



UNIVERSIDADE FEDERAL DE UBERLÂNDIA
INSTITUTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA, CONSERVAÇÃO E BIODIVERSIDADE



**HISTÓRIA DE VIDA E COMPORTAMENTO SOCIAL DO
RATO-DE-ESPINHO SEMI-FOSSORIAL *Clyomys laticeps*
(Thomas, 1909) (Rodentia: Echimyidae)**

CLAIRE PAULINE RÖPKE FERRANDO

2022

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Tese apresentada à Universidade Federal de Uberlândia
como parte das exigências para obtenção do título de doutor
em Ecologia, Conservação e Biodiversidade.

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Prof.^a Dr.^a. Natália Oliveira Leiner

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UBERLÂNDIA

Agosto - 2022

Ficha Catalográfica Online do Sistema de Bibliotecas da UFU
com dados informados pelo(a) próprio(a) autor(a).

F372 Ferrando, Claire Pauline Röpke, 1987-
2022 História de vida e comportamento social do roedor
semi-fossorial *Clyomys laticeps* (Thomas, 1909)
(Rodentia: Echimyidae) [recurso eletrônico] : História
de vida e comportamento social do roedor *Clyomys*
laticeps / Claire Pauline Röpke Ferrando. - 2022.

Orientadora: Natália Oliveira Leiner.

Coorientadora: Eileen Anne Lacey .

Tese (Doutorado) - Universidade Federal de Uberlândia,
Pós-graduação em Ecologia, Conservação e Biodiversidade.

Modo de acesso: Internet.

Disponível em: <http://doi.org/10.14393/ufu.te.2022.359>

Inclui bibliografia.

Inclui ilustrações.

1. Ecologia. I. Leiner, Natália Oliveira ,1979-,
(Orient.). II. , Eileen Anne Lacey,1961-, (Coorient.).
III. Universidade Federal de Uberlândia. Pós-graduação
em Ecologia, Conservação e Biodiversidade. IV. Título.

CDU: 574

Bibliotecários responsáveis pela estrutura de acordo com o AACR2:

Gizele Cristine Nunes do Couto - CRB6/2091

Nelson Marcos Ferreira - CRB6/3074



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ATA DE DEFESA - PÓS-GRADUAÇÃO

Programa de Pós-Graduação em:	Ecologia, Conservação e Biodiversidade				
Defesa de:	Tese, número 78, PPGECEB				
Data:	vinte e cinco de agosto de dois mil e vinte e dois	Hora de início:	14:00	Hora de encerramento:	17:30
Matrícula do Discente:	11813ECR003				
Nome do Discente:	Claire Pauline Röpke Ferrando				
Título do Trabalho:	História de vida e comportamento social do rato-de-espinho semi-fossorial <i>Clyomys laticeps</i> (Thomas, 1909) (Rodentia: Echimyidae)				
Área de concentração:	Ecologia				
Linha de pesquisa:	Ecologia de comunidades e ecossistemas				
Projeto de Pesquisa de vinculação:	Padrões de biodiversidade e processos ecológicos em ecossistemas de Cerrado na região do Triângulo Mineiro e Sudeste de Goiás (sub-bacia do Rio Paranaíba)				

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Iniciando os trabalhos o(a) presidente da mesa, Dr(a). Natalia Oliveira Leiner, apresentou a Comissão Examinadora e o(a) candidato(a), agradeceu a presença do público, e concedeu ao(à) discente a palavra para a exposição do seu trabalho. A duração da apresentação do(a) discente e o tempo de arguição e resposta foram conforme as normas do Programa.

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Claire Pauline Röpke Ferrando

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UBERLÂNDIA
2022



Ilustradora Claire Wickiestaubie

Clyomys laticeps (Thomas, 1909) no Cerrado.

“Assim como dediquei a minha dissertação, dedico a minha tese ao *Clyomys laticeps* espécie que tive o privilégio de estudar. Por meio dela pude me aprimorar como cientista e admirar ainda mais os seres vivos com os quais compartilhamos esse planeta. Espero muito que este estudo possa beneficiá-la em algum momento da história...”.

