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**Sexual and density dependent behavior in two neotropical
small mammals**

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À uma grande amiga (*In memoriam*) que
deixou uma imensa saudade.

“Try and ease the pain somehow. We'll
feel the same. Well, no one knows where
our secrets go” - Billy Corgan & James

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General abstract

1. Home range and resource selection are important ecological approaches to understand how animals occupy the space and use the resources available. Sex is an important intrinsic factor that can mediate or change how the individual uses the habitat and selects the resources. Another important factor is the population density that can limit or facilitate both the formation and use of the home range and the selection of resources.

2. Here, we present two studies, one related to the home range of the opossum *Didelphis albiventris* in an urban area and the other related to resource selection of the rodent *Thrichomys fosteri* in a region of the Pantanal. In the first study, we investigated the relationship between body mass and sex influencing the home range size. We hypothesized that males should have larger home ranges than females and larger animals should have larger home ranges. In the second study, we hypothesized that the main resource for the rodent should be the density of bromeliad stands, which protects spiny rats from predators, being potentially more important for females than males. We also hypothesized that the abundance of conspecifics should lead females to a negative selection and, lead males to a positive selection due to different sexual behaviors related to sexes.

3. We did not find any relationship between sex and weight with the home range size of *D. albiventris*. However, females showed a lower overlap of their core areas when compared to male-male overlap. The bromeliad cover was the main resource for *T. fosteri*, with an almost double selection force for females than for males. Females selected for areas with lower density of conspecifics, while male selected for higher densities. We also hypothesized that the abundance of conspecifics should lead females

to a negative selection and, lead males to a positive selection due to different sexual behaviors related to sexes.

4. Spatial limitation and urban barriers may explain the absence of effect of mass and sex on the home range of opossums. In addition, supplementary feeding with human waste and generalist habits can also limit the movement of urban animals. The low overlap of female core areas may be a response to reproductive behavior, where females need more exclusive areas for the care of their offspring. The higher selection of *T. fosteri* females for bromeliads can also be explained by the higher need of females for protection to maximize their reproductive success by survival of the offspring. In the same way, females tend to avoid areas with high density of conspecifics. On the other hand, males should maximize their reproductive success by covering a larger number of females, so they should not avoid areas with high density of individuals, even when it entails being more exposed to predators.

Resumo geral

1. Área de vida e seleção de recursos são importantes abordagens ecológicas para o entendimento de como os animais ocupam o espaço e como eles utilizam os recursos. O sexo dos animais é um fator intrínseco importante que pode mediar ou alterar em como o indivíduo usa o habitat e seleciona os recursos. Outro importante fator é a densidade populacional que pode limitar ou facilitar tanto a formação e ocupação da área de vida como a seleção dos recursos.
2. Aqui nós apresentamos dois estudos, um relacionado à área de vida do gambá *Didelphis albiventris* em uma área urbana e o outro sobre a seleção de recursos pelo roedor *Thrichomys fosteri* em uma região do Pantanal. No primeiro, investigamos a relação da massa corpórea e do sexo influenciando a área de vida, hipotetizamos que machos devem ter áreas de vida maiores que fêmeas e animais maiores devem ter áreas de vida maiores. No segundo estudo, nós hipotetizamos que o principal recurso para o roedor deve ser a formação de bromélias comum na área de estudo pois a proteção deve ser o fator chave na seleção de recursos, entretanto fêmeas devem selecionar mais esse recurso que machos. Nós também hipotetizamos que a abundância de coespecíficos deve promover uma seleção negativa pelas fêmeas e positiva para os machos, devido às diferenças comportamentais relacionadas aos sexos.
3. Não encontramos relação do sexo nem o peso com o tamanho da área de vida em *D. albiventris*, entretanto fêmeas apresentaram baixa sobreposição das áreas core entre elas do que os machos. A formação de bromélias foi o principal recurso para *T. fosteri*, entretanto a força de seleção foi quase o dobro para fêmeas que para machos. A densidade populacional leva à uma seleção negativa pelas fêmeas enquanto para machos leva à uma seleção positiva.

4. A limitação espacial e as barreiras urbanas podem ser um fator que explica a ausência de efeito da massa e sexo na área de vida dos gambás. Além disso, a suplementação alimentar em áreas urbanas e o hábito generalista também podem limitar a movimentação de animais urbanos. A baixa sobreposição das áreas core de fêmeas pode ser uma resposta do comportamento reprodutivo onde fêmeas necessitam de áreas mais exclusivas para o cuidado da prole. A seleção maior de fêmeas de *T. fosteri* por bromélias também pode ser explicada pela maior necessidade de proteção das fêmeas que possuem seu sucesso reprodutivo na sobrevivência da prole e da mesma forma, elas tendem a evitar áreas com alta densidade populacional. Já machos, maximizam seu sucesso reprodutivo cobrindo um maior número de fêmeas, assim eles devem se expor mais e não evitar áreas com alta densidade de indivíduos.

General introduction

Animals tend to move non-randomly in the landscape. Their movement is guided by the constant search for resources, whether food, reproductive mates and shelter or also by avoiding predation (Burt 1943). These movements are aimed to maximize fitness (Morales et al. 2010, Street et al. 2016). The accumulated area of this movement during animal's life is called home range and it is a key approach for ecological studies.

Through further analysis of the home range, it is possible to define different ecological and evolutionary questions such as the mating system, intraspecific competition, habitat or resource selection (Myllymäki 1977, Gaulin et al. 1988, Oka 1992, Hingrat et al. 1994, Dickson and Beier 2002).

Several related intrinsic and extrinsic variables can influence how animals create and use their home range. The main intrinsic variables include sex, body size, reproductive stage and physiology, among others (Burt 1943, Cederlund and Source 1994, Dahle and Swenson 2003, Safi et al. 2007, Gentile et al. 2012). Among the main extrinsic variables, environmental traits and intra and interspecific interactions are the most important (Valenzuela and Ceballos 2000, Loretto and Vieira 2005, Rivrud et al. 2010, Cáceres et al. 2012). However, all the interactions of those variables are not easy to access which make us separate them in order to proceed with the different ecological questions.

One key factor related to population variations is the sex. It is probably the first expected populational difference and is often easily detected. The role of sexes in population dynamics, movement, home range, behavior, habitat selection, and even morphological adaptations, brings us important evolutionary insights to understand the life histories of different species (Hendrik and Temeles 1989). For most taxa, sexual

differences begin at the morphological level (sexual dimorphism) and goes until distinct behavioral aspects (Arak 1988, Quinn and Foot 1994). Sex is often a fundamental component on studies of home range and habitat selection, with females and males responding differently (Swihart and Slade 1989, Gehrt and Fritzell 1997, Lidgard et al. 2020).

Each taxon has its idiosyncrasies in sexual variations but a very interesting group for the studies of sexual variation is mammals. Variations of sexual reproductive roles in mammals bring significant differences on how they behave, and, consequently, use the environment and select their resources (Morris 1984). In general, the most evident sexual difference in mammals -directly acting in the formation of home ranges and the habitat selection- is morphological dimorphism, in which males are normally larger than females (Cáceres and Monteiro Filho 2001, Isaac 2005). However, the main driver of mammals' sexual differences in behaviour is the great difference in the reproductive roles of males and females. The high level of parental care often carried out exclusively by females makes their reproductive success dependent on how much care mammalian mothers have with their offspring. This leads females to seek safe areas, with higher food resources in order to product milk, resulting on lesser or no overlap of home ranges (Gittleman and Thompson 2015, Hamel and Côté 2008). Males, on the other hand, base their reproductive success on the largest number of reproductive mates they can achieve, which usually results on males giving priority to areas with more reproductive mates over a high quality of resources (Clutton-Brock and Harvey 1978, Jędrzejewski et al. 2002, Boyko and Marshall 2009).

In addition to sex, population density have a great capacity to mediate ecological relationships, as they are directly linked to intraspecific competition and, consequently, the formation of home ranges, selection of resources and how the sexes deal with all

these variables (Powell 2000). In general, high population densities are expected when resources are abundant and low when they are scarce (Hairston et al. 1960, Ostfeld et al. 1993, Boyce and McDonald 1999). This resource-density relationship also directly influences how animals use the environment and whether or not they maintain exclusive areas. Following the idea of female's behavioral pattern reported in the previous paragraph, areas of high density can often be avoided by females, as they prefer more exclusive areas to obtain more resources to raise the offspring (Clutton-Brock et al. 1989). Males, which, on the contrary, maximize their reproductive effort by getting more mates, may prefer -or at least tolerate- areas of high density of conspecifics.

In this thesis, we present two studies carried out with small neotropical mammals where, using data of home range and analysis of resource selection, we investigate the effects of sexual and density related conflicts on the populations. In the first chapter, we assessed the home range of the marsupial *Didelphis albiventris* in an urban area. The key novelty is that we captured all the individuals of the study area, so we managed to analyze the entire population. The main objective was to verify the influence of sex and body mass of opossums on the characteristics of their home ranges, considering that we knew the real density of individuals in the areas. In the second chapter, we investigated the selection of resources of the rodent *Thrichomys fosteri* through a structural equation modeling approach. For that work, the home range metrics were used as a tool in order to determine the resource selection of individuals at a fine scale, within the home range. We quantified the main available resources that are important for these rodents (identified in previous studies) and, through the structural analysis, we defined the level of importance of these resources in the individual selection of *T. fosteri*. Here, the main hypothesis is that the bromeliad cover -a common plant in the region that provides protection against predators- is the main resource for *T.*

foster, modulating, at the same time, the influence of all other variables. The selection of areas with bromeliad, despite strong in general, should notably stronger for females than for males, due to the different sexual behaviors, on which females prioritize offspring survival.

