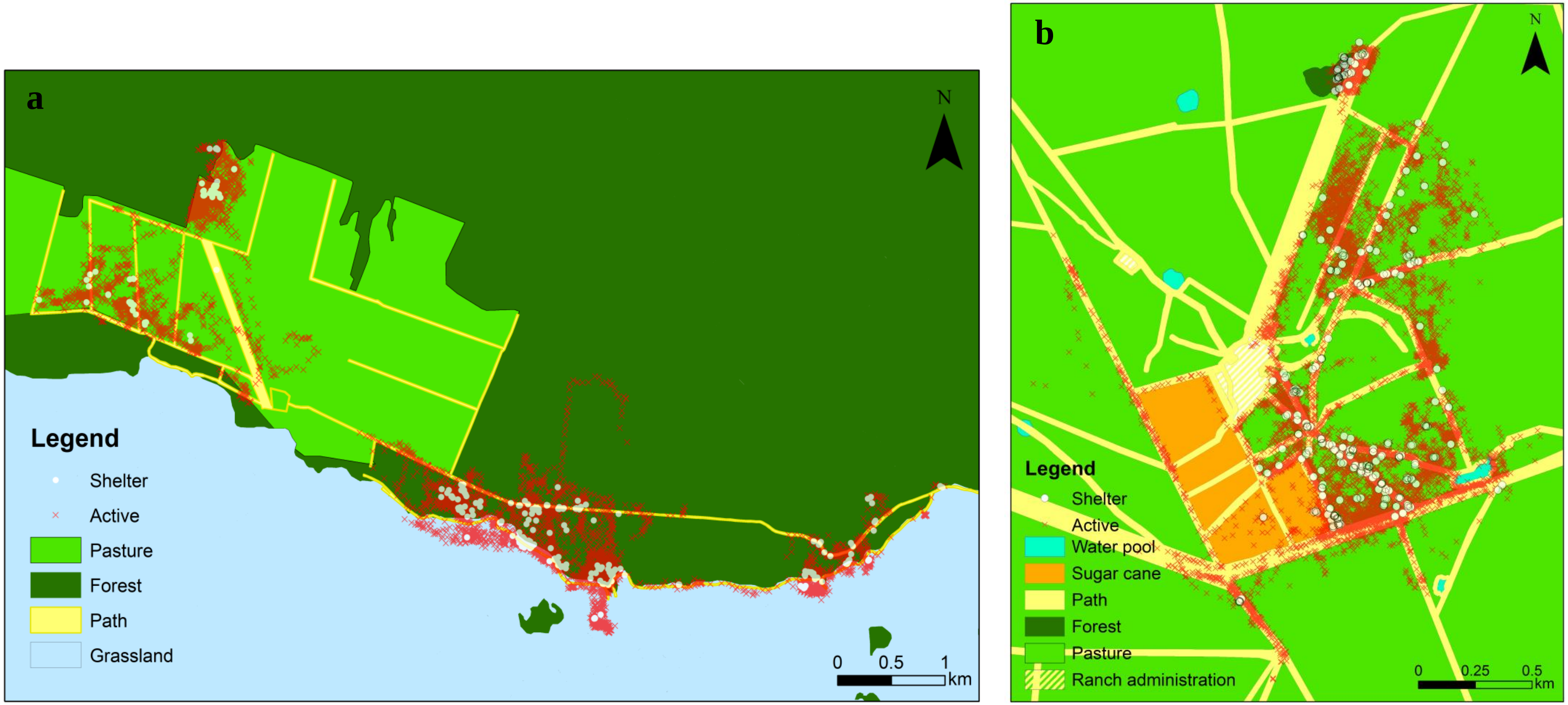


Figure 2. Thematic habitat maps classified according to vegetation features with locations of armadillo activity records (red 'x') and their shelters (white circles). Data from 26 individuals of *Tolypeutes matacus* monitored at (a) Site 1 and (b) Site 2, between November 2014 and August 2015.

Activity

The raw locations were submitted to a protocol described elsewhere (Supplementary Material) in order to account for the GPS inaccuracies and improve the detection of the shelter locations. To define the activity status of armadillos throughout the GPS tracks, we used an adaptation of the Residence Time method (Barraquand & Benhamou 2008; Supplementary Material). 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.

Resource selection

At each study site, we evaluated resource selection during active and resting periods separately. Resource selection during activity indicates the selection of areas where animals can find suitable conditions to perform activities such as foraging, displacing and finding mating partners, while selection during resting periods indicates where animals find suitable places to establish their shelters. To characterize resource selection, first we sub sampled the animal's trajectories of each activity data set to fixes with one-hour intervals.

We used Step Selection Functions (SSF; Fortin et al. 2005, Forester et al. 2009) to evaluate the effects of cover type and distance to dirt paths on the resource selection of *T. matacus*. Dirt paths comprehended features of the landscape that promoted a linear clearing, such as unpaved dirt roads, cattle tracks and fences. Fences are completely permeable for small-sized animals such as armadillos. In addition, the clearance of vegetation alongside fences turns them into linear clearings with equivalent width to cattle dirt tracks.

To prepare the data for the SSF analyses, first, we subsampled the individual trajectories composed of 5 min fixes to fixes with 60 min intervals. To account for changes across space in resource availability, we generated 30 random steps originating from each actual location of each armadillo. To do this, first we estimated the standard deviations of the Eastings (x) and Northings (y) of the locations of each armadillo. Then, we generated random steps by sorting 30 independent random samples from a random normal distribution with zero mean and the observed standard deviations of x and y of the locations, respectively, to obtain 30 x-segments and 30 y-segments. Each sampled combination of x and y segments were added to the actual UTM coordinate resulting in 30 new random coordinates of available next steps (see Calenge et al. 2009). This process was done for every observed location of each armadillo. We chose to use this process to generate random steps, instead of the traditional sorting of step lengths and angles, because it proved to be less time consuming in terms of computational process, which is important when working with large data sets such as ours.

For each observed and possible random step of each individual, we recorded the habitat type and the Euclidean distance to the closest dirt path at the step's ending point. Using RapidEye satellite imagery (taken in 2011), habitat types were classified into categories according to vegetation features of the landscape of each study site as follows: forest, pasture (both encountered in both study sites), natural grasslands (encountered only at Site 1), and sugar cane plantation (encountered only at Site 2). Values of distance to dirt 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 estimated an independent model for activity and inactivity at each study site, totaling four models. Each SSF model was fitted using a Conditional Logistic Regression (CLR) using the function 'clogit' in the package 'survival' (Therneau 2015) in R (R Core Team 2017). CLR models were conditioned to each step within individual (where observed steps were scored as 1 and random available steps were scored as 0). 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 for each model, first we fitted a LME model to the residuals of the CLR with individual identity as a random effect plus a first-order autoregressive correlation structure (Oliveira-Santos et al. 2016). Then, we fitted an autocorrelation function over the LME to identify the level of temporal autocorrelation present in the data (i.e., number of successive steps with similar values of residuals in CLR). Finally, we refitted the best CLR (based on AIC), clustering the auto-correlated successive steps, which allowed the estimation of the robust standard error of the coefficients (see Craiu et al. 2008). When plotting results, "Relative Selection Strength" was interpreted as the effect size (i.e., the exponential value of the final models coefficients; Forester et al. 2009, Avgar et al. 2017).

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) was 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 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 of connecting the most external records forming the smallest polygon without concavities (Mohr 1947). All analyses were performed using the R package 'adehabitatHR' (Calenge 2006).

We used a Student's t-test to assess if the body mass and home range size estimates of armadillos differed between study areas. We used the same approach to evaluate differences in home range size estimates and body mass between sexes. We fitted an ANCOVA model to evaluate the relationship between home range size (KUD 95%), sex and body mass. Because 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 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 least squares asymptotic model − y = a-b*exp^(-x*c) − through the function 'nls' of the 'stats' R package (R Core Team 2017).

Static interaction

We estimated the static interaction between individuals during activity and inactivity separately. First, we estimated core (KUD 50%) and home range areas (KUD 95%) of each individual during these two states, active and inactive. Then, 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 UDs are uniformly distributed and have 100% overlap. However, UDOI can be >1 if the two UDs are non-uniformly distributed and have a high degree of overlap. UDOI is a function of the product of two UDs 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. 3). During the monitoring period, the activity onset usually 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±2.9 hours) and summed to an average daily activity duration of 5.5±2.8 hours. Armadillos stayed inside their shelters for long periods, with an average of 14±6.7 hours/day and a maximum of 19.7 hours/day.

Resource selection

Tolypeutes matacus selected mainly forested areas at both study sites, regardless of activity status (Appendix 2). At Site 2, they also selected pasture areas while active, but with weaker relative selection strength. At both sites, the relative selection strength of almost all vegetation types was related to the distance to dirt paths (Fig. 4). Habitat units closer to dirt paths presented higher relative selection strength.

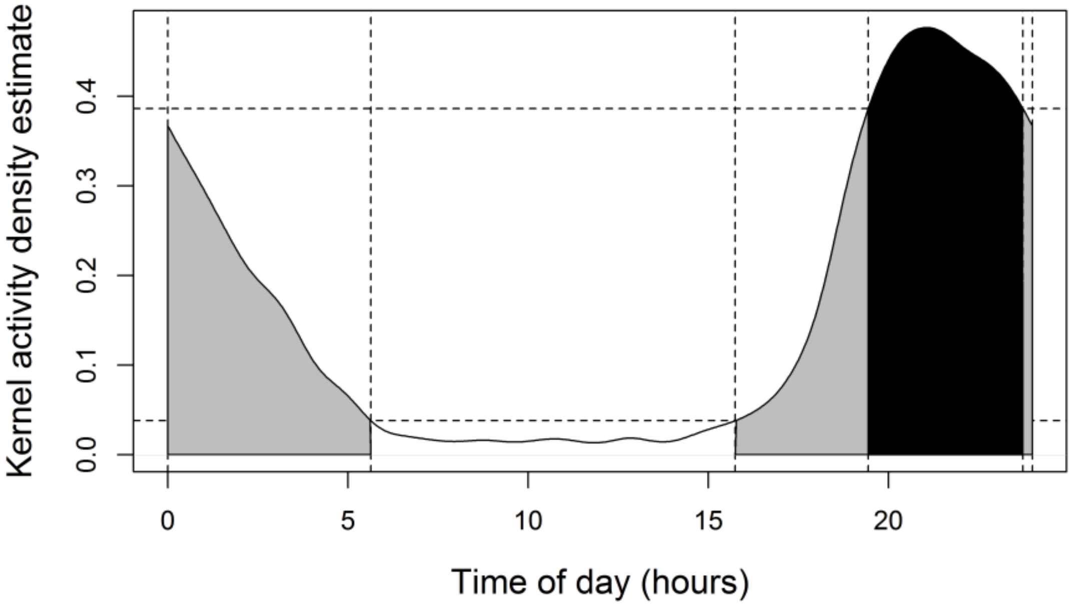


Figure 3. Kernel density estimates for the activity of *Tolypeutes matacus*. Gray areas represent the activity range (95% Kernel activity density estimates), while the black area represents core activity (50% Kernel activity density estimates) during a 24-h period. Data derived from 21,515 GPS activity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

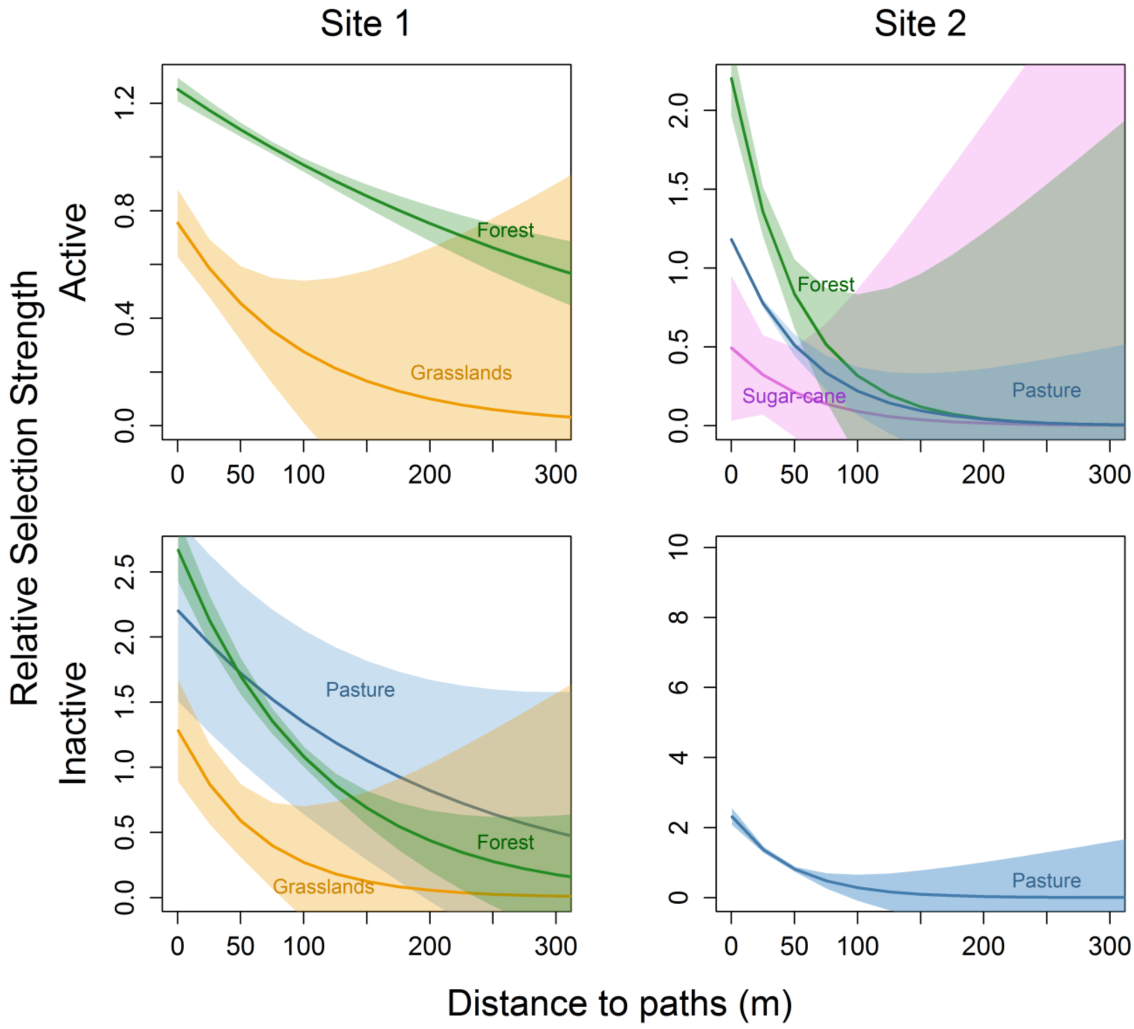


Figure 4. Relative selection strength of vegetation types according to distance to paths. Exponential coefficients and Standard error (shaded areas) of the Step Selection Function models, for active periods (top) and when in shelters (bottom) at Site 1 (left) and Site 2 (right). Lines plotted only for significant relationships (Appendix 2). Data from twenty-one *Tolypeutes matacus* monitored in the Pantanal of Brazil from November 2014 until August 2015 .

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 the data from both sites to examine the relationship between home range size, body mass and sex of all adult individuals. Since body mass and sex of the armadillos interacted to explain their home range size (Fig. 5; $F_{(1,17)}= 7.32$, $p_{\text{interaction}} = 0.05$), 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 (KUD 95% = -86.6 + 139.2 * 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. 5). Adult males were heavier than adult females (Table 1; Appendix 1) and the home range area (KUD 95%) of adult males *T. matacus* was, on average, about 2.8 times larger than the home range area of adult females (Table 1). To allow comparisons with previous studies, we also included the MCP 100% estimates in Table 1, since mean KUD 95% home range estimates differ from mean MCP estimates ($t = 2.14$, $df = 20$, $p = 0.04$).

Daily distance traveled

On a daily basis, adult males moved more than adult females (Table 1). The relationship between mean daily displacement and the square root of home range area shows an asymptotic tendency (Fig. 6). 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, $p = 0.32$).

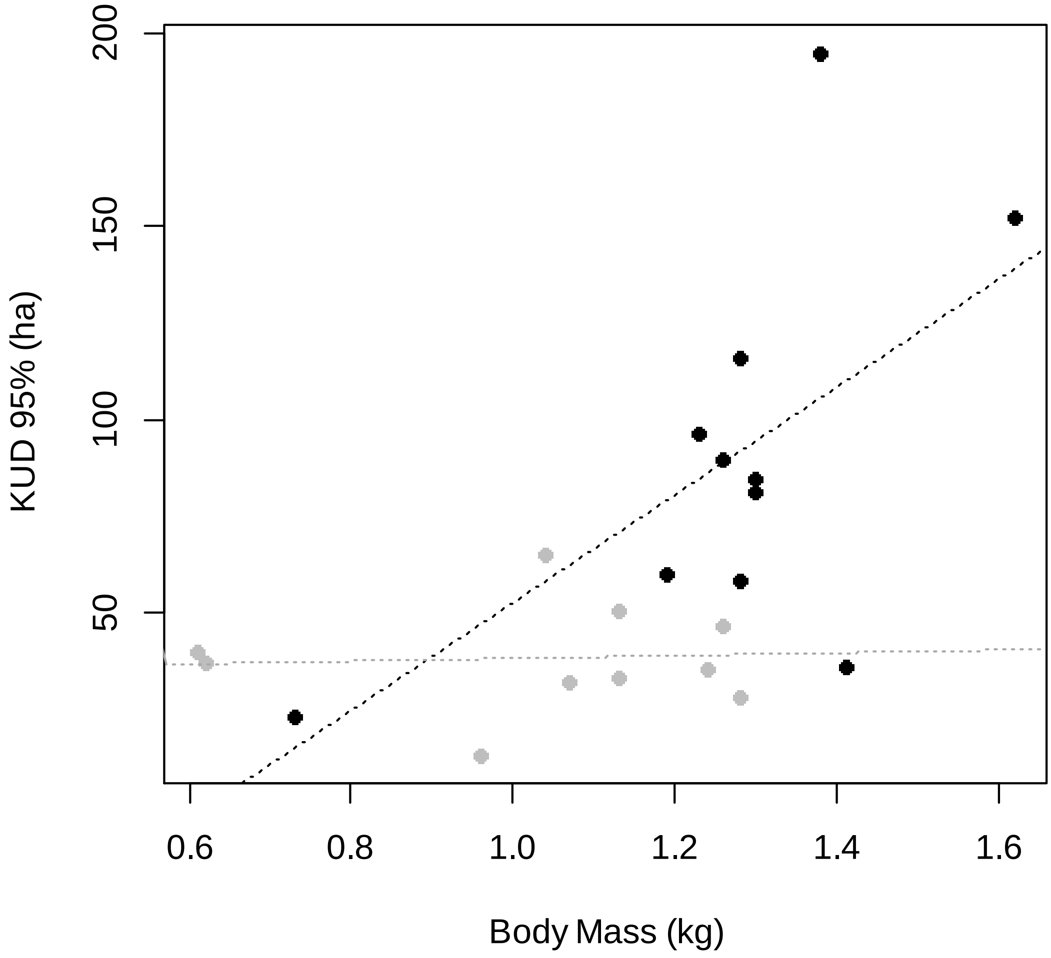


Figure 5. Relationship between body mass (kg) and Kernel Use Density home range size (KUD 95%) of twenty-one *Tolypeutes matacus* tracked at two sites in the Pantanal of Brazil, from November 2014 until August 2015. Black circles represent male armadillos and grey circles represent females. Dotted lines indicated the slope of the linear regressions for each sex.

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 18 adult individuals tracked at 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

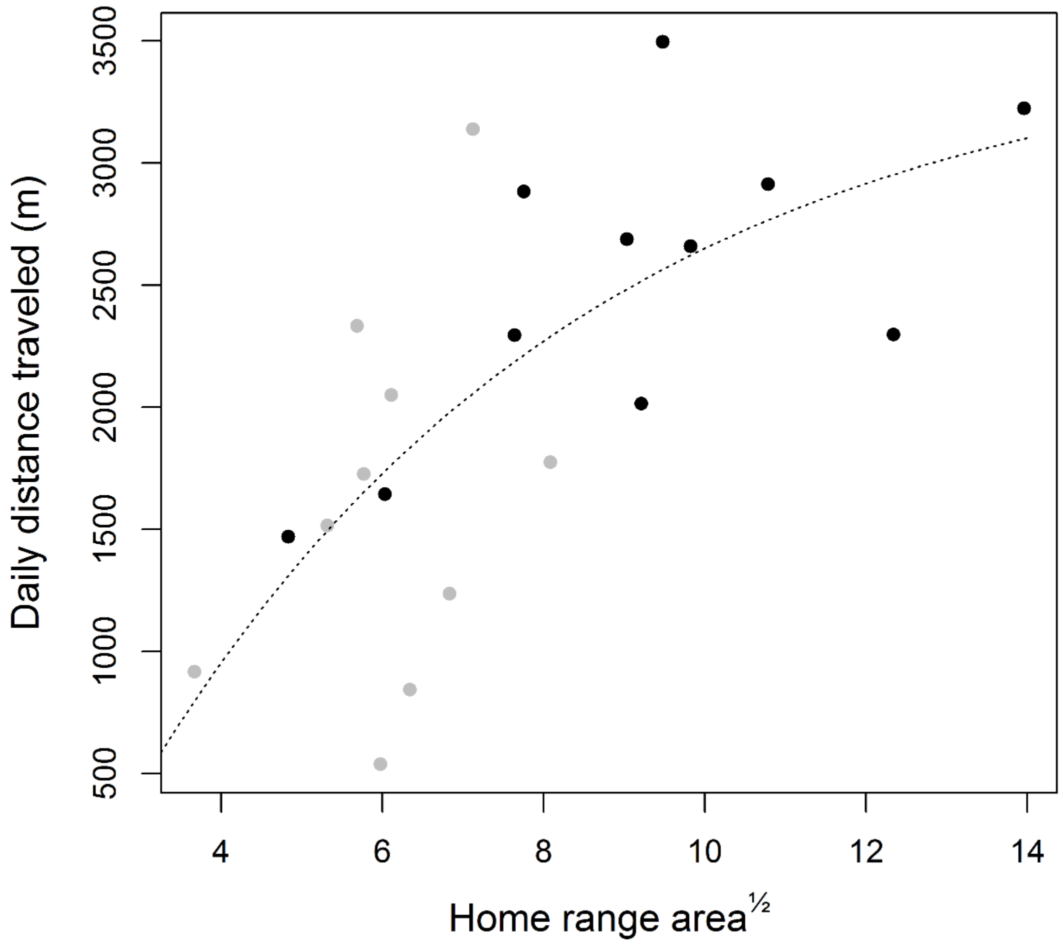


Figure 6. Relationship between mean daily distance traveled and the square root of the home range area of twenty-one *Tolypeutes matacus* tracked at two sites in the Pantanal of Brazil, from November 2014 until August 2015. Home range was estimated by the Kernel method (95%). Gray points represent females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

Static interaction

Overall, static interaction between individuals was low (Table 2). Sex and age class of armadillos influenced the probability of space use sharing between pairs of individuals (UDOI; Appendix 3). The average probability of space use sharing (UDOI) is higher when adult animals are active and at home range level (13%), when compared to inactive periods at home range level (5%) and core area level (1%), respectively (Table 2). During inactive periods, the average 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) at both home range and core area levels.

