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PERÍODO DE ATIVIDADE E PADRÕES DE USO DO ESPAÇO DO RATO-DE-ESPINHO *Clyomys laticeps* (Thomas, 1909) (Rodentia: Echimyidae)

CLAIRE PAULINE RÖPKE FERRANDO

2017

Claire Pauline Röpke Ferrando

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Dissertação apresentada à Universidade Federal de Uberlândia como parte das exigências para obtenção do título de mestre em Ecologia e Conservação de Recursos Naturais.

Orientadora
Prof.ª Dr.ª. Natália Oliveira Leiner

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Prof.ª Dr.ª Celine de Melo...Universidade Federal de Uberlândia

Prof.ª Dr.ª Natália Mundim Tôrres.......................... Universidade Federal de Uberlândia

Prof.ª Dr.ª Natália Oliveira Leiner

Universidade Federal de Uberlândia
(Orientadora)

UBERLÂNDIA
2017

Ilustradora Claire Wickiestaubie

Luna - filhote de *Clyomys laticeps* (Thomas, 1909)

"Dedico este trabalho aos roedores que tive o privilégio de estudar.

Espero muito que este estudo possa beneficiá-los

em algum momento da história...".

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RESUMO

Ferrando, C. P. R. 2017. Período de atividade e padrões de uso do espaço do rato-de-espinho *Clyomys laticeps* (Thomas, 1909) (Rodentia: Echimyidae). Dissertação de mestrado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 75 p.

Cada espécie apresenta um nicho ecológico específico composto por n-dimensões que representam as condições e recursos do ambiente em que vive. Os padrões de atividade e uso do espaço dos indivíduos revelam o comportamento nas dimensões tempo e espaço do nicho, respectivamente. Os roedores subterrâneos apresentam o hábito de escavar e viver dentro de galerias subterrâneas, e aqueles que obtêm seu alimento basicamente acima do solo (conhecidos como semi-fossoriais), são diretamente influenciados pelos fatores do ambiente quando em atividade acima do solo. Desta forma, tanto fatores ambientais quanto fatores intrínsecos (e.g. interações sociais, tamanho corporal, dieta, morfologia) influenciam na escolha do período do dia para a execução de suas atividades de sobrevivência e reprodução. Além da distribuição no tempo, os padrões de uso do espaço refletem comportamentos ecológicos e fisiológicos dos indivíduos, assim como, indicam informações de comportamento social e reprodutivo da espécie. Nós avaliamos a escolha do período de atividade acima do solo pelo rato-de-espinho semi-fossorial *Clyomys laticeps* ao longo de um ano com o uso de armadilhas fotográficas. Além disso, durante dez meses avaliamos, com o uso da técnica do carretel de rastreamento, padrões de uso do espaço frente aos fatores intrínsecos (sexo e massa corporal) e extrínseco (oferta de recurso) através do método Mínimo Polígono Convexo (95%). O nosso estudo mostrou que a temperatura teve influência sobre a escolha do período de atividade de *C. laticeps*. Este apresentou preferência por temperaturas mais baixas do dia (10-25°C), demonstrando assim atividade predominantemente noturna, independente da sobreposição de período de atividade com seus potenciais predadores. Esse resultado nos indica que a escolha do período de atividade é restringida pela ocorrência de altas temperaturas durante o dia como ocorrem no bioma Cerrado, de maneira que as vantagens dessa escolha parecem ultrapassar os custos associados à predação. Com relação ao uso do espaço, a área de vida diária do rato-de-espinho variou entre os sexos. Os machos apresentaram maior área de vida diária que as fêmeas, como provável resposta as suas maiores necessidades energéticas para a manutenção da sua massa corporal e ao seu comportamento reprodutivo. As fêmeas adultas apresentaram maior intensidade de uso do habitat, explorando mais o entorno das galerias, assim como comportamento de fidelidade às galerias durante o período de estudo. Esse padrão de uso do espaço parece estar relacionado ao cuidado maternal, uma vez que a espécie parece apresentar uma reprodução não sazonal no nosso estudo. Em relação à oferta de alimento, a variação na abundância de frutos de *Allagoptera campestris* não mostrou ser um bom preditor dos padrões de área de vida da população estudada, mesmo sendo a palmeira bastante abundante na área. A ausência de efeito da oferta de alimento sobre o tamanho da área de vida diária do *Clyomys laticeps* pode ser explicada pela atividade reprodutiva contínua dos indivíduos, assim como pela inclusão de outros itens alimentares vegetais na sua dieta quando a oferta de frutos da *Allagoptera campestris* é reduzida na área.

Palavras-chave: área de vida diária, Echimyidae, massa corporal, noturno, período de atividade, sexo, subterrâneo, temperatura.

ABSTRACT

Ferrando, C. P. R. 2017. Activity period and space use patterns of the spiny rat *Clyomys laticeps* (Thomas, 1909) (Rodentia: Echimyidae). M.S. thesis. UFU. Uberlândia-MG. 75 p.

Each species present a specific multidimentional ecological niche which dimensions correspond to their environmental conditions and resources. Individuals' activity and space use patterns reveal the behavior in the time and space niche dimensions, respectively. The subterranean rodents have the habit to dig and live underground galleries, and those that get their food basically from the above-ground (named as semi-fossorial), are directly influenced by the environmental factors when in activity above-ground. In this way, both environmental influence and intrinsic factors (e.g. social interactions, body size, diet, morphology) have influence on the daily activity period choice to perform survival and reproduction. Besides the distribution in time, the individuals' space use patterns reflect the ecological and physiological activities, as well as, indicate about the species' social and reproductive behavior. We evaluated the above-ground daily activity choice by the semi-fossorial spiny rat *Clyomys laticeps* along one year through camera traps use. Furthermore, along ten months we evaluated, with spool-and-line technique, the space use patterns in response to the intrinsic factors (sex and body mass) and extrinsic (food availability) through the Minimum Convex Polygon method (95%). Our study revealed that temperature had influence on the activity period selected by *C. laticeps*. It presented preference for lower daily temperatures (10-25°C), presenting so, a predominant nocturnal activity, independently from the activity period overlap with their potential predators. This result indicates us that the activity period choice is restricted by the occurrence of high temperatures during the day, as occur in the Cerrado biome, so that the advantages of this choice seems to exceed the costs associated to predation. In relation to space use pattern, the spiny rat's daily home range varied between sexes. Males had larger daily home range than females, as probably response to their greater energy demands to maintain their bigger body mass and to their reproductive behavior. Adult females presented larger intensity habitat use, exploring more the galleries' surroundings, as well as fidelity behavior during the study period. This space use pattern seems to be related to the maternal care, once this species seems to present a non-seasonal reproduction in our study. In relation to food availability, the palm *Allagoptera campestris'* fruit availability variation didn't prove to be a good predictor of the individuals' daily home range size, even the palm being very abundant in the study area. The absence of food's availability effect on the *Clyomys laticeps*' daily home range size can be explained through individuals' year round reproductive activity, as well as by other food items inclusion in their diet when *Allagoptera campestris'* fruits is reduced in the area.

Key words: activity period, Echimyidae, body mass, daily home range, subterranean, nocturnal, temperature, sex

INTRODUÇÃO GERAL

O nicho ecológico n-dimensional de uma espécie é definido pelo intervalo de condições bióticas e abióticas (i. e. dimensões do nicho) em que ela pode sobreviver e se reproduzir (Hutchinson 1957). Uma vez que a espécie pode se perpetuar em diferentes combinações dessas condições, a sua distribuição geográfica é definida por ocorrência e acessibilidade de áreas viáveis a sua existência, assim como pela capacidade de dispersão dos seus indivíduos (Soberón & Peterson 2005). Assim, o nicho ecológico de uma espécie reflete o conjunto de decisões dos seus indivíduos frente aos fatores extrínsecos (e.g. condições do tempo, recurso alimentar, predadores e competidores) e intrínsecos (e.g. interações sociais, tamanho corporal, dieta, idade, sexo e morfologia) do ambiente em que vivem (Roughgarden 1972; Bolnick et al. 2002, 2003; Schmidt et al. 2002; Maher & Burger 2011;).

Na dimensão tempo do nicho, o período de atividade reflete estratégias para maximizar a procura por alimentos e parceiros e minimizar o encontro com predadores e competidores (Tattersall 1987; Hut et al. 2012). Resulta da resposta do animal frente às condições abióticas e bióticas do ambiente em que ocorre, como condições da luz, temperatura ambiental, umidade relativa, precipitação e velocidade do vento e à posição trófica que ocupa em relação aos demais no ambiente (Halle 2000). O período noturno é o mais escolhido pelas espécies de roedores, concentrando nele assim as suas atividades (Bennie et al. 2014). Existem porém, também espécies de roedores diurnas, assim como as que apresentam picos de atividade bimodais ocorrendo durante os períodos de transição dia/noite no crepúsculo e aurora (Graipel et al. 2003) e em minoria, as catemerais (Tattersall 1987).

Fatores bióticos, como predação e oferta de alimento, são conhecidos por afetar a escolha do período do dia para a execução das atividades dos animais. Porém, em animais endotérmicos, como os mamíferos, a temperatura ambiental é muitas vezes o fator determinante nesta escolha, uma vez que apresentam pequena tolerância a altas temperaturas devido aos custos relacionados a termorregulação (Lagos et al. 1995; Bacigalupe et al. 2003; Angilletta et al. 2010; Bennie et al. 2014). O comportamento, fisiologia e sucesso reprodutivo dos endotérmicos dependem fortemente de uma temperatura corporal estável de forma que eles devem mantê-la ao longo de suas atividades (Angilletta et al. 2010). Assim, roedores que vivem em ambientes áridos podem apresentar diferentes estratégias para evitar condições de altas temperaturas durante as suas atividades, envolvendo processos fisiológicos e comportamentais para realizar suas atividades (Chappell & Batholomew 1981; Bacigalupe et al. 2003; Bennie et al. 2014). Alguns exemplos sendo tolerância à hipertermia, escolha por áreas menos quentes (e.g. as sombreadas e/ ou com vento) e pelo período do dia com temperaturas mais baixas (e.g. noite e crepúsculo) (Chappell & Batholomew 1981; Bacigalupe et al. 2003; Bennie et al. 2014).

Na dimensão espaço do nicho, o uso do espaço reflete as estratégias para maximizar sobrevivência e sucesso reprodutivo dos indivíduos através da escolha do local para a determinação da área a ser usada e distribuição das diferentes atividades desenvolvidas dentro da área de vida (i.e. intensidade de uso do habitat), a adoção ou não de territorialidade e a distribuição espacial da população em uma área (Prevedello et al. 2008). A ocupação de ambientes pela biota é determinada por um conjunto de características físicas, químicas e bióticas favoráveis que podem variar ao longo do tempo. Como resposta às variações de condições e recursos, o uso da área também varia tanto entre animais de diferentes espécies assim como entre indivíduos de uma mesma espécie (Burt 1943; Powell & Mitchel 2012). Dentro do uso do espaço, a área de vida, anteriormente mencionada, corresponde à área utilizada por um indivíduo nas atividades relacionadas à sobrevivência e desenvolvimento (i.e. busca por alimento) e geração de prole (i.e. acasalamento e cuidado parental) (Burt 1943; Prevedello et al. 2008).