AGRADECIMENTOS

“Obrigada a todos os seres que cruzaram o meu caminho e tornaram o doutorado um presente da vida para mim”

Uma das coisas mais importantes para a formação de um cientista é ter a confiança de pessoas com maior experiência e ter a liberdade para desenvolver suas próprias opiniões e poder defendê-las. Obrigada orientadora Natália Oliveira Leiner por ter me proporcionado isso durante os 8 anos que trabalhamos juntas! Foi um privilégio, e o continuará sendo, poder trabalhar com você! Obrigada pela tua confiança em mim e pelo apoio que sempre me deste.

Em um dos primeiros emails que a minha co-orientadora Eileen Anne Lacey me mandou ela me escreveu; “Claire, I have confidence in you and your abilities!”. Acredito que ela não se lembre disso, mas essas palavras chegaram a mim como um carinho humano que ela teve por mim durante toda a trajetória do doutorado. Mesmo distante fisicamente, Eileen sempre esteve presente, contribuindo para a nossa pesquisa com a sua visão “mais ampla da coisa”.

Se pudesse inserir mais um co-orientador, com certeza incluiria a supervisora do meu período de doutorado sanduíche em Montevideu (Uruguai), Ivanna Haydée Tomasco. Ela me mostrou o mundo da genética de forma leve e prazerosa por meio do seu amor pela pesquisa, seu carinho, alegria e jeito simples de ser! Ivanna me mostrou que podemos ser ótimos cientistas sem deixar de ser quem somos!

Agradeço imensamente à família do José Neto por ter me acolhido na sua casa em Marzagão (GO) para desenvolver meus primeiros campos do doutorado no PESCaN, enquanto o alojamento do parque estava em reforma. Uma família de grande coração acolhedor que jamais esquecerei! Obs: como era bom acordar 4h da manhã com uma mesa posta e uma térmica de café pronta para levar a campo e ser recebida com um bom almoço ou janta na volta para descansar.

Eu tenho a sorte ENORME de ter uma família que me apoia nas minhas aventuras e desventuras da vida! Tenho certeza de que o prazer com que desenvolvi o meu doutorado foi por saber que eu receberia palavras de apoio dela em qualquer dificuldade que pudesse encontrar na jornada. Além da família humana, também agradeço a minha família canina, principalmente Margarida e Stopa, os quais adotei durante o doutorado e me ajudam a superar os momentos de solidão e vivenciam os momentos alegres da vida comigo.

Agradeço muito ao meu amigo Guilherme Lima Righetto, que foi meu conselheiro acadêmico desde a graduação, por me mostrar os nortes da minha jornada cheia de lindas curvas.

O doutorado é um grande exemplo de que não caminhamos sozinhos na jornada da vida. Tive inúmeras pessoas que me ajudaram ao longo de todo o doutorado e já peço desculpas se esqueci de agradecer alguém.

Sabe, aquelas pessoas que tocam tudo e tornam a tua vida mais leve e alegre mesmo nos momentos de maior perrengue? Aqui tenho que citar a Camila Provásio e a Drielly Queiroga que me acompanharam nas noites cansativas de telemetria e de capturas. Sintam-se muito abraçadas por mim e saibam que parte desse doutorado é de vocês também! Obrigada por nunca terem me desanimado nos campos e fazerem parte da minha vida.

Marco Oliveira e Rodrigo Rossi, os homens do meu doc, hehehe. Também foram fundamentais para a realização dos meus campos do projeto, passando noites em claro no platô. Obrigada por, além da ajuda, terem cruzado o meu caminho e me dado a oportunidade de ser mais tolerante e respeitar as diferenças e o silêncio do próximo.

Um abraço de agradecimento também aos demais corajosos que se aventuraram no campo comigo: Ellen M. R. Ferrando, Fábio S. de Melo, Fernanda Rodrigues, Vitória Buzatto, Phabliny M. S. Bomfim e também aos que se aventuraram a emprestar o seu carro particular para realizar os meus campos, meus pais Marcel Ferrando e Ursula O. Röpke, (sorry pelas sequelas no carro...).

Ah Julia Oshima! O que seria de mim sem você? Essa pessoa incrível que dedicou horas para me ensinar o novo método de estimativa de área de vida, AKDE, do qual nunca tinha ouvido falar. Junto com ela, tive o apoio dos integrantes do Laboratório de Ecologia Espacial e Conservação (LEEC - Unesp, Rio Claro), que sempre esclareceram as minhas dúvidas e até mesmo construíram scripts para mim! Muito obrigada pelo suporte que me deram!