Females did not share their home ranges and core areas with other females, regardless of age class. The highest average probability of space use sharing between females is 1%, during active periods, at home range level (Table 2). Nevertheless, nursling females tended to have home ranges almost completely encompassed by their mother's home range (Fig. 7). When compared to all others, pairs of females showed a lower overlap probability at both home range and core area levels (Table 2). On the other hand, the ranges occupied by males overlapped with both males and females. In general, the probability of adult inter-sexual (M-F) space use sharing is higher than the intra-sexual probability (Table 2). 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. 7).

Dynamic interaction

Dyads were on 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 interaction, occurring during short periods in foraging locations and paths used for displacement, such as dirt roads and trails. During tolerance interactions, animals may feed in proximity (Breece & Dusi 1985) or just share a displacement route at the same time.

The analysis of proximity dynamics of different dyads can provide information about the social dynamics of three-banded armadillos. 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 the animals where in close proximity in five out of 10 days of simultaneous monitoring. The female of the dyad was lactating, although her cub (TM32; Appendix 1) was almost her size. At that time, mother and cub no longer shared a shelter every night, indicating that the cub would 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), suggests that some type of social interaction could have been taken 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 on 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 within 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 on 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 on displacement routes, but also in foraging areas and near resting shelters, portraying a higher tolerance than any other intra-sexual pair.

Table 2. 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 (a) home range level (KUD 95%) and at (b) core area level (KUD 50%) for each subset of locations. Individuals were tracked at two sites in the Pantanal of Brazil from November 2014 until August 2015.

(a)

Home range level	Adult - Adult		Adult - Juvenile		Juvenile - Juvenile			**Mean**
	Active	Inactive	Active	Inactive	Active	Inactive		
Female - Female	0.022	0.007	0.003	0	0	0	Active	0.017
							Inactive	0.005
Female - Male	0.096	0.038	0.079	0.074	0	0	Active	0.177
							Inactive	0.099
Male - Male	0.051	0.023	0.087	0.045	0	0	Active	0.121
							Inactive	0.061
Mean	0.127	0.054	0.12	0.094	0	0		

(b)

Core area level	Adult - Adult		Adult - Juvenile		Juvenile - Juvenile			**Mean**
	Active	Inactive	Active	Inactive	Active	Inactive		
Female - Female	0.001	0.007	0	0	0	0	Active	0.001
							Inactive	0.005
Female - Male	0.007	0.038	0.007	0.074	0	0	Active	0.014
							Inactive	0.099
Male - Male	0.003	0.023	0.002	0.045	0	0	Active	0.007
							Inactive	0.061
Mean	0.009	0.054	0.009	0.094	0	0		

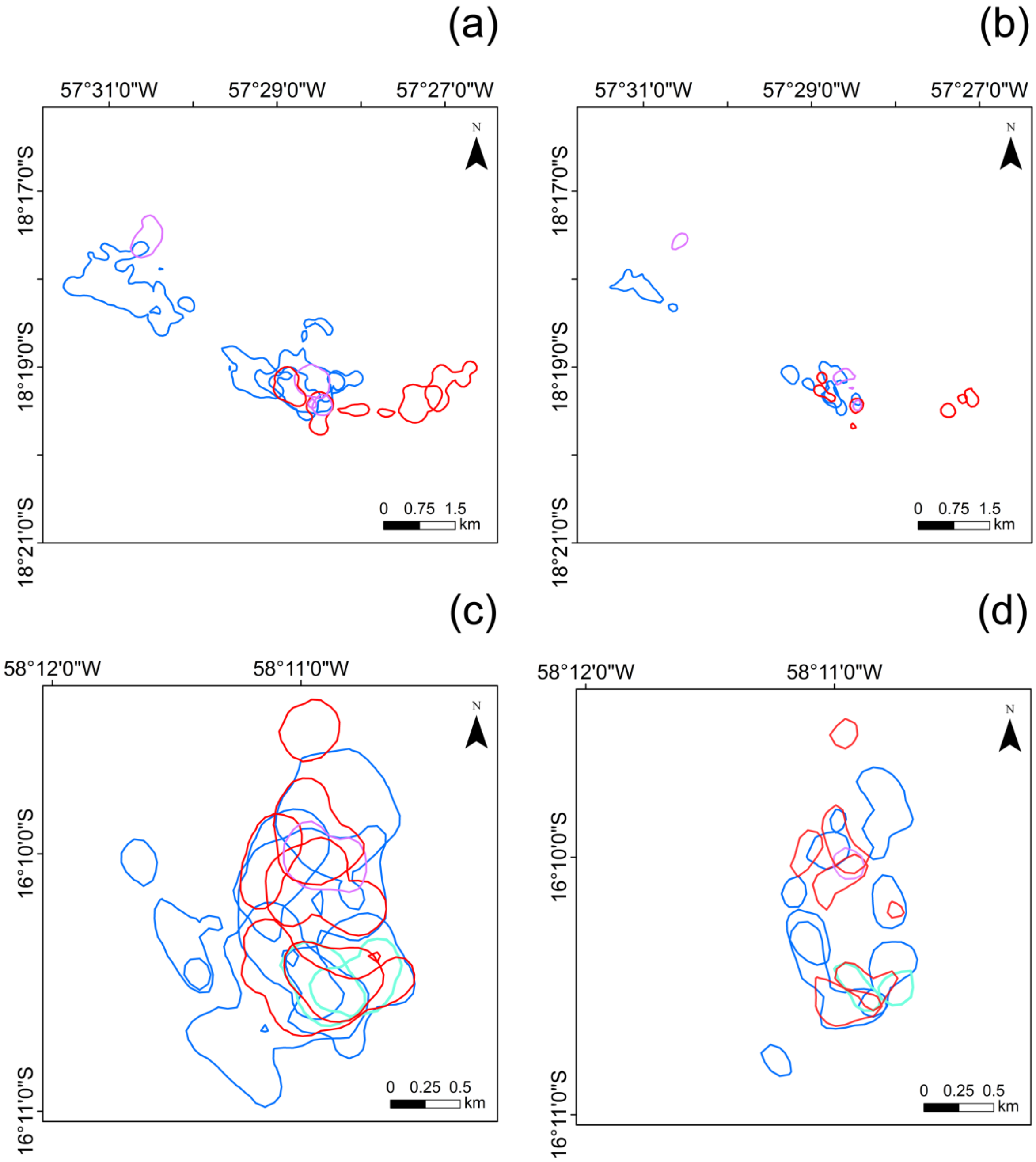


Figure 7. Spatial organization and overlap between males (blue) and females (red) of *Tolypeutes matacus.* Individuals were tracked in two sites in the Pantanal of Brazil, from November 2014 until August 2015. (a) Home range contour (Kernel 95%) and (b) core area contour (Kernel 50%) of eleven individuals tracked at Site 1. (c) Home range contour (Kernel 95%) and (d) core area contour (Kernel 50%) of fifteen individuals tracked at Site 2. Pink and light blue lines represent immature females and males, respectively.

Discussion

Activity

Even though we only monitored animals during seven months of the year, we would not expect a great variation from the observed activity pattern, since photoperiod variation is minor in the tropics, when compared to temperate zones. In addition, we did monitor animals along a broad temperature variation spectrum, which is known to be one of the main factors affecting activity pattern variation in xenarthrans (Maccarini et al. 2015, Medri & Mourão 2007; this study).

Three-banded armadillos were mainly nocturnal. Even though Eisenberg & Redford (1999) have reported a cathemeral activity for *T. matacus* and we have captured some individuals during daytime, we estimated a low probability of finding them active during 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 reported a diurnal activity pattern for the species, but this pattern may be biased by an unequal hunting effort over the hours of the day (Barrientos & Cuellar 2004, Cuéllar 2008). The activity pattern observed in the present study is similar to that reported for the congener *T. tricinctus*, which also seems to be active at the end of the afternoon and in the first half of the night (Bocchiglieri et al. 2010).

Even though we were able to monitor only a few juvenile individuals, it was possible to observe that they 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 (Meritt 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). Most carnivore species in this region present a nocturnal behavior (Astete et al. 2008), and an earlier activity onset by juveniles, could reduce their chance of encounter with most potential predators. Adult three-banded armadillos are likely to be predated only by large carnivores that have the strength to punch their thick carapace and/or a mouth big enough to fit the entire rolled animal (e.g., jaguars and maned wolves, Hannibal et al. 2015). Nevertheless, young individuals should be more vulnerable to predation by these and other smaller carnivores, due to their relatively softer carapace and smaller size when rolled up. Differences in activity behavior could also be related to variations in body mass between age classes and its consequences for thermoregulation (McNab 1980), i.e. individuals of smaller size and body mass tend to lose heat faster, especially in the colder nocturnal temperatures. Finally, behavioral and, consequently, niche changes during the life cycle of a species influence intra specific competition and population dynamics (Ebenman 1987). Hence, differences in activity behavior between age classes could reduce intra specific competition during foraging activities.

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), than *T. matacus* (5.45 hours). The short activity period 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 act as thermal shelters and are used for behavioral thermoregulation by these imperfect homeotherms (González et al. 2001, Maccarini et al. 2015).

Resource Selection

Three-banded armadillos have been reported to rest in forested areas but often leave this vegetation type to forage in open habitats (Smith 2007). In the present study, armadillos showed 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, Meritt 2008). In Central Chaco, Meritt (2008) also reports the occurrence of this species in natural grassland patches and in open thorn bush habitat. Although this vegetation type was flooded during most of our study period at Site 1, individuals used natural grassland areas in the brief period the water receded and this feature became available.

Three-banded armadillos also selected (with relatively lower strength) some modified elements of the landscape with reduced canopy cover, such as sugar cane plantations and pastureland composed of exotic grasses (*Brachiaria* spp.). In fact, exotic pastures were selected with high selection strength, ranking only behind forest areas during activity at Site 2 and resting at Site 1. Another example of use of modified elements of the landscape was recorded at Site 2, where 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. tricinctus,* 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 et al. 2010) in Northeast Brazil. Hence, even though three-banded armadillos show a strong selection for 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. Over a couple of weeks of sugar cane plowing, we saw at least three armadillos (2 *D. novemcinctus* and 1 *E. sexcinctus*) 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 source-sink dynamic 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 relative selection strength in units closer to paths. Indeed, sightings and captures of this species and its congener on dirt roads have been repeatedly reported for other areas (e.g. Meritt 2008, Bocchiglieri et al. 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 stated that this selection was likely due to the greater stability of these areas when compared to the inner part of plantations, which were 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 because they have become a conspicuous and abundant element in many landscapes (Beyer et al. 2014). The selection of human-built linear features, such as unpaved roads, has been recorded mostly for large carnivores (e.g. African wild dogs

Lycaon pictus and wolves *Canis lupus*; Gurarie et al. 2011, Latham et al. 2011, Abrahms et al. 2015). Nevertheless, small mammals (e.g. black-eared opossums *Didelphis aurita*) have been recorded to use guidelines such as plantation rows 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 them 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 their legs moving rapidly “like a clockwork toy” (Smith 2007). Like other armadillo species, they can be very noisy when moving through vegetation due to the displacement of foliage that is pushed by their 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 dog presented increasing selection strength for unpaved roads (Abrahms et al. 2015). Relative landscape permeability could also explain the high relative selection strength for pasture areas during activity at Site 2. As 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 requirements 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 ± 82.9 ha) with those reported by Barrientos & Cuéllar (2004) for *T. matacus* inhabiting areas of the Bolivian Chaco (14 ha) are not useful, 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 ± 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 having more generalist habits, such as *E. sexcinctus* (4.4kg, 17±23ha; 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, similarly to the pattern observed here.

Although little is known about the mating behavior of this genus, our results point 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, as 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 in 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 oestrus. In a long-term monitoring project with *D. novemcinctus*, McDonough (2000) reports that females tend to pair with males with high overlap of their home range. Thus, reproductive success three-banded armadillo males could be associated with body mass, because 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 oestrus, has been reported for *T. matacus* congener, *T. tricinctus* (Bernier 2003, Bocchiglieri et al. 2010, Marini-Filho & Guimarães 2010).

For mammal species, female spacing is typically dictated by resource abundance and distribution, different from males (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 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). As 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 nursling 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 (pers. obs.). 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 on rare occasions of extreme cold and in a temporary manner (Meritt 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.

Males of *T. tricinctus* also present larger home range areas (238 ±103 ha) than those of adult females (24 ±12 ha; Guimarães 1997). The similarities with the spatial patterns reported 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 encounters between two adult females contradicts 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 over years, granting them opportunity for the establishment of short and long-term social relationships (Loughry & McDonough 2001, McDonough & Loughry 2008). However, kinship analyses 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 suggest 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 them 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 sniff her. However, the female walked away each 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 on multiple occasions, the previously described reproductive behavior for this genus consisted only of 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 moving 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. Even though we monitored animals for a relatively short period, our intensive monitoring methods allowed us 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. Its home range and spacing patterns point 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 at two sites in the Pantanal of Brazil, from November 2014 until August 2015**.**

Table 3. Individuals of *Tolypeutes matacus* monitored at two sites in the Pantanal of Brazil. Animals were monitored at Site 1 from November 2014 until April 2015 and at Site 2, from June 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), subadult (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
Mean		**-**	**-**		**2,919**		**-**	**17.4**	**2,079**	**64.09**	**65.62**

Appendix 2.

Table 4. Estimates of the Step Selection Function of ten individuals of *Tolypeutes matacus* tracked at Santa Tereza ranch (Site 1), between November 2014 and March 2015.

	Status	**Coef**	**Exp (Coef)**	**SE (Coef)**	**Robust SE**	**z**	**Pr(>|z|)**	**Lower 95**	**Upper 95**
Forest	active	0.506062	1.658746	0.067343	0.082037	6.169	<0.01	1.4124	1.948
	inactive	0.729341	2.073714	0.243058	0.258083	2.826	<0.01	1.2505	3.439
Pasture	active	0.167865	1.182777	0.20736	0.14427	1.164	0.245	0.8915	1.569
	inactive	0.536118	1.709359	0.574863	0.417229	1.285	0.198	0.7545	3.8724
Grassland : Paths	active	-0.01007	0.989981	0.001216	0.001572	-6.408	<0.01	0.9869	0.993
	inactive	-0.0156	0.984517	0.00344	0.003072	-5.079	<0.01	0.9786	0.9905
Forest : Paths	active	-0.00254	0.997462	0.000361	0.000254	-10.024	<0.01	0.997	0.998
	inactive	-0.00906	0.990986	0.001221	0.00115	-7.874	<0.01	0.9888	0.9932
Pasture : Paths	active	0.000361	1.000361	0.000417	0.000252	1.436	0.151	0.9999	1.001
	inactive	-0.00493	0.99508	0.00173	0.001652	-2.986	<0.01	0.9919	0.9983

Table 5. Estimates of the Step Selection Function of eleven individuals of *Tolypeutes matacus* tracked at Duas Lagoas ranch (Site 2), from July to August 2015.

	Status	**Coef**	**Exp (Coef)**	**SE (Coef)**	**Robust SE**	**z**	**Pr(>|z|)**	**Lower 95**	**Upper 95**
Forest	active	1.491275	4.442755	0.244296	0.262758	5.675	<0.01	2.6546	7.4355
	inactive	2.104105	8.199764	0.717631	0.578067	3.64	<0.01	2.6409	25.4597
Pasture	active	0.868681	2.383765	0.191603	0.232549	3.735	<0.01	1.5112	3.7602
	inactive	0.656393	1.927826	0.551114	0.469341	1.399	0.161	0.7684	4.8369
Surgar Cane : Paths	active	-0.01692	0.983223	0.004927	0.005847	-2.894	<0.01	0.972	0.9946
	inactive	-0.02197	0.978268	0.014737	0.011388	-1.929	0.053	0.9567	1.0003
Forest : Paths	active	-0.01938	0.98081	0.004821	0.003451	-5.615	<0.01	0.9742	0.9875
	inactive	-0.00667	0.993357	0.00876	0.004897	-1.361	0.173	0.9839	1.0029
Pasture : Paths	active	-0.01684	0.983306	0.000713	0.000855	-19.7	<0.01	0.9817	0.985
	inactive	-0.02119	0.97903	0.002585	0.00313	-6.772	<0.01	0.973	0.9851

Appendix 3.

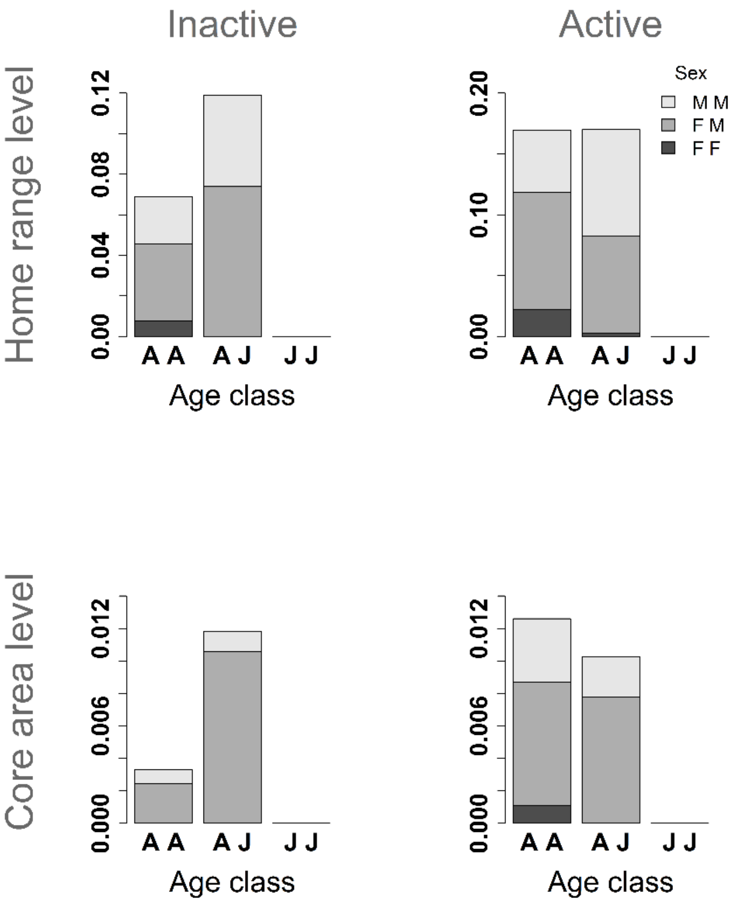


Figure 8. Joint distribution probability of pairs of *Tolypeutes matacus* of different sex and age classes, according to the UDOI index. We divided our dataset according to the activity status of the individuals ("Active" or "Inactive") and estimated the probability of space use sharing at the home range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

Appendix 4.

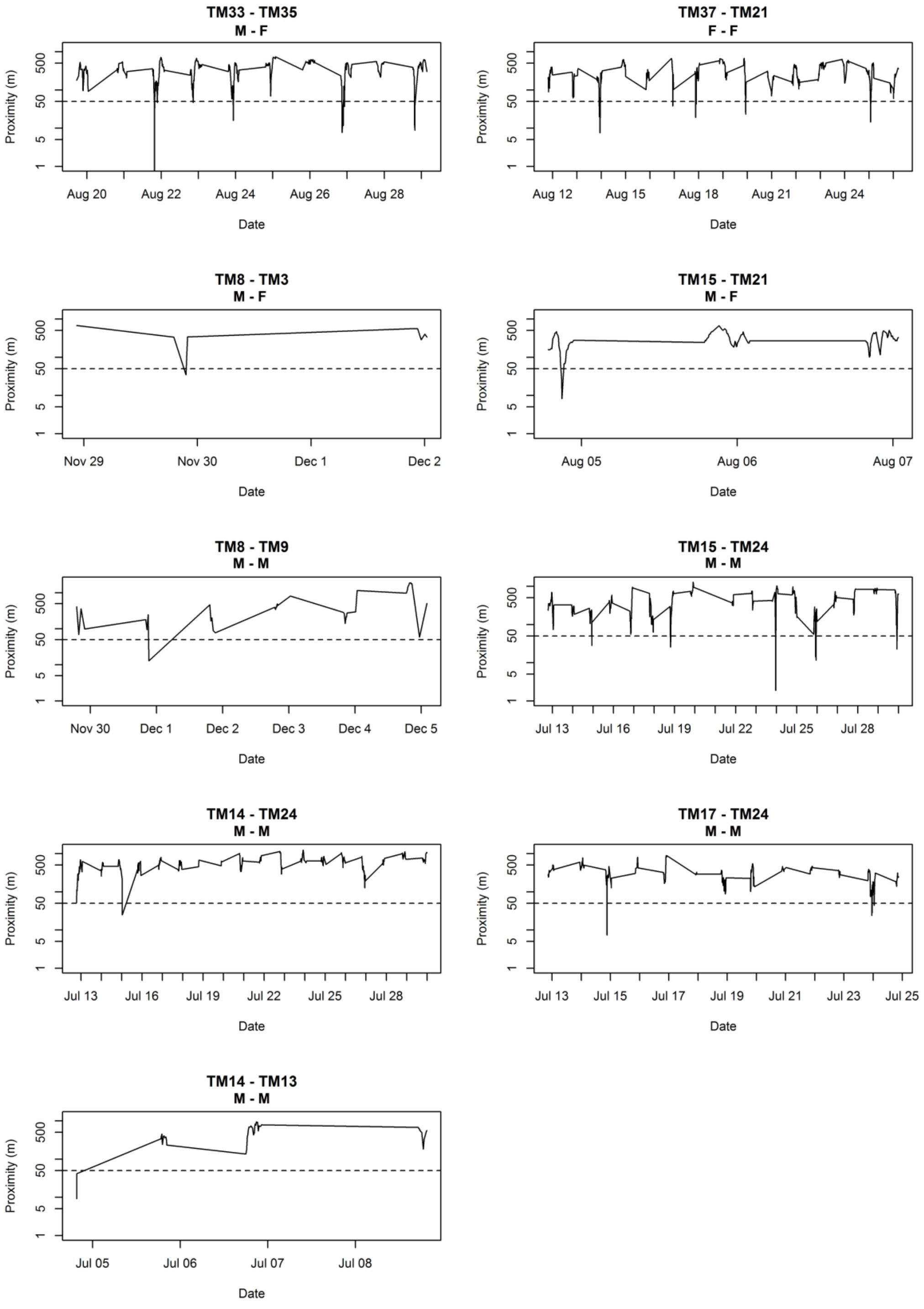


Figure 9. Proximity and encounters (distances below 50 m) between nine dyads of simultaneously monitored *Tolypeutes matacus* at two sites in the Pantanal of Brazil, from November 2014 until August 2015. Individual identification and sex of each individual of the dyad.