O uso do espaço, e consequentemente a área de vida, é fortemente influenciado por atividades dos indivíduos e os recursos alimentares disponíveis no ambiente; dois fatores amplamente associados (McNab 1963; Harestad and Bunnel 1979; Boutin 1990; Adler 2011; Emsens et al. 2013). Nos roedores, assim como em diversos outros grupos animais, fatores como tipo de dieta, distribuição e disponibilidade de alimento afetam o tamanho e sobreposição das áreas de vida (McNab 1963; Boutin 1990; Maher & Burger 2011; Tucker et al. 2014). Devido às necessidades energéticas dos animais, deve haver uma relação negativa entre tamanho da área de vida e disponibilidade de alimento de forma que os indivíduos devem aumentar o tempo e a energia gastos para suprir a demanda energética quando a quantidade de alimento no ambiente é menor; o que leva a um aumento na área de vida (Boutin 1990; Emsens et al. 2013).

Uma vez que as necessidades energéticas variam de acordo com a massa corporal (neste estudo, uma medida do tamanho do corpo) das espécies e o sexo dos indivíduos, essas variáveis também podem influenciar nos padrões de uso do espaço de roedores e outras espécies de vertebrados (McNab 1963; Rocha 1999; Adler 2011). A variação inter-sexual no uso do espaço pode ser determinada pelo dimorfismo sexual de tamanho em roedores (Batzli & Henttonen 1993; Schmidt et al. 2002), mas também por diferenças fisiológicas e comportamentais entre os sexos, que estão associadas aos seus padrões reprodutivos (Steinmann et al. 2005). Geralmente, o sucesso reprodutivo dos machos é dado pelo número de cópulas que eles conseguem obter, o que faz com que eles sejam mais vágeis durante o período reprodutivo, enquanto nas fêmeas o sucesso é determinado pela obtenção dos recursos para investimento na prole, o que as tornam mais fiéis ao sítio e, muitas vezes, territoriais durante o período reprodutivo (Emlen & Oring 1977; Ebensperger et al. 2009; Adler 2011; Maher & Burger 2011).

Os roedores (assim como outros animais) especializados em cavar e viver no subsolo são denominados de subterrâneos. Porém, as espécies subterrâneas diferem na frequência de uso da superfície para suas atividades, algumas vivendo exclusivamente no subsolo, raramente indo para a superfície, e outras administrando o tempo para a execução das suas atividades tanto na superfície quanto no subsolo (muitas vezes denominadas de semi-fossoriais ou semi-subterrâneas) (Lacey et al. 2000). Os roedores semi-fossoriais usam dimensões múltiplas do espaço escavando tocas subterrâneas para nidificação e refúgio contra predadores e estresse ambiental (Kinlaw 1999) e usando a superfície para forragear, defender territórios e procurar por parceiros (Lacey et al. 1998; Cutrera et al. 2006, 2010). Desta forma os padrões de uso do espaço destes roedores dependem tanto das condições do solo como daquelas acima dele (Burt 1943; Kinlaw 1999; Busch et al. 2000; Endries & Adler 2005).

Características da vegetação (i.e. estrutura, cobertura e biomassa), dureza do solo, pressão de predação, fatores abióticos e disponibilidade de recurso alimentar (i.e. tipo, distribuição e oferta) (Busch et al. 2000; Cutrera et al. 2006; Hayes et al. 2006) - sob influência de variações sazonais – estão entre os fatores que influenciam o uso do espaço dos roedores semi-fossoriais, assim como o sistema social que apresentam (Lacey 2000). Os roedores subterrâneos apresentam uma variedade de sistemas sociais, abrangendo desde espécies solitárias a eussociais, incluindo sistemas intermediários como colonial, social, comunal e familial (Burda et al. 2000). Eles são classificados ao longo de um contínuo que envolve o grau de sobreposição espacial entre os sexos dos indivíduos adultos, o compartilhamento ou não de galeria entre eles, a ocorrência e durabilidade do comportamento cooperativo na galeria e tipo de sistema de acasalamento (Burda et al. 2000; Lacey 2000). Nas espécies solitárias, a sobreposição espacial entre os adultos está restrita ao período reprodutivo, uma vez que não ocorre compartilhamento de galeria entre os adultos como em espécies sociais. As espécies coloniais são basicamente espécies solitárias que constroem as galerias próximas umas das outras gerando alta sobreposição espacial entre os sexos.

Os roedores da família Echimyidae (ratos-de-espinho) são representados por 90 espécies distribuídas em 23 gêneros (Fabre 2013) distribuídos ao longo da região Neotropical, encontrados desde o norte da América Central ao sul da Argentina (Adler 2011). Os roedores dessa família exploram uma variedade de hábitos, contendo gêneros essencialmente arborícolas (*Phyllomys, Kannabateomys*), terrestres (*Proechimys, Trinomys*), semi-fossoriais (*Carterodon, Clyomys, Euryzygomatomys, Trinomys*) e até mesmo semi-aquáticos (*Myocastor*), com distribuição desde áreas florestais úmidas (Mata Atlântica e Amazônia) até áreas abertas e secas (Cerrado e Caatinga) (Bonvicino et al. 2008). As informações sobre os roedores ratos-de-espinho semi-fossoriais no Brasil (*Carterodon sulcidens, Clyomys laticeps, Euryzygomatomys spinosus*, *Trinomys yonenagae*) são vagas e muitas delas de observações casuais, como no caso da espécie de *C. laticeps* (Bonvicino et al. 2008; Adler 2011; Bezerra et al. 2011).

Os indivíduos do gênero *Clyomys* Thomas, 1916 foram recentemente agrupados em uma única espécie *Clyomys laticeps* (Thomas, 1909) (Bezerra et al. 2016) e não mais em duas (*C. laticeps* e *bishopi*). Os espécimes desta espécie apresentam ampla variação fenotípica (i.e., cor de pelagem e morfológica) com ocorrência no leste do Paraguai e no Brasil nas regiões do Pantanal e Cerrado (Bonvicino et al. 2008; Patton et al. 2015), neste último já sido registrado em campos limpo e sujo, campo cerrado e cerrado sentido restrito (Mares et al. 1989). A espécie é descrita como colonial (Bezerra et al. 2016) ou social

(Burda et al. 2000) e semi-fossorial, cujas galerias apresentam interligações de túneis subterrâneos (podendo chegar a um metro de profundidade e 22 m de túneis), câmaras e várias tocas de acesso (Cunha & Belentani 2000; Lamberto 2015). Em relação à dieta, não existem estudos diretamente focados no assunto, porém estudos e observações em campo indicam o consumo de sementes de palmeiras por estes animais (Almeida & Galetti 2007; Antunes 2009; Lamberto 2015; observação pessoal), e informações sobre o período de atividade desta espécie não são conhecidos (Bezerra et al. 2016). Em resumo, são poucas as informações sobre a ecologia e biologia de *Clyomys laticeps*.

Estudos abordando a ecologia e o comportamento animal permitem entender a história natural de uma espécie. Nessa dissertação, serão abordados pela primeira vez aspectos comportamentais do rato-de-espinho *Clyomys laticeps* em dois estudos distintos, cada um compondo um capítulo da dissertação em inglês sob as normas da revista *Journal of Mammalogy*. Os estudos foram realizados em uma região de Cerrado, mais especificamente no Parque Estadual da Serra de Caldas Novas (GO, Brasil) (Fig. 1). O primeiro capítulo explora o padrão de atividade, mais especificamente o efeito da temperatura ambiental sobre a seleção do período de atividade por *C. laticeps*. O segundo capítulo aborda os padrões de uso do espaço sob influência dos fatores intrínsecos como, tamanho corporal (neste estudo, massa corporal e sexo), e extrínsecos, como oferta de recurso alimentar, na área de vida (neste estudo, área de vida diária) e intensidade de uso do habitat de indivíduos de uma população de *C. laticeps*.

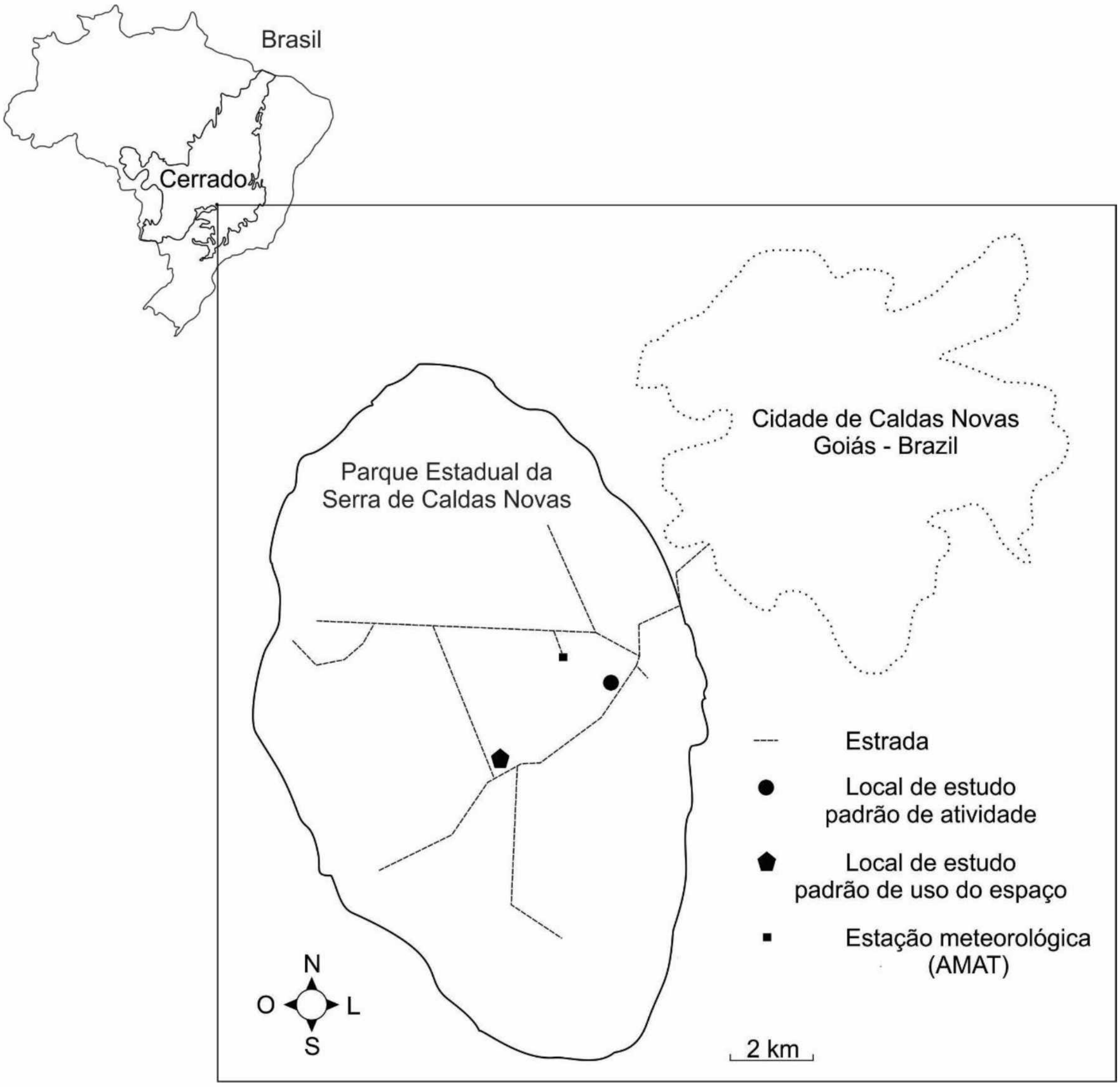

Fig. 1. Local de estudo. Parque Estadual da Serra de Caldas Novas, Goiás – Brasil.