Ao longo do meu doutorado eu fui adotada por vários laboratórios, um deles foi o Laboratório de Ixodologia (Labix - UFU) que me auxiliou desde o empréstimo de armadilhas de captura até o uso da BOD para criação de mosca de berne, hahaha. Obrigada a todos e todas por tudo e pelas conversas e cafezinhos!

O meu maior desafio do projeto de doutorado era a realização do estudo genético que implica em alto custo financeiro. Graças a todos os apoiadores do financiamento coletivo “O preço da genética”, consegui arrecadar os 12 mil reais necessários para realizar o estudo e avançar no conhecimento sobre o *Clyomys laticeps*. Um apoio fundamental para o sucesso da campanha foi do @ateliê_diverso que doou obras temáticas lindas com *C. laticeps* para os sorteios mensais entre os apoiadores.

Outro laboratório que me adotou foi o Grupo de Ecologia Comportamental e Molecular (GRECOM - UFABC) onde passei a participar das discussões de artigos e aprender um monte com as trocas de conhecimento entre os membros. Não posso deixar de fazer um agradecimento especial para dois dos membros desse lab, a Gabriela Schmaedecke que me auxiliou nas análises genéticas e a professora Cibele Biondo por ter esclarecido dúvidas em relação aos programas de análise. Muito muito obrigada, sem vocês essa parte do estudo teria sido muito mais difícil para mim, uma vez que eu tinha nenhuma experiência com o assunto.

Meus agradecimentos também ao coordenador do PPG Paulo Eugênio A. M. de Oliveira por todo o apoio que me deu durante esses anos, principalmente no momento mais tenso do doutorado, em que tive que lidar com trâmites burocráticos internacionais.

Obrigada à secretária do PPG, Juliana Pinheiro, por ser uma secretária exemplar e que está sempre pronta para tirar dúvidas e nos lembrar dos nossos direitos e deveres como pós-graduandos.

Obrigada Adriana Suzin por todos esses anos que moramos juntas! Voltar para casa era sempre uma sensação boa, a de voltar ao lar. Foi muito muito bom morar contigo e poder ter certeza de que essa parceria tornou a minha vida de doutoranda muito mais leve!

Obrigada aos membros do Laboratório Ecologia de Mamíferos do qual faço parte, que entraram durante o meu doutorado e estão criando um grupo mais unido de pesquisa. Não tive essa oportunidade no início da minha trajetória de pós-graduanda no Lema, mas estou muito feliz que vocês estão construindo esse grupo! Estarei sempre aí para ajudar no que for preciso!

Obrigada ao professor Beno Wendling pelo empréstimo do equipamento de medição de compactação de solo.

Agradeço à equipe SECIMA por ter permitido a execução do meu projeto de doutorado no Parque Estadual da Serra de Caldas Novas (PESCaN) e aos funcionários do parque, especialmente ao Maurício e Paula Tambellini por terem sido tão receptivos e por estarem fazendo um trabalho lindo para a valorização do parque.

Agradeço à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) e ao Conselho Nacional de Desenvolvimento Científico (CNPq – PELD) pelo suporte financeiro durante os quatro anos e meio de estudo.

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Ferrando, C. P. R. 2022. História de vida e comportamento social do rato-de-espinho semi-fossorial *Clyomys laticeps* (Thomas, 1909) (Rodentia: Echimyidae). Tese de doutorado em Ecologia, Conservação e Biodiversidade. UFU. Uberlândia-MG. 128 p.

RESUMO

Dados de história de vida e comportamento social são escassos para espécies com hábitos crípticos, como os roedores escavadores. As interações sociais e reprodutivas entre os indivíduos podem ser compreendidas por meio dos padrões espaciais, que consistem no conjunto dos movimentos dos indivíduos de uma população. Tais movimentos refletem estratégias individuais para maximizar o sucesso reprodutivo em resposta às condições individuais, populacionais e ambientais. Assim, os padrões espaciais de uma população determinam a estrutura genética da população e sistemas sociais da espécie. Dessa forma, com base em capturas, organização espacial e dados genéticos, nós apresentamos características da história de vida, assim como da organização social e sistema de acasalamento de uma população de vida livre do roedor escavador equimídeo *Clyomys laticeps* no Parque Estadual da Serra de Caldas Novas (GO, Brasil), situado no bioma Cerrado. A população estudada apresentou baixa densidade populacional durante todo o período do estudo, reprodução ao longo do ano todo e ausência de desvio na razão sexual, assim como ausência de dimorfismo sexual em relação à massa corporal. Adultos de *C. laticeps* frequentemente sobrepueram suas áreas de vida entre si, mas a co-ocorrência no tempo e espaço foi rara e restrita a pares de macho-fêmea, um padrão mais consistente com o hábito de vida solitário, em que cada galeria subterrânea é ocupada por um único adulto. Sexo e estação do ano não tiveram efeito sobre a sobreposição espacial das áreas de vida, o que é consistente com a evidência de reprodução não sazonal na espécie. Ainda,