Table 6. 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 aimed to evaluate how air temperature is related to variation 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*) at three sites of the Pantanal wetlands, Brazil. We used linear mixed-effects models to evaluate the variation in the timing and duration of activity patterns according to changes in air temperature. We fitted Step Selection Functions to evaluate the effects of cover type, diel cycle, and air temperature on armadillo resource selection. Our models suggest that *E. sexcinctus* activity during the daytime decreases as air temperature increases. In contrast, *T. matacus* shows less variation in its activity pattern at different air temperatures, maintaining a predominantly nocturnal activity pattern. However, as air temperature decreases, activity periods of *T. matacus* are of shorter duration and peak earlier in the day. Both species should select forested areas when experiencing air temperatures outside their thermoneutral zones. 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 behavior to achieve adequate thermoregulation.

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

Resumo

Neste estudo tivemos 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 fornecem 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 funções de "Step Selection" para avaliar os efeitos do tipo de cobertura vegetal, ciclo circadiano e temperatura do ar na seleção de recursos pelos tatus. Nossos modelos sugerem que a atividade diurna de *E*, *sexcinctus* diminui a medida que a temperatura do ar aumenta. 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. Ambas as espécies tendem a selecionar áreas florestadas quando submetidas a temperaturas fora de sua zona de termoneutralidade. 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 alterar 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). Following the global trend, the estimated mean warming for the Pantanal wetlands of Brazil ranges from 5–7°C until the end of this century (Marengo et al. 2016).

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). In general, behavioral decisions are guided by trade-offs between gaining access to resources and minimizing negative effects (e.g., physiological stress), ultimately maximizing individual fitness. In addition, even though we cannot know if species will be able to adapt fast enough to keep up with the rapid pace of climate change, adaptive responses could involve either micro-evolution and/or plasticity (which can provide shorter term responses; Bellard et al. 2012). Besides micro-evolutionary physiological adaptations, behavioral changes may involve both timing of activity and selection of habitats (Tattersall & Cadena 2010; Bellard et al. 2012, Gunderson & Leal 2016).

Changes in the use of space can be accomplished through large-scale movements, e.g. migration, or finer scale movements, e.g. habitat and microhabitat selection (Bellard et al. 2012). Habitat selection is a dynamic process that is likely to be influenced by a variety of temporally variable factors, like temperature (Sunde et al. 2014). Furthermore, diel cycles of activity allow animals to modulate their behavior according to predictable environmental changes and to choose the appropriate time for a given response or activity (Aronson et al. 1993). Ambient temperature can exert strong, direct, short-term effects on endogenous circadian rhythms, altering diel activity patterns (Rietveld et al. 1993).

The superorder Xenarthra (Mammalia) comprises armadillos (Cingulata), anteaters and sloths (Pilosa) and contains some of the most morphologically specialized terrestrial extant mammals (Möller-Krull et al. 2007). Armadillos possess low body temperatures (32.7 to 35.5°C), low basal metabolic rates (~50% of what would be expected for a non-xenarthran placental mammal with similar body mass), and high thermal conductance (130-200% of what would be expected for a non-xenarthran placental mammal with similar body mass). Like the other xenarthrans, armadillos are considered imperfect homeotherms. That is, even though armadillos are able to generate body heat like other placental mammals, they have a limited capacity to regulate it (McNab 1985). Armadillos build burrows that they use to rest, to shelter from predators, and to avoid adverse environmental conditions (McDonough & Loughry 2008). Animals that take refuge when conditions are not suitable for activity are good models for understanding how thermal constraints can affect animal behavior (Gunderson & Leal 2016). As burrowing imperfect homeotherms, armadillos should present conspicuous behavioral responses (entering or exiting burrows) to air temperature changes and, as such, are valuable models for understanding how physiology affects decision-making in mammals (Maccarini 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 thermoneutral zone is defined as the ambient temperature range where the animal's metabolic rate is independent of temperature (McNab 2002). The increased thermal conductance provided by the presence of the carapace, results in an increase of armadillos’ lower limit of thermoneutrality and leads to small differences between body temperature and environment (McNab 1985, 2002). Because this lower-limit is high in armadillos, the ambient temperature is often below it, even in tropical regions. Consequently, armadillos often need to expend more energy to keep their body heat than if the ambient temperature were within their narrow thermoneutral zone (McNab 1985).

Metabolic thermoregulation is especially costly from an energetic standpoint (Liwanag 2010), especially for these low metabolism imperfect homeotherms. To reduce such energetic costs, xenarthrans can adopt 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 screaming hairy armadillos (*Chaetophractus vellerosus*), giant anteaters (*Myrmecophaga tridactyla*) and yellow armadillos (*Euphractus sexcinctus*) as responses to temperature variation (e.g., Greegor 1985, Mourão & Medri 2007, Maccarini et al. 2015).

Here, we aim to test if air temperature drives variation 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) that has a basal metabolic rate of 42% and a thermal conductance of 172% of what would be expected for a non-xenarthran placental mammal of its size (McNab 1985). It is found in open areas, savannas, shrublands, dry and semi-deciduous forests (Eisenberg & Redford 1999). Roig (1969) proposed that 30°C would be its optimal ambient temperature, and the graphical inspection of Figure 2D of the work of McNab (1980) indicates that its thermal neutral zone ranges from 26°C to about 34°C. In addition, *E. sexcinctus* has been recorded active at instant air temperatures between 13.2 and 36.2°C in the Pantanal wetlands of Brazil (Maccarini et al. 2015; see methods section for area description).

In contrast, the southern three-banded armadillo (*T. matacus*) is restricted to the dry forests of western Brazil, Bolivia, Paraguay and Argentina (Wetzel et al. 2008). 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). It has one of the lowest basal metabolic rates amongst armadillos (31% of what would expected for a mammal of its size) and a thermal conductance of 133% of expected (McNab 1980). When resting, it can use burrows and other types of shallow shelters (Attias et al. 2016). In the studied areas, this species is mostly nocturnal (Attias et al. unpublish. data), though its activity pattern may be primarily influenced by temperature and rainfall (Eisenberg & Redford 1999). To date, many aspects of its biology and ecology are poorly known. Eisentraut (1932) stated that between 16°C and 28°C, *T. matacus* maintains a constant body temperature of about 32°C, but its body temperature increases if the ambient temperature becomes higher than 28°C. However, the graphical inspection of Figure 1A of McNab (1980) indicates that the thermal neutral zone of *T. matacus* ranges from 28°C to about 34°C.

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

Furthermore, even though both species face similar thermoregulatory constraints, they present subtle physical (i.e. body mass, carapace anatomy), physiological (i.e. thermal conductance), and ecological (i.e. diet specialization, predation susceptibility) differences. Hence, the two species can present distinct 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 need to be more flexible in relation to its activity period than *T. matacus.* This would be due to *E. sexcinctus*' relatively higher thermal conductance and tendency to forage in open habitats, which could make it more vulnerable to temperature variations. This could potentially alter the degree of overlap of the temporal niche dimension between species.

Methods

Study area

This study was carried out at three sites, 120 to 350 km apart, located in the Pantanal wetlands of midwestern Brazil (Fig. 1). The Pantanal is a large Neotropical wetland, extending 210 000 km^2 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^2 and altitude of 98 m.a.s.l. (Fig. 1), located in Corumbá municipality, Mato Grosso do Sul state. This almost pristine landscape comprises a natural mosaic of habitat types, consisting of large natural grassland areas, permanent and temporary ponds surrounded by native grassland vegetation, savanna and woodland areas (Abdon et al. 1998, Fig. 2a). At this site, we captured and monitored *E. sexcinctus* in undisturbed areas (i.e., all above mentioned habitat types).

The Santa Teresa Ranch (Site 2) is located in the Serra do Amolar Mountain Range, in Corumbá municipality, Mato Grosso do Sul state, in the western limits of the Brazilian Pantanal (18°17’51”S, 57°30’35”W; Fig. 1). The variable relief in the area (90 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, Fig. 2b). This private property is part of the Network for the Protection and Conservation of Serra do Amolar and only 3% of its 630 km^2 were converted into exotic pasture (*Brachiaria* spp.) for cattle ranching. At this site, we captured and monitored *T. matacus* in both disturbed and undisturbed habitats.

The Duas Lagoas Ranch (Site 3; 16°10’13”S, 58°11’12”W) is located in the transition zone between the Pantanal and Cerrado eco-regions, in Cáceres municipality, Mato Grosso state (Fig.1). This 74 km^2 ranch is owned by the private company Floresteca. Its main economic activity is a teak plantation (*Tectona grandis*; 42 km^2), but there are also areas of exotic pasture (*Brachiaria* sp.) dedicated to cattle ranching (12 km^2) and a small sugarcane plantation (0.24 km^2, Fig. 2c). Besides these areas, the ranch encompasses 16.3 km^2 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 (taken in 2011), the habitat types of the study areas were summarized into habitat categories as follows: forest, grassland (combining exotic and native grasslands in one category), shrubland and 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. We used this classification to make inferences about the density of arboreal vegetation cover at each habitat type and their potential temperature buffering effect. We considered forested areas as areas of high arboreal cover and temperature buffering potential (*sensu* Mourão & Medri 2007); areas of shrubland and sugar cane plantation as areas with intermediate arboreal cover and comparatively lower temperature buffering potential; and grassland areas as areas with reduced or no arboreal cover directly subjected to daily fluctuations of temperature.

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

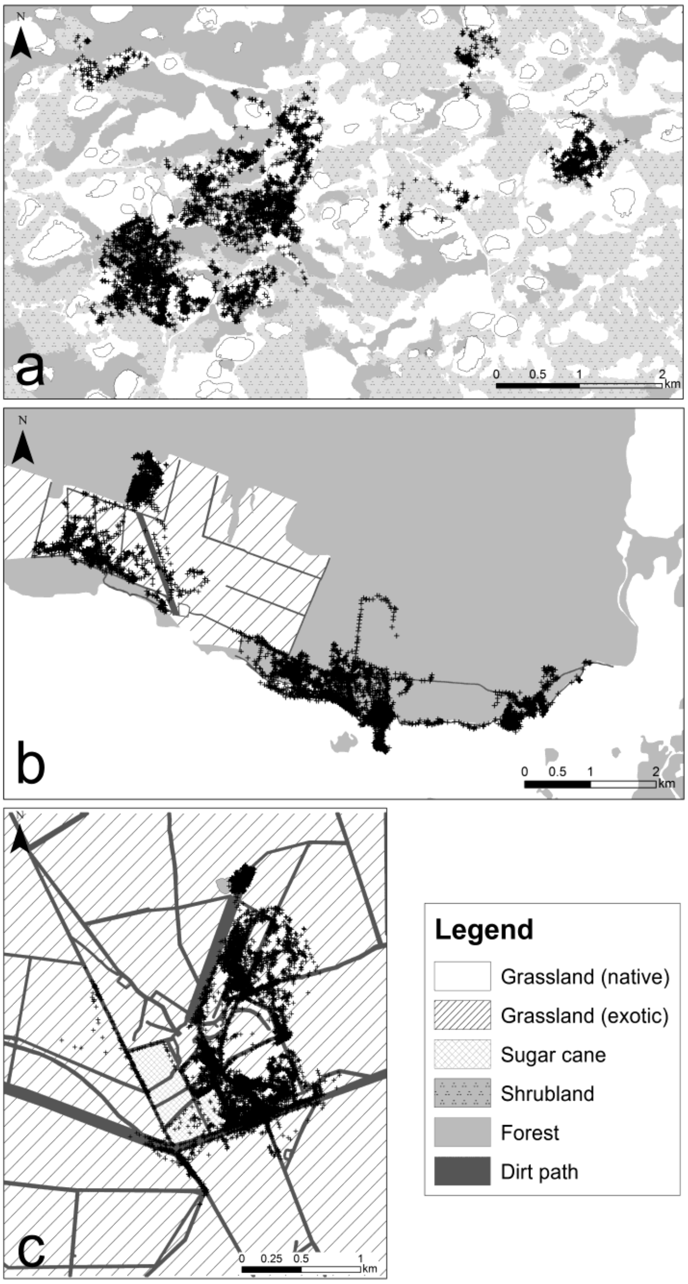


Figure 2. Locations of the monitored species (+) in different habitat categories at each study site. (a) Locations of individuals of *Euphractus sexcinctus* monitored at Site 1 between March and August 2014. (b) Location of individuals of *Tolypeutes matacus* monitored at Site 2 between November 2014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

Ethical note

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

Capture and tracking methods

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

Captured animals were temporarily contained in ventilated plastic boxes or cloth bags until processing. Information on age, sex and mass were obtained for each individual. We equipped the animals with a package containing a glue-on VHF radio (model R1920, Advanced Telemetry Systems, Inc., Isanti, 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 shield of *T. matacus*, using flexible cyanoacrylate super glue and/or epoxy resin, following a protocol commonly used for hard-shelled turtles (e.g., Seminoff 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, assess animal welfare, and to locate resting sites.

Even though all the procedures described above could be accomplished under physical restraint, some of the animals were anaesthetized through an intramuscular injection in the hind limbs to enable the collection of biological samples used in other studies simultaneously carried out in the area. 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*, Xylazine 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; Gasparotto et al. 2017).

Activity

To define the activity status of armadillos throughout the GPS tracks, we used an adaptation of the Residence Time method (Barraquand & Benhamou 2008). Active periods were characterized as the time-period an individual was not inside its shelter and was moving. Each time an individual exited a shelter, moved, and returned to a shelter was scored as an activity bout. We characterized the bout duration as the time elapsed between consecutive events of shelter exiting and shelter entering by the same armadillo. Thus, the total activity duration per day was the summed duration of all activity bouts during a 24-hour period. Because *T. matacus* was predominantly nocturnal, we estimated the total activity duration for this species as the sum of bout durations from noon of one day, until 11:59 am of the next day. Because *E. sexcinctus* is mostly diurnal/crepuscular, total activity duration for this species was estimated as the sum of bout durations from midnight until 11:59 pm of the same day.

A linear mixed-effects model (LME) was fitted to test the fixed effect of mean daily air temperature on total activity duration per day. 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. LME models were implemented through the function 'lme' of the R package 'nlme' (Pinheiro et al. 2016).

Temperature measures were taken hourly at each day of animal monitoring by automatic stations of the Brazilian National Institute of Meteorology (INMET) located in the municipality of each study site (Corumbá station, for Sites 1 and 2, and Cáceres station, for Site 3). In the abovementioned analysis, we evaluate the relationship between daily average air temperature and total daily activity duration (i.e., one measure of activity per day).

To evaluate the relationship between activity probability and hourly air temperature along the diel cycle, we first sub-sampled the individual trajectories to fixes matching one-hour intervals. The distance moved during 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. The square-root transformation of the distances moved was adopted to represent the activity index because it better captures the activity information associated with short steps, usually recorded when the armadillos were engaged in encamped activities. Also, this transformation facilitated normalization of the model residuals. When this distance was equal to zero, it was assumed that the animal was inactive during that 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 also used to build this second model and evaluate variations in the activity index along the diel cycle according to hourly changes in air temperature. Time of day was included in the model using harmonics to allow a nonlinear relationship between time of day and activity index (*sensu* Forester et al. 2009). We included two terms (c1 = cosine 2π, s1 = sine 2π) that interacted with hourly air temperature for each hourly fix of each individual. These interactions allowed us to disentangle the potential confounding effects between temperature and time of day. Hence, for each species we fitted a model that included the random nested effects of individual identity and the auto-correlation structure between consecutive steps of the same individual. For this analysis, we used hourly temperature values for each day of animal monitoring, taken from the same INMET stations for each study site, as previously described. This approach allowed us to evaluate activity thermal thresholds, changes in activity probability and activity vigor, following the conceptual framework proposed by Gunderson & Leal (2016).

Habitat selection

We used Step Selection Function (SSF; Fortin et al. 2005, Forester et al. 2009) to evaluate the effects of cover type, diel cycle, and air temperature on the resource selection of the studied species. Following Forester et al. (2009) and Avgar et al. (2017), we define “Relative Selection Strength” (RSS) as the effect size (i.e., exponential coefficients) of these SSF.

First, we subsampled the individual trajectories composed of 5 min fixes to fixes with 30 min intervals. Individual trajectories were decomposed into two components: step length and turning angle. Step length was defined as the straight-line distance between two consecutive locations and turning angles as the angular deviations between headings of two consecutive steps (Turchin 1991). To account for changes across space in resource availability, we generated 30 random steps originating from the starting location of each observed individual step. Random steps were generated by sorting independent random samples from the observed distribution of step lengths and turning angles of each individual (Oliveira-Santos et al. 2016). For each observed and random step of each individual, we recorded the hour of the day, the instantaneous air temperature (hourly measures) and the habitat type at the step's ending point. The time of day was included in the SSF to allow a nonlinear relationship between time of day and selection strength. This was implemented using harmonics, which were allowed to interact with cover type and temperature for each step from each individual. These interactions allowed us to verify the effect of temperature on the selection of habitat types by armadillos.

Thus, we fitted three SSF models in increasing order of complexity:

(Model 1) Cover type

(Model 2) Cover type + Cover type : Time of the day

(Model 3) Cover type + Cover type : Time of the day : Air temperature

SSF models were fitted using a Conditional Logistic Regression (CLR) using the function 'clogit' in the package 'survival' (Therneau 2015) in R. CLR models were conditioned to each step within individual (where observed steps were scored as 1 and random steps were scored as 0). We used Akaike 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 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 (as defined by Eisentraut (1932), and McNab (1980) for each species) and the historic range of temperatures recorded in the study areas (-1.6°C to 43°C, from 1985 until 2013; INMET). Also, because we were interested in evaluating how these imperfect homeotherms would deal with the temperatures changes expected in a global climate change scenario, we extrapolated minimum and maximum temperatures (not frequently experienced by the animals) when plotting the models. Finally, to enable a clear visualization of how activity probability varies along the day, we fixed one of the model parameters, the air temperature, and used a regular interval of 10°C between modeled temperatures.

Results

Individuals of *E. sexcinctus* were monitored for an average of 10 days (3-27 days) and *T. matacus* for 17 days (4-32 days; Appendix 1). With the sampling protocol of five-minute interval between fixes, *E. sexcinctus* had an average of 816 locations per individual (169-2 129), totaling 13 885 locations for this species. *Tolypeutes matacus* presented an average of 2 919 (218-8 248) locations per individual, totaling 61 303 locations. From these, 8 067 locations were assigned as activity records of *E. sexcinctus*, in 304 activity bouts, and 21 515 as activity records of *T. matacus*, in 617 activity bouts.

Activity

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). Our models suggest that variability in daily activity duration of *E. sexcinctus* was not explained by daily mean air temperature (t 103 = 1.44, P = 0.15). However, time of day and hourly air temperature interacted to explain the activity index (t 1 165 = 2.14, P = 0.03). Thus, our second LME model indicates that *E. sexcinctus* activity during the daytime decreases as air temperature increases (Fig 3a). At modeled air temperatures up to 30°C, *E. sexcinctus* would tend to be diurnal, with higher activity probability near noon. At intermediate temperatures (35 - 40°C), this species could be found active either at daytime or nighttime (Fig. 3a). At higher air temperatures (> 40°C), activity behavior could potentially switch and *E. sexcinctus* would tend to increase its nocturnal activity, especially in the first half of the night (Fig. 3a).

Figure 3b shows how temperature varied in the study area, both during the day (minimum amplitude = 1.4°C; maximum amplitude = 11.5°C) and between days (range of mean daily temperatures = 16 – 30°C).

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

Habitat Selection

Individuals of *T. matacus* and *E. sexcinctus* used all available habitat types in their study areas. There was almost 100% evidence (AICcWt = 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 hourly air temperature (Tables 1 and 2, respectively; see Appendix 2 and 3 for model coefficients).

The best model suggests that at air temperatures of 25°C, close to the lower limit of its thermoneutral zone, *E. sexcinctus* would use forests according to availability, irrespective of time of day (Fig. 3c). If experiencing air temperatures close to the upper limit of its thermoneutrality (35°C) or higher (45°C) during the warmest hours of the afternoon, *E. sexcinctus* would be expected to select the buffered forest areas and avoid them during the remaining hours of the day. If temperatures under its thermoneutral zone (15°C) were to be experienced during the nighttime, when activity probability is low (Fig. 3a), or in the early morning, *E. sexcinctus* would select the buffered forest areas (Fig. 3c), and it should also be sheltering in its burrows. The model suggests that the pattern of selection of shrubland areas would be similar to that observed for forests. However, when compared to forests, there would be less variability at different air temperatures and at different times of day (Fig. 3d). Finally, the model suggests that when *E. sexcinctus* experiences air temperatures within its thermoneutrality (25°C and 35°C) and above (45°C) during daytime, grassland areas would be used according to availability (Fig. 3e). However, if the same range of air temperatures were to be experienced after the sunset, grassland areas would be positively selected. In contrast, the model suggests that, at chilly temperatures (15°C), grassland areas would be slightly avoided by *E. sexcinctus* at all times of day (Fig. 3e).