CAPÍTULO 1

Rua Ceará s/n
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Clyomys laticeps' daily activity

Above-ground activity pattern of the semi-fossorial spiny rat, *Clyomys laticeps*

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Choosing a period to perform basic survival and reproduction activities follows a trade-off between the costs and benefits associated to abiotic and biotic demands, in which individuals try to maximize their fitness. Once the rodents have small tolerance to high temperatures, their activity patterns are usually thermally constrained. No information is registered about the semi-fossorial spiny rat *Clyomys laticeps* activity patterns. In this way, we assessed the above-ground activity of free-living *C. laticeps* individuals, using camera traps along one year. The studied population was more frequently active during lower temperatures, generally found during night and dawn. Hence, *C. laticeps* was nocturnal, with some degree of crepuscular activity. Its activity was restricted to temperatures between 10-25°C, with an activity peak within 19-21°C. The nocturnal activity of *C. laticeps* occurs in spite of predation risk in this period; thus, timing of activity above-ground is probably a strategy to avoid thermal stress, and the benefits of being active in this period compensate the costs of predation and competition.

Key words activity period, Echimyidae, nocturnal, subterranean, temperature

Escolher um período para realizar atividades básicas de sobrevivência e reprodução segue um *trade-off* entre os custos e benefícios associados às demandas abióticas e bióticas, nos quais os indivíduos tentam maximizar o seu sucesso reprodutivo. Uma vez que os roedores apresentam baixa tolerância a altas temperaturas, seus padrões de atividade são termicamente limitados. Não existe informação sabida sobre o padrão de atividade do rato-de-espinho semi-fossorial *Clyomys laticeps*. Desta forma, nós acessamos a atividade acima do solo dos indivíduos de vida livre do *C. laticeps* com o uso de armadilhas fotográficas ao longo de um ano. A população estudada foi mais frequentemente ativa durante temperaturas mais baixas do dia, geralmente ocorrendo ao longo da noite e amanhecer. Assim, *C. laticeps* foi noturno, com certo grau de atividade crepuscular. Sua atividade foi restrita a temperaturas entre 10-25°C, com pico de atividade entre 19-21°C. A atividade noturna de *C. laticeps* ocorre apesar do risco de predação neste período; desta forma, tempo de atividade acima do solo é provavelmente uma estratégia para evitar o estresse térmico, e os benefícios de ser ativo neste período compensam os custos da predação e competição.

Palavras-chave Echimyidae, noturno, período de atividade, subterrâneo, temperatura

Animal activity patterns are defined by the interaction between endogenous and environmental factors under which they are exposed; hence resulting from the interplay between light intensity, temperature, photoperiod, precipitation, predators and food availability (Halle 2000). The choice of a timing to perform basic survival and breeding activities is determined by a trade-off between costs and benefits, such that individuals usually tune their activities to the most favorable period of the day, thus maximizing their fitness (Halle 2000; Kronfeld-Schor and Dayan 2008; Refinetti 2008). Studies have been pointing out how predation risk (Larimer et al. 2010), food availability (Braun 1985; Bacigalupe et al. 2003) as well as temperature (Kenagy et al. 2002; Rezende et al. 2003; Levy et al. 2007) can affect when animals will be active, and how they manage to deal with these factors acting at the same time.

In endothermal animals, as mammals, temperature plays an important role in timing their activities once they have to avoid thermal stress (Bacigalupe et al. 2003; Peinke and Brown 2003; Bennie et al. 2014) in order to maintain homeostasis (Angilletta et al. 2010). Species that inhabit arid environments exhibit a variety of physiological and behavioral strategies that enable them to deal with the scarcity of water and extremes of temperature. Among these, we may point out the timing of activity restricted to periods with lower temperatures (e.g. night and twilight) (Bennie et al. 2014), shifting activity periods in response to temperature variation between seasons (Lee et al. 2010; Cid et al. 2015), hiding in burrows for body cooling (Long et al. 2005), tail use as portable parasols (Bennett et al. 1984), selecting microhabitats with higher wind speeds (Melcher et al. 1990) and even increasing the capacity of heat storage, being tolerant to hyperthermia (Chappell and Batholomew 1981; Peinke and Brown 2003).

Subterranean species that spend most of their time underground have already been hypothesized to present random activity pattern and the absence of circadian rhythms

(Nevo 1979; Buffenstein 2000; Roll et al. 2006), once these animals live in a dark stable environment (i.e. in the absence of circadian cycle). Nevertheless, a few species exhibit circadian activity rhythms, which may change between seasons as a response to seasonality in ecological conditions (Braun 1985; Kenagy et al. 2002; Marcomini and Oliveira 2003; Cutrera et al. 2006). On the other hand, semi-fossorial species that perform their activities in both space dimensions, surface and underground, should be more exposed to environmental factors than the strictly subterranean species, such that external factors may influence their daily activity timing decisions (Buffenstein 2000; Burda et al. 2007). These species usually forage and mate above-ground and use their tunnels and galleries to store food, avoid predators, nesting and eventually to forage (Kinlaw 1999). The study of the daily activity pattern in semi-fossorial species has some limitations, once they also spend time underground. In this way, in natural conditions studies have focused on the daily activity pattern above-ground, excluding the activities performed below ground (Rezende et al. 2003; Williams et al. 2014).

Clyomys laticeps (Thomas, 1909) (Rodentia: Echimyidae) is a New World hystricognath medium-sized rodent (range mass: 50 to 350g – data from our study), described as a semi-fossorial colonial or social species (Burda et al. 2000; Bezerra et al. 2016). It is distributed over east Paraguay and over Brazil in the Pantanal and Cerrado biomes (Bonvicino et al. 2008; Paiva Camilo-Alves and Mourão 2009; Patton et al. 2015), mainly in open cerrado physiognomies (Mares et al. 1989). Previous studies suggest that they present a frugivore-herbivore diet, emerging above-ground to forage for fruits and seeds and other plant parts (Almeida and Galetti 2007; Antunes 2009; pers. observ.). Activity patterns of this species are unknown (Bezerra et al. 2016), although anecdotal information suggests a diurnal habit (IUCN 2016). In this way, the aim of this study is to describe, in natural conditions, the above-ground activity patterns of *C. laticeps*. Taking into account that the time activity decision is linked with the best time for foraging (Nevo et al. 1982) and that this rodent species is distributed along areas with extreme daily temperatures, we hypothesize that they will be above-ground active during cooler day periods in regard to hyperthermia reduction risk.

MATERIALS AND METHODS

Study site: we conducted this study in the state park of Serra de Caldas Novas (PESCaN) situated in the state of Goiás (17°43' - 17°51'S e 48°40' - 48°44'W) with the approval from the Secretaria Estadual do Meio Ambiente de Goiás, Brazil (SECIMA). The park has an area of 12,315 ha which comprises a plateau formation with a mosaic of different vegetation types associated with different soil characteristics because of the local geological formation (Eiten 1978; SECIMA 2016). The area is characterized by a mosaic of physiognomies, such as forests, savanna and grassland areas (Eiten 1978). The study was developed in a savanna physiognomy named as 'cerrado sensu stricto' (woodland with low trees, shrubs and tall grass sometimes covering the ground - Ribeiro and Walter 1998). The region climate is defined by two well defined seasons: dry season from April to September and a wet season from October until March (Silva et al. 2008; AMAT 2016). The monthly mean minimum and maximum temperature varied between 16.93 °C – 33.43 °C in the wet season and 9.68 °C – 34.88 °C in the dry season, and total monthly rainfall varied between 0.0 and 675 mm (AMAT 2016).

Methods: The study was carried out monthly from August 2015 to October 2016 (except for the months of September and December 2015) in an area of 16.5ha, where we installed 13 to 20 camera traps (Bushnell 6PM and MOULTRIE M-990i) and so, through this method, we were able to study the species' activity patterns in natural conditions.

Cameras were distant at least 30 m from each other, in order to ensure independence between sampling units, once the largest gallery observed in the study site had approximately 10 m (Lamberto 2015). Each camera was disposed at 20-50 cm height, facing entrance tunnels of *Clyomys laticeps* species and individuals of *Syagrus flexuosa* palm, which fruit and seed are consumed by this rodent. Records of activity patterns were obtained by videos of 30 s (once *C. laticeps*' individuals don't stay to long in the same place) with ten seconds of interval between each registration. Cameras were active during day and night, for approximately seven consecutive nights in each month. Each camera trap was considered as a sample unit and to avoid pseudoreplication, we included in the data analysis only videos that respected the 1 h interval criteria between videos from the same camera trap. We standardized the day period from 7:00 a.m. to 5:59 p.m. and the night period from 6:00 p.m. to 6:59 a.m., since the sunrise and sunset are mostly at 6:00 a.m. and 6:00 p.m., respectively. Temperature (°C) and humidity (%) data were obtained hourly during the study period from the meteorological station (AMAT) located about 1km from the study site. We organized a spreadsheet in which for each hour of sampling the correspondent day, month, year, year season (dry or wet), temperature, humidity, number of independent videos recorded (0-2) and presence (1) or absence (0) of *C. laticeps*' activity was specified.

Statistical analysis: We carried out a chi-square test to compare frequency of activity between day and night periods as well as between the night periods (18h00 – 00h59 and 1h00 – 6h59). Moreover, to test the hypothesis of higher activity of *Clyomys laticeps* during cooler hours, we ran a logistic regression evaluating the probability of *C. laticeps* activity along the range of daily temperatures.

RESULTS

In total, we had a sample effort of 1,521 traps-nights, resulting in 81 independent records of *Clyomys laticeps* (total of 124 videos). In most records, *C. laticeps* presented a foraging behavior (70%) (eating grasses and fruits and sniffling the surface, probably searching for food), followed by escaping (fast passing movements – 13%), attention (kept standing with the head up - 12%) and burrowing (3.7%) behaviors. Neither video recorded more than one *C. laticeps* adult together, in contrast to adult with pups that were tree times observed in our study (4%) the latter ones were also registered foraging apparently alone (6.5%). Pups were registered in January, September, October and November (in different galleries). In addition to *C. laticeps*, we registered other vertebrate species, from which the most potential *C. laticeps*' predators were recorded during night and twilight (see Supporting Information S1).

