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Efeitos da disponibilidade de recursos alimentares nos parâmetros populacionais, reprodutivos, na área de uso e na condição corporal de *Rhipidomys macrurus* (Rodentia, Cricetidae)

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Sumário

Resumo	7
Abstract	8
Resumo expandido	9
<i>Material e métodos</i>	10
<i>Resultados e Discussão</i>	11
<i>Referências bibliográficas</i>	13
Introduction	16
Material and methods	18
<i>Study species</i>	18
<i>Study site</i>	19
<i>Capture procedures</i>	20
<i>Food supplementation experiment</i>	21
<i>Data analysis</i>	22
Results	26
<i>Population density</i>	26
<i>Home-range size</i>	28
<i>Reproductive activity</i>	29
<i>Body condition</i>	31
Discussion	32
References	38
Supplementary material	45

Índice de figuras

Figure 1 - Location of the study sites in Cerrado ecoregion (neotropical savanna), central Brazil, Federal District, near the city of Brasília (top right inset). The bottom map indicates the Environmental Protection Area (APA) Gama Cabeça-de-Veado, as well as the location of the two study sites, where letter A indicates the ecological and agricultural field station of University of Brasília (locally known as “Água Limpa farm – FAL”), and letter B indicates the Ecological Station Botanical Garden of Brasília (JB). The circles represent the specific locations of the study sites in FAL and JB. 20

Figure 2 - Minimum population density (in individuals per hectare) of the neotropical rodent *R. macrurus* over the sampling period in two study sites in Cerrado ecoregion (FAL and JB), central Brazil. The food supplementation experiment was conducted continuously from June 2014 (indicated by the vertical dashed line) to December 2016. Food resources were offered only in JB site. Horizontal dashed lines represent the mean minimum density of *R. macrurus* in periods before and during the food supplementation experiment (FAL = grey; JB = black). Shaded areas represent the dry season and non-shaded areas represent the rainy season. 27

Figure 3 - Mean home range sizes (in hectares) of male and female individuals of *R. macrurus*, in periods before and during food supplementation, in JB site. Error bars represent standard errors. Groups sharing distinct letters on top differ significantly, according to the pairwise Mann-Whitney U test (p [corrected] < 0.05). 29

Figure 4 - Mean percentages of reproductive *R. macrurus* females (*i.e.*, pregnant, lactating, or with perforated vulva) of the total females captured in each capture session, in relation to the rainy season ($n = 12$) and the dry season ($n = 6$), in JB site. Error bars represent standard errors. 30

Figure 5 - Mean percentages of reproductive *R. macrurus* males (*i.e.*, testes in scrotal position) of the total males captured in each capture session, in JB site,

as a function of **a**) the period before (n = 18) or during (n = 9) food supplementation and **b**) the rainy season (n = 14) or the dry season (n = 13). Error bars represent standard errors. 31

Figure 6 - Mean body condition of *R. macrurus* individuals (inferred through the Scaled Mass Index – SMI) as a function of the season (rainy or dry), for both study sites (FAL and JB). Error bars represent standard errors. Groups inside the same site sharing distinct letters on top differ significantly from each other. 32

Resumo

Uma das questões centrais da ecologia é determinar os efeitos da disponibilidade de recursos alimentares para populações de animais. Eu investiguei as respostas do roedor neotropical *Rhipidomys macrurus* a variações na disponibilidade de recursos alimentares através de um experimento de suplementação alimentar em campo durante 7 anos (2009-2016) no Cerrado (savana neotropical), no Brasil central, em duas áreas distintas de cerradão. Em uma dessas áreas, foram ofertados recursos alimentares (ração comercial para gatos moída) continuamente de junho de 2014 até dezembro de 2016. Meus resultados não mostraram um aumento na densidade populacional de *R. macrurus* em resposta a suplementação alimentar, mas as fêmeas desta espécie responderam à adição de alimento reduzindo a sua área de uso. Por outro lado, eu encontrei uma maior proporção de machos reprodutivos durante a suplementação alimentar, mas o mesmo não ocorreu para fêmeas. Essas diferenças provavelmente estão relacionadas com o sistema de acasalamento promíscuo desta espécie, em que a área de uso de fêmeas é determinada pela disponibilidade de recursos, e a área de uso de machos é determinada pela distribuição das fêmeas. Além disso, eu encontrei, em uma das áreas de estudo, uma densidade populacional de *R. macrurus* naturalmente mais alta. Somente nesta área, eu verifiquei uma piora na condição corporal dos indivíduos e uma menor proporção de fêmeas reprodutivas durante a estação seca, em comparação à estação chuvosa. Esses padrões provavelmente estão relacionados com algumas diferenças intrínsecas entre ambas as populações, como um alto nível de competição por recursos alimentares entre os indivíduos durante a estação seca na área com alta densidade.

Palavras-chave: Cerrado; pequenos mamíferos; roedor arborícola; reprodução; suplementação alimentar.

Abstract

One of the central questions in ecology is about determining the effects of food resource availability for animal populations. I investigated the responses of the neotropical rodent *Rhipidomys macrurus* to variations of food resource availability through a food supplementation experiment in the field, conducted during 7-year (2009-2016) in the Cerrado ecoregion (neotropical savanna) in central Brazil, in two distinct sites of cerrado (cerrado woodland). In one of these sites, food supplementation (milled commercial cat food) was provided continuously from June 2014 to December 2016. My results did not show an increase in population density of *R. macrurus* in response of food supplementation, but only females responded to the food addition by reducing their home range size. On the other hand, proportion of reproductive males during food-supplementation period was higher in the food-supplemented site than in the control site, but not of females. These differences are probably related to a promiscuous mating system of this species, in which female home ranges are determined by resource availability and male home ranges are determined by female distribution. Moreover, in one of the study sites *R. macrurus* population density was naturally higher than in the other one regardless the food supplementation. Only in this high-density site I found a deterioration of the body condition of individuals and a lower proportion of reproductive females during the dry season, in comparison to the rainy season. These patterns are probably related to some intrinsic differences between both populations, such as a high level of competition among individuals for food resources during the dry season in the high-density site.

Keywords: Cerrado; small mammals; long-tailed climbing mouse; reproduction; food supplementation.

Resumo expandido

Uma das questões centrais da ecologia é determinar os efeitos da disponibilidade de recursos nas populações de animais (Hunter & Price, 1992; Krebs, 2002; Sinclair & Krebs, 2002; White, 2008). Para isso, é essencial a realização de experimentos manipulativos de adição de alimentos (suplementação alimentar) em campo (Prevedello et al., 2013). Pequenos mamíferos geralmente são mais abundantes e têm ciclo de vida mais curto do que outros mamíferos, e assim, é possível que os efeitos da suplementação alimentar sejam mais facilmente e rapidamente verificados em populações de mamíferos de pequeno porte (Boutin, 1990; Prevedello et al., 2013).

A suplementação alimentar geralmente causa um aumento na densidade populacional ou na abundância de pequenos mamíferos (Boutin, 1990; Morris et al., 2011; Prevedello et al., 2013; Johnsen et al., 2017; Yin et al., 2017), e também pode causar alterações no uso do espaço (área de uso) desses animais (Jonsson et al., 2002; Schoepf et al., 2015). Estudos demonstram que o uso do espaço e territorialidade podem ser considerados preditores do sistema de acasalamento dessas espécies (Gaulin & FitzGerald, 1988; Ostfeld, 1990; Wolff, 2007; Adler, 2011). Dessa forma, a avaliação dos efeitos da suplementação alimentar na área de uso de machos e fêmeas pode contribuir para elucidar as estratégias reprodutivas e sistemas de acasalamento de cada espécie. Além da densidade populacional e área de uso, a suplementação alimentar também pode afetar outras características individuais importantes, como a atividade reprodutiva e a condição corporal (Boutin, 1990; Díaz & Alonso, 2003; Kager & Fietz, 2009; Forbes et al., 2014; Zangrandi et al., 2019).

Neste estudo, eu investiguei as respostas do roedor neotropical *Rhipidomys macrurus* (Gervais, 1855) à disponibilidade de recursos alimentares, através de um experimento de suplementação alimentar, em duas áreas distintas de cerrado na ecorregião Cerrado (definida conforme Veblen et al., 2007), no Brasil central. O Cerrado é uma ecorregião altamente sazonal, com duas estações bem definidas ao longo do ano: estação chuvosa e estação seca (Eiten, 1972), onde geralmente há uma redução da disponibilidade de recursos alimentares durante a estação seca, se comparada à estação chuvosa (Camargo

et al., 2019; Maruyama et al., 2019). Mais especificamente, eu investiguei diversos aspectos relacionados à biologia de *R. macrurus* em resposta à suplementação alimentar e à sazonalidade no Cerrado. Esses aspectos incluíram: densidade populacional, área de uso, atividade reprodutiva e condição corporal.

Material e métodos

A espécie focal deste estudo foi *R. macrurus*, um roedor neotropical (Cricetidae, Sigmodontinae), classificado como arborícola e frugívoro-granívoro (Paglia et al., 2012). Frutos compõem a maior parte da dieta de *R. macrurus*, mas esta espécie também se alimenta de invertebrados em menor quantidade (Ribeiro et al., 2019). Populações de *R. macrurus* foram monitoradas em duas áreas distintas de cerradão durante 7 anos (2009-2016) na área de proteção ambiental (APA) Gama-Cabeça-de-Veados, Distrito Federal, Brasil (Fig. 1). Uma destas áreas era localizada na área experimental e de conservação da Universidade de Brasília (“Fazenda Água Limpa – FAL”) e outra área era localizada na Estação Ecológica Jardim Botânico de Brasília (localmente conhecida como “Jardim Botânico – JB”).