Air temperature in the study areas of *T. matacus* reached its daily peak in the mid-afternoon and its lowest values right before sunrise. The best model suggests that, in most cases, the selection strength of different habitats by *T. matacus* tends to vary with the time of day and instant air temperature (Fig. 4). The model suggests that buffered forest areas would tend to be selected by *T. matacus* at the most extreme temperature scenarios, i.e. if air temperatures of 45°C were to be experienced during the daytime or if temperatures of 15°C were experienced during the nighttime (Fig. 4c). If temperatures of 15°C or 25°C were to be experienced by *T. matacus* at any time of day, it would tend to avoid sugar cane plantations (Fig. 4c). However, a positive selection of sugar cane plantations would be expected if warmer temperatures (35°C or 45°C) were experienced during the nighttime, when animals are expected to be active and out of their shelters. Finally, the model suggests an almost inverse pattern of selection for grasslands when compared to that encountered for forest areas (Fig. 4e). *Tolypeutes matacus* should select grassland areas either during the daytime, when experiencing low temperatures (15°C) or, after sunset, when experiencing warmer temperatures (35°C or 45°C). At intermediate temperatures of about 25°C, which are likely to fall within its thermoneutral zone, the model suggests that grassland areas would be used according to their availability.

Table 1. Ranking of the three competing Step selection function models fitted to characterize resource selection of *Euphractus sexcinctus*. Models account for the effects of vegetation cover type, diel cycle variation (time of day) and hourly air temperature. Number of parameters (K), relative difference between models (ΔAIC), weight of the model (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.

Model	**K**	**ΔAIC**	**AICc Wt**	**Cum Wt**	**LL**
Cover type + Cover type : Time of day : Air temperature	23	0	1	1	-14 743.96
Cover type + Cover type : Time of day	11	17 160.49	0	1	-23 336.21
Cover type	3	17 213.13	0	1	-23 370.54

Table 2. Ranking of the three competing Step selection function models fitted to characterize resource selection of *Tolypeutes matacus*. Models account for the effects of vegetation cover type, diel cycle variation (time of day) and hourly air temperature. Number of parameters (K), relative difference between models (ΔAIC), weight of the model (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.

Model	**K**	**ΔAIC**	**AICc Wt**	**Cum Wt**	**LL**
Cover type + Cover type : Time of day : Air temperature	29	0	1	1	-87 108.41
Cover type + Cover type : Time of day	14	32.27	0	1	-87 139.54
Cover type	4	52.64	0	1	-87 158.73

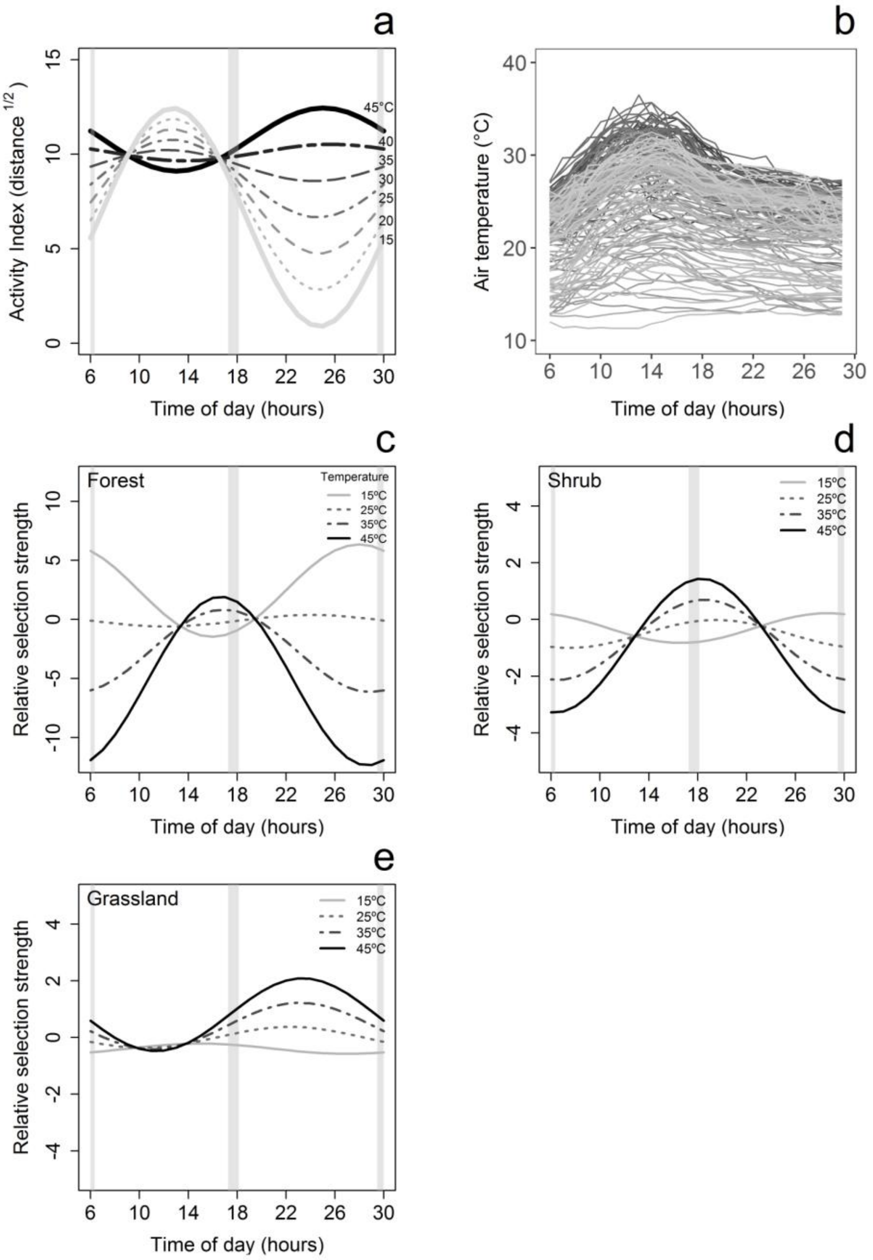


Figure 3. Models of activity pattern and relative habitat selection strength by *Euphractus sexcinctus* throughout the day, at different air temperatures. (a) Activity index probability estimates throughout the day at varying instant air temperatures according to LME model. (b) Daily variation of air temperature at the study site during the study period. Selection strength of (c) forests, (d) shrublands, and (e) grasslands at four air temperature scenarios according to the best fit model (see Table 1 and Appendix 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 17 armadillos tracked at Site 1 (see Fig.1), from March to August 2014.

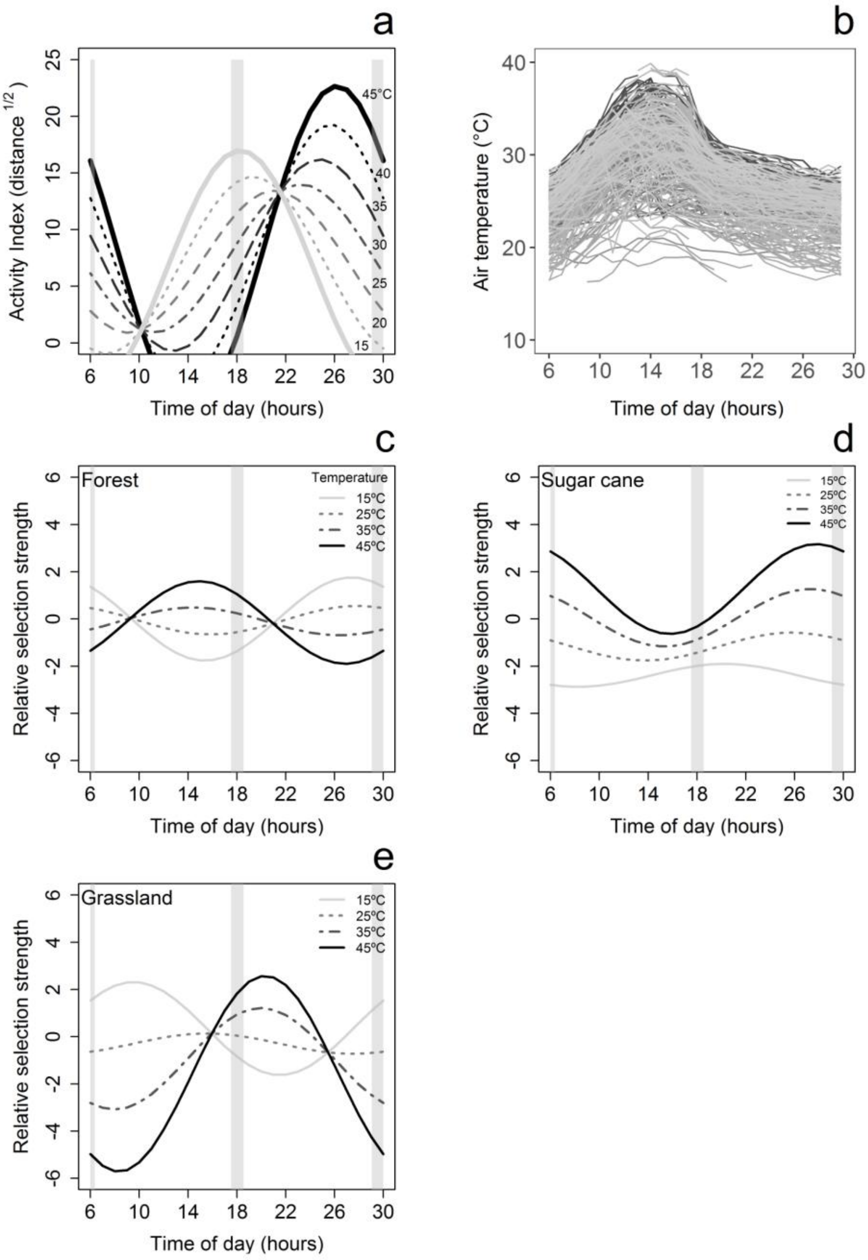


Figure 4. Models of activity pattern and relative habitat selection strength by *Tolypeutes matacus* throughout the day, at different air temperatures. (a) Activity index probability estimates throughout the day at varying instant air temperatures according to LME model. (b) Daily variation of air temperature at both study sites during the study period. Selection strength of (c) forests, (d) grasslands, and (e) sugar cane plantations at four air temperature scenarios according to the best fit model (see Table 2 and Appendix 3). 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 diel activity and habitat selection for these imperfect homeotherms.

The influence of air temperature on activity has been reported for other imperfect homeotherms, such as anteaters, sloths, echidnas, pangolins and other armadillos (McNab 1980, Greegor 1985, 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 (i.e., at warmer hours of the day) in cold winters and more nocturnal in summers (Greegor 1985, Layne & Glover 1985, Pietersen et al. 2014). *Tolypeutes matacus* and *E. sexcinctus* have a mainly tropical distribution (Feijó et al. 2015) and are physiologically adapted to relatively warm air temperatures (Eisentraut 1932, Roig 1969, McNab 1980). Our studied species also tend to adjust their activity behavior as a function of air temperature and seem to vary their activity behavior on a scale of days. 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.

Because armadillo burrows can buffer the external air temperature and work as thermal shelters (Maccarini et al. 2015), the decision to remain inside or leave a burrow constitutes a behavioral thermoregulation strategy for armadillos. Hence, as in other armadillo species, the short activity duration of the studied species, and the tendency to have 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).

Once an animal makes a decision to leave its thermal shelter, i.e. timing of activity, it can engage on different types of activity and adopt additional strategies of behavioral thermoregulation, like choosing the most appropriate habitat feature to perform its activities (Gunderson & Leal 2016). Our models indicate that, besides the variation in activity patterns, temperature can also be related to changes in habitat selection by armadillos. The influence of temperature on the activity behavior and relative 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).

Regardless of their timing of activity, models indicate that *E. sexcinctus* tends to avoid forests while active, but it tends select them while inactive (as suggested by Medri 2008). 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 low body temperature of 34.2°C, mean that *E. sexcinctus* can be very susceptible to air temperature changes (Maccarini et al. 2015). Furthermore, the tendency to be active in open vegetation areas makes this species especially susceptible to gain heat through direct exposure to solar radiation or to radiative heat loss on cold nights. Hence, the reliance on burrow use for thermoregulation should be especially conspicuous for *E. sexcinctus*. This would result in more variability in diel activity patterns when compared with *T. matacus*, as our models indicated. The tendency to avoid forests during activity could indicate that *E. sexcinctus* tends to handle air temperature variation mostly through activity behavior variation. Alternatively, it could be related to predator avoidance, because 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). In addition, if the limits of thermoneutrality of *T. matacus* proposed by Eisentraut (1932; 16-28ºC) represented the species' physiology at our study sites, this could explain the comparatively smaller variability in the diel activity patterns of *T. matacus* and the predominantly nocturnal activity suggested by the models.

The models for *T. matacus* indicate that they could select forests for both activity and resting, depending on air temperature. Their relatively higher flexibility in habitat selection, when compared to *E. sexcinctus*, could be due to its comparatively thicker carapace and its defensive behavior of rolling into a ball, which grants *T. matacus* fewer natural predators. It is likely that only large carnivores, such as jaguars and manned wolves, can overcome *Tolypeutes* defenses. *Tolypeutes* stand out for having one of the lowest body temperatures (33°C) and metabolic rates (31% of what would expected for a mammal of its size) amongst armadillos, probably due to their 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. Besides being thicker, the carapace of *Tolypeutes* covers a much larger proportion of the body (leaving only the distal extremities of its limbs exposed to environmental conditions) when compared to other armadillo species (M. Superina pers. comm., August 2017). In addition, when the carapace is closed or partially closed, the air trapped between the body and the carapace can further reduce thermal conductance (McNab 1985). However, 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. This could also explain their comparatively shorter activity duration on colder days. Nevertheless, this assumption should be further explored for *T. matacus* by evaluating the variation in body and shelter temperature as functions of air temperature variation (e.g. Camilo-Alves & Mourão 2006, Maccarini et al. 2015).

As air 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 could adopt different behavioral responses to air temperature variation. As daily temperature increases *E. sexcinctus* tends to adopt a more nocturnal behavior (like *T. matacus* already has) whereas *T. matacus* tends to forage in open vegetation areas (like *E. sexcinctus* already does). These changes potentially increase the overlap of the temporal and spatial niche dimensions between the two species, setting the stage for a potential increase in 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 on hot days. The buffering effect should be proportional to arboreal vegetation cover, granting shrubland and sugar cane areas an intermediate level of temperature buffering, when compared to forest and grassland areas. Hence, imperfect homeotherms could select 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 in many other parts of South America, one of the main threats to the conservation of the Pantanal is habitat conversion. More than 40% of the forest and savanna habitats have been altered for cattle ranching through the introduction of exotic grasses in the Pantanal (Harris et al. 2005), and if conversion rates continue to follow the historic trend, a complete loss of native vegetation can be expected by 2045 (Silva et al. 2011). 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, because 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 burrowing imperfect homeotherms, armadillos should present a conspicuous response to temperature variation. Here, we provide a specific example of the dynamic nature of activity patterns and habitat selection and illustrate how thermal constraints vary over the diel cycle and among days. More generally, models like those presented here can be used to better understand the consequences of climate change on animals inhabiting Neotropical savannas, highlighting the importance of habitat heterogeneity for the long-term conservation of animal species in a scenario of global climate change.

Appendix 1

Individual information on animals captured for the study and monitoring effort.

Table 1. Individuals of *Euphractus sexcinctus* (ES) and *Tolypeutes matacus* (TM) monitored at three sites in the Pantanal of Brazil. Here we present information on: Study site (Site) - 1 (Nhumirim Ranch), 2 (Santa Teresa ranch), 3 (Duas Lagoas ranch); Sex of individuals - male (M), female (F); Age class - adult (A), subadult (S) and juvenile (J); Body mass (kg); Number of locations obtained through GPS telemetry (N Locations (GPS)); Date of first animal capture (Date of capture); Total monitoring time span; Absolute number of days that the animal was tracked with GPS telemetry.

	Species	Id	Site	Sex	Age class	Body mass (kg)	N Locations (GPS)	Date of capture	Monitoring time span (days)	GPS Tracking period (days)
1	ES	ES01	1	M	A	4.9	169	02-feb-14	4	4
2	ES	ES02	1	F	A	4.62	506	07-mar-14	131	11
3	ES	ES03	1	F	A	4.96	212	09-mar-14	4	3
4	ES	ES05	1	F	A	4.36	530	12-mar-14	6	6
5	ES	ES06	1	F	A	5.96	1,331	13-mar-14	21	21
6	ES	ES07	1	M	J	1.6	944	15-mar-14	14	14
7	ES	ES08	1	M	A	4.46	1,069	16-mar-14	154	17
8	ES	ES09	1	F	A	5.42	1,949	17-mar-14	127	27
9	ES	ES10	1	F	A	3.32	264	18-mar-14	4	4
10	ES	ES11	1	M	A	4.02	340	19-mar-14	13	7
11	ES	ES12	1	M	A	3.8	1,141	20-mar-14	16	16
12	ES	ES13	1	M	A	4.72	195	19-apr-14	6	6
13	ES	ES15	1	M	A	4.78	1,087	23-apr-14	119	19
14	ES	ES17	1	M	A	5.12	591	04-jun-14	11	11
15	ES	ES18	1	F	A	4.86	2,129	10-jun-14	21	17
16	ES	ES19	1	M	A	4.96	815	07-jul-14	8	6
17	ES	ES20	1	M	A	4.82	613	10-jul-14	10	10
18	TM	TM2	2	F	S	1.04	3,256	08-nov-14	131	19.9
19	TM	TM3	2	F	A	1.24	895	11-nov-14	127.5	28.6
20	TM	TM4	2	F	S	0.62	3,040	14-nov-14	74	25.2
21	TM	TM5	2	M	A	1.3	1,799	20-nov-14	87.1	19.2
22	TM	TM6	2	M	A	1.38	2,556	22-nov-14	69.6	17
23	TM	TM7	2	F	A	1.26	351	23-nov-14	20.5	9
24	TM	TM8	2	M	A	1.62	1,664	27-nov-14	122.3	23.9
25	TM	TM9	2	M	A	1.3	263	27-nov-14	54.9	6.3
26	TM	TM10	2	F	A	1.13	1,616	24-jan-15	30.6	18.5
27	TM	TM12	2	F	J	0.61	218	25-feb-15	6.1	5.1
28	TM	TM13	3	M	A	1.41	1,078	03-jul-15	12	4.18
29	TM	TM14	3	M	A	1.23	5,396	03-jul-15	36.6	26.4
30	TM	TM15	3	M	A	1.28	8,248	04-jul-15	39.5	32.9
31	TM	TM16	3	M	A	1.26	1,197	05-jul-15	7.7	5.15
32	TM	TM17	3	M	A	1.28	4,420	05-jul-15	35.53	17.9
33	TM	TM21	3	F	A	1.28	4,664	07-jul-15	51	21.9
34	TM	TM24	3	M	S	0.73	3,705	10-jul-15	20.4	17.6
35	TM	TM30	3	F	A	0.96	5,056	23-jul-15	34.8	20.1
36	TM	TM33	3	M	A	1.19	2,632	02-aug-15	27.5	10.7
37	TM	TM35	3	F	A	1.07	4,841	10-aug-15	19.3	18.8
38	TM	TM37	3	F	A	1.13	4,408	10-aug-15	17.6	17.6
Mean TM				**-**	**-**		**2,919**		**-**	**17.4**