Chapter 1 – Density and space use of white-eared opossum in an urban area

Abstract: Animal home ranges provide important information about how sexual differences change the individual space use. Here, we investigate the home range and its overlap in individuals of *Didelphis albiventris* in an urban area in the Brazilian Savannah. We used a rigorous method of capture-mark-recapture and we are able to capture and tag all individuals from the population. We aimed to test the effects of sex and body weight over the home range sizes and to evaluate if female to female overlap is larger than what would be expect by a baseline (male-female interactions). Seven opossums (four females and three males) were captured and monitored from December 2016 through July 2017. Males and females showed no difference in the size of home ranges areas and the body mass was not a significant factor. Females have a much lower and core area overlap with each other than expected in the female-male ratio. Space limitations and human barriers, in addition to human wastes that serve as food, must act to homogenize home ranges, in addition opossums are generalists and the search for food resources may not be as large as for more specialized groups. The low overlap of the females core area is might be explained by the reproductive behavior of the individuals, where females need more exclusive areas to breed and mane their offspring.

Introduction

Home range - a classical approach about animals' lives and movement - was firstly defined by Burt (1943) as the area used by an individual in order to realize all its regular activities as food gathering, search and use of shelters, reproductive behaviors and, occasional sallies outside the area. As such, it is a key characteristic of animal lives. Many factors may influence home range characteristics (as size, shape and overlap between individuals) and those factors might be related to individual and environmental characteristics. Individual characteristics include sex, body mass, physiological and health conditions, and reproductive stage (Burt 1943, Cederlund & Source 1994, Dahle & Swenson 2003, Safi et al. 2007, Gentile et al. 2012). Habitat type, temperature, seasonality and resource availability are examples of environmental components that influence the characteristics of home range (Valenzuela & Ceballos 2000, Loretto & Vieira 2005, Rivrud et al. 2010, Cáceres et al. 2012).

Two of the most important individual factors that influence the characteristics of home range are the effects of sex and body mass, which can greatly influence home range size. Generally, heavier animals have larger home range sizes because their bodies demand more energy. Thus, heavier animals must move through larger areas in order to obtain their energetic demands (McNab 1963, Milton & May 1976, Ofstad et al. 2016). This effect might be straightforward, but many other aspects of animal life can influence their body mass. As a result, it might be one of the key determinant home range size. An individual's sex is also a strong influencer in home range behavior, influencing its size. In many taxa and species, sexual dimorphism related to body size is common, and individuals of the sex with heavier body size might have larger home range sizes as a direct consequence of their body size (Lewis & Saliva 1987, Rocha 1999). In addition, males tend to cover larger areas during the breeding season in order

to find more reproductive females (Tufto et al. 1996, Gehrt & Fritzell 1997, Steinmann et al. 2005). On the other hand, mammalian females have a high level of parental care and this characteristic directly influences their home range. Smaller but more stable areas are preferred, leading to smaller home ranges, territorial behavior, and low overlap (Wolff 1993). Clearly, both body mass and sex can influence home range size and in some cases even interact and influence home range together.

Sex can also influence home range overlap, due to the energetic differences between sexes. Females tend to have smaller home range overlap among them when compared to male-male overlap (Sunquist et al. 1987, Cáceres & Monteiro-Filho 2001, Leiner & Silva 2009). One reason for a smaller home range overlap for females might be the taxing nature of pregnancy. Pregnancy requires a large amount of resources and time, making the relative demand for mates smaller than the competition for food (Ostfeld 1985, 1990). Meanwhile males' reproductive success is much more dependent on female availability (Ostfeld 1990). If females have more exclusive areas, it may become difficult for males to access each female (Soderquist 1995) so they should move between females' home ranges in order to get as many mates as possible and, consequently overlap their areas with other males (Loretto & Vieira 2005, Moraes-Junior & Chiarello 2005). Thus individual sex can influence home range overlap has a consequence of the difference in energetic investment for reproduction.

There are a plethora of methods to measure home range overlap (e.g. Fieberg & Kochanny 2010, Winner et al. 2018), however there are sources of inaccuracy that remain largely unaddressed by existing methods. First, overlap is frequently estimated by calculating home range overlap between individuals that were fitted with radio or GPS collars. Due to the high costs of these equipments, the number of animals tracked are often a small percentage of the population. As a result, much of these analyses

underestimate existing overlap since there is an unknown number of individuals that might be using the same area as the tracked individuals. A second issue is the interdependence between areas and overlap. Many studies frequently find that individuals show little overlap in “core” areas when compared to the total home range (Kerr & Bull 2006, Kapfer 2014). It is often implied that animals are enforcing exclusivity in these “core” areas and thus have some form of territorial behavior (Barg et al. 2004). However, one should expect, by simple geometry, a reduction in overlap between two shapes when those are reduced in size.

Hence, to indicate a presence of territoriality without this effect, one should present a baseline reduction to compare with the observed reduction. A suitable baseline might be intersex home range overlap. In this scenario, the benefits of contact with a member of the opposing sex should offset competition requirements and reduce the likelihood of territorial protection. Thus, it could serve as a baseline against which to measure overlap levels in order to infer territoriality. A third source of bias is the tendency to measure overlap in a pairwise fashion among individuals. This might make it difficult to measure how defensive or permissive an animal is. A large overlap among several animals may configure a situation where they all share a single large region with several exclusive pockets or a situation that no individual has any exclusive area. Thus, pairwise measures of overlap are not good descriptors of how much exclusive area one animal has at its disposal. To attempt to remedy these inaccuracies, we opted to conduct a study in an area where all individuals are known and are being tracked. This way we can actually measure exclusive areas and properly infer its impact on animal energetics.

The white-eared opossum, *Didelphis albiventris* Lund 1840 is a useful model for this analysis, a common marsupial that occurs in the eastern and central-western portions of Brazil, Paraguay, Uruguay, the northern and central regions of Argentina,

and southern Bolivia (Cerqueira & Tribe 2008). It is a medium sized animal with a body mass varying between 500 through 2000 g in adult individuals (Emmons & Feer 1997), and is classified as frugivore-omnivore (Fonseca et al. 1996). The white-eared opossum is a nocturnal and solitary species, except for the reproductive season; as most of didelphids marsupials the promiscuous mating system is registered for the species (Ryser 1992, Pires et al. 1999, Cáceres & Monteiro-Filho 2001). It is commonly found in urban areas due to your generalist behaviors (Cabrera and Yepes 1960, Fonseca et al. 1982) and it is mainly terrestrial but can occasionally climb trees (Cunha and Vieira 2002, Loretto & Vieira 2005). This species is an excellent model to conduct home range studies with controlled population numbers. Its relatively high abundance makes it easier to find the species in many places with diverse environments. Thus, if there are any areas with the logistical prerequisites to conduct a complete census of the population, it is more likely we would find this species there than other, rarer, mammal species. Further, the species is known to occur in urban environments, which allow us to study the effects of this environment in its home ranges. Animal's home range is influenced by the human modifications and regarding the changes in it, a general pattern is the reduction of home ranges when compared to animals in natural environments (Tucker et al. 2018). Two explanations are attributed to this phenomenon 1) The main and most intuitive explanation is that reducing available areas consequently reduces home ranges (Adkins and Stott 1998; Piccolo et al. 2000) and 2) especially for animals associated with human food and waste sources, they need to move less to find resources (Wright et al. 2012, Yirga et al. 2015). As *D. albiventris* is a species largely spread in urban areas it becomes an interesting model to test home range's aspects including sexual patterns. The patches of native vegetation inside urban areas also provide a

singular landscape model to capture virtually the whole population, when associated with a rigorous capture method (which we describe in the next section of this paper).

In this paper we aimed to 1) test the effects of sex and body weight over the home range sizes; 2) evaluate if female to female overlap is larger than what would be expected by a baseline (male-female interactions). In relation to the first aim, we hypothesize that males have larger home ranges than females and heavier animals have larger home ranges than the lesser. In relation to the second aim, we hypothesized that males and females have high home range and core area overlap however, the intersexual overlap will be smaller especially the female's overlap.

Methods

Study area

We carried out this study in an urban Cerrado (Brazilian Savannah) fragment with approximately 34 ha in the Campus of the Federal University of Mato Grosso do Sul (UFMS), Campo Grande, Mato Grosso do Sul, Brazil (20°30'26.78" S, 54°37'2.22" W). The fragment is surrounded by houses, buildings, wastelands and a scientific experimental farm owned by UFMS (Figure 1). The Brazilian Cerrado has an original area of approximately 2 million km² in central Brazil (Ratter et al. 1997) and comprises different types of vegetation formations. We found three typical vegetation formations of the Brazilian Savannah within the study area: gallery forest following the watercourses, woodland savannah, which consists of a forest formation with typical Cerrado's tree species and shrubby savannah, the "typical" Cerrado blending grassland, shrubs and low trees (Eiten 1972).