Temperature and humidity varied from 9.7°C to 38.95°C and 11.5% to 99% during the day period, while during the night they varied from 8.85°C to 34.75°C and 0 to 99%, respectively. The mean day and night temperature were 27°C and 20°C, and the humidity's values were 49% and 69%, respectively. Humidity and temperature were inversely related (correlation: $r = -0.776$) and *Clyomys laticeps* were active above-ground whenever humidity reached 30% or higher. Activity of *C. laticeps* was mainly registered at night ($x^2_{0.05, 2} = 36.8$, $P < 0.001$, gl = 1), from 6 p.m. to 6:59 a.m., although we registered single bouts of activity at 1:00 p.m. and 4:00 p.m. and crepuscular activity at 7:00 – 7:59 a.m. (Fig. 1). The spiny rat was registered in temperatures ranging from 10-25°C, being observed more often between 19-21°C (58%, Fig 2a); hence there is a higher probability of *C. laticeps* activity during cooler periods of the day (logistic regression: $x^2_{0.05, 2} = 4.64$, $P < 0.03$) (Fig. 2b). Individuals were more frequently active above-ground between 1 a.m. and 6:59 a.m. ($x^2_{0.05,2} = 11.21$, $P = 0.001$, gl = 1), which corresponded to the period with lower temperatures (below 20°C in 62% of the time) when compared to the first night period (between 6:00 p.m. and 0:59 a.m., which had temperatures above 20°C in 79% of the time).

DISCUSSION

Small endotherm animals, like rodents, have small tolerance to high temperatures because of thermoregulation metabolic costs (McNab 2002). Species from arid or semiarid regions are usually nocturnal due to high daytime temperatures, whereas species from high altitudes and latitudes, tend to be diurnal in a strategy of compensation of heat loss in times when ambient temperature is low, thus reflecting the importance of thermal constraints in rodent activity patterns (Bennie et al. 2014). The spiny rat *Clyomys laticeps* was constrained by the high daytime temperatures in the Brazilian savanna (i.e. Cerrado), presenting an unimodal nocturnal above-ground activity pattern lasting until dawn, in contrast to the existing anecdotal information about its activity pattern, suggesting a diurnal habit (IUCN 2016). Above-ground activity was restricted to low temperatures (10-25°C), especially between 19-21°C, and was mostly associated to food searching behaviors. Actually, even the single diurnal bouts of activity recorded occurred within the range of temperatures in which they were observed active. Finally, it seems that *C. laticeps* is more active between 1:00 a.m. and 6:59 a.m. due to the lower temperatures present in this period.

Other studies in subterranean rodents also found temperature influencing their daily activity patterns, so that they shift them in response to seasonal and daily temperature variation, in a way to avoid thermal stress. The diurnal ground squirrel (*Urocitellus parryii*), coruro (*Spalacopus cyanus*) and degus (*Octodon degus*) change their activity from an unimodal pattern - in cold days - to a bimodal one - in warm days, avoiding thermally stressful conditions during the middle of the day (Kenagy et al. 2002; Rezende et al. 2003; Williams et al. 2014). In relation to thermal constraints, the diurnal rodents tend to have high variability in diel activity, while nocturnal ones generally show small variability (Kronfeld-Schor and Dayan 2008), once the latter ones don’t need to shift in relation to the diurnal temperature variations as the diurnal ones sometimes have to, since they already accomplish their activities within the diel period with daily lower temperatures. Apparently, this seems to be the case of *C. laticeps*, that didn’t shift its activity pattern along seasons (i.e. wet and dry season).

Decisions regarding activity patterns reflects a behavioral trade-off between costs of exposure to predators, thermoregulation and benefits associated to food availability and distribution (Halle 2000). Since rodents have small tolerance to high temperatures, thermoregulatory balance may often overrun the role of other survival demands in their diel activities decisions. Bacigalupe et al. (2003) showed that activity patterns of degus involve a trade-off between thermoregulation and foraging, in which first individuals avoid thermal stress and then select areas according to food availability during the warmer season. *Clyomys laticeps* foraging primarily occurs above-ground, thus food availability may influence their activity time. However, herbivore subterranean rodents can vary in proportions of plant items according to the food supply throughout the year (Busch et al. 2000) so probably minimizing the importance of food in determining activity patterns in this species. Nevertheless, competition with other species for the available food items may change foraging behavior (Hughes et al. 1994; Bouskila 1995) and even incur in temporal niche partitioning between rodents, thus altering activity patterns of the coexisting species (Jones et al. 2001). Hence, future studies should test behavioral trade-offs between foraging and thermoregulation in *C. laticeps*, by using experiments manipulating food abundance and competitor densities in different temperatures.

In relation to predation risk, subterranean rodents also take into account the thermal constrains, so that the decision is the best made for their survival (Lagos et al. 1995). *Clyomys laticeps* is exposed to many potential predators in PESCaN, including mainly nocturnal carnivorous mammals, as *Cerdocyon thous, Lycalopex vetulus*, *Conepatus semistriatus* and *Eira barbara* (see Supporting Information S1, Tôrres 2004 and Lemos et al. 2011). Although we didn't measure attack and/or consumption rate by diurnal and nocturnal predators, Arruda Bueno (2003) pointed out a high consumption rate of *C. laticeps* by the nocturnal maned wolf (*Chrysocyon brachyurus*), and a lower consumption by owl species (*Tyto alba* and *Athene cunicularia*). Hence, we know that *C. laticeps* is highly susceptible to predation during the night, nevertheless they are more active during this period, thus probably using other strategies to avoid predation risks. Probably, the use of burrow systems by this species may confer advantage over their predators (Kinlaw 1999; Larimer et al. 2010), although Arruda Bueno (2003) demonstrated that they have a low escape response when compared to smaller rodents. Few studies have evaluated the interplay between thermal and predation risks on daily activity patterns of subterranean rodents, although Lagos et al. (1995) found that *Octodon degus* limit their activity and space use according to thermal constraints rather than predation risks. In this way, we may suggest that *C. laticeps* tune their activity according to daily temperature fluctuations, once they use other strategies to avoid predation (Ebensperger & Blumstein 2006; Brown and Peinke 2007; Larimer et al. 2010). Nevertheless, future studies should consider the role between predation risks and thermal constraints on *C. laticeps* and other subterranean rodents daily activity patterns.

To our knowledge, this is the first study detailing *C. laticeps*' daily activity patterns above-ground. Our results point out the importance of temperature fluctuations on *C. laticeps* activity, which were restricted to lower temperatures occurring during the night. We suggest that the nocturnal habit is related to thermal constraints, and that the benefits of being active during periods of lower temperatures compensate the costs of predation and competition.

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SUPPORTING INFORMATION

Supporting Information S1. Vertebrate species recorded along the study at Parque Estadual da Serra de Caldas Novas (GO - Brazil), and their corresponding activity periods. Asterisks correspond to potential *Clyomys laticeps* predators. N = nocturnal, D = diurnal and C = crepuscular.

Class	Order	Family	Species	Popular name	Activity
Mammalia	Carnivora	Canidae	*Cerdocyon thous* (Linnaeus, 1766) *	Cachorro-do-mato	N
			Lycalopex vetulus Lund, 1842 *	Raposa-do-campo	N
		Mephitidae	*Conepatus semistriatus* (Boddaert, 1785) *	Jaratataca	N
		Mustelidae	*Eira barbara* (Linnaeus, 1758) *	Irara	N/C
	Cingulata	Dasypodidae	*Cabassous unicinctus* (Linnaeus, 1758)	Tatu-do-rabo-mole	D
			Dasypus novemcinctus Linnaeus, 1758	Tatu-galinha	D
			Priodontes maximus (Kerr, 1792)	Tatu-canastra	D
	Pilosa	Myrmecophagidae	*Myrmecophaga tridactyla* Linnaeus, 1758	Tamanduá-bandeira	N/D
			Tamandua tetradactyla (Linnaeus, 1758)	Tamanduá-mirim	N
	Rodentia	Echimyidae	*Thrichomys apereoides* (Lund, 1839)	Punaré	N
			Clyomys laticeps (Thomas, 1909)	Rato-de-espinho	N
	Cetartiodactyla	Cervidae	IN	-	N
Reptilia	Squamata	Teiidae	*Tupinambis* sp. Daudin, 1802 *	Teiú	D
Aves	Cariamiformes	Cariamidae	*Cariama cristata* (Linnaeus, 1766)	Seriema	D
	Strigiformes	Strigidae	*Megascops choliba* (Vieillot, 1817)	Corujinha-do-mato	N

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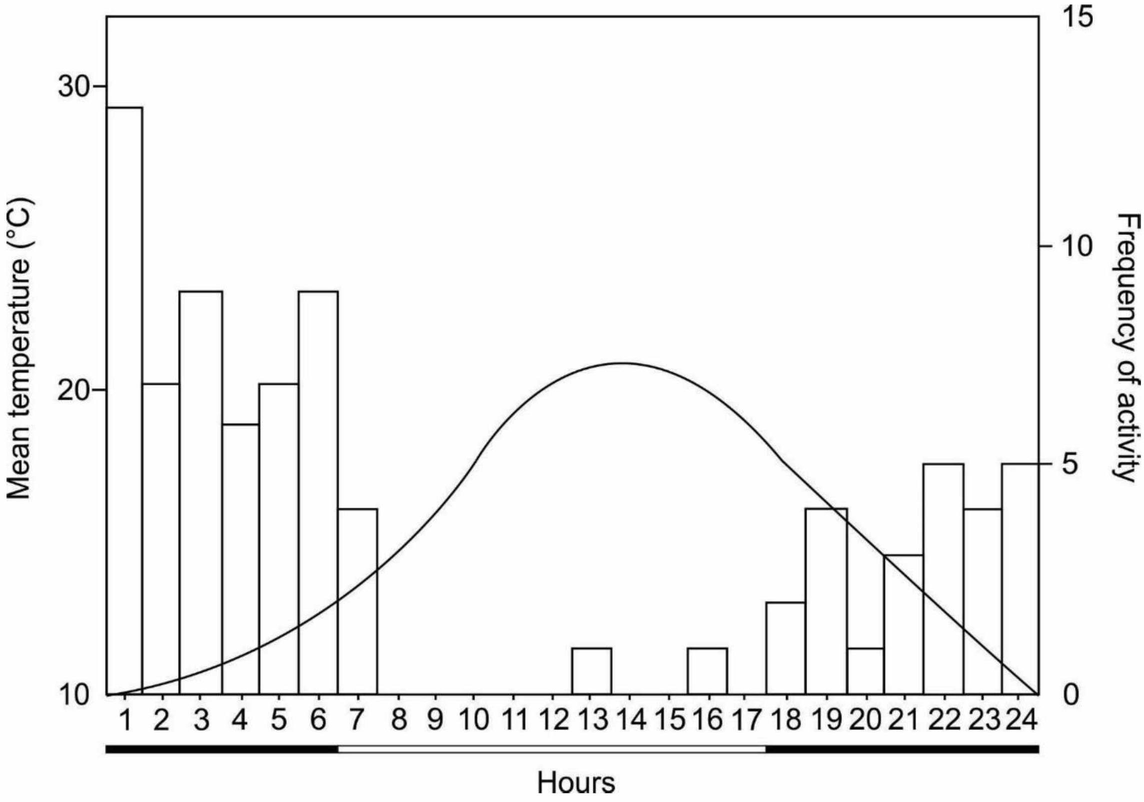

Fig. 1. *Clyomys laticeps* frequency of activity (bars) according to mean temperature (continuous line) along 24h (night and day represented by filled and not filled zone of the bar, respectively) at Parque Estadual da Serra de Caldas Novas (GO - Brazil).