Appendix 2

Model coefficients of the selected Step Selection Function model used to characterize resource selection by *Euphractus sexcinctus*. Step Selection Function (SSF; Fortin et al. 2005, Forester et al. 2009) was used to evaluate the effects of cover type (savanna, forest, shrubland, grassland), diel cycle (s1, c1), and air temperature (t.ar) on the resource selection of the studied species. The time of day was included in the SSF to allow a nonlinear relationship between time of day and selection strength. This was implemented using harmonics, which were allowed to interact with cover type and temperature for each step from each individual. These interactions allowed us to verify the effect of temperature on the selection of habitat types by armadillos. SSF model was fitted using a Conditional Logistic Regression (CLR) using the function 'clogit' in the package 'survival' (Therneau 2015) in R. Here we present values of model coefficients (coef); exponential values of model coefficients (exp(coef)), standard error (se(coef)), z-score, lower (lower .95) and upper (upper .95) limits of the 95% confidence interval.

```
Call:
coxph(formula = Surv(rep(1, 72625L), pres == 1) ~ habitat + habitat:t.ar + 
    habitat:c1r + habitat:s1r + habitat:c1r:t.ar + habitat:s1r:t.ar + 
    strata(strata), data = peba.rep30, method = "exact")

  n= 46035, number of events= 9207 
   (26590 observations deleted due to missingness)

                                 coef  exp(coef)   se(coef)      z Pr(>|z|)    
habitatforest               6.267e+00  5.267e+02  1.142e+00  5.488 4.06e-08 ***
habitatgrasslands          -1.003e+00  3.667e-01  6.731e-01 -1.491 0.136069    
habitatsavanna              5.485e-03  1.006e+00  1.468e+00  0.004 0.997019    
habitatshrub:t.ar          -2.065e-02  9.796e-01  5.719e-02 -0.361 0.718020    
habitatforest:t.ar         -2.551e-01  7.748e-01  6.332e-02 -4.030 5.59e-05 ***
habitatgrasslands:t.ar      4.004e-02  1.041e+00  5.417e-02  0.739 0.459774    
habitatsavanna:t.ar                NA         NA  0.000e+00     NA       NA    
habitatshrub:c1r            6.604e-01  1.936e+00  1.556e+00  0.425 0.671201    
habitatforest:c1r           6.244e+00  5.148e+02  1.732e+00  3.605 0.000313 ***
habitatgrasslands:c1r      -8.194e-01  4.407e-01  1.428e+00 -0.574 0.566078    
habitatsavanna:c1r                 NA         NA  0.000e+00     NA       NA    
habitatshrub:s1r            1.805e+00  6.082e+00  1.529e+00  1.181 0.237694    
habitatforest:s1r           7.025e+00  1.124e+03  1.698e+00  4.138 3.51e-05 ***
habitatgrasslands:s1r       1.305e-01  1.139e+00  1.346e+00  0.097 0.922752    
habitatsavanna:s1r                 NA         NA  0.000e+00     NA       NA    
habitatshrub:t.ar:c1r      -2.383e-02  9.765e-01  5.987e-02 -0.398 0.690628    
habitatforest:t.ar:c1r     -2.306e-01  7.940e-01  6.633e-02 -3.477 0.000507 ***
habitatgrasslands:t.ar:c1r  4.417e-02  1.045e+00  5.485e-02  0.805 0.420655    
habitatsavanna:t.ar:c1r            NA         NA  0.000e+00     NA       NA    
habitatshrub:t.ar:s1r      -9.179e-02  9.123e-01  5.969e-02 -1.538 0.124101    
habitatforest:t.ar:s1r     -2.856e-01  7.515e-01  6.561e-02 -4.353 1.34e-05 ***
habitatgrasslands:t.ar:s1r -1.475e-02  9.854e-01  5.207e-02 -0.283 0.776944    
habitatsavanna:t.ar:s1r            NA         NA  0.000e+00     NA       NA    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

                           exp(coef) exp(-coef) lower .95 upper .95
habitatforest               526.6838  0.0018987  56.18151 4.937e+03
habitatgrasslands             0.3667  2.7272350   0.09803 1.372e+00
habitatsavanna                1.0055  0.9945296   0.05660 1.786e+01
habitatshrub:t.ar             0.9796  1.0208655   0.87570 1.096e+00
habitatforest:t.ar            0.7748  1.2906440   0.68438 8.772e-01
habitatgrasslands:t.ar        1.0409  0.9607499   0.93602 1.157e+00
```

```
habitatsavanna:t.ar              NA         NA        NA        NA
habitatshrub:c1r             1.9356  0.5166337   0.09174 4.084e+01
habitatforest:c1r          514.8218  0.0019424  17.26672 1.535e+04
habitatgrasslands:c1r        0.4407  2.2691451   0.02683 7.238e+00
habitatsavanna:c1r               NA         NA        NA        NA
habitatshrub:s1r             6.0820  0.1644186   0.30381 1.218e+02
habitatforest:s1r         1123.8335  0.0008898  40.33033 3.132e+04
habitatgrasslands:s1r        1.1394  0.8776605   0.08150 1.593e+01
habitatsavanna:s1r               NA         NA        NA        NA
habitatshrub:t.ar:c1r        0.9765  1.0241159   0.86833 1.098e+00
habitatforest:t.ar:c1r       0.7940  1.2594073   0.69723 9.043e-01
habitatgrasslands:t.ar:c1r   1.0452  0.9567898   0.93863 1.164e+00
habitatsavanna:t.ar:c1r          NA         NA        NA        NA
habitatshrub:t.ar:s1r        0.9123  1.0961345   0.81157 1.026e+00
habitatforest:t.ar:s1r       0.7515  1.3306036   0.66085 8.547e-01
habitatgrasslands:t.ar:s1r   0.9854  1.0148613   0.88975 1.091e+00
habitatsavanna:t.ar:s1r          NA         NA        NA        NA

Rsquare= 0.003   (max possible= 0.475 )
Likelihood ratio test= 148.3  on 18 df,   p=0
Wald test            = 113.2  on 18 df,   p=7.772e-16
Score (logrank) test = 123.2  on 18 df,   p=0
```

Appendix 3

Model coefficients of the selected Step Selection Function model used to characterize resource selection by *Tolypeutes matacus*. Step Selection Function (SSF; Fortin et al. 2005, Forester et al. 2009) was used to evaluate the effects of cover type (sugar cane, forest, grassland, floodable open vegetation), diel cycle (s1, c1), and air temperature (t.ar) on the resource selection of the studied species. The time of day was included in the SSF to allow a nonlinear relationship between time of day and selection strength. This was implemented using harmonics, which were allowed to interact with cover type and temperature for each step from each individual. These interactions allowed us to verify the effect of temperature on the selection of habitat types by armadillos. SSF model was fitted using a Conditional Logistic Regression (CLR) using the function 'clogit' in the package 'survival' (Therneau 2015) in R. Here we present values of model coefficients (coef); exponential values of model coefficients (exp(coef)), standard error (se(coef)), z-score, lower (lower .95) and upper (upper .95) limits of the 95% confidence interval.

```
Call:
coxph(formula = Surv(rep(1, 787835L), presabs == 1) ~ habitat +
    habitat:t.ar + habitat:c1 + habitat:s1 + habitat:c1:t.ar +
    habitat:s1:t.ar + strata(strata), data = ssf1, method = "exact")

  n= 787835, number of events= 25420

                           coef exp(coef)  se(coef)      z Pr(>|z|)
habitatcana           -5.515114  0.004025  2.342865 -2.354 0.018572 *
habitatestrada        -2.729628  0.065244  1.332986 -2.048 0.040584 *
habitatmata           -1.227113  0.293138  1.250483 -0.981 0.326439
habitatpasto          -1.765961  0.171022  1.361263 -1.297 0.194529
habitatcampo:t.ar     -0.063784  0.938208  0.051405 -1.241 0.214677
habitatcana:t.ar       0.121886  1.129625  0.078534  1.552 0.120658
habitatestrada:t.ar    0.060535  1.062405  0.014452  4.189  2.8e-05 ***
habitatmata:t.ar      -0.004937  0.995075  0.025068 -0.197 0.843862
habitatpasto:t.ar            NA        NA  0.000000     NA       NA
habitatcampo:c1       -2.529325  0.079713  1.659905 -1.524 0.127565
habitatcana:c1        -0.468296  0.626068  1.772014 -0.264 0.791569
habitatestrada:c1      0.561176  1.752733  0.420937  1.333 0.182479
habitatmata:c1         2.916721 18.480590  0.787765  3.703 0.000213 ***
habitatpasto:c1              NA        NA  0.000000     NA       NA
habitatcampo:s1        4.281941 72.380790  1.668389  2.567 0.010273 *
habitatcana:s1        -1.326277  0.265464  1.619186 -0.819 0.412729
habitatestrada:s1      0.251542  1.286007  0.378937  0.664 0.506813
habitatmata:s1         1.961597  7.110675  0.726701  2.699 0.006948 **
habitatpasto:s1              NA        NA  0.000000     NA       NA
habitatcampo:t.ar:c1   0.087588  1.091539  0.060973  1.437 0.150856
habitatcana:t.ar:c1    0.041923  1.042815  0.071074  0.590 0.555286
habitatestrada:t.ar:c1 -0.009768  0.990279  0.016341 -0.598 0.549992
habitatmata:t.ar:c1   -0.099028  0.905717  0.029257 -3.385 0.000712 ***
habitatpasto:t.ar:c1         NA        NA  0.000000     NA       NA
habitatcampo:t.ar:s1  -0.181822  0.833750  0.062752 -2.897 0.003762 **
habitatcana:t.ar:s1    0.057697  1.059394  0.064157  0.899 0.368482
habitatestrada:t.ar:s1  0.002574  1.002578  0.014782  0.174 0.861754
habitatmata:t.ar:s1   -0.062044  0.939842  0.027093 -2.290 0.022021 *
habitatpasto:t.ar:s1         NA        NA  0.000000     NA       NA
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

                       exp(coef) exp(-coef) lower .95 upper .95
```

```
habitatcana             0.004025  248.41832 4.079e-05    0.3973
habitatestrada          0.065244   15.32718 4.785e-03    0.8896
habitatmata             0.293138    3.41137 2.527e-02    3.4000
habitatpasto            0.171022    5.84719 1.187e-02    2.4647
habitatcampo:t.ar       0.938208    1.06586 8.483e-01    1.0377
habitatcana:t.ar        1.129625    0.88525 9.685e-01    1.3176
habitatestrada:t.ar     1.062405    0.94126 1.033e+00    1.0929
habitatmata:t.ar        0.995075    1.00495 9.474e-01    1.0452
habitatpasto:t.ar             NA         NA        NA        NA
habitatcampo:c1         0.079713   12.54503 3.080e-03    2.0627
habitatcana:c1          0.626068    1.59727 1.942e-02   20.1819
habitatestrada:c1       1.752733    0.57054 7.681e-01    3.9996
habitatmata:c1         18.480590    0.05411 3.946e+00   86.5492
habitatpasto:c1               NA         NA        NA        NA
habitatcampo:s1        72.380790    0.01382 2.751e+00 1904.4034
habitatcana:s1          0.265464    3.76699 1.111e-02    6.3425
habitatestrada:s1       1.286007    0.77760 6.119e-01    2.7027
habitatmata:s1          7.110675    0.14063 1.711e+00   29.5447
habitatpasto:s1               NA         NA        NA        NA
habitatcampo:t.ar:c1    1.091539    0.91614 9.686e-01    1.2301
habitatcana:t.ar:c1     1.042815    0.95894 9.072e-01    1.1987
habitatestrada:t.ar:c1  0.990279    1.00982 9.591e-01    1.0225
habitatmata:t.ar:c1     0.905717    1.10410 8.552e-01    0.9592
habitatpasto:t.ar:c1          NA         NA        NA        NA
habitatcampo:t.ar:s1    0.833750    1.19940 7.373e-01    0.9429
habitatcana:t.ar:s1     1.059394    0.94394 9.342e-01    1.2013
habitatestrada:t.ar:s1  1.002578    0.99743 9.739e-01    1.0321
habitatmata:t.ar:s1     0.939842    1.06401 8.912e-01    0.9911
habitatpasto:t.ar:s1          NA         NA        NA        NA

Rsquare= 0   (max possible= 0.199 )
Likelihood ratio test= 352.9  on 24 df,   p=0
Wald test            = 332.8  on 24 df,   p=0
Score (logrank) test = 318.3  on 24 df,   p=0
```

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 behavior 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 tend to peak earlier in the day. Hence, we are a step closer to defining effective measures for *T. matacus* conservation in Brazil, where this species is still reported as Data Deficient.

Conspicuous and locally abundant species such as the armadillos in the Pantanal 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, we 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 presents a tendency to shift its activity pattern from diurnal to nocturnal as temperature changes. In addition, both studied species tends to select forested areas when subjected to temperatures outside its thermoneutral zone. The conspicuous behavioral responses of armadillos and other xenarthrans, coupled with armadillo species richness (20 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.

Literature cited

Abba AM, Sauthier DEU, Vizcaíno SF. 2005. Distribution and use of burrows and tunnels of *Chaetophractus villosus* (Mammalia, Xenarthra) in the eastern Argentinean pampas. Acta Theriologica 50: 115-124.

Abba AM, Vizcaíno SF, Cassini MH. 2007. Effects of land use on the distribution of three species of armadillos in the Argentinean pampas. Journal of Mammalogy 88: 502-507.

Abba AM & Superina M. 2010. The 2009/2010 Armadillo Red List Assessment. Edentata 11(2): 135-184.

Abdon MM, Silva JSV, Pott VJ, Pott A & Silva MP. 1998. Utilização de dados analógicos do Landsat-TM na discriminação da vegetação de parte da sub-região da Nhecolândia no Pantanal. Pesquisa Agropecuária Brasileira 33: 1799-1813.

Abrahms B, Jordan NR, Golabek KA, McNutt JW, Wilson AM & Brashares JS. 2015. Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads. Animal Conservation 19: 247-255.

Aronson BD, Bell-Pedersen D, Block GD, ..., & Zucker I. 1993. Circadian rhythms. Brain Research Reviews 18: 315-333.

Astete S, Sollmann R & Silveira L. 2008. Comparative ecology of jaguars in Brazil. Cat News Special Issue 4: 9-14.

Attias N, Miranda FR, Sena LMM, Tomas WM & Mourão GM. 2016. Yes, they can! Three-banded armadillos *Tolypeutes* sp. (Cingulata: Dasypodidae) dig their own burrows. Zoologia 33: e20160035.

Avgar T, Lele SR, Keim JL & Boyce MS. 2017. Relative Selection Strength: Quantifying effect size in habitat and step selection inference. Ecology and Evolution 7(14): 5322-5330.

Barraquand F & Benhamou S. 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. Ecology 89(12): 3336-3348.

Barrientos J, Cuellar L. 2004. Área de acción de *Tolypeutes matacus* por telemetría y seguimiento por hilos en Cerro Cortado del Parque Kaa-Iya. In: Memorias VI Congreso de Manejo de Fauna Silvestre en Amazonia y Latinoamérica. Iquitos, Wildlife Conservation Society, pp. 120-124. Available online at: http://manejofaunasilvestre.org/Congresos/Iquitos-2004/ Ponencias.aspx [Accessed: 08/08/2016]

Bellard C, Bertelsmeier C, Leadley P, Thuiller W & Courchamp F. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15: 365-377.

Bernier D. 2003. North American regional studbook for the Southern three-banded armadillo (*Tolypeutes matacus*). Chicago, Lincoln Park Zoo, 49pp.

Bertrand MR, DeNicola AJ, Beissinger SR & Swihart RK. 1996. Effects of parturition on home ranges and social affiliations of female white-tailed deer. Journal of Wildlife Management 60(4): 899-909.

Beyer HL, Haydon DT, Morales JM, Frair JL, Hebblewhite M, Mitchell M & Matthiopoulos J. 2010. The interpretation of habitat preference metrics under use-availability designs. Philosophical Transactions of the Royal Society B 365: 2245-2254.

Beyer HL, Gurarie E, Börger L, Panzacchi M, Basille M, Herfindal I, Van Moorter B, Lele SR & Matthiopoulos J. 2014. 'You shall not pass!': quantifying barrier permeability and proximity avoidance by animals. Journal of Animal Ecology 85(1): 43-53.

Bianchi RC, Olifiers N, Gompper ME & Mourão GM. 2016. Niche partitioning among mesocarnivores in a Brazilian wetland. PLoS ONE 11: e0162893

Bocchiglieri A, Mendonça AF & Henriques RPB. 2010. Composição e diversidade de mamíferos de médio e grande porte no Cerrado do Brasil central. Biota Neotropica 10(3): 169-176.

Bolkovic ML, Caziani SM, Protomastro JJ. 1995. Food habits of the three-banded armadillo (Xenarthra: Dasypodidae) in the dry Chaco of Argentina. Journal of Mammalogy 76: 1199-1204.

Borges PAL, Tomás WM. 2008. Guia de rastros e outros vestígios de mamíferos do Pantanal. Corumbá, Embrapa Pantanal, 148pp.

Boyce MS. 2006. Scale for resource selection functions. Diversity and Distributions 12: 269-276.

Boyce MS & McDonald L. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14(7): 268-272.

Brice PH, Grigg GC, Beard LA & Donovan JA. 2002. Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. Australian Journal of Zoology 50: 461–475.

Burnham KP & Anderson DR. 2002. Model selection and multi-model inference: A practical information–theoretic approach. Springer-Verlag, London. 488 pp.

Cagnacci F, Boitani L, Powell RA & Boyce MS. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B 365: 2157-2162.

Calenge C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516-519.

Calheiros DF & Fonseca WC. 1996. Perspectivas de estudos ecológicos sobre o Pantanal. Embrapa CPAP, Corumbá, Mato Grosso do Sul.

Camilo-Alves CSP & Mourão GM. 2006. Responses of a specialized insectivorous mammal (*Myrmecophaga tridactyla*) to variation in ambient temperature. Biotropica 38: 52-56.

Carbone C, Cowlishaw G, Isaac NJB & Rowcliffe M. 2005. How far do animals go? Determinants of day range in mammals. The American Naturalist 165(2): 290-297.

Carter TS, Encarnação CD. 1983. Characteristics of burrows by four species of armadillos in Brazil. Journal of Mammalogy 64: 103-108.

Clutton-Brock TH. 1989. Mammalian mating systems. Proceedings of the Royal Society of London B 236: 339-372.

Craiu RV, Duchesne T & Fortin D. 2008. Inference methods for the conditional logistic regression model with longitudinal data. Biometrical Journal 50: 97-109.

Creel S, Creel NM, Creel AM & Creel BM. 2016. Hunting on a hot day: effects of temperature on interactions between African wild dogs and their prey. Ecology 97: 2910-2916.

Cuellar E. 2002. Census of the three-banded armadillo *Tolypeutes matacus* using dogs, southern Chaco, Bolivia. Mammalia 66: 448-451.

Cuellar E. 2008. Biology and ecology of armadillos in the Bolivian Chaco. In: The biology of the Xenarthra (Eds. SF Vizcaíno & Loughry WJ). Gainesville, University Press of Florida.

Desbiez AL, Borges PAL & Medri IM. 2006. Chasing behavior in yellow armadillos, *Euphractus sexcinctus*, in the Brazilian Pantanal. Edentata 7: 51-53.

Ebenman B. 1987. Niche differences between age classes and intraspecifi competition in age-structured population. Journal of Theoretical Biology 124: 25-33.

Eisenberg JF, Redford KH. 1999. Mammals of the Neotropics - the central Neotropics: Ecuador, Peru, Bolivia, Brazil. Chicago, The University of Chicago Press, vol. 1, 609 pp.

Eisentraut M. 1932. Biologische Studien im bolivianischen Chaco. IV. Die Wärmeregulation beim Kugelgürteltier (*Tolypeutes conurus* Js. Geoff.). Zeitschrift für vergleichende Physiologie 18: 174-185.

Emerling CA & Springer MS. 2015. Genomic evidence for rod monochromacy in sloths and armadillos suggests early subterranean history for Xenarthra. Proceedings of the Royal Society of London B 282: e20142192.

Fahrig L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21: 1003-1015.

Feijó A, Garbino GST, Campos BATP, Rocha PA, Ferrari SF, Langguth A. 2015. Distribution of *Tolypeutes* Illiger, 1811 (Xenarthra: Cingulata) with comments on its biogeography and conservation. Zoological Science 32: 77-87.

Fieberg J & Kochanny CO. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69(4): 1346-1359.

Forester JD, Im HK & Rathouz PJ. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90: 3554-3565.

Fortin D, Hawthorne HL, Boyce MS, Smith DW, Duchesne T. & Mao JS. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86: 1320-1330.

Fortin D, Morris DW & McLoughlin PD. 2008. Habitat selection and the evolution of specialists in heterogeneous environments. Israel Journal of Ecology and Evolution 54: 311-328.

Garland T Jr. 1983. Scaling the ecological cost of transport to body mass in terrestrial mammals. American Naturalist 121:571-587.

Gasparotto VPO, Attias N, Miranda FR, Soresini GCG, Canena AC, Mourão G. 2017. Chemical immobilization of free-ranging yellow armadillos (*Euphractus sexcinctus*) for implantation of intra-abdominal transmitters. Journal of Wildlife Diseases 53(4): 896-900.

Giné AF, Cassano CR, Almeida SS & Faria D. 2015. Activity budget, pattern and rhythm of maned sloths (*Bradypus torquatus*): Responses to variations in ambient temperature. Mammalian Biology 80: 459-467.

González EM, Soutullo A & Altuna CA. 2001. The burrow of *Dasypus hybridus* (Cingulata: Dasypodidae). Acta Theriologica 46: 53-59.

Greegor DH. 1985. Ecology of the little hairy armadillo *Chaetophractus vellerosus*. In: The evolution and ecology of armadillos, sloths and vermilinguas (Ed GG Montgomery), pp. 397-405. Smithsonian Institution Press, Washington.

Greene HW. 2005. Organisms in nature as a central focus for biology. Trends in Ecology & Evolution 20(1): 23-27.

Guimarães MM. 1997. Área de vida, territorialidade e dieta do tatu-bola, *Tolypeutes tricinctus* (Xenarthra, Dasypodidae), num Cerrado do Brasil Central. Brasília, Master's Dissertation, Programa de Pós-graduação em Ecologia, Universidade de Brasília, 64 pp. Available online at: http://www.pgecl.unb.br/images/sampledata/arquivos/dissertacoes/1990a1999/1997/Marilia%20Marques%20Guimareas.PDF [Accessed: 08/08/2016]

Gunderson AR & Leal M. 2016. A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global climate change. Ecology Letters 19: 111-120.

Gurarie E, Suutarinen J, Kojola I, Ovaskainen O. 2011. Summer movements, predation and habitat use of wolves in human modified boreal forests. Oecologia 165: 891-903.

Hannibal W, Duarte LA, Santos CC. 2015. Mamíferos não voadores do Pantanal e entorno. Campo Grande, Natureza em Foco, 224 pp.

Harestad AS & Bunnell FL. 1979. Home range and body weight - A reevaluation. Ecology 60(2): 389-402.

Harley CDG. 2011. Climate change, keystone predation, and biodiversity loss. Science 334: 1124-1127.

Harris M, Tomas W, Mourão GM, Silva CJ, Guimarães E, Sonoda F & Fachim E. 2005. Safeguarding the Pantanal wetlands: Threats and conservation initiatives. Conservation Biology 19: 714-720.

Hernandez SM, Gammons DJ, Gottdenker N, Mengak MT, Conner LM, Divers SJ. 2010. Technique, safety and efficacy of intra-abdominal transmitters in nine-banded armadillos. The Journal of Wildlife Management 74: 174-180.

Hut RA, Kronfeld-Schor N, van der Vinne V & De la Iglesia H. 2012. In search of a temporal niche: Environmental factors. Progress in Brain Research, vol. 199, 1st ed (Eds. A Kalsbeek, Merrow M, Roenneberg T & Foster RG), pp. 281–304. Elsevier, Salt Lake City.

Hutto RL. 1985. Habitat selection by non breeding, migratory land birds. In: Habitat selection in birds (Ed. ML Cody), pp. 455–476. New York, NY Academic Press.

ICMBio, Instituto Chico Mendes para a Conservação da Biodiversidade. 2017. Plano de ação nacional para a conservação do tatu-bola. http://www.icmbio.gov.br/portal/faunabrasileira/plano-de-acao-nacional-lista/4808-plano-de-acao-nacional-para-conservacao-do-tatu-bola. Accessed in 20/08/2017.

Kernohan J, Gitzen RA & Millspaugh JJ. 2001. Analysis of animal space use and movements. In: Radio tracking and animal populations (Eds. JJ Millspaugh & Marzluff JM), pp. 125-166. Academic Press, San Diego.

Krebs JR & Davies NB. 1993. An introduction to behavioural ecology. 3rd ed. Wiley-Blackwell, Oxford.

Kronfeld-Schor N, Dayan T. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34: 153-181.