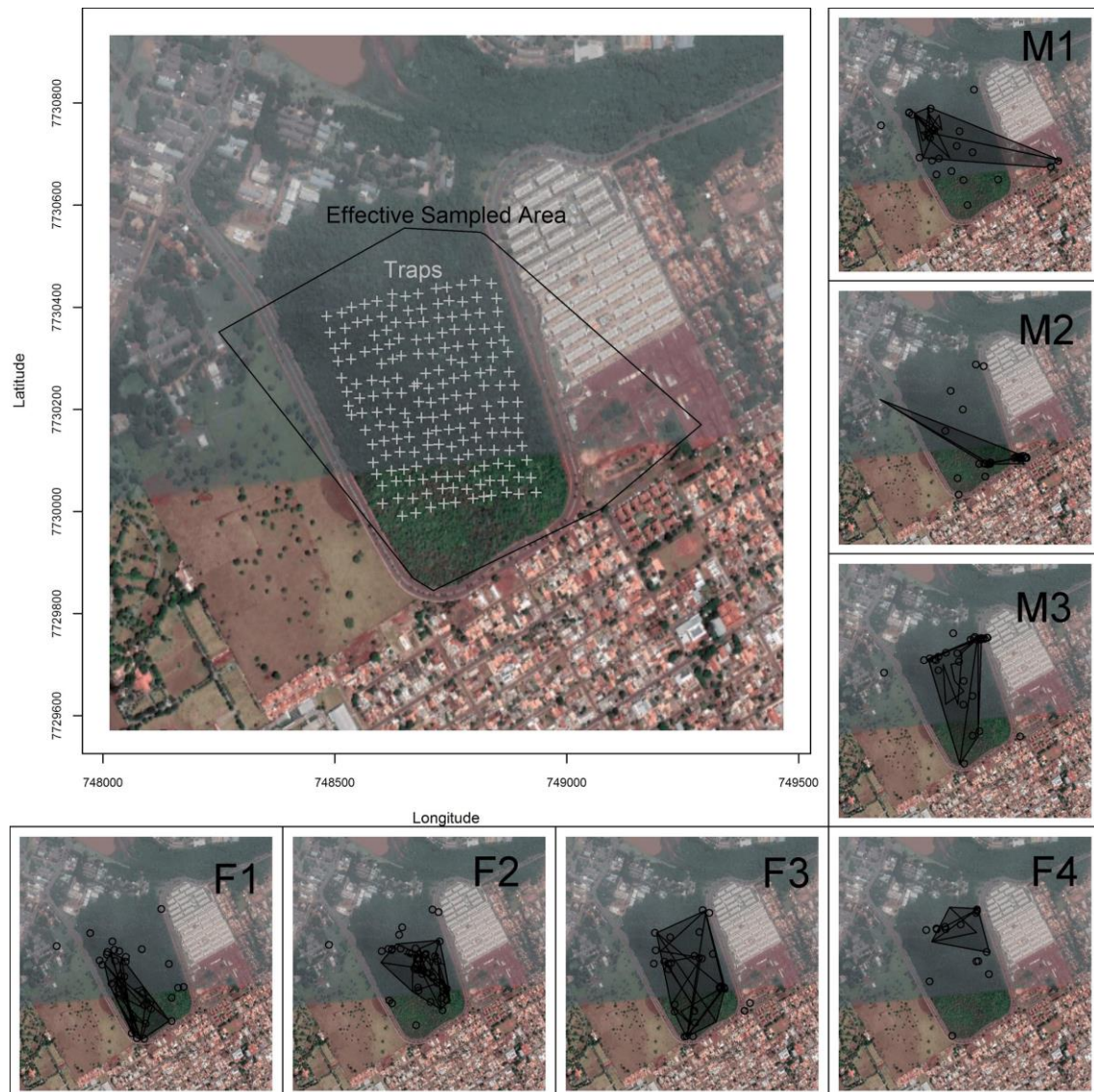


Figure 1 - Study area, capture grid (based on GPS coordinates) and individual home range (MCP 100%) for all individuals of *Didelphis albiventris*.

Capture, handling and tracking

We captured and tagged the individuals of *D. albiventris* monthly between December 2016 through July 2017. The captures, handling and tracking were licensed by the Brazilian Environment Institute, IBAMA (SISBIO License 51900) and by UFMS' animal ethics committee (CEUA-UFMS Process 745/2016). We also developed the capture and handling according to the American Society of Mammalogists guidelines (Sikes et al. 2016). We set a capture grid of 208,000 m² with 220 Tomahawk traps (Tomahawk Live Trap Co., Hazelhurst, Wisconsin) apart 30 m each other (Figure 1). We placed the traps on the ground and we baited them with a banana slice and peanut butter. Baits were replaced daily. Traps remained open for five consecutive nights per month, except in July 2017 when we carried out 16 consecutive nights of capturing (see Density Estimation in Methods section). The total effort employed during the 8 months of sampling was 11,250 night traps. For each captured individual we recorded the date and capture site, sex and body mass. Individuals were tagged with numerical ear-tags on both ears. As all the individuals were considered as adults we tagged them with a VHF collar (weight < 6% of individual body mass; Tigrinus, Timbó, Santa Catarina). We radio-tracked the opossums almost daily between June 2017 and August 2017 (3 months). Tracking was carried out twice a day, at daytime and at night. During the capture sessions, we did not track individuals at night to avoid affecting capture success. We tracked the individuals until seeing them or identifying their shelters. When this was not possible, we located animals by removing the antenna from the VHF receiver and reducing the radio gain as minimum as possible. If VHF signal is audible without antenna and minimum gain, we guarantee the animal was located within less than 2 m from the radio receiver (we tested this procedure previously). After

location was determined we used a portable GPS device to take the geographic coordinates.

Abundance and density estimation

Once we aimed to investigate home range overlap among individuals, we first ensured we captured and radio-tracked virtually all individuals that composed the population. Thus in July 2017, we began a capture session that would stop just when we were sure that we had captured and radio tagged every individual in the studied population. Departure from the second capture night, we daily estimated population abundance (see model parametrization below), and just stopped capturing when 95% confidence intervals of abundance estimation were less than one individual. That would mean we are at least 95% sure we have no new individual to be captured.

We estimated the abundance of opossums by applying a closed capture model over our capture-mark-recapture data. We chose the Huggins' conditional parametrization found in RMark package available in R environment. This parametrization presents two inner parameters in its likelihood formulation: capture detectability (p) and recapture detectability (c), while abundance (N) is estimated as a derived parameter. We ran three models with different effects on detectability to figure out the detection structure that best fit our detection history. The models were (1) null model: detectability was constant among capture occasions; (2) behavior model: capture probability was different from recapture probability (i.e. behavior response to first capture), and (3) time model: detectability varied among capture occasions. Models were ranked based on Akaike Information Criteria (AIC), where those with $\Delta AIC < 2$ were considered with similar support. If just one model match the $\Delta AIC < 2$ criteria, that

model was considered the best. However, if more than one model match the $\Delta AIC < 2$ criteria, we model averaged them. Abundance was then derived from best model(s).

For translating abundance, estimation into density is necessary to divide the abundance estimated by the area occupied by individuals (hereafter, effective sampled area). This area is usually much larger than the area covered by the traps (sampled area), and there is a long debate about how to approach it [see details in Foster & Harmsen (2012)'s review]. Here, we opted by dividing the estimated abundance by the area created by the joined home ranges of all tracked individuals. In our specific case, we believe it was the best choice once we were able to virtually capture and track each individual in the population (see results). This population census gave us the opportunity to overcome every limitation of standard methods of effective sampled area estimation (e.g. HMMDM or MMDM; Foster & Harmsen 2012), and therefore to provide reliable density values.

Home range estimation

We estimated home range size using the Minimum Convex Polygon (MCP, Mohr 1947) method considering 100% of locations. We check the confidence and stabilization of our estimations by building an accumulation curve (number of locations X accumulated area) for each individual. Only asymptotic curves were considered to reach reliable home range size estimation. Home range estimations were performed in adehabitatHR package (Calenge 2006) available at R environment. We tested the effects of sex, body mass, and sex-body mass interaction on home range size using a general linear model. The number of locations taken by individuals was included as covariate in the model to control for spurious sampling effect. Both home range size and body mass

were log-transformed. We compared body mass between males and females using a t-test.

Home range overlap

We measured home range overlap among individuals using the HR method that computes the proportion of area used of one animal covered by the area used of other (i.e. pair of individuals; Fieberg & Kochanny 2005). Here we are specifically interested in estimating the proportion of exclusive home range between not only pairs, but also taking account of all individuals within the population. Therefore, our modified overlap estimation computed the proportion of area used by one individual covered by any other individual within the population. We split these calculations in three parts to account for our sexual hypothesis: (1) proportion of one female's area used covered by any other female (female-female); (2) proportion of one male's area used covered by any other male (male-male), and (3) proportion of one male's/female's area used covered by any other individual of opposite sex (male-female). We measured overlap, using MCP considering two levels of locations: 100% (home range) and 50% (core area) of locations.

We tested the fixed effect of sex, level of locations (home range and core area) and the interaction term sex-level of locations on area used overlap (i.e. area exclusivity) using a general linear mixed model. For the sex (categorical variable), male-female class (intersexual overlap) was set as reference class. Individual identity was included as random effect because each individual had its overlap measured in 4 different ways: home range and core area within and between sexes. For this model, we were specifically interested in the significance of sex variable or the interaction term

sex-level of locations. If main effect of sex was significant but interaction not, we would expect females had less intrasexual overlap in both home range and core area than the observed in the reference class (intersexual: male-female). Otherwise, if interaction was significant but main effect of sex not, we would expect female intrasexual overlap decreasing emerged only in core area level, but not in home range.