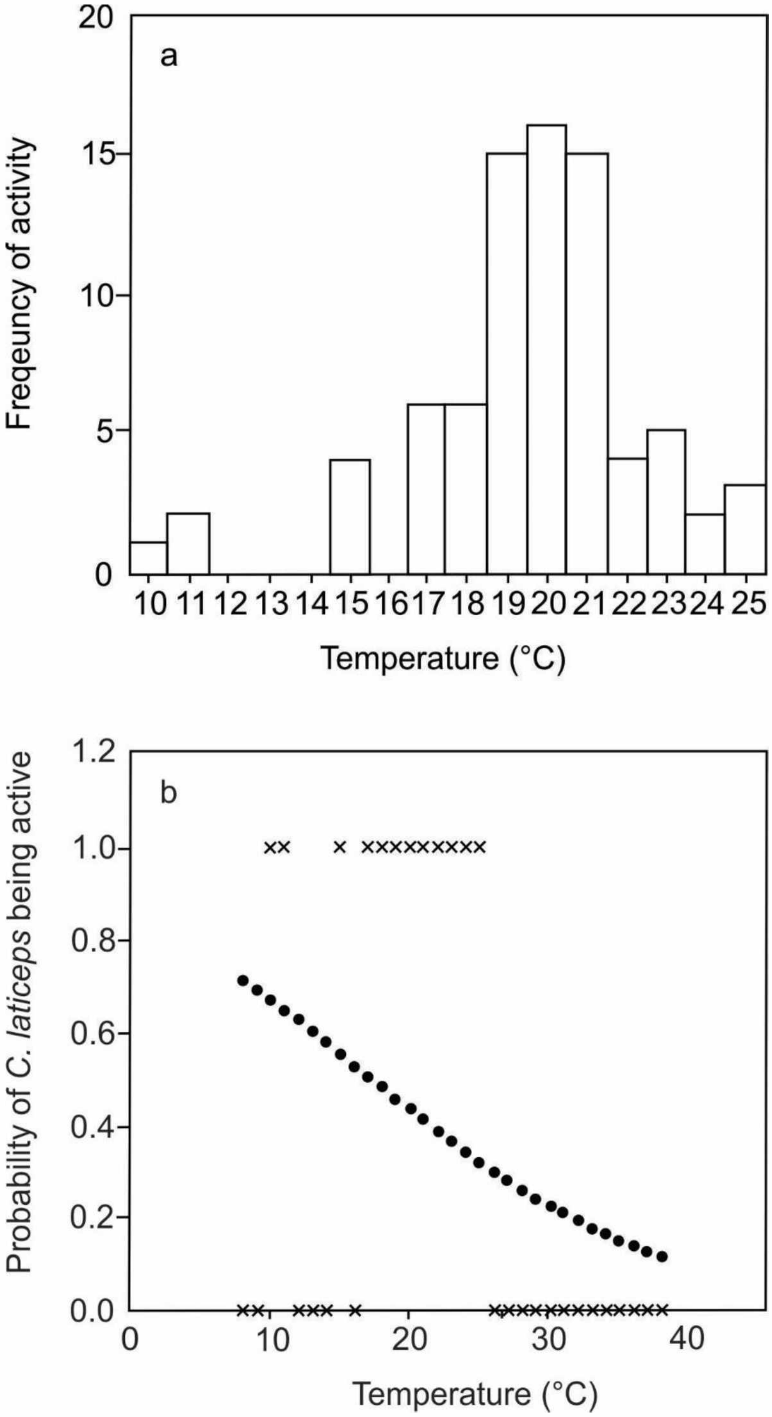

Fig. 2. a) Frequency of activity of *Clyomys laticeps* within the range of temperatures in which they were registered, and **b)** Probability of *C. laticeps* being active according to temperature fluctuation at Parque Estadual da Serra de Caldas Novas (GO - Brazil).

CAPÍTULO 2

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Clyomys laticeps' space use

Effects of body mass and sex on space use of the spiny rat, *Clyomys laticeps*

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The animal's home range represents the space used for their nutritional, social and reproductive activities, and the intensity of habitat use, the distribution of these activities within its home range. Hypothesis about the influence of extrinsic and intrinsic factors over the space use patterns have been predicted, allowing us to further understanding of individual behavior, their social interactions and population dynamics. In this study, we evaluated how space use patterns of the semi-fossorial rodent *Clyomys laticeps* was affected by their body mass and sex, as well as by food availability, by measuring their daily home range and intensity of habitat use. Adult males had larger daily home range size than females in response to their greater body mass and strategic reproductive behavior. Furthermore, adult females had greater intensity of habitat use, presenting site fidelity, which probably mirrors the offspring care throughout the year in response to the apparently non-seasonal reproduction of *C. laticeps* found in our study. Differently from expected, food availability variation (in this study, *Allagoptera campestris* palm fruits) had no influence on the space use patterns of *C. laticeps*. As in other subterranean herbivorous rodents, shifts in proportion of consumed food items according to their availability may explain the lack of a negative relationship between palm fruit abundance and *C. laticeps* daily home range.

Key words: body mass, daily home range, Echimyidae, intensity of habitat use, semi-fossorial, sex

A área de vida de um animal representa o espaço usado para as suas atividades nutricionais, sociais e reprodutivas, e a intensidade do uso do habitat, a distribuição destas atividades dentro da sua área de vida. Hipóteses sobre a influência de fatores extrínsecos e intrínsecos sobre estes padrões do uso do espaço têm sido feitas, permitindo ainda, o entendimento do comportamento individual, suas interações sociais e dinâmicas populacionais. Neste estudo, nós avaliamos como padrões de uso do espaço do roedor semi-fossorial *Clyomys laticeps* foi afetado pela sua massa corporal e sexo, assim como oferta de alimento, medindo a sua área de vida diária e intensidade do uso do habitat. Machos adultos apresentaram maior área de vida diária que as fêmeas em resposta ao seu maior tamanho corporal e seu comportamento reprodutivo estratégico. Além disso, as fêmeas adultas apresentaram maior intensidade de uso do habitat, apresentando fidelidade às galerias, o que provavelmente representa o seu comportamento de cuidado com a prole ao longo do ano em resposta a aparente reprodução não-sazonal de *C. laticeps* observada no nosso estudo. Diferentemente do esperado, a variação da oferta de alimento (neste estudo, frutos da palmeira *Allagptera campestris*) não teve influência nos padrões do uso do espaço do *C. laticeps*. Como em outros roedores subterrâneos herbívoros, mudanças na proporção dos itens consumidos de acordo com a sua disponibilidade pode explicar a ausência de uma relação negativa entre abundância dos frutos da palmeira e área de vida diária do *C. laticeps*.

Palavras-chave: área de vida diária, Echimyidae, intensidade do uso do espaço, massa corporal, semi-fossorial, sexo

Animal movements reflect individual decisions to enhance fitness in response to environmental conditions, biotic interactions and intrinsic ecological factors. Several extrinsic factors, such as predators, weather conditions, habitat heterogeneity and food resource, and intrinsic ones such as population density, body size, social interactions and diet may affect movements and space use patterns of individuals within a population (Fisher et al. 2003; Cutrera et al. 2006, 2010; Maher and Burger 2011; Grassel et al. 2015). Understanding patterns of use of space and the factors that influence them is essential, due to the link between use of space and population dynamics (e.g. Fernandez et al. 1997) and community structure (Vieira and Monteiro Filho 2003). Space use patterns encompass variables as home range (area required for their normal activities like food gathering, mating, and caring for young), intensity of habitat use (individuals' activities distribution within a home range), spatial organization of individuals and habitat selection (Burt 1943; Prevedello et al. 2008).

Within mammals, both extrinsic (e.g food distribution, availability and quality) and intrinsic factors (e.g. body size and sex) affect home range size and intensity of habitat use of individuals (Burt 1943; Adams 2001; Powell and Mitchel 2012). According to the habitat-productivity hypothesis (Harestad and Bunnel 1979), home range size decreases when food is abundant, since individuals may occupy smaller areas to meet their energetic demands (Endries and Adler 2005; Quirici et al. 2010; Maher and Burger 2011). Correlative and food supplementation studies have already provided evidence supporting this hypothesis (Boutin 1990; Emsens et al. 2013). Since energy requirements determine animal movements, big-bodied individuals usually have to explore larger areas, translated into larger home ranges, to satisfy their higher energetic demands (McNab 1963). The positive relationship between home range size and body mass has been commonly studied between species, but limited attention has been given to this hypothesis within species (Schmidt et al. 2002; Tucker et al. 2014). Finally, physiological and behavioral differences between sexes often result in contrasting effects of reproduction on male and female space use patterns. Usually, males explore large areas to obtain access to more mating partners, while female movements are associated to food availability and not reproductive activity (Emlen and Oring 1977; Ostfeld 1985; Schmidt et al. 1997; Ebensperger 2001; Adler 2011; Maher and Burger 2011). Both extrinsic and intrinsic factors vary seasonally and along years, resulting in home range dynamics within individuals.

Subterranean rodents, those specialized in digging and underground living, present a range of behaviors related to their activity patterns, mating and social systems, as a response to environmental and ecological conditions which they are exposed (Ebensperger 1998; Maher and Burger 2011). They exhibit a variety of social systems, and they are classified according to spatial overlap between adults, mating system and occurrence of cooperative breeding, thus ranging from solitary to eusocial species, including intermediate systems such as colonial, social, communal and familial breeders (Burda et al. 2000; Lacey 2000). The major dichotomy between solitary and social species is defined by the occurrence and extent of burrow system sharing (i.e. subterranean gallery) and spatial overlap between adults. In this way, solitary species present burrow sharing restricted to mother-offspring or male and females during the mating period (Ebensperger 1998; Burda et al. 2000; Lacey 2000). In social species, at least one adult member of each sex shares a burrow system regardless of the reproductive season (Lacey 2000). The colonial species are basically solitary animals who build their burrow systems in close vicinity to each other (Burda et al. 2000), with high spatial overlap between home ranges of individuals of both sexes. In this way, home range size of males and females is usually similar in males and females of social and colonial species (Turrini et al. 2008; Santos and Lacey 2011), since male access to females is facilitated through gallery sharing and gallery proximity, respectively (Lacey 2000; Santos and Lacey 2011). On the other hand, in solitary species, males usually present larger home ranges than females, since they are forced to find their mates during the breeding season (Zuri and Terkel 1996; Lacey et al. 1998; Bennett et al. 2000; Lacey 2000).