Foram utilizadas armadilhas Sherman® para amostrar as populações de *R. macrurus*. O esforço amostral total durante os 7 anos de amostragem foi de 58.032 armadilhas-noite, 29.016 armadilhas-noite em cada área. A configuração das grades de amostragem e o esforço amostral foram iguais em ambas as áreas durante todo o período do estudo.

O experimento de suplementação alimentar foi realizado de junho de 2014 a dezembro de 2016 (2,5 anos). O suplemento alimentar escolhido foi ração comercial para gatos moída, que foi ofertada *ad libitum* dentro de comedouros desenvolvidos especificamente para este estudo (material suplementar; Fig. 1; veja mais em Mendonça et al., 2017). Os comedouros foram dispostos homogeneamente em linhas diagonais ao longo da grade de amostragem e também ao longo de uma zona tampão de 30 metros de largura ao redor da grade de amostragem (material suplementar; Fig. 2). Apenas a área JB recebeu adição de alimento, enquanto a área FAL foi escolhida como controle para o experimento de suplementação alimentar. A disponibilidade de frutos nas áreas

de estudo foi amostrada durante os anos 2009 e 2010 através da contagem de frutos no sub-bosque e dossel em oito transectos aleatórios em cada área.

Para determinar a densidade populacional de *R. macrurus*, eu utilizei o método do MNKA (número mínimo de animais vivos - *minimum number of individuals know alive*; Krebs, 1989). Para o cálculo da área de uso, eu utilizei o método do MPC (mínimo polígono convexo) apenas para os indivíduos com 5 ou mais capturas. Para mensurar a atividade reprodutiva de *R. macrurus*, eu calculei a proporção de indivíduos reprodutivos, utilizando apenas campanhas onde no mínimo 4 indivíduos de cada sexo foram capturados ao total. Assim, eu calculei a proporção de machos reprodutivos (*i.e.* escrotados), e a proporção de fêmeas reprodutivas (*i.e.* grávidas, lactantes ou com vulva perfurada) em relação ao total de indivíduos de cada sexo capturados em cada campanha. Para estimar a condição corporal dos indivíduos, eu utilizei o índice de massa padronizado (*Scaled Mass Index* – SMI; Peig & Green, 2009, 2010).

Resultados e Discussão

Neste estudo, eu verifiquei uma maior densidade populacional de *R. macrurus* na área JB durante praticamente todo o período amostral, em comparação à área FAL (Fig. 2). No entanto, não verifiquei um aumento na densidade populacional em resposta a suplementação alimentar. A pressão de predação pode ter contribuído para impedir o aumento da densidade populacional de *R. macrurus* em meu estudo, considerando a diversidade de predadores de pequenos mamíferos no Cerrado (França et al., 2008; Marinho-Filho & Juarez, 2002; Telles & Dias, 2010). Além da predação, a competição indireta com outra espécie dominante nas minhas áreas de estudo (*Gracilinanus agilis*), a qual respondeu à suplementação alimentar aumentando a sua densidade populacional no mesmo período (Sano, 2017), também pode ter contribuído para impedir o aumento da densidade populacional de *R. macrurus* em meu estudo.

Apesar disso, as fêmeas de *R. macrurus* responderam à suplementação alimentar reduzindo a sua área de uso, enquanto os machos, não (Fig. 3). Outros estudos similares também exibem esse mesmo padrão (Jonsson et al., 2002; Schoepf et al., 2015). Esses resultados estão de acordo com a hipótese de que

o uso do espaço está relacionado com o sistema de acasalamento em pequenos mamíferos (Gaulin & FitzGerald, 1988; Ostfeld, 1990; Wolff, 2007). Um sistema de acasalamento promíscuo, onde machos não defendem territórios e sua área de uso é determinada para maximizar o acesso às fêmeas, é comum em pequenos mamíferos, especialmente na região neotropical (Gaulin & FitzGerald, 1988; Steinmann et al., 2005, 2009; Wolff, 2007). Meus resultados estão de acordo com a suposição de que *R. macrurus* possui um sistema de acasalamento promíscuo, onde o fator determinante no tamanho da área de uso para fêmeas é a disponibilidade de recursos alimentares, e para machos, é a disponibilidade de fêmeas para acasalar.

Já em relação à atividade reprodutiva, eu detectei um aumento na proporção de indivíduos reprodutivos de *R. macrurus* em resposta à suplementação alimentar para os machos (Fig. 5a), mas não para as fêmeas. Considerando que, para pequenos mamíferos solitários, o custo fisiológico de cada evento reprodutivo (incluindo gravidez e lactação), é mais alto para fêmeas do que para machos (Speakman, 2008), os machos poderiam responder mais prontamente à adição de alimento do que as fêmeas.

Em relação à sazonalidade no Cerrado, os dados de disponibilidade de frutos apontaram para uma menor disponibilidade de frutos durante a estação seca, se comparado a estação chuvosa (material suplementar; Fig. 3). Isso está de acordo com outros estudos no Cerrado (Camargo et al., 2019; Maruyama et al., 2019). Meus dados também indicaram que não houve diferenças significativas na disponibilidade de frutos entre as duas áreas (material suplementar; Fig. 3).

Ainda em relação à sazonalidade no Cerrado, eu verifiquei uma redução da proporção de fêmeas reprodutivas (Fig. 4), assim como uma redução do índice de condição corporal dos indivíduos (Fig. 6) durante a estação seca, em comparação à estação chuvosa. No entanto, isso ocorreu na área JB, mas não na área FAL. A baixa disponibilidade de frutos durante a estação seca certamente deve estar relacionada a esses resultados, pois frutos compõem a maior parte da dieta de *R. macrurus* (Ribeiro et al., 2019). Porém, devido ao fato de que esses resultados foram observados somente na área JB, e não na área FAL, esse padrão provavelmente está relacionado à algumas diferenças

intrínsecas entre essas populações, como um maior nível de competição por recursos alimentares durante a estação seca na área com maior densidade populacional de *R. macrurus* (JB), comparado à área com menor densidade populacional (FAL).

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Introduction

One of the central questions in ecology is about determining the factors that affect animal density in natural conditions (Krebs, 2002; White, 2008). Both bottom-up (e.g., food resources availability) and top-down effects (e.g., predation pressure), are potentially relevant for determining density patterns observed for animals in natural conditions (Hunter & Price, 1992; Sinclair & Krebs, 2002). The relative importance of each of these factors in distinct environments is still source of debate (White, 2008, 2019; Krebs, 2009; Salo et al., 2010; Pierce et al., 2012; Prevedello et al., 2013; Schmidt, McIntyre, et al., 2018). For clarifying that and bringing advancement to population ecology, the conduction of field experiments based on experimental manipulations is essential (Prevedello et al., 2013). Moreover, specific individual responses to manipulated factors (e.g., food supplementation), such as body condition, reproductive condition, and space use, must also be understood.

Bottom-up (ascending) and top-down (descending) control can affect species differently, depending on their specific characteristics, such as diet, body size and life history (Hunter & Price, 1992; Sinclair & Krebs, 2002). For small mammal populations, several studies point out bottom-up control as the main factor limiting those populations, which is related to food resource availability. Most of these studies also demonstrate an increase in population density of small mammals during food supplementation experiments (Boutin, 1990; Báez et al., 2006; Previtali et al., 2009; Krebs et al., 2010; Prevedello et al., 2013; Johnsen et al., 2017; Yin et al., 2017; Schmidt, Rexstad, et al., 2018; White, 2019). Moreover, the availability of resources may also affect how these animals use the space, determining their home-range size and territory establishment (Jonsson et al., 2002; Schoepf et al., 2015).

The evaluation of the effects of food supplementation on use of space by small mammals may also provide insights on mating systems of these animals. Small rodents adopt several distinct mating strategies, ranging from monogamy to promiscuity (Waterman, 2007; Wolff, 2007) and their mating systems are intrinsically related to home range size and territoriality (Gaulin & FitzGerald, 1988; Ostfeld, 1990; Wolff, 2007). The evaluation of sex-related responses in

home range sizes, induced by changes in resource availability, may contribute to elucidating reproductive strategies adopted by several species whose mating systems are still unknown.

In addition to use of space, other crucial individual characteristics, such as reproductive activity and overall body condition, are potentially affected by food supplementation (Boutin, 1990; Díaz & Alonso, 2003; Kager & Fietz, 2009; Morris et al., 2011; Forbes et al., 2014; Zangrandi et al., 2019). Reproduction is one of the most important aspects of the life history of an animal and food supplementation can potentially affect the proportion of reproductive individuals in populations of small mammals, as well as litter size, number of weaned offspring and recruitment (Boutin, 1990; Doonan & Slade, 1995; Jonsson et al., 2002; Díaz & Alonso, 2003; Kager & Fietz, 2009; Prevedello et al., 2013; Yin et al., 2017). In its turn, body condition of an animal represents the “energy capital accumulated in the body as a result of feeding” (Peig & Green, 2009). It is important to assess the body condition of individuals because it can be an indicator of an animal’s health and its ability to deal with environmental stress (Jakob et al., 1996; Peig & Green, 2009). The lack of information about the effects of food addition on crucial individual biological aspects for several species, mainly those occurring in tropical environments (Prevedello et al., 2016), still hinders our understanding on the general effects of ascending factors on small mammal populations.

In this study I investigated the responses of the long-tailed climbing mouse *Rhipidomys macrurus* (Gervais, 1855) to food resource availability through a food-supplementation experiment in the Cerrado ecoregion (neotropical savanna; Veblen et al., 2007). This is a highly seasonal ecoregion, with well-marked rainy and dry seasons along the year (Eiten, 1972). This seasonality causes a high within-year variation in food resource availability, with Cerrado animals having to cope with a lower resource availability during the dry season compared to the rainy season (Camargo et al., 2019; Maruyama et al., 2019). Because of this characteristic, the Cerrado is an interesting region for the conduction of food-supplementation experiments, allowing the investigation of small mammal responses to the addition of food during the entire year with the consequent suppression of the period of low availability of resources.