Results

We captured seven individuals (four females and three males) (Table 1) within 35 captures. Both null model and behavior model received high support ($\Delta AIC < 2$; cumulative $w = 99\%$; Table 2). Model-averaged estimates of probability of capture (0.30; $IC_{95\%} = 0.19-0.44$) and probability of recapture (0.31; $IC_{95\%} = 0.23-0.41$) did not indicate clear behaviour effect (i.e. trap happy effect). Model-averaged abundance estimate was 7.02 individuals ($IC_{95\%} = 7.00-7.32$), suggesting we have captured virtually every individual in the population. Since all captured individuals were also radio-tracked, we were able to estimate the area occupied by the entire population (0.41 km^2 ; Figure 1), which yielded a density estimation of 17.06 individuals/ km^2 ($IC_{95\%} = 17.01-17.81$).

As said early, all captured individuals were radio-tracked (Table 1) whose home range estimates were considered stabilized for six of them (except ID M1, Figure 2). Males and females had similar body mass ($t = 0.11$, $df = 5$, $p = 0.91$) (mean = 754 g, range = 495-1000 g). Mean home range size was 10.08 ha ($SD = 4.46$), with no effect of sex ($t = 0.45$, $df = 5$, $P = 0.69$), body mass ($t = 0.04$, $df = 5$, $P = 0.96$), number of locations ($t = -0.56$, $df = 5$, $P = 0.63$) nor interaction between sex and body mass ($t = -0.36$, $df = 5$, $P = 0.75$).

Mean home range overlap was 81% between males and females (range = 59% to 99%), 63% among males (range = 53% to 78%), and 69% among females (range = 60% to 82%). Mean core area overlap was 50% between males and females (range = 14% to 80%), 10% among males (range = 0% to 24%), and 7% among females (range = 0% to 12%). As expected, we found the main effect of level of locations on home range overlap (32% of reduction; $t = -4.09$, $df = 16$, $p < 0.01$), i.e. home range overlap was larger than core area overlap. We found no main effect of sex on area overlap since both female-female ($t = -1.65$, $df = 16$, $p = 0.12$) and male-male ($t = -1.51$, $df = 16$, $p = 0.14$) did not present differences when compared to male-female values (reference class) (Figure 3). However, we also found effect of interaction term (sex-level of locations), which means that the effect of level of locations depended on which sex comparisons we did. The reductions on area overlap (from home range to core area) were more pronounced among females (61% of reduction; $t = -2.25$, $df = 16$, $p = 0.04$) when compared to male-female reductions (32% of reduction) (Figure 3). On the other hand, reductions observed in male-male were not higher than those observed in male-female ($t = -1.42$, $df = 16$, $p = 0.17$) (Figure 3).

Table 1. Informations about sex, weight (g), number of locations and home range size (ha) for all individuals of *Didelphis albiventris*.

ID	Sex	Weight (g)	Locations	MCP100 (ha)
F1	F	495	33	7.77
F2	F	780	23	8.91
F3	F	800	15	17.31
F4	F	770	32	5.24
M1	M	645	44	13.38
M2	M	790	29	5.54
M3	M	1000	28	12.43

Table 2.—Model's rank for detectability and abundance estimation. p = probability of capture; c = probability of recapture; k = number of parameters; AIC = Akaike Information Criterion; Δ AIC = delta Akaike Information Criterion; w = Akaike weight; cumulative w = cumulative Akaike weight.

Model	Model Description	k	AIC	Δ AIC	w	Cumulative w
Null model	$p(.) = c(.)$	1	141.12	0.00	0.72	0.72
Behavior	$p(.) \neq c(.)$	2	143.11	1.98	0.27	0.99
Habitat model	$p(\text{time}) c(.)$	16	168.28	27.16	<0.01	1.00

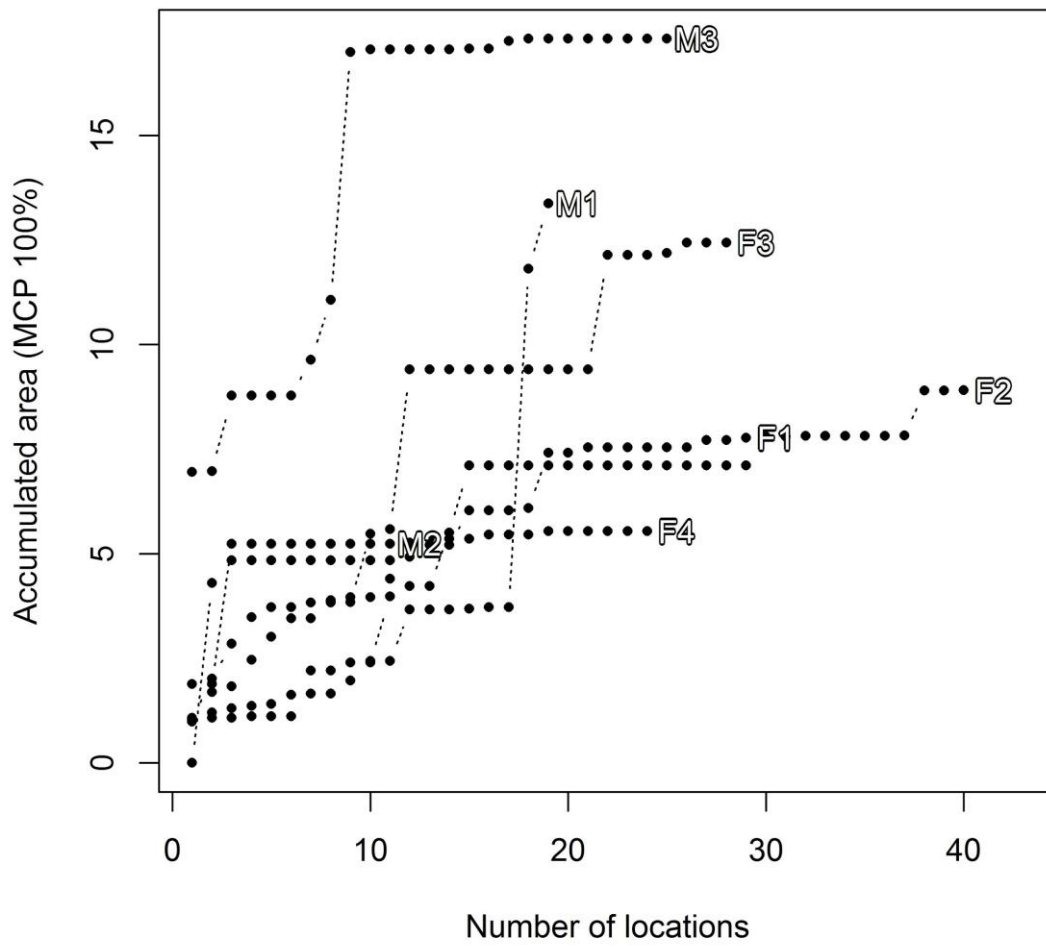


Figure. 2 - Accumulated locations forming the stabilized home range area for the most of individuals.