The spiny rat *Clyomys laticeps* (Thomas, 1909) (Rodentia: Echimyidae), is a New World hystricognath medium-sized rodent (range mass: 50 to 350g) distributed over east Paraguay and over Brazil in the Pantanal and Cerrado biomes (Bonvicino et al. 2008; Paiva Camilo-Alves and Mourão 2009; Patton et al. 2015). It has been recorded mainly in open cerrado physiognomies, like those called as campo limpo, campo sujo, campo cerrado and cerrado *strictu sensu* (Mares et al. 1989). Previous studies suggest a semi-fossorial and social (Burda et al. 2000) or colonial (Bezerra et al. 2016) habit and a frugivore-herbivore diet, including primarily palm seeds (Almeida and Galetti 2007; Antunes 2009; pers. observ.). Records in the literature suggest that the breeding may be seasonal (Patton et al. 2015). Pregnant females were already registered in the dry season (June and September) and in the wet season (December) and those that were analyzed, had a single embryo (Bishop 1974; Vieira 1997). Young specimens with incomplete dentition were taken in December and April (Bishop 1974) and Vieira (1997) observed that the juveniles weaned and grew during the wet season.

Studies about spatial and social organization are absent in some terrestrial echimyids species like the semi-fossorial rodent *Clyomys laticeps* (Adler 2011). Hence, for the first time we evaluate the role of extrinsic and intrinsic factors (food abundance, body mass and sex) on the use of space of this species. In this study, daily home range area, which reflects individual home range in a small time scale (Prevedello et al. 2008), and intensity of habitat use, will act as surrogates of use of space by *C. laticeps*. Then, the following hypotheses will be tested 1) in a social or colonial organization, as assumed for *C. laticeps*, movement is not different between sexes due to burrow sharing and proximity between individuals, 2) individual movement is positively related to body mass in response to energy demands, and 3) individual movement is negatively related to habitat productivity, due to easy access to food resources in productive environments. Thus, our study predictions are: 1) daily home range size and intensity of habitat use will be similar between *C. laticeps* males and females, 2) individuals of *C. laticeps* with greater body mass will present larger daily home ranges than individuals with lower body mass, and 3) daily home range size in *C. laticeps* will increase in periods of low *Allagoptera campestris*' fruit availability, and decrease in periods of its greater availability.

MATERIALS AND METHODS

Study area: The study took place in Serra de Caldas Novas state park (PESCaN), a mountain chain of 750-1043 m situated in Goiás - Brazil (17°43' - 17°51'S and 48°40' -

48°44’W). The study site has an area of approximately 12,315 ha, with several savanna physiognomies, like open grasslands, savanna woodlands and shrub savannas (Eiten 1978; SECIMA 2016). The study was developed at the top of the mountain plateau in a savanna physiognomy called ‘cerrado campo sujo', which is characterized by sparse distribution of shrubs intermixed with herbaceous plants (Ribeiro and Walter 1998). The region climate is defined by a dry season from April to September and a wet season from October to March (Silva et al. 2008; AMAT 2016). During the study, mean minimum temperature was 9.68 °C and mean maximum temperature was 34.88 °C in the dry season, while mean temperature ranged from 16.93 °C to 33.43 °C in the wet season. Total monthly rainfall varied between 0.0 and 675 mm (AMAT 2016).

Data collection: *Clyomys laticeps* individuals were live trapped monthly, in a 20 ha area, from January to October 2016. In each trapping session, 41 Sherman live traps (43 x 12.5 x 14.5 cm; Equipos Fauna) were baited with a mixture of peanut butter, banana and oat, and set at the entrance of active burrows along different burrow systems (defined as subterranean galleries containing more than five burrow entrances) during five consecutive nights. The active galleries were defined as those with burrows with soil recently removed, rest of consumed fruits and feces in the burrow entrances. The number of traps in each gallery was proportional to the number of burrows in each gallery. Traps were checked every morning and the captured animals were weighed, sexed and ear-tagged. Larger individuals (body mass ≥ 150g) were equipped with a spool-and-line device and posteriorly released at their point of capture, while smaller individuals (body mass ≤ 150g) were released after recording their data. Those individuals who died accidentally in the livetraps were posteriorly dissected. Livetrapping was approved by the

Secretaria Estadual do Meio Ambiente de Goiás, Brazil (SECIMA) and IBAMA, CONCEA.

Home range: Captured individuals were tracked using the modified spool-and-line device method – spool-and-line in a backpack (Mendonça et al. 2010). The quilting cocoons, with approximately 4.1g and 140 m of line, were covered in heat-shrinking plastic and then fixed on a curved piece of cardboard (3.5 x 4 cm) with masked tape. This device was fixed to the back of the animals forming a backpack following Mendonça et al. (2010) with some modifications. Each individual received a specific spool quilting cocoon color for posterior identification. The backpacks were marked with a number and weighted approximately 5-6g, and it was only used when its weight was 5% or less of the animal's weight (Sikes et al. 2016). One of the line's end was tied on a fixed point and then the rodent was released at the same point where it was captured.

On the next day, we mapped the rodent trajectory along the released thread. We measured the distance between points of trajectory change with a measure tape and the orientation to the next point with a compass (i.e. azimuth). The depart point of measurement was the burrow where the individual took refuge after releasing. Every time that the rodent entered in a burrow, we assumed (measured) the distance and orientation from that burrow to the nearest where it came out again, we did so, only in cases where the specimen didn't get out again from the same burrow it entered. We were only able to map the thread when the trajectory was above-ground, once it wasn't possible to track the line inside the galleries' tunnels, hence daily home range was estimated mainly from above-ground. The daily home range (DHR) was estimated (once the individuals could move more than the 140 m in one night) as the total area occupied by an individual and determined using the 95% minimum-convex-polygon (MCP) that encompassed all tracked points using CALHOME software (Kie et al. 1996) (see Loretto and Vieira 2005 for more details). In cases in which the animal walked the 140m in more than one day, the DHR (m^2) was only calculated for the day when we tracked more than 35m (Loretto and Vieira 2005). The intensity of habitat use (IU) was defined as the total thread released by the animal (in our case, the sum of the distances between all measure points) divided by the square root of the DHR (area of MCP) (Loretto and Vieira 2005). Individuals' moving patterns with repetitively short straight-line distances usually use smaller areas, thus presenting greater IU, than those with repetitively large straight-line distances.

Food resource: The food resource chosen was the palm *Allagoptera campestris* once we supposed that its fruits and seeds are *Clyomys laticeps*' main resource, based on the palm's high abundance in the area and the previous knowledge of *C. laticeps'* feeding on the palm's fruits and seeds (pers. observ.). Food availability was evaluated along five transects of 300 m, with a width of 4 m, equidistant 100 m. The estimates of food availability were carried out every two months (i.e. April, June, August and October 2016) since we assumed that the evaluated food didn't change greatly between months. We counted the number of *Allagoptera campestris'* infrutescences (Mart.) Kuntze available along each transect in each month of sampling. For resource availability, we counted the number of green fruits (which they already consume) from 150 infrutescences along the transects, and calculated the mean number of fruits per infrutescences in each month of sampling. The period between April and June was classified as the period with low fruit availability (<3,000), whereas the period between August and October was categorized as the period with high (>9,000) available fruits.

Statistical analysis: Based on the assumption that there is sexual size dimorphism in rodents and that body mass affects home range size (Schmidt et al. 2002), we first compared body mass between males and females using a Mann-Whitney non-parametric test due to data distribution. Individuals captured along the study that had more than 200g

(12 females and 10 males) were considered as adults, based on the body mass of captured pregnant females (mean = 216g) and body mass variation (Fig. 1a). Then, to test the difference between male and female daily home range (DHR) size we carried out an ANCOVA, using body mass as a covariate, DHR size as the response variable and sex as the predictor variable. We applied a similar test using intensity of habitat use (IU) as the response variable that was square-root transformed. For this last analysis, we excluded two outliers (one female and one male) to avoid violating ANCOVA assumptions. To test the positive association between DHR size and body mass of *C. laticeps* we ran a linear regression between the variables, using body mass as the independent variable and DHR size as the dependent variable.

And finally, to test the negative relationship between food availability and DHR size, we performed a Mann–Whitney rank-sum tests comparing DHR size between periods of low and high abundance of food. Here, we didn't consider the home range data from January, February and July, since the resource availability study was only made in April, June, August and October. Since some males and females were recaptured more than once, we were able to organize our data so that similar number of different females and males were similar between the two periods of food availability (e.g. data of the individual which was captured in both periods was only considered from the period where we consider it as a sample unit), so that the sex effect over home range couldn't affect the results ('low' period = three males and three females; 'high' period = three males and four females). Pregnant females were also considered in our analyses, since we noticed that pregnant and non-pregnant females could have the same body mass, thus making it difficult to identify them in the field. All analyses were performed with the software SYSTAT 10.2 assuming 95% confidence interval, and since some individuals were captured more than one time, for them, we considered the mean of their data for our study results. We did the same analysis assuming just the first individuals' data registered – simulating only one capture per individual - and the same results were found, except for the test where we evaluated the sexual body mass dimorphism. Even so, we assumed the mean data for this test, because we believe that the females captured in January and February were pregnant (Fig. 1a), and we believe that assuming the mean values would be more accurate.

RESULTS

Total trapping effort was 3,690 trap-nights, resulting in 31 captured individuals (19 females and 12 males) from 15 different active burrow systems. Nine individuals were caught more than once in different sampling months (6 females and 3 males). We captured a single individual in four burrow systems, including one with a single adult male, one with a single adult female and 2 with juvenile females (>100 g). On the other hand, we captured more than one individual in 11 burrow systems. Among these, adult males and females were captured in the same burrow system (n = 7), and in some of them, with other adults (n = 3, in two of them, one more male and in the remaining, another female) and juveniles (n = 4, in three, one more female and in the remaining, another male). We also captured adults of the same sex in a burrow system (n = 2), and one male and one female with female pups (<100 g) in the same burrow (n = 2). All individuals captured in the same gallery were caught in different days, except for one case in which we captured an adult female and male in the same night of capture.

We registered females with larger body mass (more than 300g) between January and February, suggesting pregnancy. Interestingly, the same females lost weight from March on (Fig. 1a). Pregnant females were recorded in April (2 females with 250 g), July (278 g) and October (287 g), after necropsy of 10 individuals that were found dead in the traps. In April, one of the females had a neonate with 24g (with eyes and ears formed, the body almost furred, and upper and lower incisors erupted), while the other one had a tiny, unformed embryo, probably in the initial phase of gestation, similar to the one we found in October (< 2 g). In July, we observed a two grams' embryo, which we could already recognize the body parts. Moreover, two pups from two different galleries (52 and 61 g respectively) were captured in March and June, supporting the evidence of female reproduction in this period.

From the total of individuals captured, we were able to track 10 females and seven males which were used in our analysis. Our data indicated the occurrence of sexual size dimorphism, with males 10% heavier than the females ($\bar{x}$ = 296.63g and $\bar{x}$ = 269.12g respectively) ($U = 30$, $n_1 = 12$, $n_2 = 10$, $P = 0.04$) (Fig. 1b). Mean DHR size of *C. laticeps* was 628m^2 ($SD = 341$), with males ($\bar{x}$ = 748.1m^2) presenting larger DHR than females ($\bar{x}$ = 199.8m^2) (ANCOVA: $F_{1,14} = 2.82$, $P = 0.01$) (Fig. 2a), thus refuting our first hypothesis. In contrast, females had a greater IU than males ($\bar{x}$ = 6.58 and $\bar{x}$ = 4.14, respectively) (ANCOVA: $F_{1,12} = 4.382$, $P = 0.02$) (Fig. 2b). In fact, recaptured females were always captured in the same burrow system, indicating site fidelity. On the other hand, males were usually trapped in different burrow systems at each month (except for two males). Moreover, spool-and-line tracking also revealed males visiting more than one burrow system, which was unusual among females (except for one female).