Populations of *R. macrurus* were analyzed in two study sites of cerrado (cerrado woodland in the Cerrado ecoregion) sampled for 7 years. In one of these study sites, additional food was offered from the 4th year until the end of the study (duration of 2.5 years). I evaluated several aspects of this rodent's biology in relation to food supplementation and also in relation to annual climatic seasonality in Cerrado. These aspects included population density, home range size, reproductive activity and body condition of individuals. Considering my study system and focal species, my expectations were: (i) food supplementation causes an increase in population density of *R. macrurus*; (ii) during food supplementation, home range size of *R. macrurus* females is significantly reduced; (iii) during food supplementation, there is a greater proportion of reproductive individuals of *R. macrurus*, for both females, and males; (iv) during the dry season, the period of lowest fruit availability in the Cerrado ecoregion (Camargo et al., 2019; Maruyama et al., 2019), I expected a deterioration in the body condition of *R. macrurus*, because fruits are the main item in the diet of this rodent (Ribeiro et al., 2019); moreover, (v) I expected that during food supplementation, this possible deterioration of the body condition in the dry season would not occur.

Material and methods

Study species

The long-tailed climbing mouse, *R. macrurus*, is a neotropical rodent (Cricetidae, Sigmodontinae) found in woodland and forest formations of the Cerrado ecoregion (neotropical savanna), but can also be found in the Atlantic forest, and possibly in some regions in northeastern Brazil (Costa et al., 2011; Sancha et al., 2011). This species has an average body mass between 60 and 70 grams, it is arboreal and classified as frugivorous- omnivorous (Paglia et al. 2012), with fruits being the main item of its diet, although it also feeds on invertebrates to a lesser extent (Camargo et al., 2016, 2018; Ribeiro et al., 2019).

Study site

This study was conducted in the Cerrado ecoregion (Veblen et al., 2007; Batalha, 2011) in central Brazil, also known as the neotropical savanna. According to Batalha (2011), the Cerrado ecoregion is composed of three biomes: tropical grassland (campo limpo), savanna (campo sujo, campo cerrado, and cerrado sensu stricto) and cerrado woodland (cerradão). As part of a long-term project on small mammal ecology in study sites of cerradão, small mammal populations were monitored in two study sites of cerradão from October 2009 to December 2016. The monitored study sites were located about 16 km from the Brasília city, in the Environmental Protection Area (APA) Gama Cabeça-de-Veados (Fig. 1), which has about 11,400 ha of continuous protected area (Fonseca & Silva Júnior, 2004; Câmara, 2008). One of these sites (with an area of 7.53 ha) was located in the ecological and agricultural field station of the University of Brasília, (locally known as “Água Limpa” farm, hereafter referred to as ‘FAL’, from the original name in Portuguese; 15° 56' 49,0" S and 47° 56' 42,8" W). The other site (with an area of 27.33 ha) was located in the Ecological Station of the Botanical Garden of Brasília, (hereafter referred to as ‘JB’; 15° 55' 32,8" S and 47° 49' 58.4" W).

The climate in Cerrado ecoregion is tropical and markedly seasonal (“AW” Köppen [1948] continental climate) with a rainy season and a dry season (Eiten, 1972). The average annual rainfall during the sampling period near my study sites was 1,381 mm, with more than 94% of this rainfall occurring between months October and April (rainy season; data from the meteorological station RECOR/IBGE). The average annual rainfall recorded over 25 years (from 1980 to 2004) is 1,440 mm, with an average annual temperature of 22.1°C (data from the meteorological station RECOR/IBGE).



Figure 1 - Location of the study sites in Cerrado ecoregion (neotropical savanna), central Brazil, Federal District, near the city of Brasília (top right inset). The bottom map indicates the Environmental Protection Area (APA) Gama Cabeça-de-Veado, as well as the location of the two study sites, where letter A indicates the ecological and agricultural field station of University of Brasília (locally known as “Água Limpa farm – FAL”), and letter B indicates the Ecological Station Botanical Garden of Brasília (JB). The circles represent the specific locations of the study sites in FAL and JB.

Capture procedures

Rhipidomys macrurus populations were monitored in two phases. The first phase was conducted from October 2009 to September 2012, when a trapping grid was established, composed of 144 (12 × 12) capture stations spaced at 15-m intervals, covering 2.72 ha in each site. During this phase, 12 capture sessions were conducted in each site, with intervals of 1 – 3 months between sessions. In this phase, a capture session consisted of six consecutive nights with 160 Sherman live traps (11.0 × 12.5 × 37.0 cm and 9.0 × 9.5 × 23.0 cm), 80 placed on

the ground and 80 in the understory, in randomly selected capture stations within the grid. The 2nd phase of the study was from September 2012 to December 2016; when the grid conformation was changed to 9 × 9 capture stations spaced at 15-m intervals (1.44 ha total area covered) for all sampled study sites. In each of these study sites, 162 Sherman live traps were placed per session, evenly distributed on the ground (81) and in the understory (81). 18 capture sessions were conducted in each site in the second phase of the study. The total capture effort was 58,032 night-traps (29,016 night-traps in each study site). Trapping grid configuration and efforts were identical for both sites during the entire period of the study.

During the capture sessions, the live traps were checked and baited daily in the morning with a mixture of cod liver oil, cornmeal, banana, vanilla essence and peanut butter (Amendocrem®). Captured animals were identified, weighed, sexed, ear-tagged (model 1005-1; National Band and Tag, Newport, Kentucky), and released at the same point of capture. All field methods were consistent with the animal care guidelines of the American Society of Mammalogists (Sikes et al., 2016) and were approved by Ethics Committee on Animal Experiments of the Universidade de Brasília.

Food supplementation experiment

Food supplementation was conducted continuously in JB site from June 2014 to December 2016. For that, it was offered milled commercial cat food (Golden Gatos® salmon, Grandfood, Dourado, SP, Brazil, 3.91 kcal/g) *ad libitum* through feeders developed specifically for this long-term experiment (Mendonça et al., 2017). Feeders were replenished every 2-3 weeks (according to the consumption rates) so that feeders were never empty during this experiment. This commercial cat food was used primarily for evaluation the responses of a marsupial (Mendonça et al., 2017; Zangrandi et al., 2019) but it is a nutritionally balanced food and *R. macrurus* fed frequently inside the feeders, as assessed through camera traps and hair traps (Mendonça A. F., pers. obs.).

The feeder consisted of a polypropylene plant pot (18 cm x 14 cm - diameter x depth), a polypropylene plant saucer (17 cm x 3 cm), a PVC tube (4 cm x 15 cm), and a smaller pot (7 cm x 4.5 cm) fixed to the bottom of the feeder

by 3M VHB adhesive tape (supplementary material; Fig. 1). Entomological glue (Colly Química Ltda., Capivari, SP, Brazil) was used on the inner walls to avoid the access of arthropods to the food (see Mendonça et al., 2017 for details).

In the JB site, which was randomly selected for the addition of resources, 27 feeders were placed inside the internal trapping grid, and 30 in an external buffer area to the trapping grid (supplementary material; Fig. 2). This conformation was chosen to minimize the populational crowding effect in the internal trapping grid due to the addition of food, as suggested in Prevedello et al. (2013). During capture sessions for population sampling of the rodent *R. macrurus*, the feeders were closed and made unavailable to the animals. Throughout this experiment 205.66 kg of food was offered in JB site, of which 151.66 kg was consumed.

Fruit resource availability was evaluated in the study sites during years 2009 and 2010. Fruits in the canopy and understory were counted along 8 random linear transections of 20 x 5 m in each sampling campaign. There were 3 sampling campaigns during the dry season and 3 during the rainy season, in each area. The obtained data indicated that there was a lower fruit availability in the dry season, compared to the rainy season, in both study sites (supplementary material; Fig. 3). Studies in the Cerrado are in agreement with these results (Camargo et al., 2019; Maruyama et al., 2019). The data also suggested there was no significant difference in fruit availability between the two study sites (supplementary material; Fig. 3).

Data analysis

In order to calculate *R. macrurus* population density, I divided the minimum number of individuals known alive (MNKA; Krebs, 1989) for the effective sampling area (in hectares) for each capture session, for each site. To calculate the effective sampling area, I added the radius of the mean home range of *R. macrurus* to the four sides of the original trapping grid area. The resulting estimates corresponded to the minimum populational density of *R. macrurus* for each capture session, in individuals per hectare.

I built the population density models with the ordinal number of the capture session as a fixed effect variable to remove the influence of the order of capture

sessions in the model, and thus reduce the temporal autocorrelation. I tested for autocorrelation of model residuals using the autocorrelation function (ACF). In the presence of significant autocorrelation, I added a first-order autoregressive correlation component to the model, and tested the model again for residual autocorrelation. I used the R package “nlme” for adding the correlation component to the model (Pinheiro et al., 2019).

I estimated home range size of *R. macrurus* individuals using the minimum convex polygon (MCP), through the R package “adehabitatHR” (Calenge, 2006). I calculated the home range size only for those individuals with 5 or more captures in 4 or more different capture points. In a preliminary analysis, I separated the data into sex (males and females), season (rainy and dry), and food supplementation (before and during), and calculated the home range size for each individual, with the identification of the individual as a random factor. The season had no significant effect on the home range size of *R. macrurus* ($F = 1.553$, $p = 0.22$). Thus, I separated the data in sex and supplementation and calculated home range sizes again for each individual. I verified that the number of captures of each individual had a strong effect on home range size, thus I added the number of captures of each individual in the model as a random factor using the R package “lme4” (Bates et al., 2015).