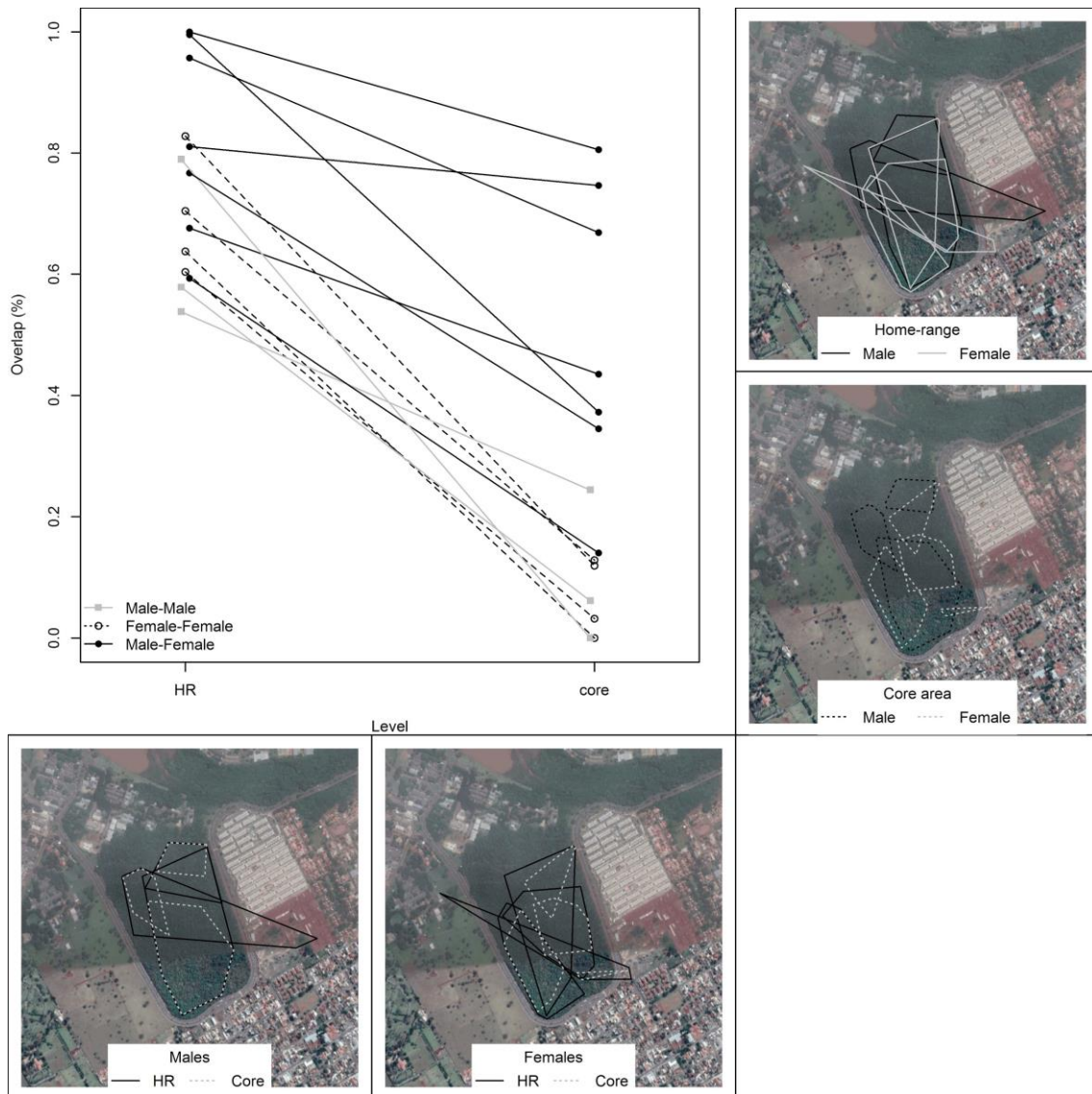


Figure 3 - Home range and core areas overlapping for all individuals of *Didelphis albiventris* separated by sex.

Discussion

We captured all individuals from the area, which allowed us to know the individuals' real exclusive home ranges. Most studies that evaluated home range and its overlap normally do not capture all the individuals. Consequently, the real density of individuals might be inaccurate. Thus, the real amount of home ranges in an area and their overlap can be imprecise. Once we have all the individuals tagged and tracked, we have a real spatial organization of home ranges and consequently their overlap. This approach is more effective than the usual pairwise overlap approach because unknown individuals may lead us to make wrong assumptions about the use of space, exclusive areas (including territoriality) and matting systems.

Heavier animals, regardless of sex showed no larger home ranges. The same pattern was found for *D. albiventris* by Almeida et al. (2008). However, Sanches et al. (2012) showed that heavier opossums had larger home ranges and the same pattern was reported for other species of the genera (Cajal 1981, Cáceres & Monteiro-Filho 2001, Cáceres 2003). Our study was carried out in a large urban area inside University campus, which is limited and surrounded by streets, houses and wastelands whose seem to work as a barrier, since only two opossums occasionally leave the boundaries of the area. The study area is also characterized by low human density, an altered landscape and low natural resources, which might probably limit its potential colonization by opossums. In addition, there is evidence that individuals of the congeneric *D. virginiana* reduce their movement and home range in urban areas when compared with individuals from natural areas because of the high availability of human wastes, which decreases the search for food (Wright et al. 2012). All those anthropic disturbances can restrict

home range size and prevent the size effect being manifested (Ditchkoff et al. 2006, Šálek et al. 2014, Tucker et al. 2018).

Another possible explanation for the lack of mass effect on the size of the home ranges is the food habits of *D. albiventris*, which is classified as omnivorous with high prevalence of invertebrates on diet (Cáceres 2002). Due to the high availability of resources for generalist and insectivorous animals, there is a tendency of less movement in the search for food resources, when compared to specialist or carnivorous animals, which need to move more to find their strictest resources (Gittleman and Harvey 1981, Tucker et al. 2014, Fauvelle et al. 2017). Thus, this reduction in movement mediated by the intrinsic availability of the resources can also act in the homogenization of the individuals' home range even if they have different body mass.

There were no significant differences in home range size for males and females. These results are similar to those estimated by other authors (Almeida et al. 2008, Sanches et al. 2012), but differ from the pattern observed for Brazilian marsupials (Vieira & Palma 1996, Pires et al. 1999, Cáceres & Monteiro-Filho 2001, Galliez et al. 2009, Shibuya et al. 2017), including the genera *Didelphis* (Petrides 1949, Gardner 1973, Tyndale-Biscoe & Mackenzie 1976, Fonseca & Kierulff 1989, Cherem et al. 1996). One possible explanation for our results is the apparent lack of sexual dimorphism regarding the body mass of the species (Cáceres & Monteiro-Filho 1999, Almeida et al. 2008). Other factors besides sexual dimorphism may also influence home range size such as reproductive period and seasonality, where males and females may exhibit changes in home range size due to behavioral changes. Males might increase their home range areas only during the reproductive season and females might increase their monopoly over an area during this period (Sunquist et al. 1987, Ryser 1992, Cáceres 2003, Loretto & Vieira 2005). The reproductive period for *D. albiventris* in the

Cerrado biome is reported for the rainy season, from November through April (Mares & Ernest 1995) and our radio tracking was carried out in a relatively short period (June through August) outside the reproductive period. The tracking was done during the middle of the winter, which is the driest season in the region and probably the worst season for reproduction.

Home range overlap was larger than core areas overlap for all comparisons (male-female, male-male, and female-female) which is expected due to geometric reduction from home range to core area. However, females' core area overlap was smaller than male-female core area overlap, what did not occur for males. These results show us that, on core area scale, females have more exclusive areas than males. This result is in accordance with existing knowledge on mating systems reinforcing that gestation, lactation and infanticide costs elicit more territorial behavior in females (Ostfeld 1985, 1990, Wolff 1993). It is reported that females of *D. aurita* and *D. virginiana* reduce their core areas overlap during the reproductive season and they have a certain level of territorial behavior (Ryser 1995, Cáceres 2003) which can reflect an exclusivity of core areas, including in periods outside the breeding season. Again, monitoring a minimum period of one year and identifying the reproductive period could elucidate the aspects of a possible territorial behavior in females of *D. albiventris*. On the other hand, the higher overlap of the males' core areas might be related to their more generalist reproductive behavior when compared to females as we stated previously. Apparently, males cover larger areas in general, which should lead to a higher general overlap even outside the reproductive season.

Chapter 2. Sexual and density dependence effects on bromeliad spine rat's space use revealed by structural resource selection function

Abstract

Animal movement is often guided by resource distribution, which highlights the importance of understanding the habitat selection process. Different biological traits, such as sex, can influence resource selection. Here, we investigate the factors driving resource selection in the spiny rat *Thrichomys fosteri*, using a Structural Equation Model approach over the Resource Selection Function design perspective. We radio-tracked 39 individuals and evaluated three resources that are considered key to the species (bromeliad cover, arthropod biomass and conspecific abundance) in the individual habitat selection of bromeliad spiny rats. We hypothesized that the bromeliad cover is the main resource for individuals because it offers protection against predation, and should also directly influence prey availability and intraspecific competition. As expected, bromeliad cover was the main resource structuring habitat selection among the three modelled covariates, being the strength of selection almost twice for females than for males. Arthropod biomass negatively influenced conspecific abundance, which, in turn, affected habitat selection differently by sex (positively for males and negatively for females). We showed how sexual differences in behavior influence the habitat selection process, with females more associated with bromeliad cover, due to their territorialism and bigger need to protect their offspring. For the same reason, females avoid high population abundances while males select it, possibly guided by the search for reproductive mates and the absence of territoriality.

Key-words: Echimyidae, Habitat Selection, Home Range, Protection, *Thrichomys fosteri*

Introduction

Habitat selection is a fundamental part of animal behavior because it modulates evolution, population dynamics, intra and interspecific interactions, as well as key components of communities' composition (Morris 2003). As animals usually do not move randomly across space, habitat selection emerges as an important driver of individuals movement, shaping its distribution and abundance (Beyer et al. 2010, Van Moorter et al. 2016, Boyce et al. 2016). The distribution of resources is the main modulator of whether an area is selected or avoided in relation to what is available (Morris 1987). Despite this relationship being so strong to the point trophic resources concentration is used as a direct proxy to habitat selection, other factors should be important for habitat selection such as the density of conspecifics. For example, high densities can increase competition for food resources; however, it can dilute the effect of predation or even indicate a large number of available sexual mates (Turchin & Kareiva 1989, Klimley et al. 1996, Lehtonen & Lindström 2008). Furthermore, predation intensity and risk perception have been also considered important components in habitat selection (Jordan et al. 1997, DeCesare et al. 2014). Hence it is mandatory the understanding on how individuals integrate information about conspecifics density and risk during their habitat choices.

Iteroparous populations are age- and sexually structured, in which different individuals can require and perceive resources differently to maximize their survival. Sexual differences in habitat selection can be related to sexual dimorphism where body differences between the sexes could explain how resources are selected through different energy requirements and/or risk of predation (Schoner 1967, 1968). In mammals, the role of the sexes is generally well marked, with females being primarily responsible for parental caring. Mammalian females need to breastfeed (which means a

high energy cost) and protect the litters from predation and infanticide. Thus, females tend to maximize shelter quality and use areas of reduced predation pressure and conspecific competitions (Clutton-Brock et al. 1981, Hoogland & Foltz 1982, Stacey 1982). These requirements often lead the mammalian mother to prioritize areas of better food quality and protection than males (Grignolio et al. 2007, Oliveira et al. 2018).