As expected by our second hypothesis, DHR size increased significantly with an increase in *C. laticeps* body mass (Fig. 3; regression: $R^2 = 0.45$, $F_{1,15} = 12.38$, $P = 0.003$). Hence, larger individuals (mean body mass = 296.67g) moved through larger areas than smaller individuals (mean body mass = 193g). Finally. We failed to support the habitat-productivity hypothesis in *C. laticeps*; actually DHR size didn't differ between periods of low and high abundance of palms ($U = 9$, $n_1 = 7$, $n_2 = 6$, $P = 0.086$).

DISCUSSION

Among subterranean rodents, usually solitary species present males with larger home range sizes than females, whereas social species present similar home range sizes between sexes (Lacey et al. 1998; Bennett et al. 2000; Lacey 2000; Turrini et al. 2008). Although *Clyomys laticeps* is considered social (Burda et al. 2000) or colonial (Bezerra et al. 2016), in our study males presented larger DHR size than females. This difference may be explained by the sexual size dimorphism in this species (Fig. 3). Once males presented larger body mass than females in *C. laticeps*, it is expected that male greater energy demands would result in larger movements by this sex (Nevo 1999), as already demonstrated in *Ctenomys talarum* (Cutrera et al. 2006) and other mammal species (Mcloughlin and Ferguson 2000; Scantlebury et al. 2006). In fact, our study indicated a positive relationship between DHR and body mass of individuals, although we believe that this relationship is an artifact of the role of sexual size dimorphism on movements of each sex. Schmidt et al. (2002) also found an influence of body mass on daily movement patterns of *Dicrostonyx groenlandicus*, which was associated to intersexual differences in body mass in this species.

Mating systems may also play a role on the observed difference between male and female movements in *C. laticeps*. Usually, male spatial organization in mammals is determined by female distribution, since their reproductive success depends on the number of copulations they obtain (Emlen and Oring 1977; Ostfeld 1990). On the other hand, female movements are tuned by food and nest availability (Ostfeld 1990). In our study system, not only males presented larger DHR than females but we observed that males visited more than one burrow system during spool-and-line tracking (including systems separated by 100 meters) and were seldom recaptured at the same system

(14.3%), whereas females were always recaptured at the same burrow system, remaining close to their burrows while foraging. These results provide evidence of a promiscuous/polygynous mating system in *C. laticeps*, in which larger male movements may be a result of their attempts to copulate with a great number of females, as already demonstrated in other rodent species (Bond and Wolff 1999; Harris and Leitner 2004; Cooper and Randall 2007) and proposed by Adler (2011) as an appropriate strategy for mate searching in echimyid species with polygynous mating systems.

Moreover, females presented higher IU when compared to males, indicating site fidelity by the former sex. Such behavior may be reinforced by the presence of offspring in the nest (Wolff and Peterson 1998). Although little is known about breeding season in *C. laticeps*, our results point out to a non-seasonal breeding season, with births occurring throughout the year, as already discussed in previous studies (Bishop 1974; Vieira 1997). Both larger males movements and higher IU by females were already found in solitary subterranean rodents, such as *Ctenomys talarum* (Cutrera et al. 2006) and *Spermophilus mohavensis* (Harris and Leitner 2004), respectively. On the other hand, social species usually present similar home range size between sexes (Lacey 2000) and site fidelity in both sexes (Boellstorff and Owings 1995; Santos 2004; Taraborelli 2006; Ebensperger et al. 2009). Hence, our results refute our original hypothesis that in a colonial or social organization, movement is not different between sexes, so casting a doubt on the previously idea that *C. laticeps* presents colonial or even social behavior.

Previous studies have already demonstrated that an increase in habitat productivity usually leads to reduced home range size (Harestad and Bunnel 1979), although we failed to find this relationship in our study site. DHR of *C. laticeps* was not affected by the availability of *Allagoptera campestris* fruits, as for example the availability of *Astrocaryum standleyanum* influences home range size of agoutis (Emsens et al. 2013).

Diet of most subterranean rodents is based on a mixture of plant items, like roots, tubers, bulbs, starks and leaves (Busch et al. 2000). Little is known about the diet of *C. laticeps*, although we have evidence that they eat seeds of other species and grasses. Most species. species that spend time above-ground for food gathering, as some *Ctenomys* species, *Spalacopus cyanus, Dipodomys ingens* and *Octodon degus* (Braun 1985; Busch et al. 2000; Ebensperger and Hurtado 2005) tend to forage more on aerial plant parts, although food items vary in proportion according to dietary preferences, species foraging behavior and seasonal availability (Busch et al. 2000). Hence, it is possible that C. *laticeps* include fruits from other species and other plant parts during the period of low availability of *A. campestris* fruits, or meet most of their energy requirements eating hoarded seeds, a behavior already demonstrated for this species (Almeida and Galetti 2007). At the same time, the absence of a negative relationship between individual daily home range size and food availability may be explained by the continuous reproductive activity of females in the population studied. Such non-seasonal reproduction may favor reduced movements by females, to ensure maternal care and pup protection, and greater movement by males to provide greater access to reproductive females (Bond & Wolff 1999). Future studies on diet and possible food switching by this species may clarify the lack of relationship between fruit availability and use of space.

Little is known about the social organization of subterranean echimyid rodents, although anectodal information suggests *C. laticeps* presents a colonial and a social system (Burda et al. 2000; Bezerra et al. 2016). Arantes (2011), studying a *C. laticeps* population in São Paulo, demonstrated that the genetic structure of the population resembles a solitary species, in spite of aggregation of burrows, which only indicates a gregarious habit that could be related to resource distribution or soil characteristics (Ebensperger 1998). Our results regarding space use patterns support Arantes' (2011) suggestion of a solitary social system in *C. laticeps*, once larger male movements when compared to females are common among solitary subterranean rodents (Lacey 2000). This difference in home range sizes between sexes is also an indicative of a promiscuous/ polygynous mating system, which is further supported by the observed site fidelity in females and the observation that males visit several burrows, probably to increase their mating opportunities (Bond and Wolff 1999). However, considering the entire study periods, we captured more than one individual in a few subterranean systems, including pairs of adults or adults plus juveniles or pups, indicating burrow sharing not restricted to the mother-offspring relationship. According to Lacey (2000), sociality depends on burrow sharing and spatial overlap between adults. Although burrow sharing between adult *C. laticeps* suggests possible social interactions between individuals, it is unclear if male and female simultaneous use of a burrow system is restricted to mating interactions. Moreover, our methods fail to evaluate if individuals overlap their home ranges, as occur in social species, or if they use discrete portions of their burrow systems, thus avoiding their conspecifics as in solitary species (Lacey 2000). Hence, we can only infer about *C. laticeps* mating system, which could occur in spite of social or solitary habits (Shier and Randall 2004; Adler 2011). In this way, future studies with radiotracking are needed to clarify *C. laticeps* social system.

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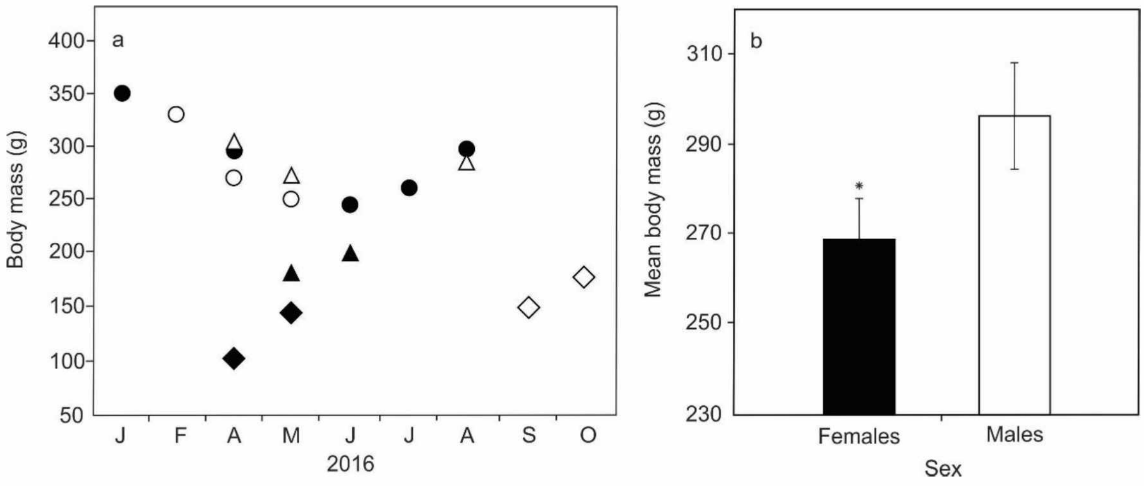

Fig. 1. a) Variation in body mass (g) of recaptured young (<200g) and adult (>200g) *Clyomys laticeps* females (each symbol type represents a different female, n = 6) from x to y at Parque Estadual da Serra de Caldas Novas (GO - Brazil). **b)** Mean (± standard error) body mass of *Clyomys laticeps* females (n = 12) and males (n = 10) with more than >200g captured from January to October 2016 at Parque Estadual da Serra de Caldas Novas (GO - Brazil). Asterisk (*) denote statistical differences between sexes for the same body mass estimation method ($P < 0.05$).

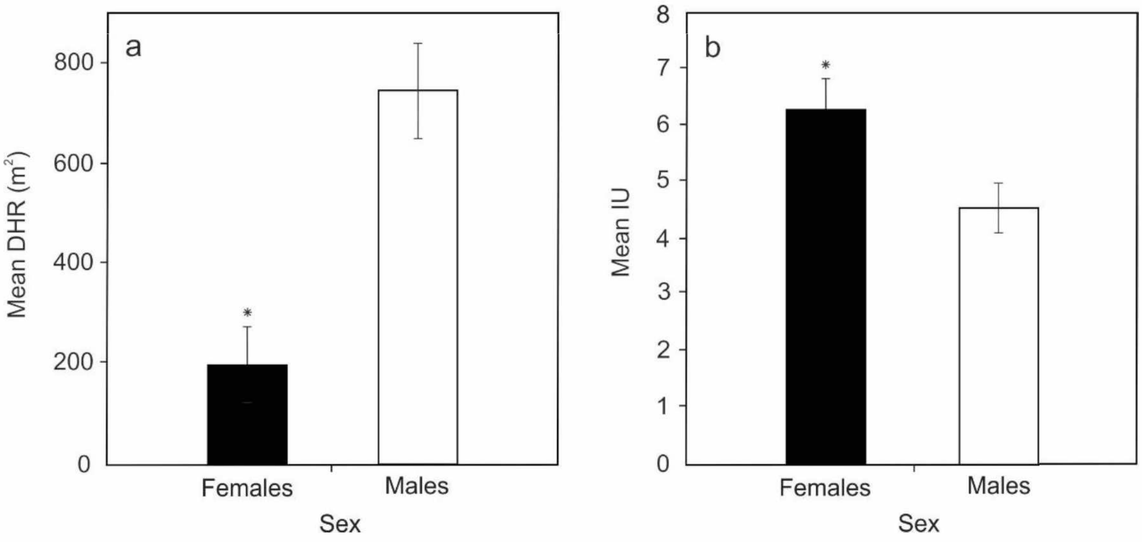

Fig. 2. a) Mean (± standard error) daily home range size of *Clyomys laticeps* females' (n = 10) and males' (n = 7) and **b)** mean (± standard error) intensity of habitat use of *C. laticeps* females' (n = 9) and males' (n = 6) at Parque Estadual da Serra de Caldas Novas (GO - Brazil) from January to October 2016. Asterisks (*) denote statistical differences between sexes for the same DHR and IU estimation method ($P < 0.05$).