I calculated the proportion of reproductive individuals only for capture sessions in which 4 or more individuals were captured in total. The correlation of the proportions of reproductive males (*i.e.* testes in scrotal position) and reproductive females (*i.e.* pregnant, lactating or perforated vulva) was low ($r = -0.19$), therefore I decided to analyze reproductive males and reproductive females separately. This proportion data has a binomial distribution because it was calculated by dividing the number of reproductive individuals by the total number of individuals captured in that particular capture session (Warton & Hui, 2011). Thus, I utilized a binomial distribution to test this data, as suggested by Warton & Hui (2011). I tested models for overdispersion observing the ratio between the residual deviance and the degrees of freedom, and also with the overdispersion test from the R package “qcc” (Scrucca, 2004).

I utilized the Scaled Mass Index (SMI) as the body condition index for *R. macrurus* individuals, which represents the standardized body mass of each

individual to the average head-body length of all individuals (L_0) sharing the same body mass to head-body length relationship (Peig & Green, 2009, 2010). I chose the Scaled Mass Index because it is considered to be the best non-invasive indicator of the relative size of energy reserves and other body components of individuals, and because it is the body condition index that best controls for the mass and length relationships of individuals compared to other body indexes, including the residuals of a linear regression between mass and length (Peig & Green, 2009, 2010).

I followed the instructions of Peig & Green (2009) in order to estimate the SMI for each individual. I calculated " L_0 " as the average head-body length of all *R. macrurus* individuals. I used the R package "smatr" (Warton et al., 2012) for building the standardized major axis regression between body mass and head-body length of individuals, and for estimating the correlation coefficient " b_SMA ". Pregnant females and juvenile individuals (body mass < 30 g) were excluded of this analysis. I included only the first capture of each individual in each capture session, and I used only data before the start of the supplementation experiment in order to calculate " b_SMA ".

In order to test whether I could merge data of both sexes and both study sites to calculate the " b_SMA " coefficient, I tested the relationship between body mass and head-body length of *R. macrurus* individuals (both variables log transformed) with a SMA regression, accounting for the factors sex and site (analysis of covariance). I found no difference for males and females (slope: likelihood ratio statistic = 0.64, $p = 0.42$; intercept: Wald statistic = 0.016, $p = 0.90$), nor for individuals of different study sites (slope: likelihood ratio statistic = 0.027, $p = 0.87$; intercept: Wald statistic = 0.016, $p = 0.90$). Thus, I merged data from both sexes and both study sites to build the SMA regression (supplementary material; Fig. 4) and to estimate the regression coefficient " b_SMA ", whose estimated value was approximately 2.317. The average head-body length " L_0 " of all *R. macrurus* individuals throughout the study, in both study sites, was estimated at 118.33 mm. Then, I calculated the SMI for the first capture of each individual in each capture session, and I built linear mixed models considering each individual as a random factor.

For all statistical analysis, I first build full models with all the variables and possible interactions between them. In order to decide which variables remained in the final models for the tests, I performed a model selection process with single term deletion tests, utilizing the “drop1” function from the R package “stats” (R Core Team, 2019). I excluded a single variable from the model at a time (the variable in which the exclusion resulted in a best-fit model, comparing to others), and the new model with one less variable was then subjected to the same process again. I repeated this until it was no longer possible to improve the fit of the model (by excluding a variable) compared to the model before.

I proceed to this model selection process only as a preliminary analysis in order to define which was the best-fit model, the final model, which contained the variables for the statistical tests. I tested the model residuals for normality (with histograms, normal q-q plots and with the Shapiro-Wilk normality test) and for homogeneity of variances (with the visualization of residuals plotted against model fitted values and model variables, and with Levene's test for homogeneity of variances), when using linear models and parametric tests (for population density, home range size and body condition). All analyzes were performed using R software (R Core Team, 2019).

For the population density analysis, the factor ‘season’ (levels: ‘dry’ and ‘rainy’) was excluded from the model during the initial model selection process. The final models for population density included only the factor ‘supplementation’ (levels: ‘before’ and ‘during’) and the number of the capture session as explanatory variables. For the JB site, there was no significant temporal autocorrelation of the model residuals (supplementary material; Fig. 5a). For the FAL site, however, because of the temporal autocorrelation detected in model residuals (supplementary material; Fig. 5b), I included a first order autoregressive correlation component in the model. After that, the residuals no longer showed significant autocorrelation (supplementary material; Fig. 5c). I used the Autocorrelation Function (ACF) to test for temporal autocorrelation in the model residuals.

For female reproductive activity, the final binomial GLM (Generalized Linear Model) included only the supplementation factor, the season factor and the number of the capture session as explanatory variables. Interactions terms

between factors were excluded during the initial model selection process. There was not enough data to build the binomial GLM for the FAL site, so I built it only for the JB site. For male reproductive activity, the final binomial GLM included supplementation and season factors as explanatory variables (the interaction term between those factors was excluded from the model during the model selection process). There was not enough data to build the GLM for the FAL site, so I built it only for the JB site.

For the body condition of *R. macrurus* individuals, the factor 'supplementation' was excluded from the model, for both study sites, during the preliminary model selection process. The final models for body condition in both study sites included only the factors sex and season as explanatory variables, with the Scaled Mass Index (SMI) as the response variable, and each individual as a random factor.

Results

Population density

I captured a total of 233 individuals of *R. macrurus*, of these 161 individuals (95 males, 61 females and 5 individuals in which sex could not be determined) were captured 666 times (including recaptures) in the JB site, and 72 individuals (41 males, 30 females and 1 individual in which sex could not be determined) were captured 237 times (including recaptures) in the FAL site.

Rhipidomys macrurus occurred in lower population densities in the FAL site compared to JB site, since average population densities of *R. macrurus* in FAL were between 40% and 50% of the values in JB, for both before and during food supplementation (Fig. 2). The food supplementation had no significant effect on population density in JB site ($F = 1.046$, $p = 0.315$). However, I detected an increase of nearly 77% in *R. macrurus* population density in FAL site during the period of the food supplementation experiment ($\text{Chisq} = 4.553$, $p = 0.033$), even though there was no food addition in the FAL site (Fig. 2).

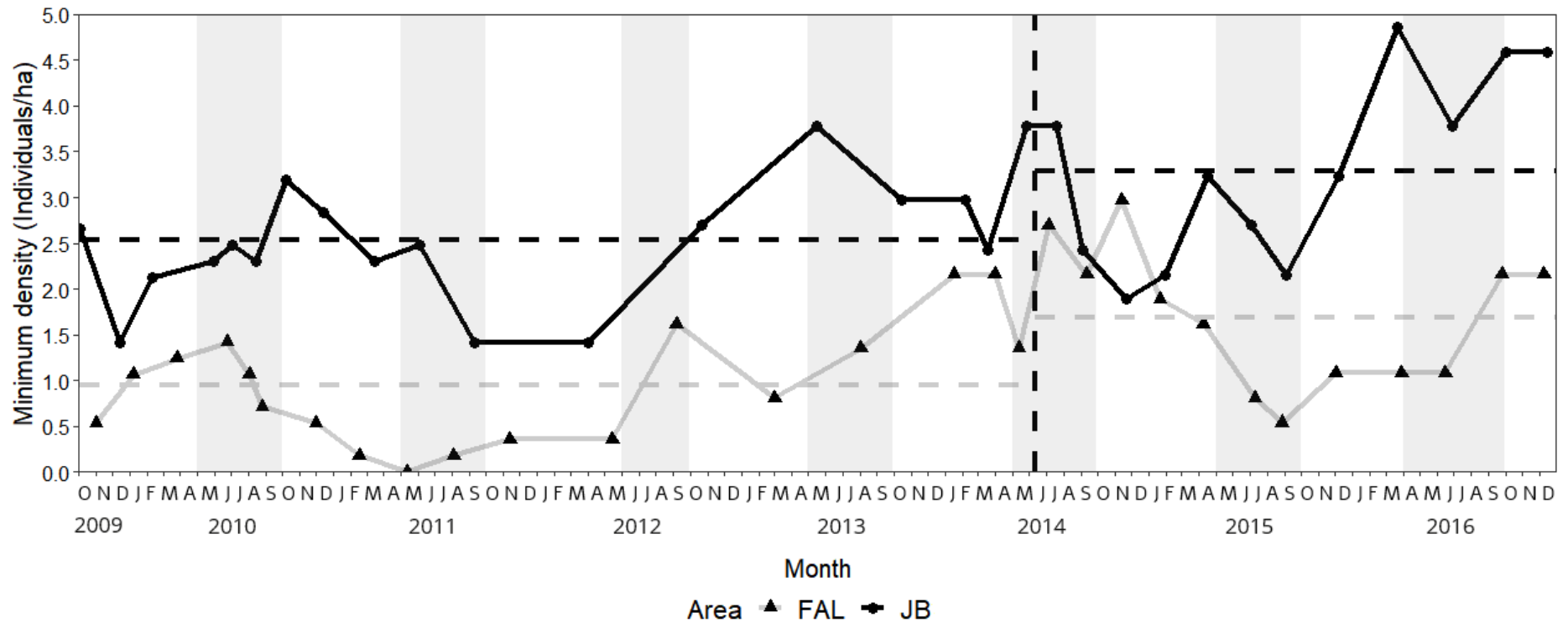


Figure 2 - Minimum population density (in individuals per hectare) of the neotropical rodent *R. macrurus* over the sampling period in two study sites in Cerrado ecoregion (FAL and JB), central Brazil. The food supplementation experiment was conducted continuously from June 2014 (indicated by the vertical dashed line) to December 2016. Food resources were offered only in JB site. Horizontal dashed lines represent the mean minimum density of *R. macrurus* in periods before and during the food supplementation experiment (FAL = grey; JB = black). Shaded areas represent the dry season and non-shaded areas represent the rainy season.