Latham ADM, Latham MC, Boyce MS & Boutin S. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northwestern Alberta. Ecological Applications 21: 2854-2865.

Layne JN & Glover D. 1985. Activity patterns of the common long-nosed armadillo *Dasypus novemcinctus* in south-central Florida. In: The evolution and ecology of armadillos, sloths and vermilinguas (Ed GG Montgomery), pp 407-417. Smithsonian Institution Press, Washington.

Lele SR, Keim JL & Solymos P. 2017. ResourceSelection: Resource selection (probability) functions for use-availability data. R package version 0.3-2. https://CRAN.R-project.org/package=ResourceSelection

Lele SR & Keim JL . 2006. Weighted distributions and estimation of resource selection probability functions. Ecology 87(12): 3012-3028.

Liwanag HEM. 2010. Energetic costs and thermoregulation in Northern fur seal (*Callorhinus ursinus*) pups: The importance of behavioral strategies for thermal balance in furred marine mammals. Physiological and Biochemical Zoology 83: 898-910.

Long JA, Nelson TA, Webb SL & Gee KL. 2014. A critical examination of indices of dynamic interaction for wildlife telemetry studies. Journal of Animal Ecology 83: 1216-1233.

Long JA. 2014. wildlifeDI: Calculate indices of dynamic interaction for wildlife telemetry data. R package version 0.2. https://CRAN.R-project.org/package=wildlifeDI

Loughry WJ, Superina M, McDonough CM & Abba AM. 2015. Research on armadillos: a review and prospectus. Journal of Mammalogy 96(4): 635-644

Loughry WJ & McDonough CM. 1998. Spatial patterns in a population of nine-banded armadillos (*Dasypus novemcinctus*). The American Midland Naturalist 140(1): 161-169.

Loughry WJ & McDonough CM. 2001. Natal recruitment and adult retention in a population of nine-banded armadillos. Acta Theriologica 46(4): 393-406.

Loughry WJ & McDonough CM. 2013. Beyond natural history: some thoughts about research priorities in the study of xenarthrans. Edentata 14: 9-14.

Maccarini TB, Attias N, Medri IM, Marinho-Filho J, Mourão GM. 2015. Temperature influences the activity patterns of armadillo species in a large neotropical wetland. Mammal Research 60: 403-409.

Macdonald DW, Ball FG & Hough NG. 1980. The evaluation of home range size and configuration using radio tracking data. In: A handbook on biotelemetry and radio tracking: Proceedings of an International Conference on Telemetry and Radio Tracking in Biology and Medicine (Eds CJ Amlaner & MacDonald DW), pp. 405-424. Pergamon Press, Oxford.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL & Erickson WP. 2002. Resource selection by animals: Statistical design and analysis for field studies. 2nd ed. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Marengo JA, Alves LM & Torres RR. 2016. Regional climate change scenarios in the Brazilian Pantanal watershed. Climate Research 68: 201-213.

Marini-Filho OJ, Guimarães MM. 2010. Comportamento sexual de tatu-bola (*Tolypeutes tricinctus*, Dasypodidae). Edentata 11: 76-77.

Mazerolle MJ. 2016. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-0. https://cran.r-project.org/package=AICcmodavg.

McDonough CM. 1997. Pairing behavior of the nine-banded armadillo (*Dasypus novemcinctus*). The American Midland Naturalist 138: 290-298.

McDonough CM. 2000. Social organization of nine-banded armadillos (*Dasypus novemcinctus*) in a riparian habitat. The American Midland Naturalist 144(1):139-151

McDonough CM & Loughry WJ. 2008. Behavioral ecology of armadillos. In: The biology of the Xenarthra (Eds SF Vizcaíno & Loughry WJ), pp 281–293. University Press of Florida, Gainesville.

McNab BK. 1980. Energetics and the limits to a temperate distribution in armadillos. Journal of Mammalogy 61: 606-627.

McNab BK. 1985. Energetics, population biology, and distribution of xenarthrans, living and extinct. In: The evolution and ecology of armadillos, sloths and vermilinguas (Ed GG Montgomery), pp 219–232. Smithsonian Institution Press, Washington.

McNab BK. 2002. Short-term energy conservation in endotherms in relation to body mass, habitats, and environment. Journal of Thermal Biology 27: 459-466.

Medri IM. 2008. Ecologia e história natural do tatu-peba, *Euphractus sexcinctus* (Linnaeus, 1758), no Pantanal da Nhecolândia, Mato Grosso do Sul. PhD thesis, University of Brasília, Brasília.

Medri IM, Mourão GM, Rodrigues FHG. 2011. Ordem Cingulata. In: Mamíferos do Brasil (Eds. NR Reis, Peracchi AL, Pedro WA & Lima IP), p. 75-90. Londrina, Author's Edition.

Meritt D. 2008. Xenarthrans of the Paraguayan Chaco. In: The biology of the Xenarthra (Eds. SF Vizcaíno & Loughry WJ), p294-299. University Press of Florida, Gainesville.

Millspaugh JJ, Nielson RM, McDonald L, Marzluff JM, Gitzen RA, Rittenhouse CD, Hubbard MW & Sheriff SL. 2006. Analysis of resource selection using utilization distribution. Journal of Wildlife Management 70: 384-395.

Mittermeier RA, Mittermeier CG, Brooks TM, Pilgrim JD, KonstantWR, da Fonseca GAB & Kormos C. 2003. Wilderness and biodiversity conservation. Proceedings of the National Academy of Science 100: 10309-10313.

Mohr CO. 1947. Table of equivalent populations of North American Mammals. The American Midland Naturalist 37: 223-249

Möller-Krull M, Delsuc F, Churakov G, Marker C, Superina M, Brosius J, Douzery EJP & Schimtz J. 2007. Retroposed elements and their flanking regions resolve the evolutionary history of Xenarthran mammals (armadillos, anteaters, and sloths). Molecular Biology and Evolution 24: 2573-2582.

Mourão GM & Medri IM. 2007. Activity of a specialized insectivorous mammal (*Myrmecophaga tridactyla*) in the Pantanal of Brazil. Journal of Zoology (London) 271:187-192.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D & Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105: 19052-19059.

Noss AJ. 2013. Seguimiento del corechi (*Tolypeutes matacus*) por medio de carreteles de hilo en el Chaco Boliviano. Edentata 14: 15-22.

Oliveira-Santos LGR, Zucco CA & Agostinelli. 2013. Using conditional circular kernel density functions to test hypotheses on animal circadian activity. Animal Behaviour 85(1): 269-280.

Oliveira-Santos LGR, Forester JD, Piovezan U, Tomas WM & Fernandez FAS. 2016. Incorporating animal spatial memory in step selection functions. Journal of Animal Ecology 85: 516-524.

Pianka ER. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

Pietersen DW, McKechnie AE & Jansen R. 2014. Home range, habitat selection and activity patterns of an arid-zone population of Temminck's ground pangolin *Smutsia temminckii.* African Zoology 49: 265-276.

Pinheiro J, Bates D, DebRoy S, Sarkar D & R Core Team. 2016. nlme: Linear and nonlinear mixed effects models. R package version 3.1-126. http://CRAN.R-project.org/package=nlme

Powell RA. 2000. Animal home ranges and territories and home range estimators. In: Research techniques in animal ecology: controversies and consequences (Eds. L Boitani & Fuller TK), pp. 65-110. Columbia University Press, New York.

Prevedello JA, Forero-Medina G & Vieira MV. 2010. Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. Journal of Animal Ecology 79: 1315-1323.

Quantum GIS Development Team. 2017. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Development Core Team. 2017. R: A language and environment for statistical computing. The R Foundation for Statistical Computing.

Redford KH. 1985. Food habits of armadillos (Xenarthra: Dasypodidae). In: The evolution and ecology of armadillos, sloths and vermilinguas (Ed GG Montgomery), pp 429–437. Smithsonian Institution Press, Washington.

Reinert HK. 1993. Habitat selection in snakes. In: Snakes: ecology and behavior (Eds RA Seigel & Collins JT), pp. 201-240. McGraw-Hill, New York.

Reis ML, Mourão GM, Vaz SM, Belentani SCS & Anacleto TCS. 2015. Avaliação do risco de extinção de *Tolypeutes matacus* (Desmarest, 1804) no Brasil. Processo de avaliação do risco de extinção da fauna brasileira. ICMBio. http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/lista-de-especies/7112-mamiferos-tolypeutes-matacus-tatu-bola.html

Rietveld WJ, Minors DS & Waterhouse JM. 1993. Circadian rhythms and masking: an overview. Chronobiology International 10: 306-312.

Roig VG. 1969. Termorregulación en *Euphractus sexcinctus* (Mammalia: Dasypodidae). Physis 29: 27-32.

Samuel MD & Fuller MR. 1994. Wildlife Radiotelemetry. In: Research and management techniques for wildlife and habitats (Ed. TA Bookhout), pp. 370-418. The Wildlife Society, Bethesda.

Sanborn CC. 1930. Distribution and habits of the three-banded armadillo (*Tolypeutes*). Journal of Mammalogy 11: 61-69.

Sandell M. 1989. The mating tactics and spacing patterns of solitary carnivores. In: Carnivore Behavior, Ecology and Evolution (Ed. JL Gittleman). Ithaca, New York, Cornell University Press.

Seminoff JA, Resendiz A, Nichols WJ. 2002. Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. Marine Ecology Progress Series 242: 253-265.

Sikes RS, & the Animal Care and Use Committee of ASM. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97(3): 663-688.

Silva MC & Oren DC. 1993. Observations on the habitat and distribution of the Brazilian three-banded armadillo *Tolypeutes tricinctus*, a threatened Caatinga endemic. Mammalia 57: 149-152.

Silva JSV, Abdon MM, Silva SMA, Moraes JA. 2011. Evolution of deforestation in the Brazilian Pantanal and surroundings in the timeframe 1976 - 2008. Geografia 36: 35-55.

Smith P. 2007. Southern three-banded armadillo *Tolypeutes matacus* (Desmarest, 1804). In: Fauna Paraguay: Handbook of the Mammals of Paraguay (Ed. P Smith), vol. 2. Available online at: http://www.faunaparaguay.com/mammhb2.html [Accessed: 08/08/2016]

Sunde P, Thorup K, Jacobsen LB & Rahbek C. 2014. Weather conditions drive dynamic habitat selection in a generalist predator. PLoS ONE 9: e88221.

Superina M & Boily P. 2007. Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). Comparative Biochemistry and Physiology A 148: 893-898.

Superina M & Loughry WJ. 2012. Life on the half-shell: Consequences of a carapace in the evolution of armadillos (Xenarthra: Cingulata). Journal of Mammalian Evolution 19: 217-224.

Tattersall GJ & Cadena V. 2010. Insights into animal temperature adaptations revealed through thermal imaging. The Imaging Science Journal 58: 261-268.

Therneau T. 2015. A package for survival analysis in S. version 2.38. http://CRAN.R-project.org/package=survival.

Tomas WM, Campos Z, Desbiez ALJ, Kluyber D, Borges PAL & Mourão G. 2013. Mating behavior of the six-banded armadillo *Euphractus sexcinctus* in the Pantanal wetland, Brazil. Edentata 14: 87-89.

Tortato FR, Layme VMG, Crawshaw Jr. PG & Izzo TJ. 2015. The impact of herd composition and foraging area on livestock predation by big cats in the Pantanal of Brazil. Animal Conservation 18: 539-547.

Turchin P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72: 1253-1266.

Viscaíno SF & Milne N. 2002. Structure and function in armadillo limbs (Mammalia: Xenarthra: Dasypodidae). Journal of Zoology 257: 117-127.

Vynne C, Keim JL, Machado RB, Marinho-Filho J, Silveira L, Groom MJ & Wasser SK. 2011. Resource selection and its implications for wide-ranging mammals of the Brazilian Cerrado. PLoS ONE 6(12): e28939.

Wetzel RM, Gardner AL, Redford KH & Eisenberg JF. 2008. Order Cingulata. In: Mammals of South America. Vol. 1: Marsupials, Xenarthrans, Shrews and Bats (Ed. AL Gardner), pp. 128-156. University of Chicago Press, Chicago.

Worton BJ. 1987. A review of models of home range for animal movement. Ecological Modelling 38: 277-298.

Worton BJ. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59(4): 794-800.

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 these 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 at 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).

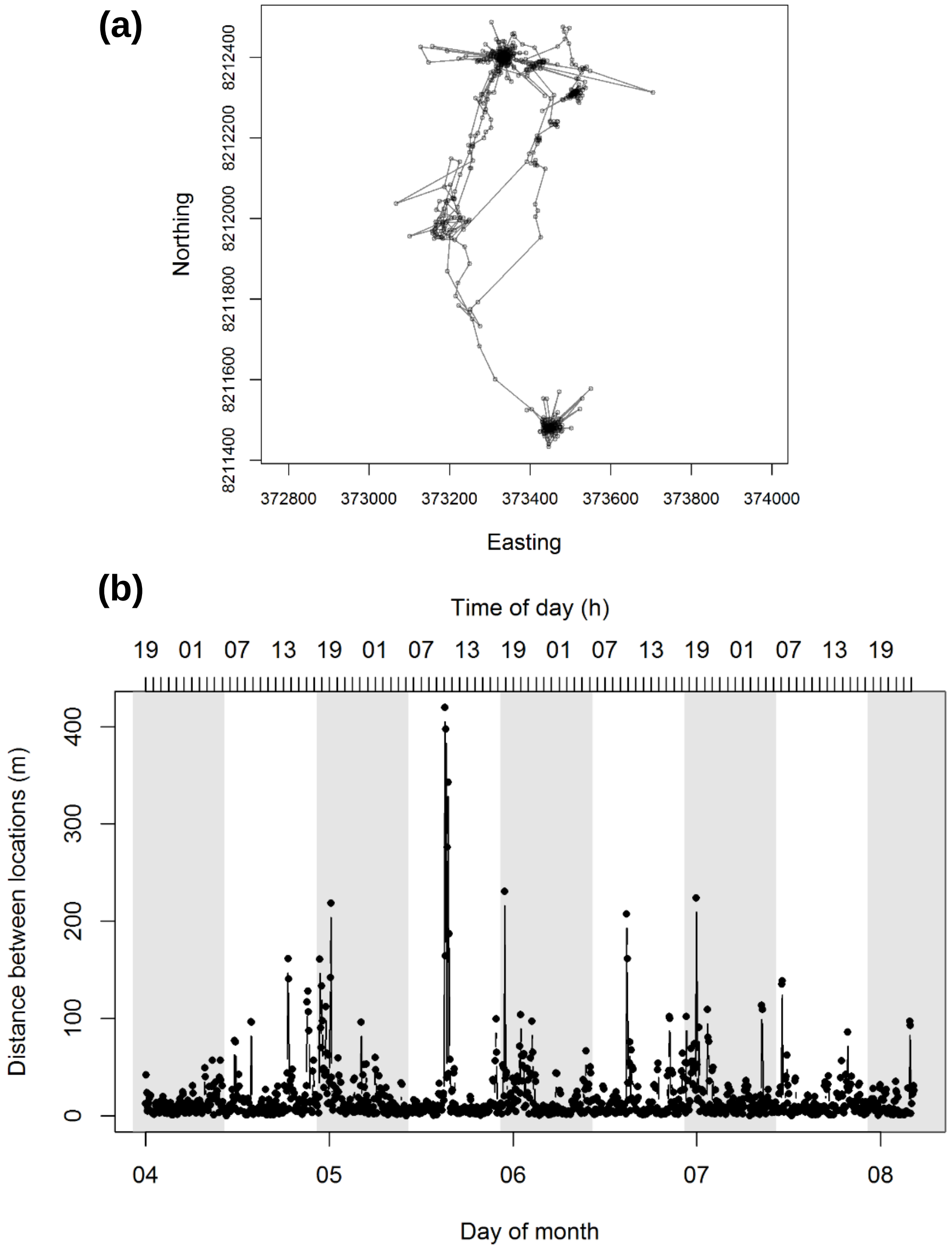


Figure 1. Original track (a) and distances moved between locations (b) by an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. . Coordinates are in Universal Transverse Mercator coordinate system (UTM, zone 21K). The errors created when the animal enters its shelter are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

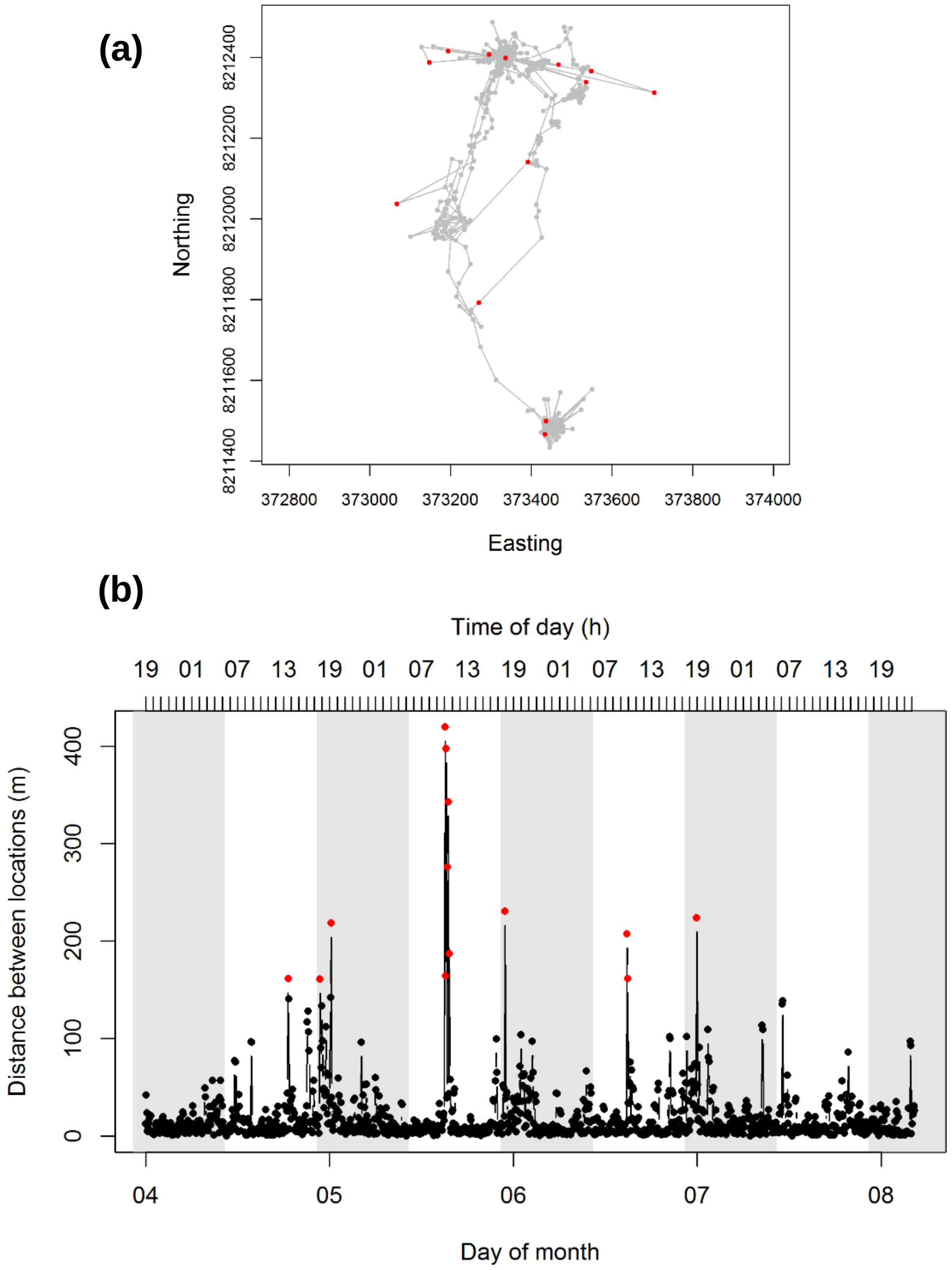


Figure 2. GPS track (a) and distances moved between locations (b) by an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. Locations with speeds higher than the 99% quantile are marked in red. Coordinates are in Universal Transverse Mercator coordinate system (UTM, zone 21K).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

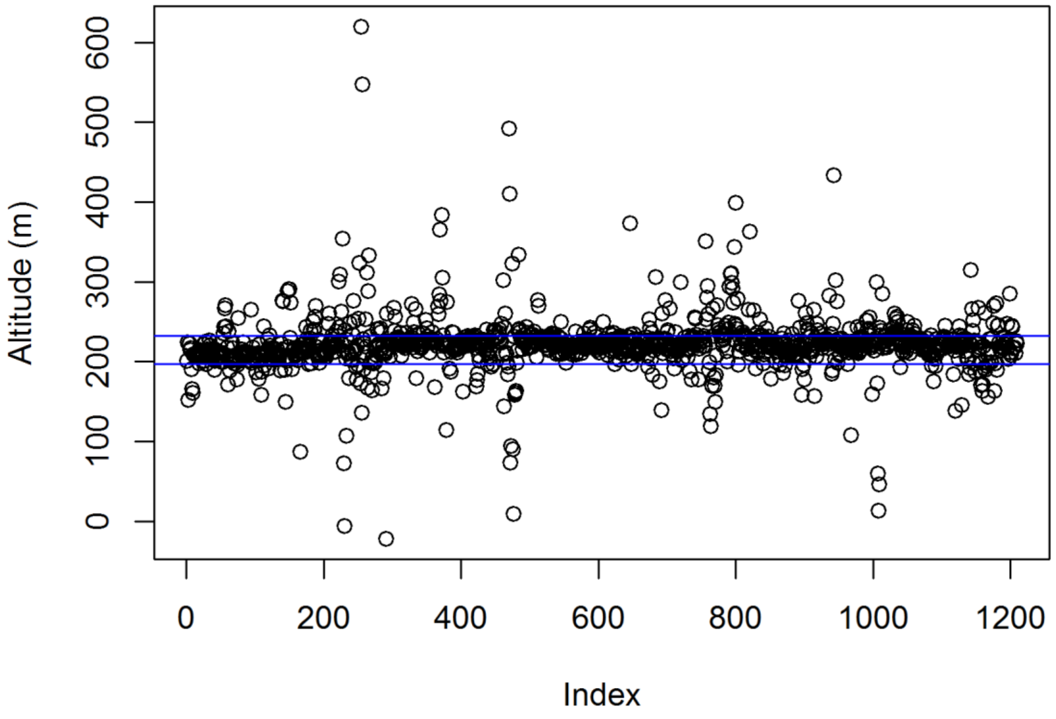


Figure 3. Altitudes associated with each location of the original track of an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. Blue lines indicate the range of altitude of the study area.