Sexual differences in habitat selection might not be a direct response to different reproductive behaviors related to sexes. Instead, these differences would be a way of decreasing intraspecific competition in a population, or just reflect the nesting habits of females. As females are usually restricted to the nests, they tend to occupy nearby habitats, and may even perform different habitat selection outside the breeding season (Morris 1984). Sexual differences in habitat selection can also be linked to intrinsic components of the habitat such as degree of habitat heterogeneity (Bowers & Smith 1979). In addition, sexual differences in habitat selection can also be a mechanism for reducing intraspecific competition (Bowers & Smith 1979, Morris 1984). Thus, the analysis of each population and how males and females interact with key resources is essential to define the role of sex on habitat selection.

Small mammals are an interesting model to test hypotheses on habitat selection, as they have a tight relationship with the variation of small-scale habitat resources (Morris 1987, Stapp 1997, Jorgensen & Demarais 1999, Moura et al. 2005). Furthermore, they have a wide variety of mating systems and sexual behaviors (Clutton-Brock 1989, Adler 2011) that can directly influence habitat selection. Here, we quantified the influence of resources on individual habitat selection using the Structural Resource Selection Function (SRSF) in a small rodent in the Echimyidae family, the spiny rat *Thrichomys fosteri* Thomas, 1903. Its density is relatively low (0.9 to 3.03 individuals / ha; Antunes, PC unpublished data) and its presence is linked to bromeliad

stands (more information in the “Methods” section) which provide shelter against predators (Antunes 2009, Antunes et al. 2016). The mating system of the local population was recently inferred (considered promiscuous) and other aspects of the population's sexual behavior were described (Antunes et al. 2020). Because of these characteristics and previous knowledge, this species becomes a very interesting model to understand how sex can shape resource selection.

According to the previous and theoretical background of *T. fosteri*'s ecology, we evaluated the influence of the following variables in individual habitat selection of spiny rat's males and females: bromeliad cover, arthropods biomass and conspecific abundance. We hypothesize that 1) bromeliad cover should be the most important variable in individual selection, particularly for females, due to its protective function; 2) the bromeliad cover should also positively influence the two other variables: arthropods biomass and conspecific abundance; 3) arthropod biomass should also be an important variable in individual selection, with no expected difference for sexes; 4) arthropod biomass should positively influence population abundance; 5) conspecific abundance (due to the different sexual strategies of females and males) should generate a different scenario for each sex, where females should avoid areas with high population abundance and males should select for.

Methods

Study area

We carried out the study in two forested areas of the Pantanal of Brazil. The first capture site is a continuous forested area located at Nhumirim Ranch (18°57.5' S, 56°37.1' W) and the second one comprised two forest patches of 0.41 ha and 0.15 ha

located at Alegria Ranch (19°9.14' S, 56°47.9'W and 19°8.7' S, 56°47.77' W) (Figure 4). Both areas are located in the Pantanal region called Nhecolândia. Mean annual precipitation is about 1,000 mm and mean temperature ranges from 29.1 °C in January to 22 °C in June (Garcia 1984). The flood regime of the area (which is due to river overbanking at other regions of the Pantanal) occurs due to local rainfall at the Nhecolândia. This process creates two sharply distinct seasons. The rainy season (more than 120 mm/month) extends from November to March or April, and the dry season (less than 40 mm/month) extends from June to August (Rodela 2006). Different types of vegetation occur in the area, such as continuous forests (called '*cordilheiras*'), forest patches ('*capões*'), shrubby savannah, grasslands and monodominant formations. Permanent and temporary bodies of water such as lagoons, "salinas" (bodies of water with high amounts of alkaline compounds), and swamps also make up the elements of the landscape (Alho et al. 1987). Due to their higher elevation, forested areas are not subjected to flooding. At these areas, some species stand out for their abundance and specific morphological aspects, as the acuri palm (*Attalea phalerata*) and the caraguatá bromeliad (*Bromelia balansae*) (Figure 5). The palms usually occupy the center of the forest patches while the bromeliads -due to higher sunlight availability- tend to occupy the forest edges. The bromeliad also forms monodominant stands with high abundance (in some areas the dominance is about 100%) and height up to 2m.

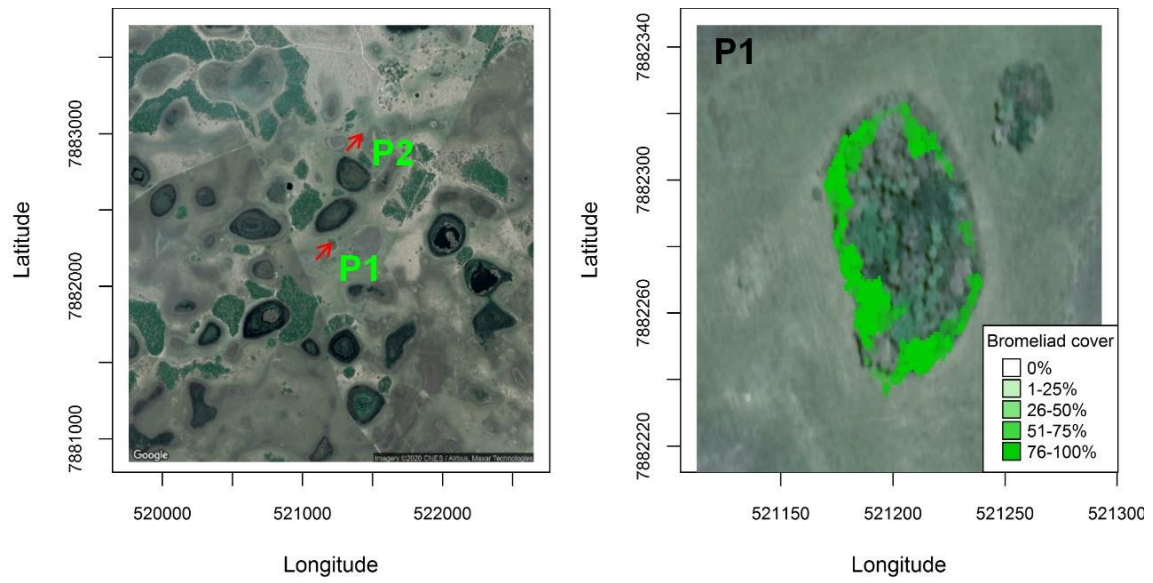


Figure 4 - Overview of the landscape of Nhecolândia subregion. The two sampled patches (P1 and P2) are on the left. Patch 2 with bromeliad cover distribution across its boundaries.



Figure 5 – Caraguatá bromeliad (*Bromelia balansae*). A) Part of bromeliad stand and B) one individual of *B. balansae*.

Animal capture and handling

The captures of *T. fosteri* occurred in two phases, one on each of two study areas. Both phases followed a capture-mark-recapture (CMR) process developed according to the American Society of Mammalogists guidelines (Sikes et al. 2016) and licensed by the Brazilian Environment Institute, IBAMA (SISBIO numbers 23116-1 and 51900), and by the UFMS' animal ethics committee (CEUA-UFMS Process 745/2016). For the first phase we carried out monthly captures between July 2010 and June 2012 (except March 2011) in a grid of 200 x 240 m (4.8 ha). The grid was composed of 143 capture sites separated by 20 m. Each capture site contained a Tomahawk™ trap (45 x 16 x 15 cm; Tomahawk Live Trap Co., Hazelhurst, Wisconsin) and a Sherman trap (Metalúrgica Miranda, Nova Veneza, Santa Catarina, Brazil), alternating between two sizes (30 x 8 x 9 cm or 43 x 12.5 x 14.5 cm). We placed the traps on the ground, 1 - 2 m apart from each other. For the second phase, we carried out the study during August through October 2018 at two forest patches (patch 1 and patch 2). We located the traps differently for each patch matching its respective bromeliad stand configuration. For the patch 1, where bromeliads are distributed at the edge of the forest patch, we set 118 traps in that area, on the ground, 1.5 m apart from each. For patch 2, where bromeliads are present throughout the area, we constructed a grid covering all the patch area (0.15 ha) with 150 traps separated by 2 m. Antunes et al. (2016) revealed that bromeliad cover is the most important resource for spiny rats due to the protective effect it provides, conditioning the species' occurrence. Thus, we placed the traps along the entire length of the bromeliad cover. We used the same bait for both phases, banana and peanut butter, replaced daily. Traps remained open for 5 consecutive nights. For each captured individual we recorded the date, capture site, sex, and body weight. We weighed individuals with a 5-g precision spring scale (Pesola AG

LightLine, Baar, Switzerland). Individuals were marked with numerical ear-tags on both ears (National Band and Tag Co., Newport, Kentucky). Those individuals able to carry the VHF collar (weight < 3% of individual body weight) were equipped with it (Telenax®, Playa del Carmen; Mexico, and Tigrinus®, Timbó, Brazil).