Home-range size

In JB site, a preliminary analysis indicated no significant effect of season on home range size of *R. macrurus* ($F = 1.553$, $p = 0.22$). Thus, I tested only the effects of sex and supplementation (and their interaction) on this response variable. Considering that >98% of the individuals whose home ranges were estimated before food supplementation were not the same individuals whose home ranges were estimated during food supplementation, I did not have to worry about data dependence. Prior to food supplementation, home range sizes were about 0.59 ha for males and 0.50 ha for females. The interaction term between factors sex and supplementation was significant ($F = 6.963$, $p = 0.01$). During supplementation, mean home range sizes of the females dropped around 65% (0.17 ha). In this period females also had significant smaller home range sizes than males, whose home range sizes were not affected by food supplementation (pairwise Mann-Whitney U test, with corrected p values with the Hommel method; Fig. 3). In FAL (control site) I could not perform statistical comparisons due to small sample sizes, but females did not show a marked reduction during food supplementation as in JB (supplementary material; Fig. 6).

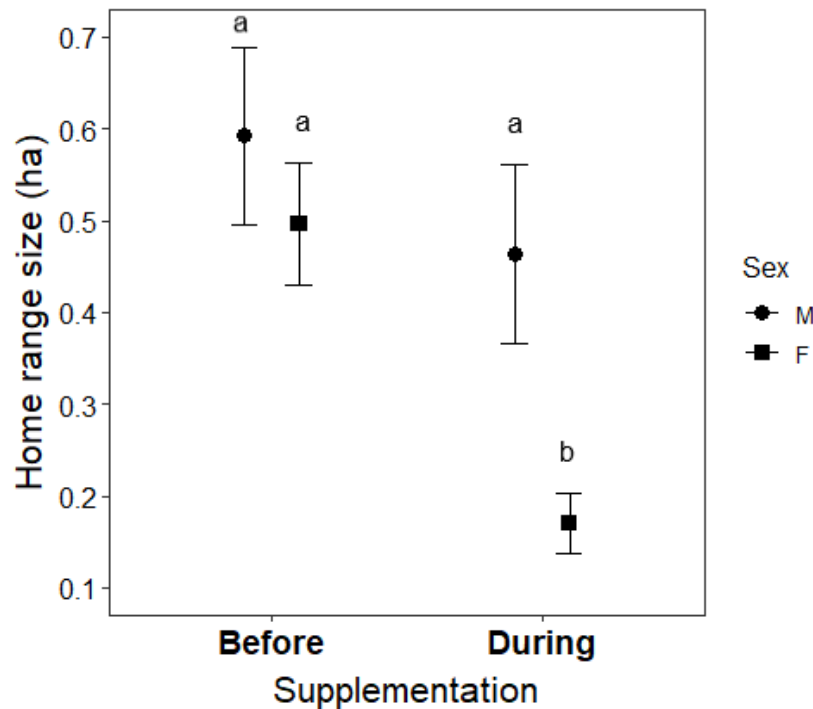


Figure 3 - Mean home range sizes (in hectares) of male and female individuals of *R. macrurus*, in periods before and during food supplementation, in JB site. Error bars represent standard errors. Groups sharing distinct letters on top differ significantly, according to the pairwise Mann-Whitney U test (p [corrected] < 0.05).

Reproductive activity

In JB site, I found a significant effect of the season (LR Chisq = 6.357; p = 0.012) on the proportion of reproductive females. In this site, the proportion of reproductive females was nearly 50% lower in the dry season compared to the rainy season (Fig. 4). Limited sample sizes did not allow statistical comparisons for the FAL data, but this reduction in female reproductive activity during the dry season apparently did not occur in this site (supplementary material; Fig. 7). The proportion of reproductive females was not affected by food supplementation (LR Chisq = 3.081; p = 0.079). The ratio between the residual deviance and degrees of freedom in the JB site GLM was 1.912 and the overdispersion test from the

“qcc” R package did not detect overdispersion in the GLM (Obs. Var / Theor. Var = 0.178; Statistic = 3.024; $p = 0.999$).

In relation to the reproductive activity of *R. macrurus* males, both food supplementation (LR Chisq = 12.459; $p = 0.0004$) and season (LR Chisq = 3.855; $p = 0.0496$) had significant effects on the proportion of reproductive individuals in JB site. Food supplementation increased in about 76% the proportion of reproductive males in JB (Fig. 5a), and 44% more males were captured in reproductive condition during the dry season, compared to the rainy season (Fig. 5b). The ratio between the residual deviance and degrees of freedom of the GLM was equal to 1.813 and the overdispersion test from the “qcc” R package did not detect overdispersion in the GLM (Obs. Var / Theor. Var = 0.152; Statistic = 3.947; $p = 1$). In the FAL site, the reproductive activity of the males did not seem to be differ between the both periods considered (before and during food supplementation (supplementary material; Fig. 8).

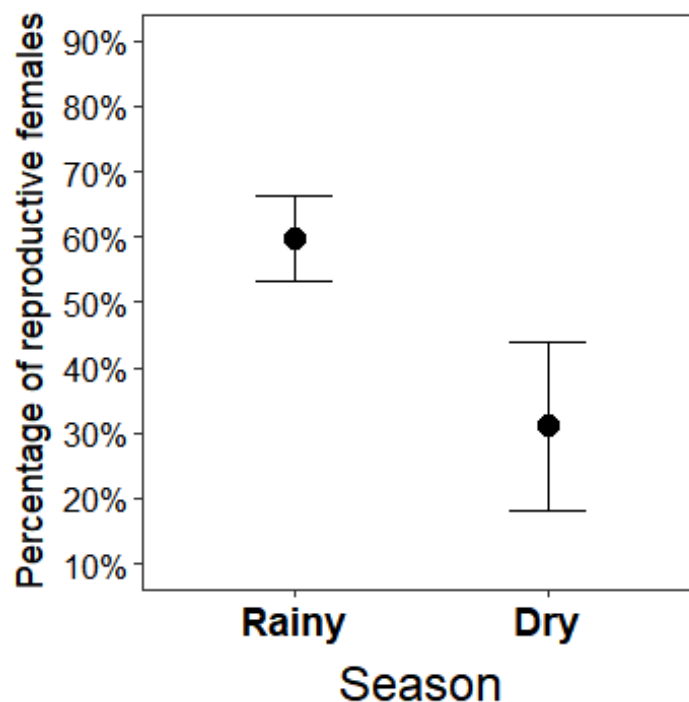


Figure 4 - Mean percentages of reproductive *R. macrurus* females (*i.e.*, pregnant, lactating, or with perforated vulva) of the total females captured in each capture session, in relation to the rainy season ($n = 12$) and the dry season ($n = 6$), in JB site. Error bars represent standard errors.

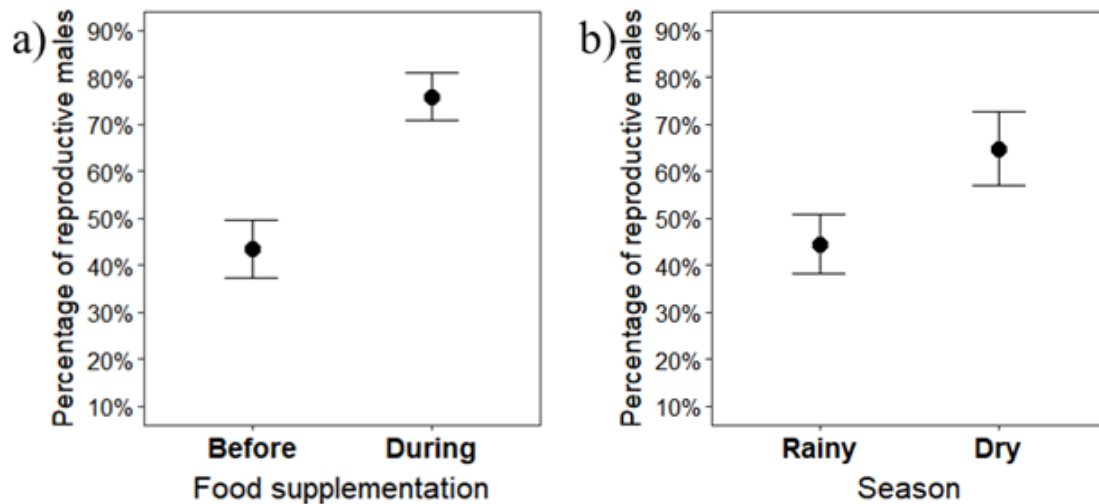


Figure 5 - Mean percentages of reproductive *R. macrurus* males (*i.e.*, testes in scrotal position) of the total males captured in each capture session, in JB site, as a function of **a)** the period before ($n = 18$) or during ($n = 9$) food supplementation and **b)** the rainy season ($n = 14$) or the dry season ($n = 13$). Error bars represent standard errors.

Body condition

The factor 'supplementation' was excluded from the body condition models during the model selection process. The factor 'season' (rainy or dry) had a significant effect on the Scaled Mass Index (SMI) of *R. macrurus* individuals for the JB site ($F = 4.682$, $p = 0.031$), but not for the FAL site ($F = 1.261$, $p = 0.265$). SMI values were lower in JB site during the dry season, compared to the rainy season (Fig. 6). Sex had no significant effect on the Scaled Mass Index (SMI) of the individuals in any of the study sites (JB: $F = 1.412$, $p = 0.235$; FAL: $F = 0.429$, $p = 0.515$).