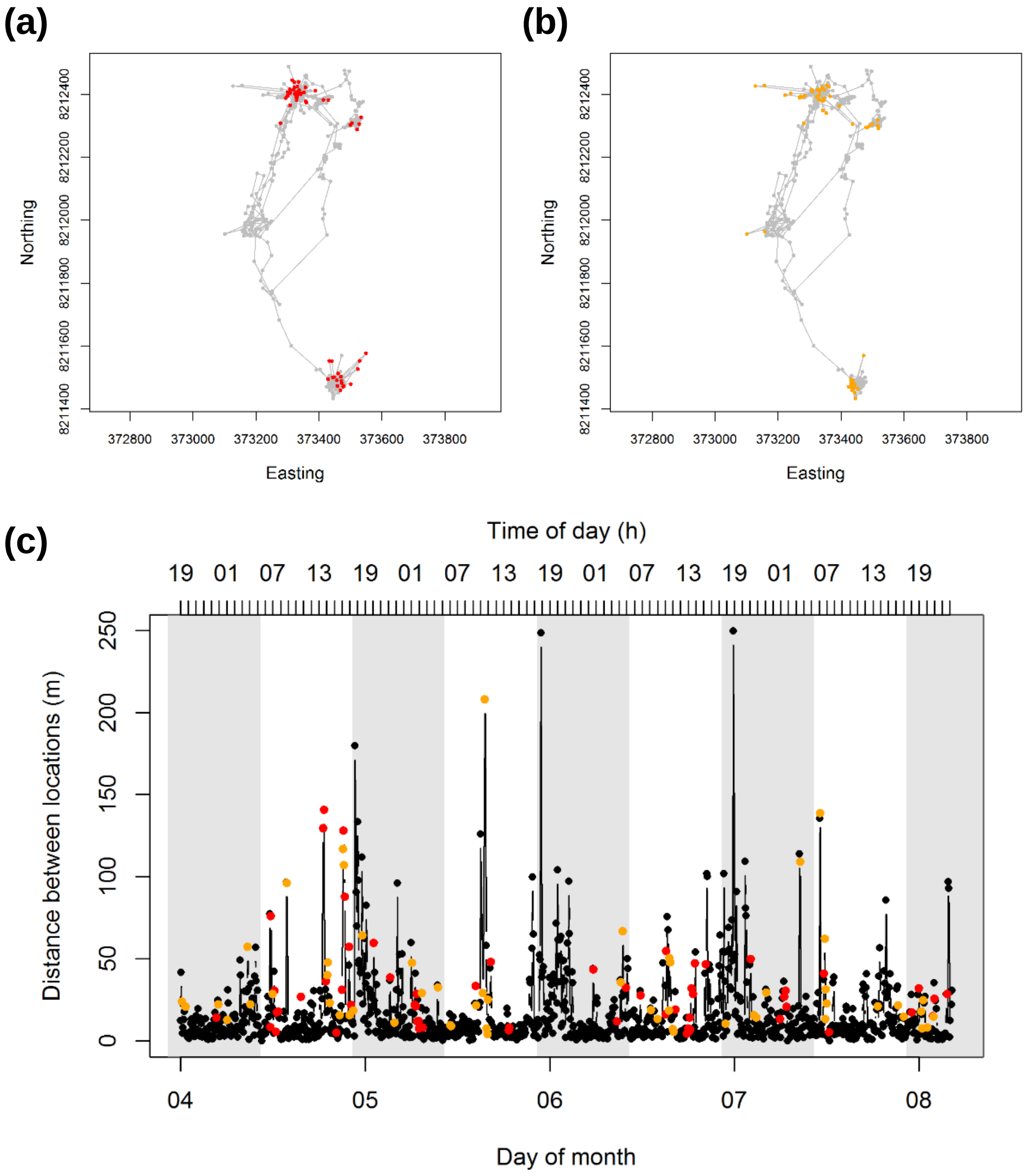


Figure 4. GPS track and distances moved between locations by an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. In red, locations with altitudes higher than the 95% quantile and, in orange, location with altitudes lower than the estimated 5% quantile. Coordinates are in 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 though 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 spent 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).

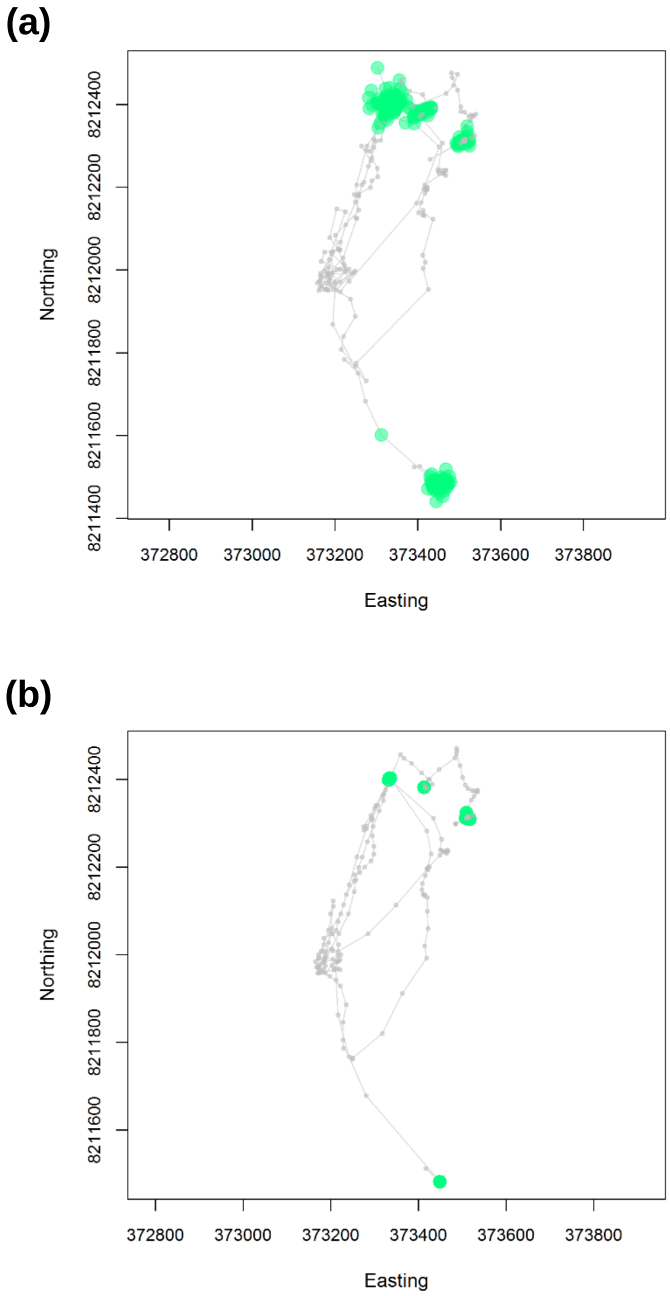


Figure 5. Shelter locations (green) as identified by the Residence time method (where the animal spent more than one hour inside a 20 meters radius). Identification of shelter location prior (a) and after (b) the estimation of the average shelter coordinates. Data from an individual of *Tolypeutes matacus*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

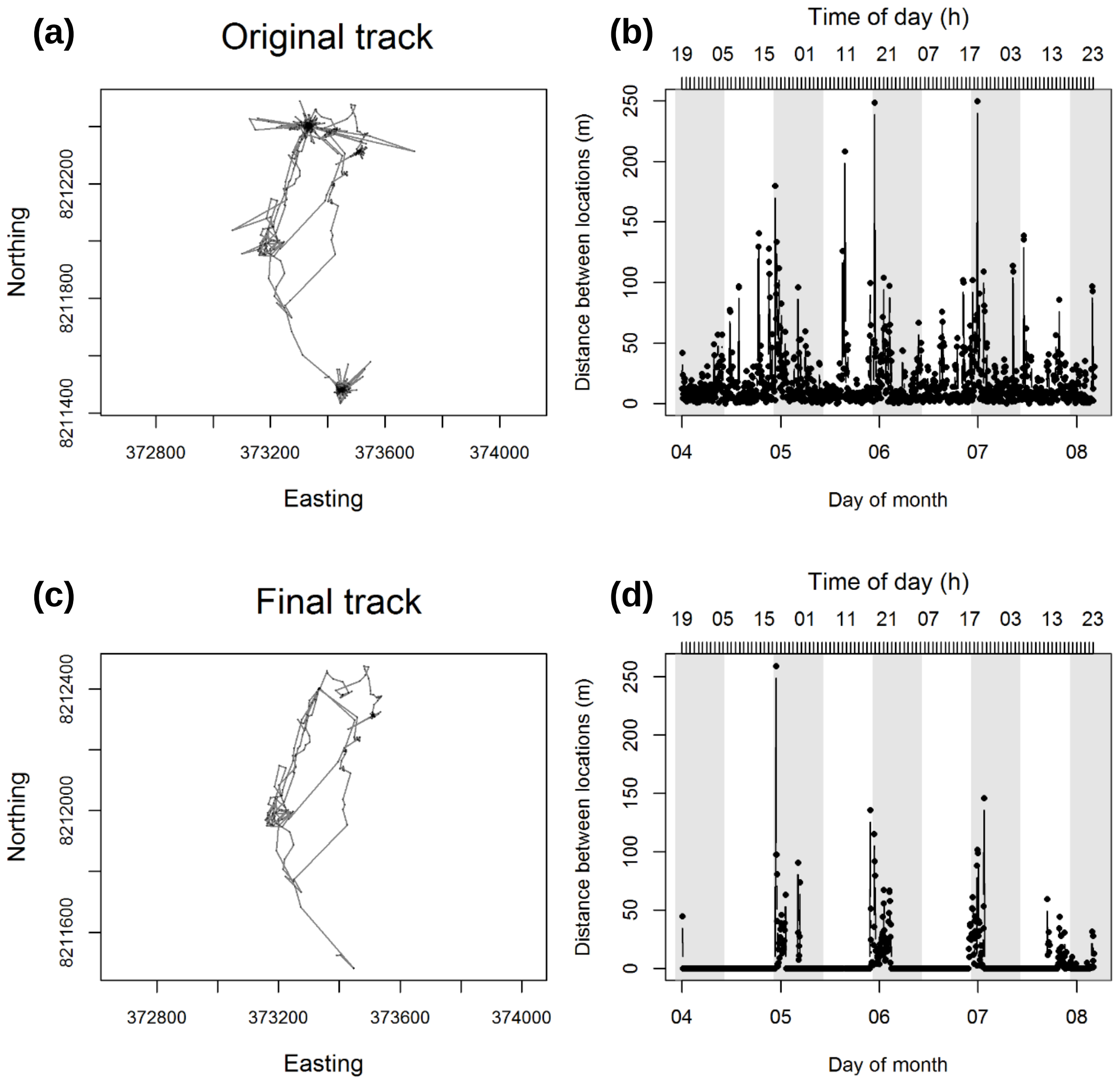


Figure 6. GPS track and distance moved between locations by the same individual (a and b) before and (c and d) after being subjected to our protocol for identification and correction of GPS errors. Data from an individual of *Tolypeutes matacus* tracked at Duas Lagoas ranch in August 2015. Coordinates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

Below follows an 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)
```

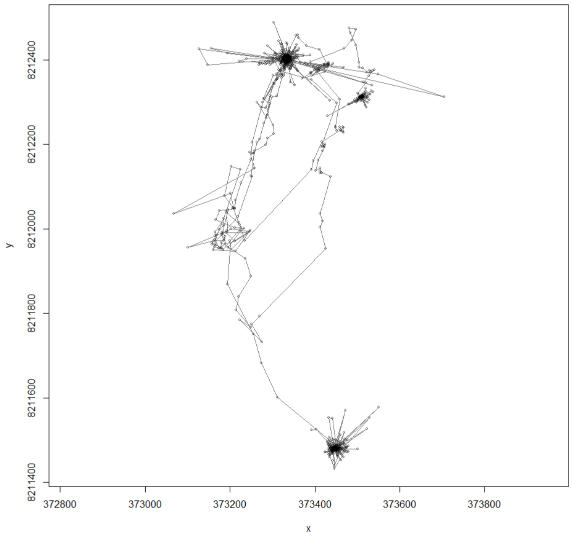
Load data:

```
Tm13<- read.csv("~/Doutorado_UFMS/GPSdata/TM13/Tm13l.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)
```

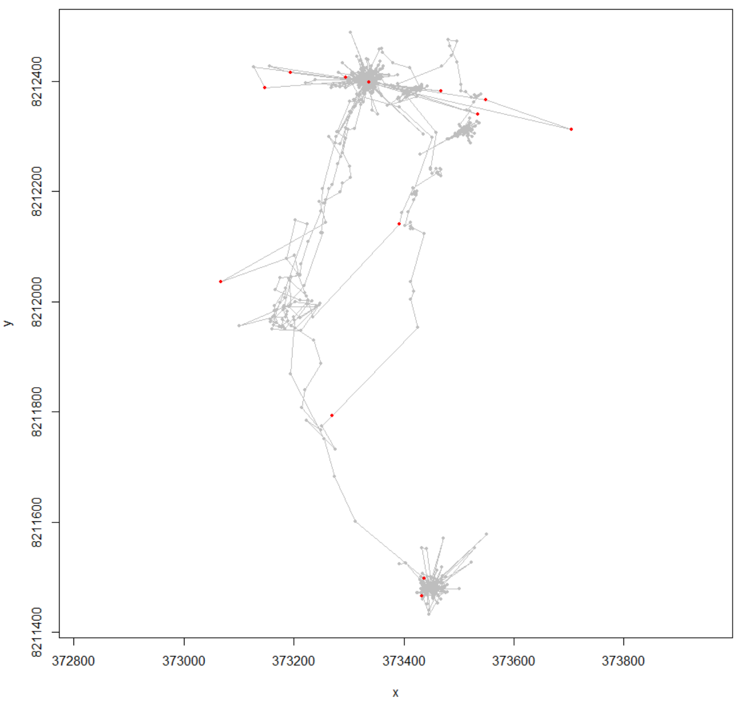
Filtering away points from the raw data where velocity > 99% (m/sec)

```
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"))
```



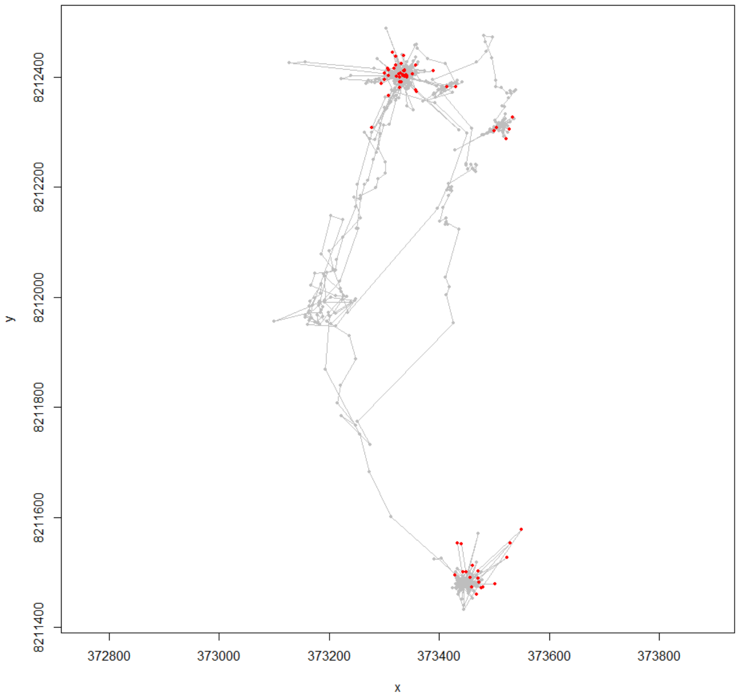
```
Temporary subset of the track data filtered by velocity
armadillo.temp <-subset(armadillo, V < v.max, na.rm=T)
```

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
```

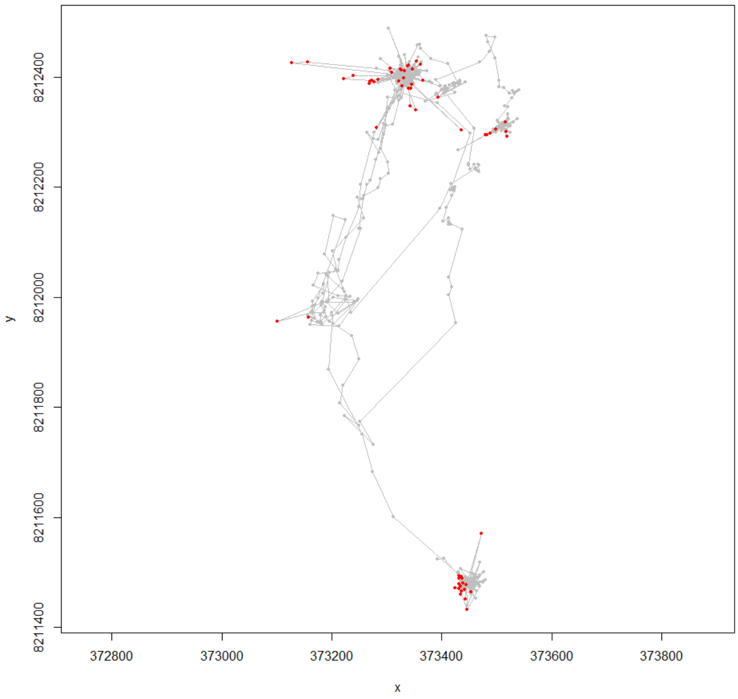
```
with(armadillo.temp, plot(x,y, asp=1, pch=19, cex=0.5, col="grey",
type="o"))
with(subset(armadillo.temp, armadillo.temp$alt > alt.max),
points(x,y, asp=1, pch=19, cex=0.5, col="red"))
```



```
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
```

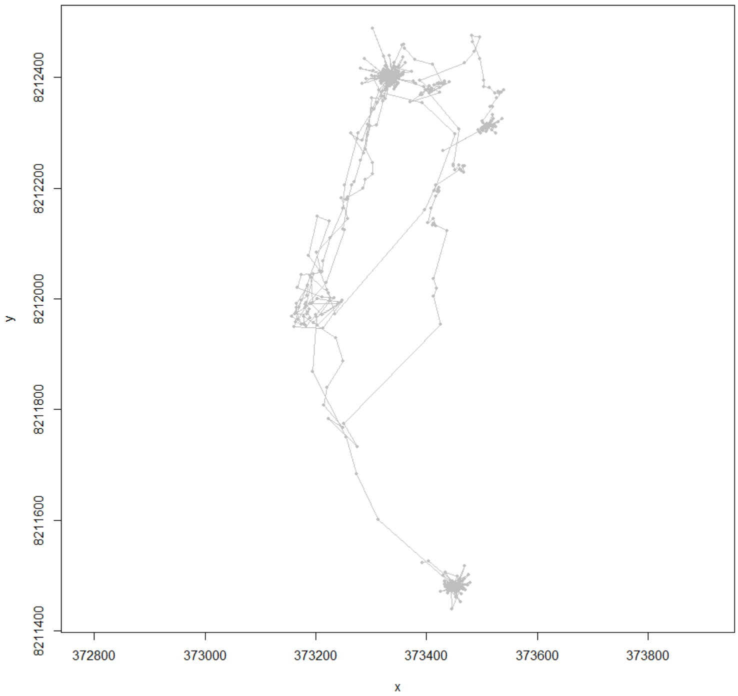
```
with(armadillo.temp2, plot(x,y, asp=1, pch=19, cex=0.5, col="grey",
type="o"))
with(subset(armadillo.temp2, armadillo.temp2$alt < alt.min),
points(x,y, asp=1, pch=19, cex=0.5, col="red"))
```



```
#Filtered by velocity and altitude
armadillo2 <- subset(armadillo.temp2,armadillo.temp2$alt > alt.min,
na.rm=T)
```

Creating the filtered track objects

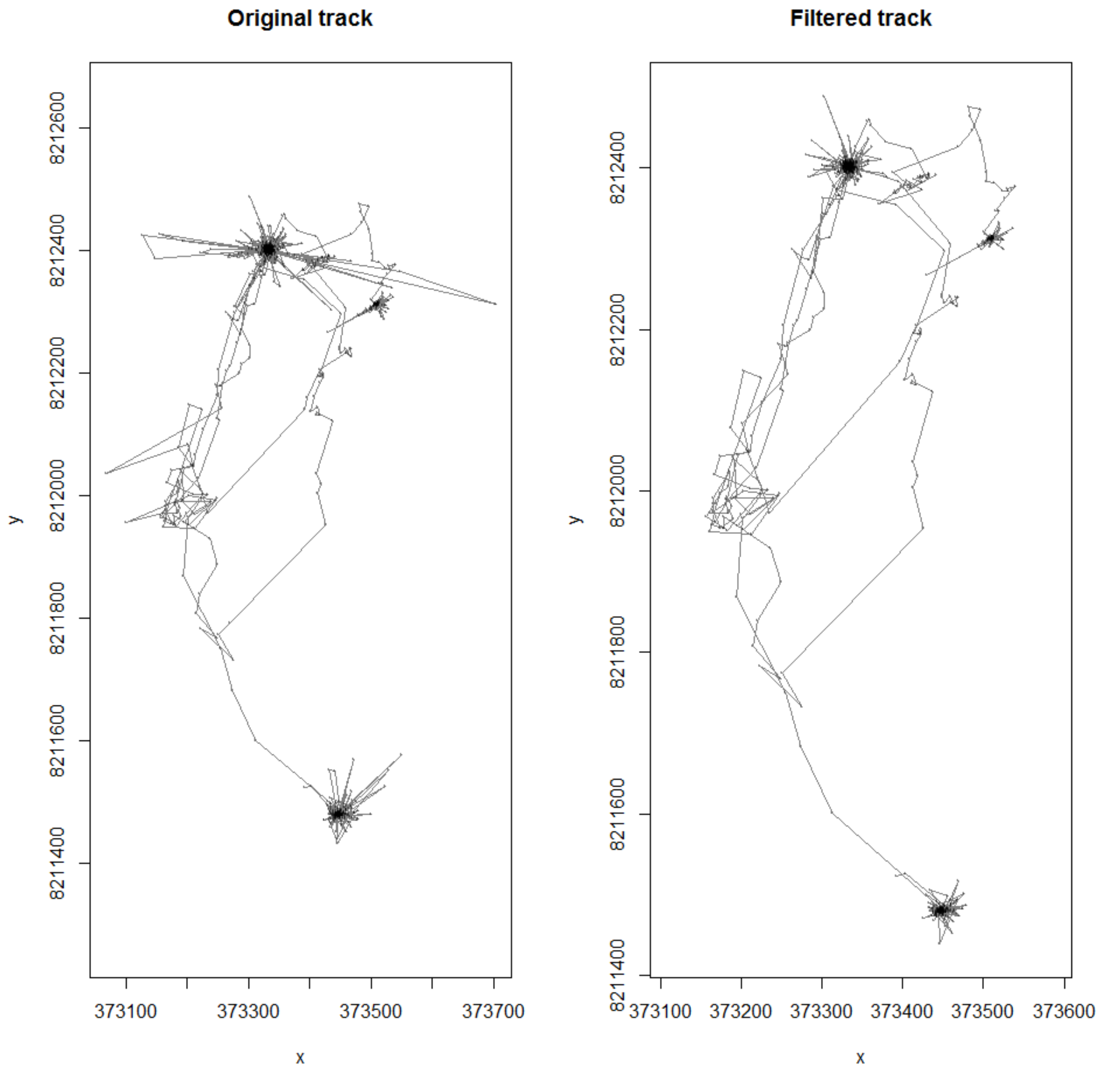
```
armadillo2$id<- 'tm13'
with(armadillo2, plot(x,y, asp=1, pch=19, cex=0.5, col="grey",
type="o"))
```



```
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
```