Movement tracking

We used two methods in order to obtain the individual locations: CMR and radio telemetry. Regarding CMR, animals were caught as described in the subsection “Animal capture and handling”, registering the capture location. Regarding telemetry, individuals were radio-tracked for different periods in the two study phases. For the first phase, we radio-tracked 21 individuals monthly between April 2011 and August 2012 (17 months). For the second phase we radio-tracked 17 individuals from August through October 2018. The tracking process was the same for both phases: we carried out tracking twice a day, at daytime and at night, with a minimum interval of 2 h between locations. During the capture periods, we did not track individuals at night to avoid affecting capture success; otherwise we continued obtaining locations throughout the 24 h. We tracked the individuals until seeing them or identifying their shelters. When this was not possible, we located animals by removing the antenna from the VHF receiver and reducing the radio gain to less than a half of the maximum gain. We tested this procedure previously, and it guaranteed a location error of less than 3 m. After we find an individual, we determined its exact location by the distance in meters to the nearest capture site. All capture sites in the grid or edge were numbered and georeferenced, so we were able to accurately determine the exact location of each individual. We removed

all VHF collars after the end of the study, except for four individuals whose equipment malfunctioned.

Home range estimation

We used the home range estimation as a tool to delimit the use area of each individual in order to determine the resource selection. We estimated the home ranges for all individuals that had at least 5 locations, using both the Minimum Convex Polygon (MCP, Mohr 1947) method and the kernel density estimation (Kernel, Worton 1989). For CMR data, we only considered the first capture of each individual in each month to avoid dependence among locations, since the baited traps attract and intercept individuals and prevent their free movement. For the radio telemetry data, we assumed independence of the locations because the 94% of temporally adjacent location pairs were obtained with at least 5 h between them. If the animal did not move between two consecutive locations, the last location was discarded. We estimated the area used by applying a kernel probability density estimation through a bivariate normal fixed-kernel method under 95% (home range) and 50% (core home range) probability isopleths. The smoothing parameter (h) was set to the mean reference value (h_{ref} —Worton 1995), estimated separately for each individual ($h_{ref} \bar{X} \pm SD = 12.43 \pm 8.85$ m). Whenever the home range included non-contiguous contours generated from only one location, we excluded this location and the resulting area. In the following analyses, we considered only individuals with enough locations to produce stable home-range estimates. We assessed home-range estimate stability by examining a graph of the home range size estimates as a function of the number of locations; when the curve reached an asymptote, we considered the home range area “stable”. We performed all home-range

size estimates using the `mcp.area()` and `kernel.area()` functions in the `adehabitatHR` (Calenge 2006) package of R environment (R Core Team 2012).

Resource covariates

We accessed 3 resource variables within each spiny rat's home range: caraguatá bromeliad cover, arthropod biomass and abundance of conspecifics. Caraguatá bromeliad is very abundant in the area forming large stands and its density positively affects the probability of occupancy by this species (Antunes 2009). Bromeliads also provide a protective effect by decreasing the movement and attack of predators due to its thorny and dense conformation (Figure 5), even making predators noisier and quickly to notice. As we stated earlier, spines' rats are highly associated with bromeliad stands. Thus, we assumed that bromeliad cover was an important resource for the spiny rats. We measured the bromeliad cover once because its distribution, density and biomass are not affected by seasonality, being stable for long periods of time. For the first phase we evaluated the bromeliad cover in 893 plots (10x10 m) covering the entire capture grid, plus the home range of the spiny rats that were located outside the grid. For the second phase we evaluated the bromeliad cover for the entire patch 2 in 36 plots (4x4 m), and for the patch 1, as the traps were arranged in a circular pattern, we evaluated the bromeliad cover in plots (4x4 m) centered at each capture site. Bromeliad cover was estimated in each plot using 5 cover categories (0%, 1–25%, 26–50%, 51–75%, and 76–100% of bromeliad cover).

Arthropods are an important food resource for spiny rats ($n = 63$ fecal samples, relative frequency = 98.4%, Antunes 2014). Therefore, we considered them as an important resource for the species. In order to assess the temporal variation in this resource for the first phase of the study, we sampled arthropod biomass every 2 months

for 5 days using 36 pitfall traps. Pitfall traps were regularly spaced every 40 m in a 200×200 m grid, which overlapped the capture grid. As the second phase was a short-term study, we just accessed the arthropod biomass once in September 2018. For patch 1 we disposed one pitfall trap in each capture station and for patch 2 we disposed 85 pitfall traps between each capture station. Pitfall traps were made with a 500-ml plastic cup, filled with 200 ml of a mixture of water, 70% alcohol, and a drop of dish soap. Arthropods sampled in each pitfall trap were preserved in 70% alcohol and then oven-dried (at 60°C for 24 h) and weighed to calculate the biomass.

Intraspecific competition was estimated by the abundance of conspecifics across the grid/patches because high population densities should lead to a reduction of resource availability per capita. We estimated the abundance of conspecifics along the capture grid/patch by counting the number of individuals caught in each trap station per month. Since arthropod biomass and conspecific abundance were measured in points instead of plots, we applied an ordinary kriging interpolation method (package `gstat` in R environment) to estimate raster maps of these two resources covering the home ranges of each individual (see Antunes et al. 2016).

Structural Resource Selection Function

We analysed resource selection under the third order of selection (sensu Johnson 1980), i.e. where individuals allocate their time within their home ranges. Therefore, used and available resources were measured within home range. Used resources were measured by intercepting all observed locations with the three maps of resources. We randomly sampled 500 locations within each individual's home range to assess resource availability. Note that resource use and availability were independently measured for

each individual. Because biomass of arthropods and abundance of conspecifics have monthly maps, the interception of observed and available locations considered the month when locations were registered (see Antunes et al. 2016). Used locations were coded as 1's and available locations as 0's, following a standard case-control design commonly used in Resource Selection Function approach (Manly et al. 2002).

Resource Selection Function (RSF) has been largely solved using Conditional Logistic Regression (CLR; Duchesne et al. 2010). In CLR, a logistic regression is applied over data, but conditioned by the individual identity, which matches the case-control design (i.e. used resources by one individual are compared with resources available within the home range of that individual). However, CLR assumes, as any linear model, that the modeled covariates are independent. It could be the case for the most resource selection studies, which just evaluate habitat classes. However, this assumption of independence would be hardly met when modeled resource covariates are prey and conspecifics, once they also respond and interact with habitat evaluated in the RSF. In other words, a target individual can select for some habitat class and for areas with high prey biomass, but in turn prey biomass can also be structured in according to habitat classes.

Cause-effect structure among modeled covariates can be accommodated using Structural Equation Modeling (SEM). Furthermore, the SEM approach allows us to estimate direct and indirect effects on the target response, which could enlighten our understanding on the underlying ecological context of habitat selection. Therefore, here we applied a SEM to solve our RSF. The case-control design is accommodated by using mixed linear models (Shibley 2016), in which individual identity was modeled as a random intercept. Our Mixed Structural Resource Selection Function (mixed-SRSF)

(Ortega et al. 2019) was then solved using *piecewiseSEM* package (Shipley 2016) available in R environment. The model structure follows:

(equation 1) Habitat selection \sim bromeliad cover + conspecifics abundance + prey biomass + bro:cons + bro:prey + prey:cons + bro:sex + cons:sex + prey:sex

(equation 2) conspecific abundance \sim bromeliad cover + prey biomass

(equation 3) prey biomass \sim bromeliad cover;

where equation 1 was modeled with binomial distribution ($\text{used}[1]/\text{available}[0]$), and all three equations included individual identity as random intercept.

We looked for sexual differences in habitat selection, i.e. how different sexes perceive and demand resources, by including in equation 1 interactions between sex and the three resource covariates.

Results

We captured 126 individuals (73 males and 53 females) in the first phase and 19 individuals in the second phase. Out of these 19, 15 individuals (7 females and 8 males) were captured in patch 1, and 4 individuals (2 females and 2 males) in patch 2, totalling 83 captures. Within all those individuals, we radio-tracked 21 individuals in the first phase and 13 individuals from the second phase, obtaining a total of 449 locations (Table 3)

Bromeliad cover had strong direct and indirect effects on the habitat selection of spiny rats. As a direct effect, selection for bromeliads was stronger for females ($\beta = 0.99$) than for males ($\beta = 0.47$). Bromeliad cover also directly influenced arthropod

biomass ($\beta = 0.08$, $p < 0.05$) and conspecific abundance ($\beta = 0.22$, $p < 0.05$). Arthropod biomass did not have a significant effect on habitat selection (conspecific abundance = 0), however its effect turned negative with the increase of conspecific abundance (interaction between insect biomass and conspecific abundance; $\beta = -0.28$, $p < 0.05$). Arthropod biomass also had a negative effect on conspecific abundance ($\beta = -0.03$, $p < 0.05$). Conspecific abundance drove a different, opposite effect on habitat selection regarding the sex: a negative effect for females ($\beta = -0.09$, $p < 0.05$) and a positive effect for males ($\beta = 0.06$, $p < 0.05$) (Figure 6).

Table 3 - Informations about total number of locations (captures + telemetry) sex and difference of days between first and last location of monitored individuals of *Thrichomys fosteri*.