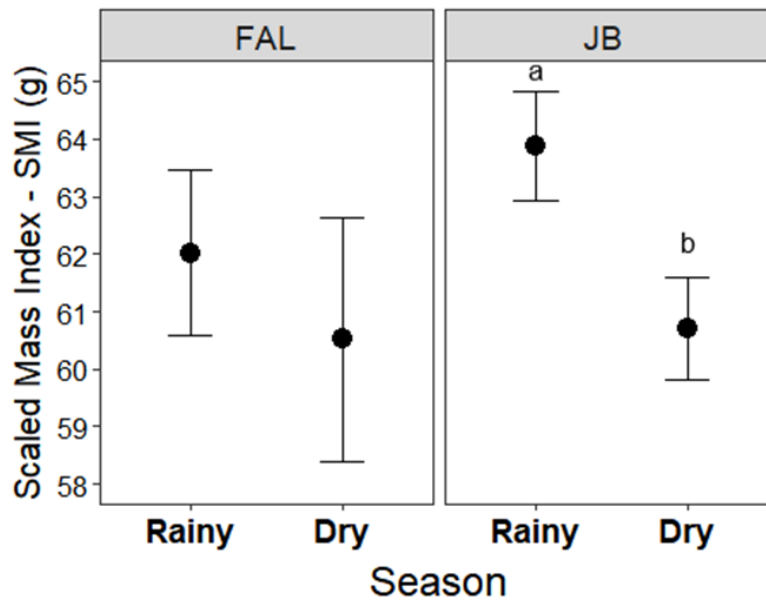


Figure 6 - Mean body condition of *R. macrurus* individuals (inferred through the Scaled Mass Index – SMI) as a function of the season (rainy or dry), for both study sites (FAL and JB). Error bars represent standard errors. Groups inside the same site sharing distinct letters on top differ significantly from each other.

Discussion

I investigated the effects of food resource availability (through food supplementation) on long-tailed climbing mouse (*R. macrurus*) populations, evaluating their responses at a populational and individual level, in a highly seasonal environment. There was no increase in rodent population density in response to experimental food supplementation. Females responded to this supplementation, however, by reducing their home range size but with no changes in the proportion of reproductive individuals. On the other hand, males responded with no changes in home range size, but increased the proportion of reproductive individuals in the food-supplemented site. I found no changes in body condition caused by food supplementation, but in one of the study sites (JB) individuals were in better body condition in the rainy season in comparison to the dry season.

The results indicated a high variability in density along the seven years of the study in both study sites, with *R. macrurus* density ranging from 0 to ~5 individuals per hectare, but with no clear effects of food supplementation. Thus, my expectation regarding population density was not confirmed, because there was no significant increase in population density of *R. macrurus* in response to food supplementation in JB site. In FAL site however, there was an increase in mean *R. macrurus* population density during the food supplementation period (even though food was not provided in FAL site), and this indicates a natural populational increase of *R. macrurus* during this period in this site, unrelated to my food supplementation experiment. It is possible that the much lower density observed in FAL prior to food supplementation in comparison to JB allowed the population in this former site to grow during the food-supplemented period because of other factors not investigated in the present study (e.g., variation in the availability of natural resources). The distance of the study sites to the nearest human settlement was 3 times lower in FAL site (690 m), compared to JB site (2180 m). Thus, human-induced disturbance in the vicinity of FAL site could explain, at least partially, the much lower *R. macrurus* density I found in this site, compared to JB site.

Not all studies with small mammals in the literature showed an increase in population density in response to food supplementation (Díaz & Alonso, 2003), but a meta-analysis study indicated a general positive effect of food supplementation on small-mammal population densities (average increase of 1.5 times in population density) for open populations with no reduction in predation pressure (Prevedello et al., 2013). This review did not report, however, detectable effects of food supplementation on survival, with immigration explaining most of the increase in population densities in 'open' small mammal populations (Prevedello et al., 2013). Similarly, my study populations were 'open', since there were no fences for limiting rodent movement. The extra feeders that were placed outside the trapping grid forming a boundary strip (i.e., the buffer area) could have helped in avoiding the sampled population to be artificially crowded with immigrants (Prevedello et al., 2013). Other factors, such as predation pressure or competition may have counterweighed a potential population increase in my study (Ford and Pitelka, 1984; Harris and Macdonald, 2007).

Predation is one of the factors that can prevent or reduce the expected population density increase of small mammals in food-supplementation experiments (Prevedello et al., 2013). Predator exclusion may cause higher survival and abundance of rodents, compared to control sites (Morris et al., 2011). The 'crowding effect' (caused mainly by immigration) of small mammals during food supplementation experiments may cause aggregation of predators in the experiment site, thus regulating the increase in population density (Prevedello et al., 2013). In some cases, only in sites with predator exclusion an increase in population density in response to food supplementation was observed (Huitu et al., 2003). Predation pressure on small rodents is surely high in the study sites, considering the high diversity of predators that occurs in the Cerrado in central Brazil, including reptiles, raptors, and mammals (França et al., 2008; Marinho-Filho & Juarez, 2002; Telles & Dias, 2010). Moreover, because my study areas are near human settlements, domestic animals like domestic cats could also be preying upon small mammals. Thus, the potentially high predation pressure in my study sites could have been responsible, at least partially, to the lack of response of *R. macrurus* to food supplementation verified in the present study.

Besides predation pressure, both intraspecific and interspecific competition can have significant effects during food supplementation experiments. In my study, I found naturally higher population density of *R. macrurus* in JB site (compared to FAL site). This high density could have caused a greater intraspecific competition pressure in this site, which could limit the increase in population density. Studies in the literature showed the effects of interspecific competition, in which only one or few small mammal species increased its population density in response to food supplementation, whereas other species did not, or even suffered a decrease in population density during food supplementation experiments, sometimes resulting in lower rodent diversity (e.g., Brown & Munger, 1985; Banks & Dickman, 2000; Koekemoer & Van Aarde, 2000; Harris & Macdonald, 2007; Orland & Kelt, 2007). In my study sites, the dominant small mammal species in terms of abundance was the marsupial *G. agilis* (Sano, 2017). For this species, there was a significant increase in population density in my study sites as a response to food supplementation (Sano, 2017). Therefore, the indirect competition between *G. agilis* and *R.*

macrurus in my study sites could have contributed to the lack of response of *R. macrurus* population density to food supplementation found in my study.

In relation to home range size, my expectation about the effects of food supplementation on *R. macrurus* individuals was confirmed, since females in the JB site responded to food supplementation by reducing their home range size by 65%. Other studies with small mammals also showed similar results (Jonsson et al., 2002; Schoepf et al., 2015). The female's reduction in home range size in periods of food abundance could not only be a strategy to save energy during lactation by reducing physical activity (Speakman et al., 2001; Speakman, 2008), but also a strategy to avoid predation risk (Norrdahl & Korpimäki, 1998). Studies show that greater mobility is associated with an increase in predation risk for voles, and there is evidence that these animals may reduce their mobility as a strategy to increase their survival probability (Norrdahl & Korpimäki, 1998; Ims & Andreassen, 2000). Those are likely the reasons why I found such sharp reduction in home range size of *R. macrurus* females in response to food supplementation.

Contrary to the pattern observed for females, I found no difference in home range size of *R. macrurus* males in response to food supplementation. Males do not need to forage only for food resources, but also for available females to mate with. Therefore, the availability of females for mating should be the determining factor of male home range size in small mammal species, as opposed to food resource availability (Adler, 2011; Shibuya et al., 2017). My results on female-only reduction in home range size only in the study site provided with additional food resources (JB) are in agreement with the hypothesis that spacing patterns are strongly related to mating systems in small mammals (Gaulin & FitzGerald, 1988; Ostfeld, 1990; Wolff, 2007). A promiscuous mating system in which males do not defend territories and their home range is established for maximizing the access to females is common for small rodents, particularly in the neotropical region (Gaulin & FitzGerald, 1988; Steinmann et al., 2005, 2009; Wolff, 2007). Food supplementation experiments reported in the literature generally indicate different sex-related responses in the use of space for solitary promiscuous small mammals, in which females may reduce significantly their home range size in response to food supplementation, whereas males do not (Jonsson et al., 2002;

Schoepf et al., 2015). My results provide support for the assumption that *R. macrurus* has a promiscuous mating system, considering that males did not reduce their home range size in response to an increase in food resources availability, but females did.

In relation to reproductive activity, during food supplementation I detected an increase in the proportion of reproductive individuals for males but not for females. This pattern is not in agreement with my expectation, considering that food supplementation generally causes an increase in the proportion of reproductive individuals for both males and females, in small mammals (Boutin, 1990; Díaz & Alonso, 2003; Kager & Fietz, 2009; Morris et al., 2011; Forbes et al., 2014). Considering that the physiological costs of a single reproductive event are significantly higher for females comparing to males (Speakman, 2008), it is likely that males can respond to food addition more readily than females, as I detected based on the proportion of reproductive individuals.

It should be noted, however, that the proportion of reproductive females is not the only measure of female reproductive activity, and other aspects such as litter size, proportion of weaned offspring, and recruitment can also show improvement during food supplementation experiments (Jonsson et al., 2002; Díaz & Alonso, 2003; Kager & Fietz, 2009; Prevedello et al., 2013; Yin et al., 2017). Even a decrease in the proportion of reproductive females as a response to food supplementation and, at the same time, an increase in female reproductive effort through higher recruitment of juvenile individuals has already been reported (Doonan & Slade, 1995). Therefore, although my study with *R. macrurus* did not indicate higher proportion of reproductive females during food supplementation, females during this period could have had larger litters and/or higher proportion of weaned offspring. Considering that these parameters (*i.e.*, litter size, proportion of weaned offspring) cannot be easily measured for my study species in the field, some possible effects of food supplementation on the reproductive activity of *R. macrurus* might have been undetected.

The results also indicated a lower proportion of reproductive females during the dry season in comparison to the rainy season verified only in JB site. The data on fruit availability in my study sites suggests that there is a lower fruit availability during the dry season, compared to the rainy season, for both study

sites (supplementary material; Fig. 3). Studies in the literature confirms this pattern in the Cerrado ecoregion (Camargo et al., 2019; Maruyama et al., 2019). But this data also suggests that there is no significant difference in fruit availability between my study sites (supplementary material; Fig. 3). Fruits are possibly the most relevant food resource for *R. macrurus*, since they are the main item in the diet of this species (but this rodent also feeds on invertebrates to a lesser extent; Ribeiro et al., 2019). Thus, the lower proportion of reproductive females during the dry season only in one of my study sites could be caused by the combined effects of high competition pressure and lower fruit availability in the dry season in comparison to the rainy season. These combined factors may also have caused the deterioration of the body condition of individuals of *R. macrurus* during the dry season only in JB site, which confirmed my previous expectation. This deterioration was not observed in the FAL site, where there was no significant difference in body condition between seasons.