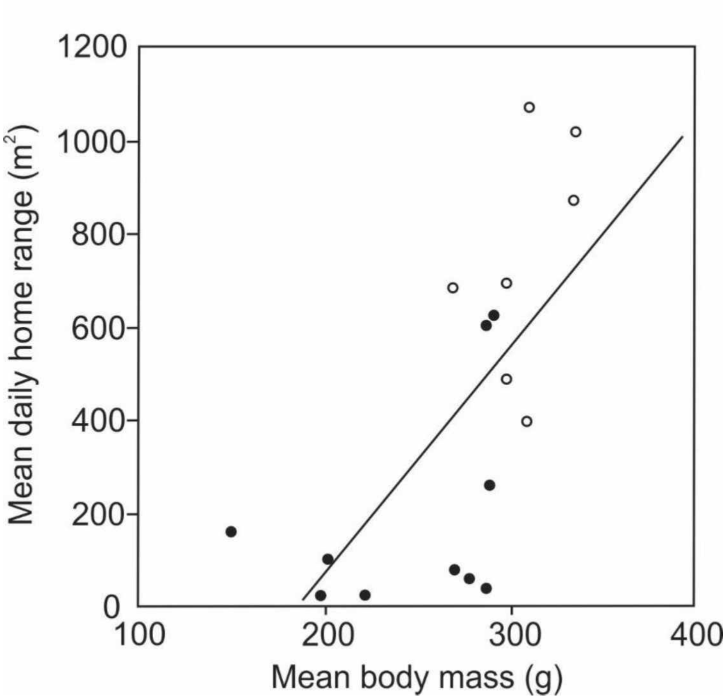

Fig. 3. Relationship between mean daily home range size (m^2) and mean body mass (g) of *Clyomys laticeps* individuals captured between x and y at Parque Estadual da Serra de Caldas Novas (GO - Brazil). Open symbols identify males and black symbols females ($P < 0.05$).

DISCUSSÃO GERAL E CONCLUSÕES

Quando, onde e como um organismo gasta o seu tempo e energia em suas atividades são decisões que afetam a sobrevivência e o sucesso reprodutivo do animal (Halle 2000). De maneira geral, a temperatura tende a ser um dos principais fatores influenciando o período de atividade de animais endotérmicos (Halle 2000; Bennie et al. 2014), em função dos altos custos de termorregulação em condições de estresse térmico (Tracy 1977). Em roedores semi-fossoriais e/ou subterrâneos, o padrão de atividade é caracterizado pelo conjunto de atividades realizadas tanto no ecótopo subterrâneo quanto no da superfície (Kinlaw 1999). Nessas espécies, a atividade acima do solo é determinada pela flutuação da temperatura (Benedix 1994; Halle 2000; Rezende et al. 2003), especialmente em espécie que vivem em ambientes com temperaturas extremas (Lagos et al. 1995; Bacigalupe et al. 2003; Vivanco et al. 2010), dado que atividades realizadas em condições de estresse costumam apresentar menor desempenho (Torres-Contreras & Bozinovic 1997; Peinke & Brown 2003; Long et al 2005).

Clyomys laticeps restringiu sua atividade acima do solo, que esteve associada principalmente ao comportamento de forrageio, à faixa de temperatura entre 10°C e 25°C, com maior frequência de atividade entre 19-21°C. Dessa maneira, a atividade foi mais frequente no período noturno e ao amanhecer, mesmo sendo a maioria dos seus potenciais predadores também ativos nesse período (ver Tabela 1 do capítulo1; Tôrres 2004; Lemos et al. 2011). Os riscos de predação podem ser minimizados através de estratégias como, redução de tempo ativo acima do solo (Larimer et al. 2010), escolha das noites mais escuras (Brown & Peinke 2007) e uso das tocas como refúgio (Kinlaw 1999). Estudos abordando a relação entre os efeitos limitantes da temperatura e do risco de predação sobre horário de atividade em roedores subterrâneos são escassos, de maneira que pesquisas nessa direção deveriam ser realizadas em *C. laticeps*. De qualquer forma, os resultados não excluem a possibilidade de atividade diurna pelo *C. laticeps* dentro das galerias, uma vez que as temperaturas ao longo dos túneis subterrâneos variam pouco em relação as do ambiente e diminuem com a profundidade em que estes estão localizados (Burda et al. 2007; Lamberto 2015). Ao mesmo tempo, os dados indicam que os custos associados ao estresse térmico são cruciais para a escolha do período de atividade, e que os benefícios associados a essa escolha aparentemente compensam os custos de risco de predação no período noturno, que pode ser diminuído através de outras estratégias de escape de predadores.

Os indivíduos vivem em conflitos de demandas de forma que precisam alocar tempo e energia a fim de conseguir cumprir as suas atividades. Dentro do tempo restringido pela temperatura, os indivíduos de *Clyomys laticeps* podem apresentar sua melhor performance nas suas funções acima do solo (Brown et al. 1993). As decisões associadas ao uso do espaço por *C. laticeps* parecem refletir diferenças comportamentais e fisiológicas entre os sexos, além do próprio sistema de acasalamento e comportamento social da espécie. A maior vagilidade dos machos de *C. laticeps* parece ser explicada pela existência de dimorfismo sexual de tamanho e por um sistema de acasalamento promíscuo/poligínico (Emlen & Oring 1977; Cutrera et al. 2006; Scantlebury et al. 2006), em que a maior mobilidade dos machos é decorrente de uma estratégia para copular com um número maior de fêmeas (Emlen & Oring 1977). Esse mesmo padrão já foi observado em diferentes espécies de roedores subterrâneos solitários (Bennett et al. 2000; Busch et al. 2000; Lacey 2000; Cutrera et al. 2006). Juntamente com o comportamento de dispersão dos machos, a maior fidelidade das fêmeas às galerias subterrâneas dá suporte à ocorrência de um sistema de acasalamento poligínico em *C. laticeps*. Geralmente, em reproduções sazonais, o padrão de dispersão intersexual varia ao longo do ano (Cooper & Randall 2007), porém quando este padrão se mantém, é uma evidência de uma atividade reprodutiva não-sazonal, o que é indicado em *C. laticeps* pelos registros de fêmeas grávidas na população (ver capítulo 2).

Diferente do esperado, a abundância de recursos não influenciou o uso do espaço de indivíduos de *C. laticeps*. Em geral, o movimento das fêmeas de roedores é determinado pela abundância e distribuição de recursos alimentares, enquanto o movimento dos machos é diretamente afetado pela distribuição das fêmeas (Emlen & Oring 1977; Ostfeld 1985). No sistema estudado, a ausência dessa relação pode ser explicada pela atividade reprodutiva contínua dos indivíduos, de maneira que as fêmeas devem manter áreas de vida restritas a proximidade das galerias para cuidar de sua prole, enquanto os machos usam o espaço na tentativa de garantir o acesso ao maior número de fêmeas (Bond & Wolff 1999). Ao mesmo tempo, é possível que a ausência da relação entre abundância de frutos de *Allagoptera campestris* e o tamanho da área de vida diária de *C. laticeps* esteja associada a inclusão de outros itens alimentares na dieta desse roedor em períodos de baixa disponibilidade dos frutos dessa palmeira. Por exemplo, o roedor *Microtus oeconomus* apresentou mudança sazonal de dieta e seletividade conforme a variação de oferta de plantas (Soininen et al. 2013). Mudanças sazonais em função da oferta de alimento nos roedores herbívoros têm sido reportadas em outros estudos (Puig et al. 1999; Harris & Leitner 2004; Quirici et al 2010).

Pouco é sabido sobre a história natural de roedores subterrâneos equimídeos, especialmente no que diz respeito a socialidade, com exceção da espécie *Trinomys yonenagae* (Santos 2004; Santos & Lacey 2011). Informações anedóticas têm sugerido que *Clyomys laticeps* apresenta um sistema colonial e social (Burda et al. 2000; Bezerra et al. 2016). Junto com os dados genéticos de Arantes (2011), nossos resultados sobre o padrão do uso do espaço sugerem um comportamento solitário nesta espécie. No nosso estudo, os machos apresentaram maior movimento diário quando comparados com as fêmeas; um resultado comumente encontrado em espécies de roedores subterrâneos solitários (Lacey 2000). De acordo com Lacey (2000), a socialidade depende do compartilhamento de galerias e sobreposição espacial entre os adultos. Em espécies solitárias, geralmente cada indivíduo usa porções discretas das galerias subterrâneas, sem sobreposição da área de vida, enquanto em espécies sociais o grau de sobreposição das galerias é alto (Lacey 2000). Embora tenha havido compartilhamento de galerias entre adultos de *C. laticeps*, sugerindo interações sociais, ainda permanece a dúvida se esse comportamento está restrito a interações reprodutivas. Além disso, nossos métodos não permitiram avaliar o grau de sobreposição entre os indivíduos.

Tendo em vista os resultados do presente estudo, foi possível entender comportamentos de *Clyomys laticeps* relacionados às dimensões temporal e espacial do seu nicho sob as condições ambientais em que vive. Observamos que a temperatura limita o tempo para *C. laticeps* executar as suas atividades diárias como procura por alimento e parceiros de forma a evitar altos custos da termorregulação. Machos e fêmeas apresentaram movimentos diários e intensidade do uso de habitat distintos, o que parece refletir o uso de diferentes estratégias de otimização do sucesso reprodutivo, como procura por parceiros e cuidado com a prole, respectivamente. Apesar de avançar no entendimento da ecologia da espécie, os métodos utilizados não permitiram entender a organização e comportamento social de *C. laticeps*. Os dados obtidos sobre período de atividade e uso do espaço estão diretamente relacionados com a socialidade de roedores subterrâneos (Ebensperger 1998; Lacey 2000; Ebensperger & Blumstein 2006), porém a relação entre essas variáveis não ficou clara no nosso estudo. Dessa forma, sugerimos estudos futuros com uso de equipamentos de radiotelemetria, que permitirão avaliar a sobreposição das áreas de vida e atividade dentro e fora das galerias, facilitando o entendimento da relação entre a estrutura social de *C. laticeps* em função de sua história natural e de características do ambiente.

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