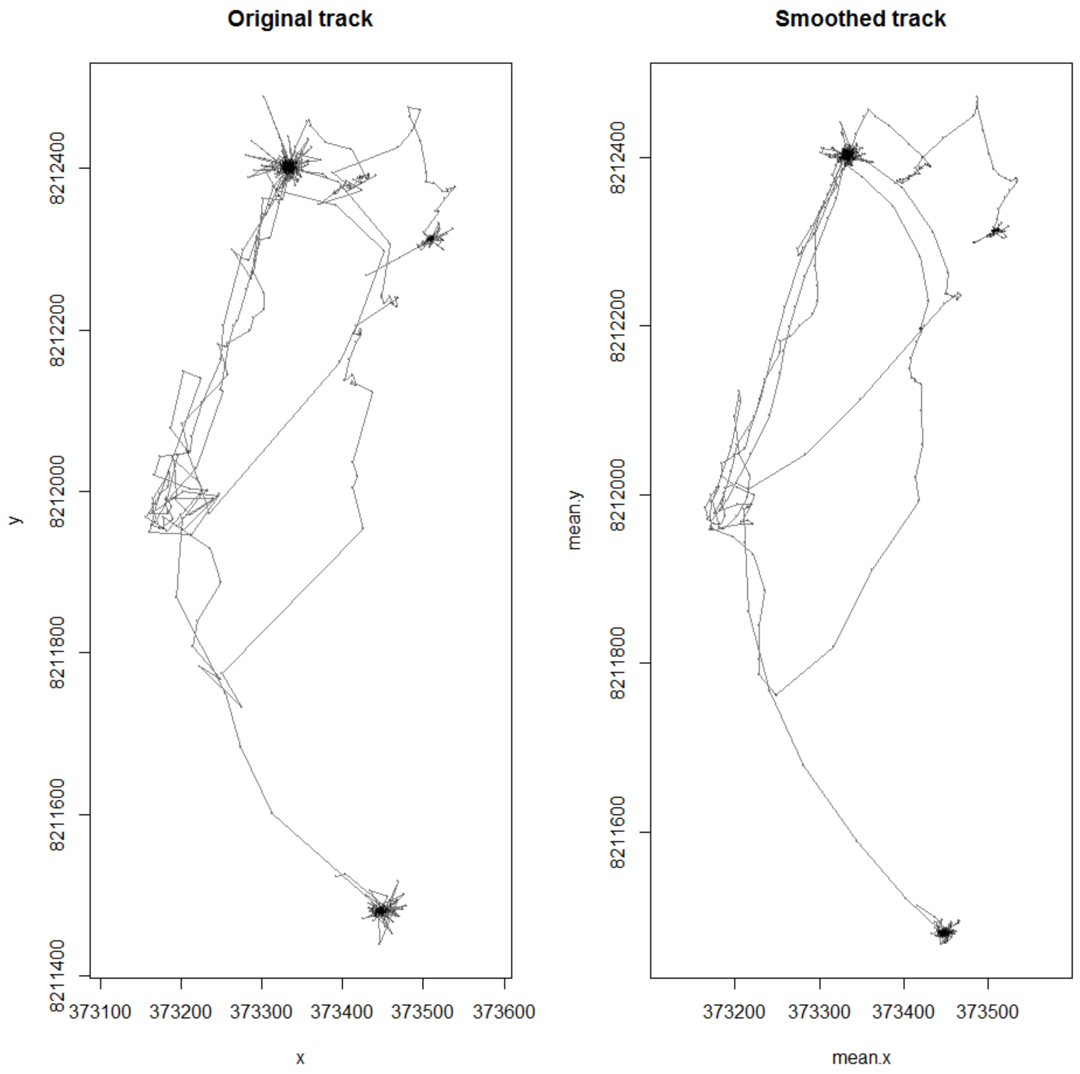
Apply a rolling mean of 3 to the filtered track 'armadillo2'

```
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:

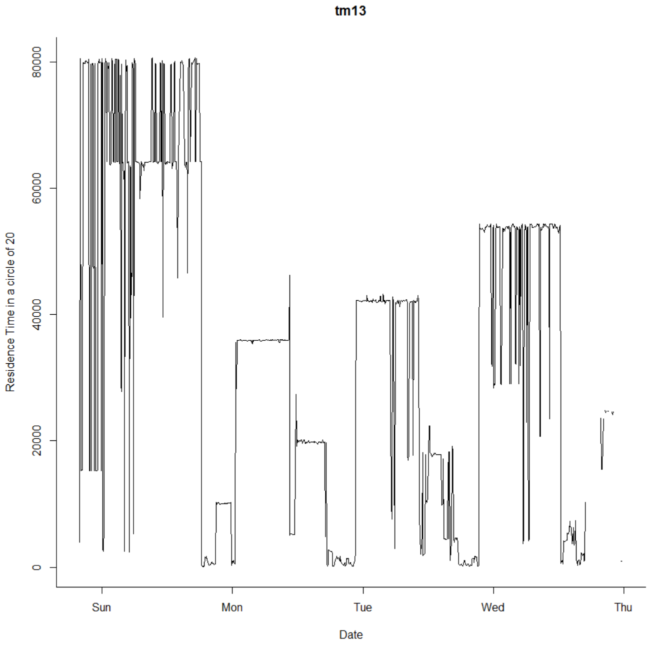
```
par(mfrow=c(1,2))
with(armadillo2, plot(x,y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Original track"))
with(armadillo2, plot(mean.x,mean.y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Smoothed track"))
```



```
#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"))
```

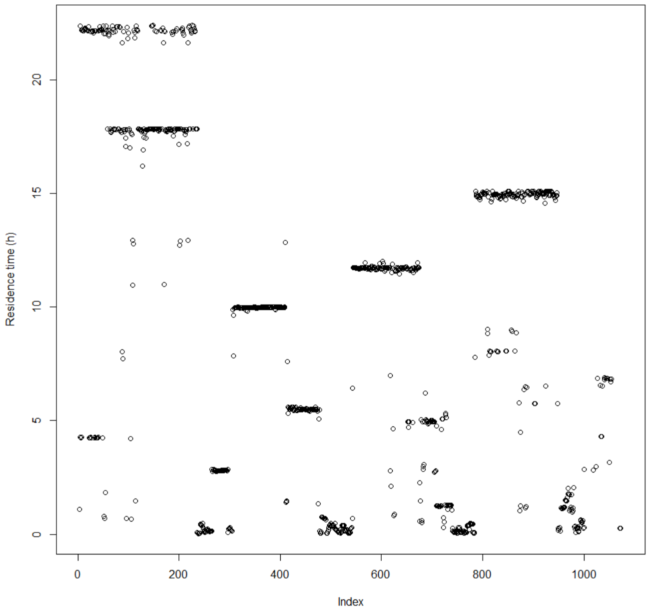
Residence time

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



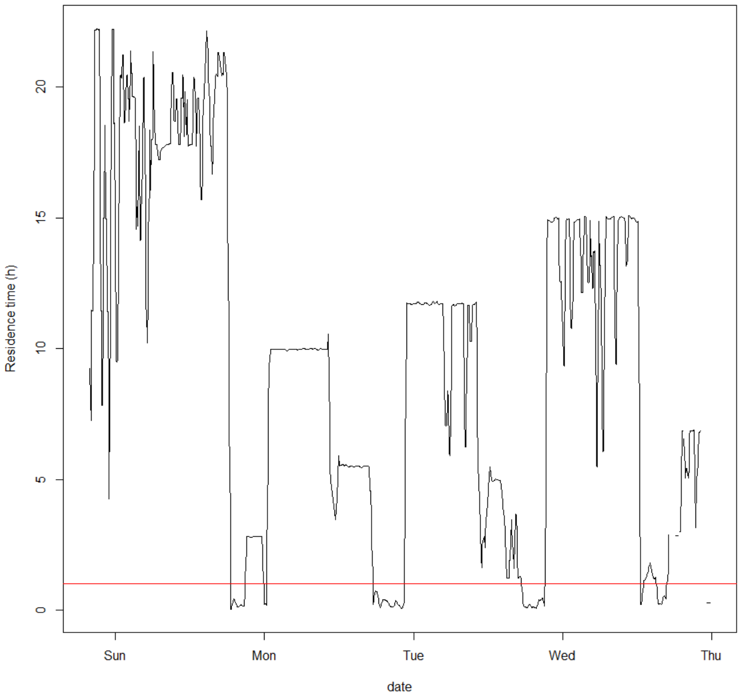
Extract the residence time vector and convert to hours:

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



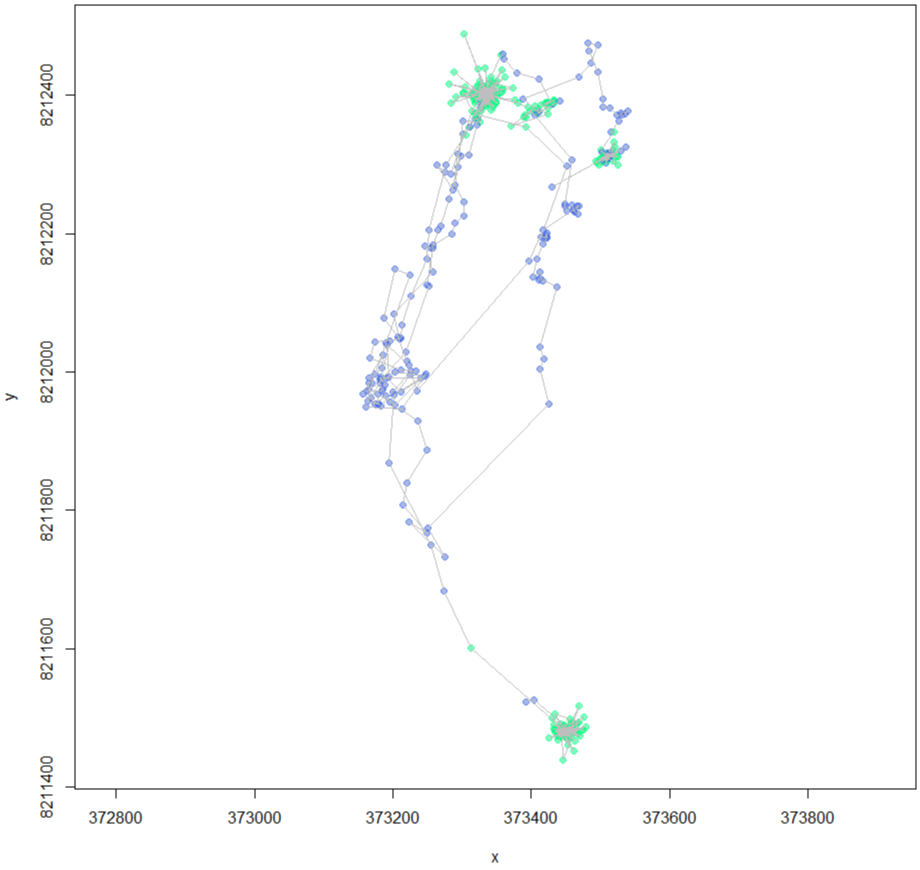
Apply a rolling mean to remove "spurious" departures (i.e. flatten the cycles)

```
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
```


Residence time (h)
0
5
10
15
20
Sun
Mon
Tue
Wed
Thu
date

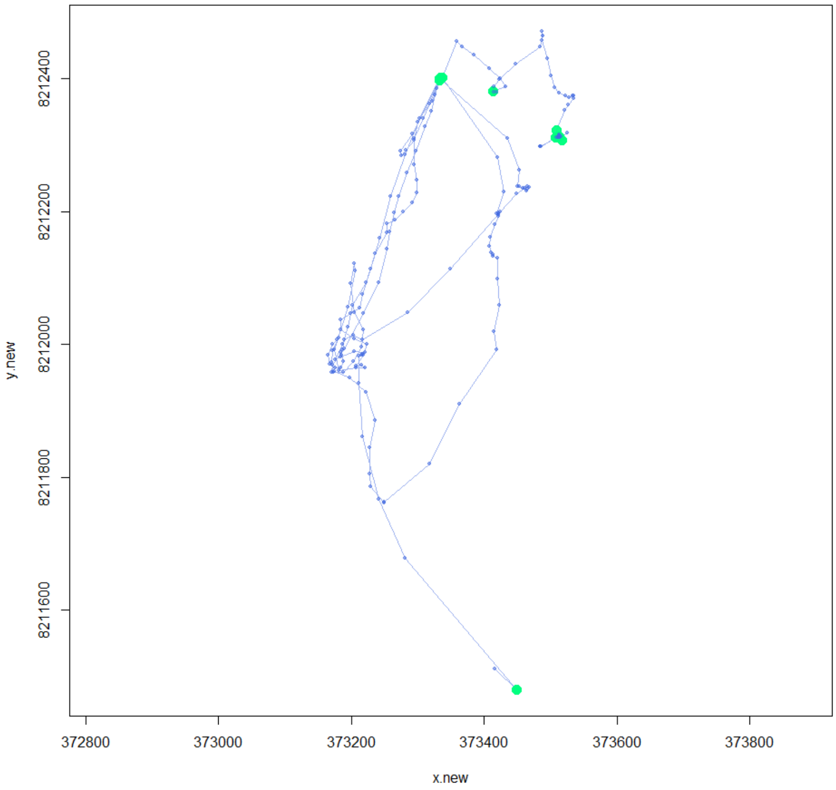
Assigning points to "In Burrow" (i.e. inactivity periods) based on the window-of-five smoothing + time threshold of 1 hour + radius of 20m

```
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")})
```



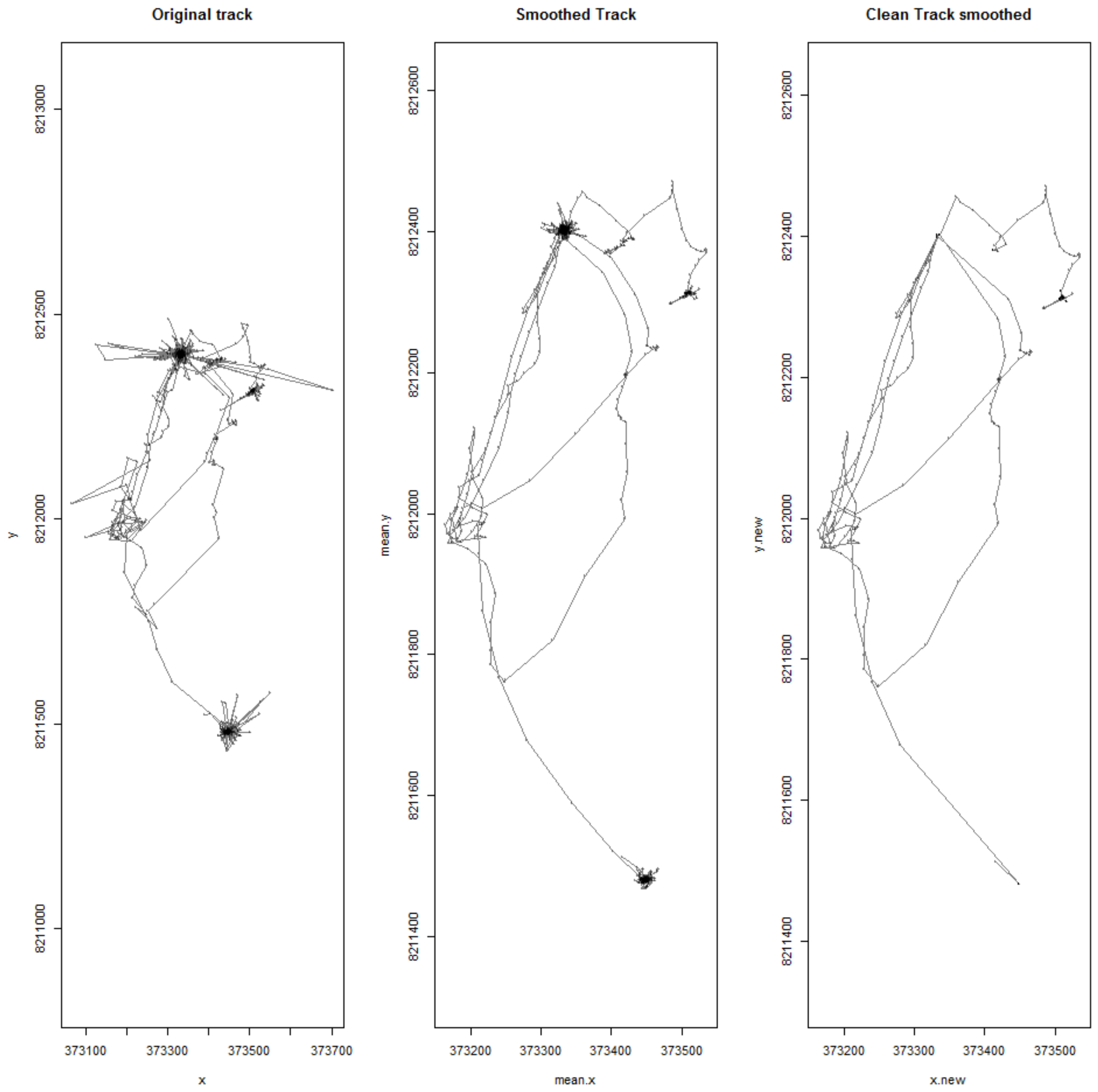
Define shelter locations by averaging the points assigned as 'In Burrow':

```
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])
}

#Ploting 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

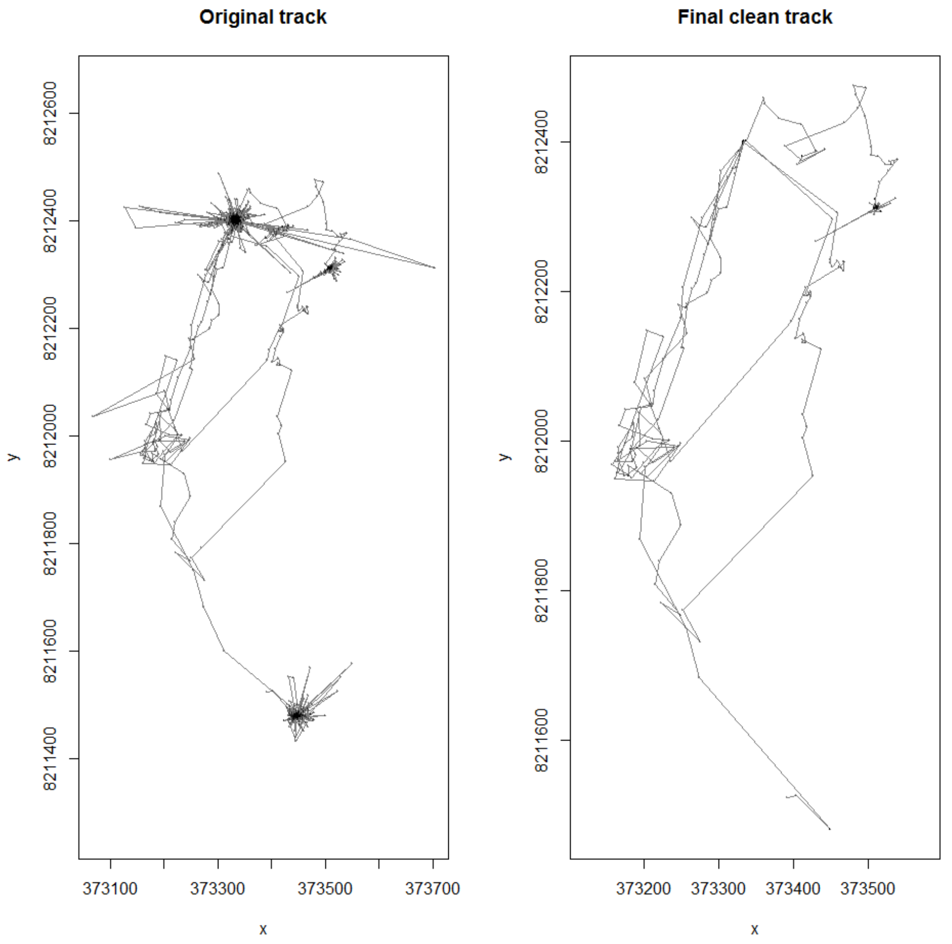
```
par(mfrow=c(1,3))
with(armadillo, plot(x,y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Original track"))
with(armadillo2, plot(mean.x,mean.y, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5), main = "Smoothed Track"))
with(armadillo2, plot(x.new,y.new, asp=1, type="o", cex=.05,
col=rgb(0,0,0,.5),main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



Creating a new track without the errors

Mantaining 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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