In addition to the seasonal changes in body condition in the food-supplemented site, food supplementation did not change *R. macrurus* body condition in any of the seasons. This indicates that availability of natural food resources (mainly fruits) is more important for maintaining the body condition of individuals of this species than the additional food that was provided (milled cat food). It is possible that the body condition of this frugivorous-omnivorous species (Ribeiro et al. 2019) is not markedly affected by the kind of food provided in my study. However, direct observations in field, and data from camera traps and hair traps, indicated that this species frequently fed on the food provided (Mendonça A. F., pers. comm.). Some other behavior aspects, such as territoriality and active defense of resource sources, may have limited the access of part of the study population to the feeders and caused the observed lack of changes in body condition induced by food supplementation.

My study highlights different responses of males and females to food supplementation. I found that *R. macrurus* home range size was related to food resource availability for females, but not for males. In contrast, I found a higher proportion of reproductive individuals during food supplementation only for males, but not for females. These differences are probably related to a promiscuous mating system of this species and low reproduction costs to males, which can

respond more promptly to an increase in food resource availability. In one of my study sites, I found a naturally higher *R. macrurus* population density, and only in this same site I found a deterioration of the body condition of individuals and a lower proportion of reproductive females during the dry season, in comparison to the rainy season. These patterns are probably related to some intrinsic differences between both populations, such as a high level of competition among individuals for food resources during the dry season in the high-density site.

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Supplementary material



Figure 1 – Feeder installed on top of a tree trunk, fixed with an elastic band, during the food supplementation experiment in one of my study sites, in a cerradão (cerrado woodland) study site, in the Cerrado ecoregion (neotropical savanna), central Brazil.

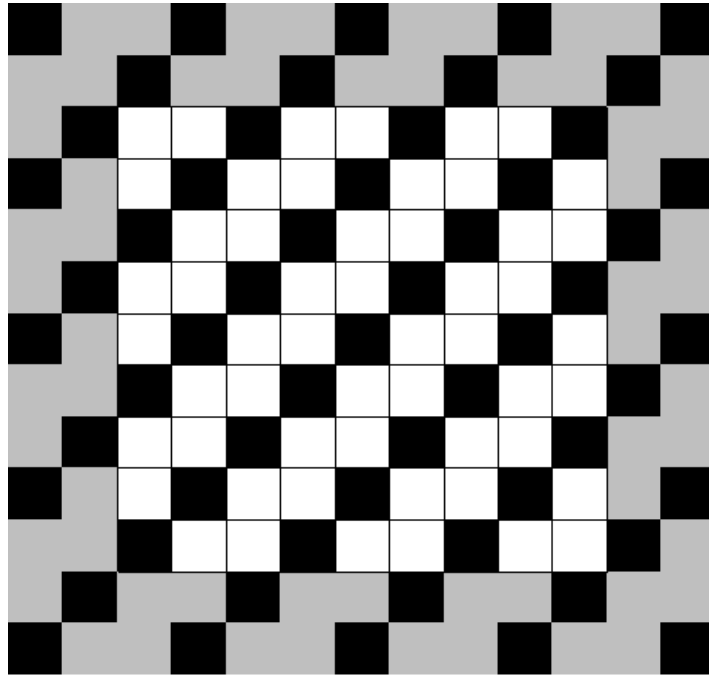


Figure 2 – Schematic representation of the distribution of feeders and capture stations in JB study site for the food supplementation experiment. The internal grid (white squares – 9 x 9) is where traps were placed to capture small mammals. The gray area around the internal grid is the external buffer area. The black squares represent sites where feeders were placed. There was no food addition in FAL site.

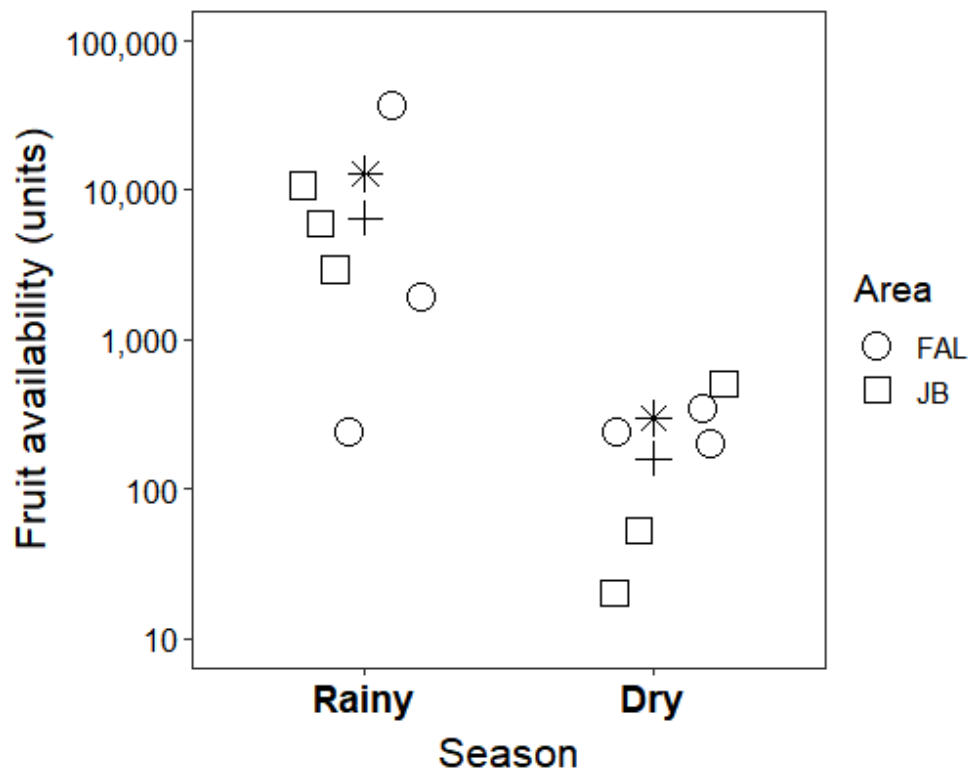


Figure 3 – Fruit availability (in units) in relation to season (rainy or dry) in both study sites (FAL and JB) in Cerrado ecoregion, central Brazil, Federal District. Fruit availability was evaluated between years 2009 and 2010, through eight linear transections of 20 m x 5 m in each area, chosen at random, where fruits in the understory and canopy were counted. Each symbol represents the fruit availability (in units) for a given sampling campaign, except the star, which represents mean values in FAL site, and the cross, which represents mean values in JB site.

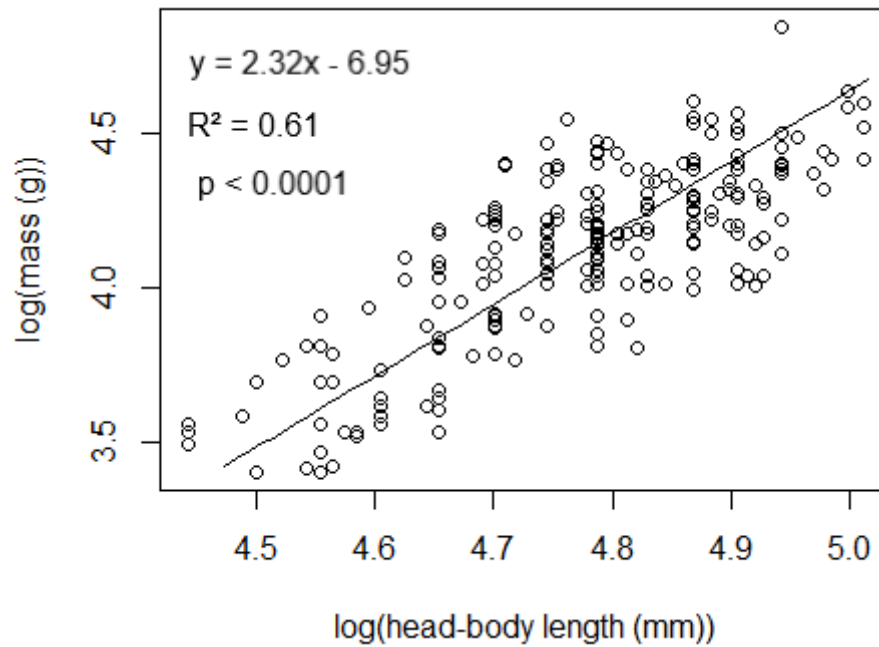


Figure 4 – Standardized Major Axis regression (SMA regression) between body mass (in grams) and head-body length (in millimeters) of individuals of the long-tailed climbing mouse (*R. macrurus*). I used data from both sexes and both study sites (FAL and JB), but only data before the start of the food supplementation experiment was included ($n = 225$). Both variables were transformed to their natural logarithm.