ID	N	Sex	Tracking time (days)
1	6	F	36.00
2	24	F	19.73
3	32	F	112.00
4	34	F	54.00
5	34	F	89.17
6	44	F	30,29
7	50	F	93.02
8	52	F	110.00
9	57	F	111.00
10	60	F	112.00
11	60	F	112.00
12	89	F	113.34

13	5	M	35.00
14	7	M	5.00
15	11	M	15.14
16	15	M	108.00
17	25	M	18.77
18	26	M	42.06
19	26	M	17.33
20	30	M	54.00
21	31	M	35.52
22	33	M	54.00
23	33	M	100.00
24	41	M	97.00
25	42	M	41.72
26	43	M	173.79
27	43	M	55.39
28	47	M	99.17
29	50	M	60.39
30	54	M	50.69
31	61	M	70.06
32	81	M	323.73
34	166	M	349.04
33	83	M	149.92

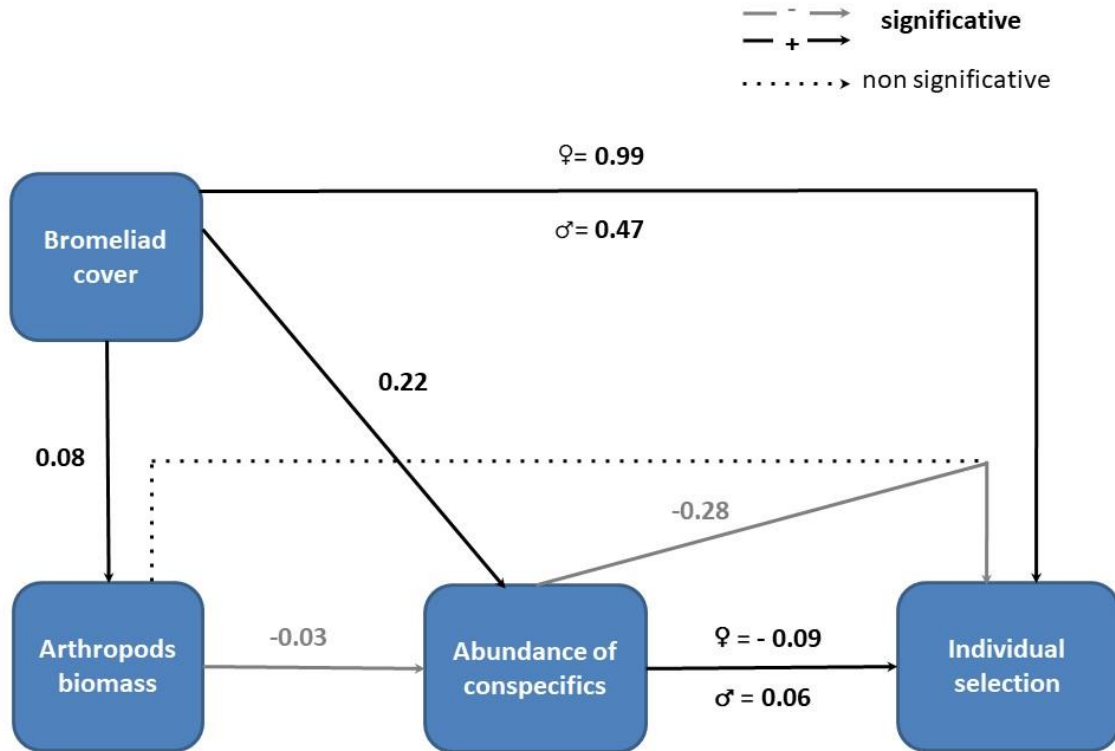


Figure 6 - Mixed-SEM model showing how the three studied resources influence the individual habitat selection of *Thrichomys fosteri* of the Pantanal of Nhêcolandia (Brazil). The solid arrows represent significant effects and the dashed arrow represents a not significant result. Each relationship is accompanied by the respective standardized path coefficient (β), which represents the relative strength of the corresponding effect. When the interaction between the covariate and sex was significant, the coefficient for each sex is provided.

Discussion

Our SRSF allowed us disentangling the effects of each resource on the final habitat selection process, as well as including the intrinsic sex variable that could mask the conclusions on individual's selection. In addition, this technique provides the direction and intensity of direct and indirect effects of the environmental variables. This integrative and mechanistic approach allows us to understand the role of each variable, including the order of importance and hierarchy in individual selection (Lefcheck 2016, Ortega et al. 2019).

Bromeliad cover was the main determinant habitat selection. Bromeliad cover promotes an important protection factor for several animals that occupy the region's landscape and it is an important shelter against predators for *T. fosteri* (Antunes et al. 2016, Menezes et al. 2018). The protection of bromeliads is further corroborated by our data. Both males and females selected areas with bromeliads. However, the strength of selection for bromeliad cover was not the same among sexes. For females, it was twice more important than for males. This difference is likely caused by its function as shelter/protection since there is no interaction effect between bromeliad and insect abundance on habitat selection. Since small mammal females have their reproductive success based on the number of litters that survive (Ostfeld 1985, 1990, Wolff 1993), accessing more protected areas should be a key-factor for reproductive success. On the other hand, males have their reproductive success based on the largest number of reproductive pairs (Stockley et al. 1994, Coltman et al. 2002, Kappeler 2012). Moreover, *T. fosteri* is a promiscuous species (Antunes et al. 2020), which would probably lead males to expose themselves (in open areas, without bromeliad cover) almost twice as much as females. Thus, we believe that the different strength of selection of both sexes for bromeliad cover should be related to reproductive behaviors.

Arthropod biomass did not influence individual habitat selection and it was negatively related to population abundance (although with a very small effect). One of the most expected cause and effect relationships in ecology is that the abundance of food resources in an area leads to more consumers (Morris & MacEachern 2010, Wasko & Sasa 2012, Corriale et al. 2013). However, in this work, we found two results contrary to this general pattern. Despite the importance of arthropods in the diet of *T. fosteri* (Antunes et al. 2014), the reduction in conspecific abundance with the increase in arthropod biomass can be explained as an indirect effect by means of competition. Then, in an area where trophic resources are abundant, higher competition between individuals is also expected (Pafilis et al. 2009, Ronconi & Burger 2011), which may explain the reduction in population abundance. Increases in food resources can lead to an increase in territoriality, and then, a decrease in population density (Imre et al. 2004, Carpenter 2015). In *T. fosteri*, there is evidence of territoriality in females (Antunes et al. 2020), and in our model the individual selection of females is directly and negatively influenced by the conspecific abundance. Thus, it is possible that this avoidance among individuals is a mechanism to evade competition. An intrinsic characteristic of arthropods as a resource is its high, renewable, and widespread biomass in tropical environments (Wolda 1978, Silva et al. 2011). This ubiquity may allow individuals from *T. fosteri* to gather enough food even if feeding from areas with low abundance of arthropods. Therefore, they would need to concentrate their foraging in resource rich areas, and would show low selection for those areas. This trend has also been found in insectivores, which tended to prioritize the structure of the habitat over spatial differences in abundance of their prey when selecting habitat (Wolfe et al. 2014). Thus, it should be more advantageous from a competitive point of view to avoid arthropod hotspot areas and to obtain this resource in adjacent areas.

Bromeliad cover also had a high direct effect on the abundance of conspecifics, which was the second most important variable modulating habitat selection. If the density of bromeliads increases the protection against predation, it would be expected to find a higher population density at these places (Lewontin and Levins 1989, Jacobson et al. 2015). However, females avoid places with high conspecific density, probably due to their sexual behavior, especially territoriality. In addition, high-density habitats might also reduce the individual fitness (Morris 1989). Therefore, there is a trade-off in the habitat selection of females, modulated by their need to find areas with greater protection while avoiding overcrowded areas (Metzgar 1971). Anyhow, the avoidance strength generated by conspecific density is quite small when compared to direct benefits provided by decreased predation risk. This suggested that the selection of areas with greater protection is more important than the avoidance of conspecifics by females. On the other hand, as males do not have territorial behavior and their sexual behavior tends to maximize reproductive pairs, they are more likely to be attracted to overcrowded areas.

General Conclusion

In the first chapter I investigated how different reproductive strategies between sexes lead to emergence of intrapopulation variability in exclusivity of area use. Using rigorous capture-recapture methods, we capture all individuals of *D. albiventris* from the sampled area. We found that opossum mass was not related to the size of the home range and aspects related to the area characteristics as its size, anthropic barrier as streets as well as other urban modifications such as human waste that can be used as food may have contributed to an absence of the mass effect. The sex also did not influence the size of the home range, although other studies indicate that opossums alter characteristics of their home ranges such as size during the reproductive season, which was not possible to evaluate in this work. Home range overlap was high and similar for all combinations of the sexes; however, in the scale of core area, females had much less overlap among them than males had among them, when compared to the male-female control ratio. This result may be evidence that females use more exclusive areas than males and this may be related to the reproductive strategies of the sexes.

In the second one, we looked at how different reproductive strategies between sexes also lead to emergence of intrapopulation variance in habitat selection, and then, in the spatial distribution of sexes through a heterogeneous space. Coupling RSF under SEM approach (SRSF) allowed us to disentangle the role of the different resources, as well as their underlying mechanistic interactions, in *T. fosteri* habitat selection. The bromeliad cover was the most important resource for individuals, modulating the selection process directly and indirectly. Directly, the coverage of bromeliads doubled selection strength by females when compared to males. Probably the need to obtain greater protection for the care of offspring lead females to select areas with bromeliads

to a greater strength than males. Meanwhile, males might expose themselves more in order to maximize reproductive success. Sex also affected the influence of the abundance of conspecifics on habitat selection, with females avoiding areas of higher density and males selecting them. The same explanations related to the different sexual behavior of females and males should explain these differences. Finally, arthropod biomass negatively influenced population abundance, possibly because areas with a large amount of food resources should be more conducive to competition. Furthermore, this food resource is quite abundant and fastly renewable in tropical areas, which makes individuals to avoid areas with a high concentration of this resource.

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