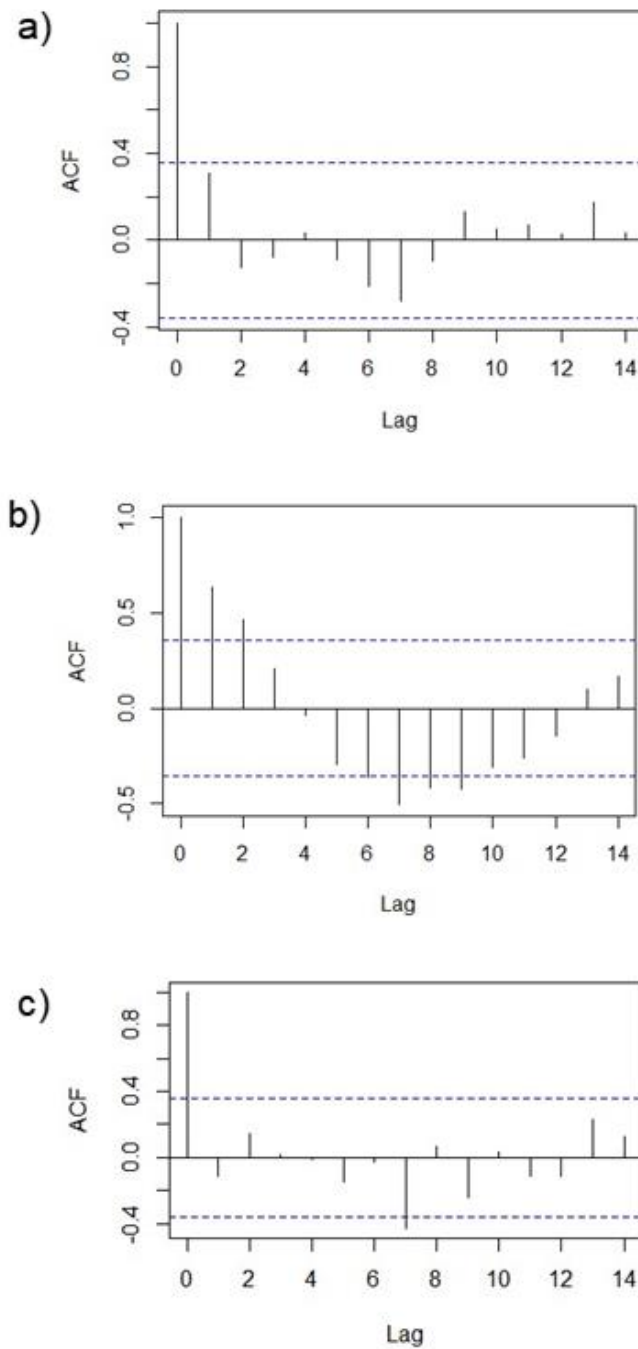


Figure 5 – Autocorrelation function (ACF) of model residuals of *R. macrurus* population density models. The zero lag always has a perfect correlation of 1, because it measures the correlation of each residual with itself. The lag 1 represents the correlation of each residual with the last residual, the lag 2 represents the correlation of each residual with the last but one residual, and so on. The horizontal dashed lines represent the confidence intervals. **a)** Autocorrelation function (ACF) of model residuals from the simple linear model in

JB site. **b)** Autocorrelation function (ACF) of model residuals from the model in FAL site, without the correlation component. **c)** Autocorrelation function (ACF) of model residuals from the model in FAL site, with the correlation component added into the model.

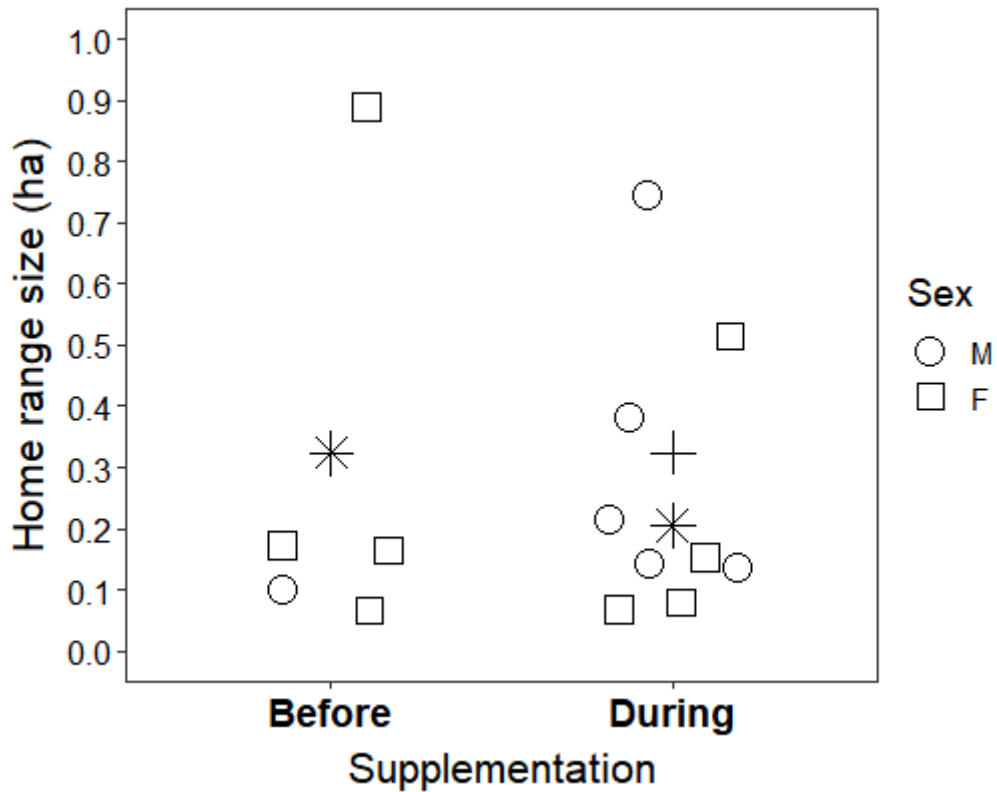


Figure 6 – Home range size (in hectares) of individuals of the neotropical rodent *R. macrurus*, as a function of the period before or during the food supplementation experiment, in FAL site, where there was no food addition. Each symbol represents the home range size of a single individual, except the cross, which represents mean values for males, and the star, which represents mean values for females.

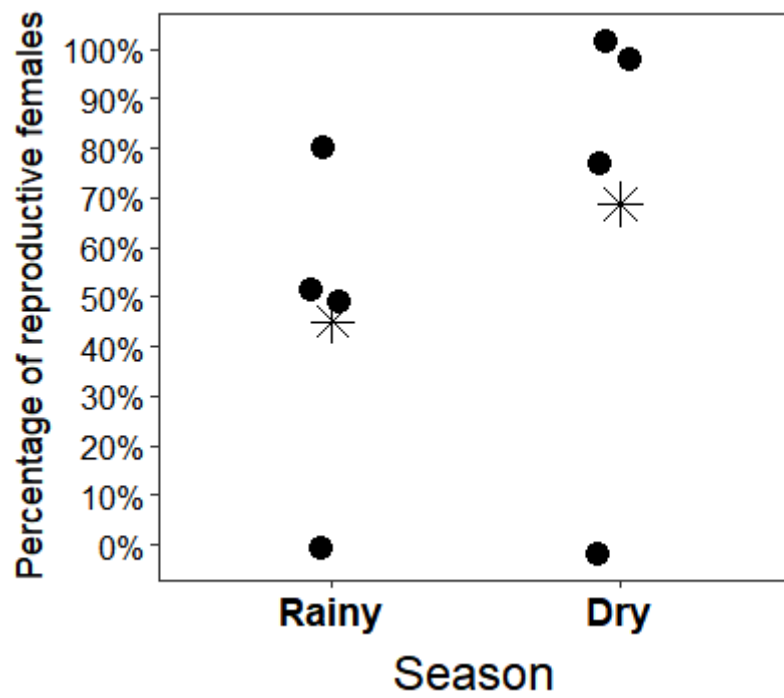


Figure 7 - Percentages of reproductive *R. macrurus* females (*i.e.*, pregnant, lactating or perforated vulva) of the total females captured in each capture session, in relation to season, in FAL site. Each dot corresponds to values in one capture session. The stars represent mean values for the groups.

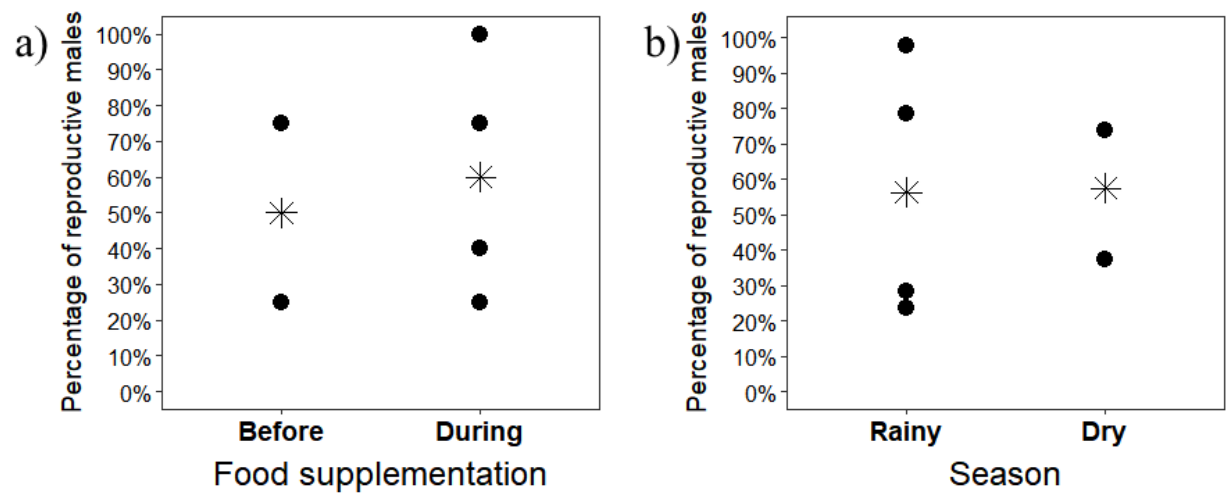


Figure 8 - Percentages of reproductive *R. macrurus* males (*i.e.*, testes in scrotal position) of the total males captured in each capture session, in relation to season, in FAL site. Each dot corresponds to values in one capture session. The stars represent mean values for the groups.