machos sobrepuseram espacialmente à várias fêmeas e vice-versa, sugerindo um sistema de acasalamento em que ambos os sexos copulam com múltiplos parceiros. Por meio de dados de paternidade e maternidade, foi possível confirmar que fêmeas e machos frequentemente acasalaram com mais de um parceiro e compartilharam os parceiros com outros indivíduos do mesmo sexo. A estrutura genética espacial e a alta diversidade genética na população de *C. laticeps* estudada revelou a dispersão natal de ambos os sexos, promovendo baixos níveis de endogamia. Nossos resultados sugerem que a baixa densidade populacional pode favorecer a vida solitária e a dispersão frequente em *C. laticeps*, uma vez que os custos dos indivíduos associados à ocupação de territórios (e.g. competição), escavação (e.g. gasto energético para escavação) e dispersão (e.g. risco de predação) devem ser mínimos. Assim, os resultados obtidos nesse estudo contribuem para a compreensão dos fatores que promovem convergência e divergência na evolução da organização e comportamento social entre roedores equimídeos, assim como entre roedores escavadores.

Palavras-chave: dinâmica populacional, Echimyidae, estrutura genética, organização social, roedor escavador, sistema de acasalamento genético, sistema de acasalamento social.

Ferrando, C. P. R. 2022. Life history and social behavior of the semi-fossorial spiny rat *Clyomys laticeps* (Thomas, 1909) (Rodentia: Echimyidae). Ph.D. thesis. UFU. Uberlândia-MG. 128 p.

ABSTRACT

Life history and social behavior data are lacking for species with elusive habits, as burrowing rodents. Social and reproductive interactions among individuals can be understood through spatial patterns, which consist of the set of movements of the individuals in a population. These movements reflect individual strategies to maximize reproductive success in response to individual, populational and environmental conditions. Therefore, the spatial patterns of a population determine the genetic structure of populations and social system of species. Therefore, based on captures, spatial organization and genetic data, we unravel life history traits, as well as social organization and mating system of the free-living burrowing echimyid rodent, *Clyomys laticeps* at Parque Estadual da Serra de Caldas Novas (GO, Brazil), situated in the Cerrado biome. The population studied presented constant low density throughout the study, breeding activity throughout the year and a lack of biased sex ratio and dimorphism in body mass. *Clyomys laticeps* adults frequently overlapped their home ranges with each other, but co-occurrence in time and space was rare and was limited to male-female pairs, a pattern that is most consistent with a solitary lifestyle in which each adult individual occupies a distinct burrow system. Neither sex nor season of the year affected spatial overlap in the population; this outcome is consistent with evidence suggesting that reproduction in this species occurs throughout the year. Moreover, individual males overlapped spatially with multiple females and vice versa, evidence suggesting a mating system in which both sexes mate with multiple partners. Indeed, through parentage data, it was possible to confirm

that females and males frequently mate with more than one partner and share them with other individuals of the same sex. Moreover, spatial genetic structure and high genetic diversity in the studied *C. laticeps* population revealed that dispersal by both sexes promoted inbreeding avoidance. The low population density may favor the solitary behavior and frequent dispersal in *C. laticeps*, since the individual costs associated to territory occupancy (e.g. competition), burrowing (e.g. energy demand to dig) and dispersal (e.g. predation risk) may be minimum. Collectively, results obtained may contribute to understand the factors that promote convergence and divergence in social evolution between echimyid rodents as well as between burrowing rodents.

Key words: burrowing rodent, Echimyidae, genetic mating system, genetic structure, population dynamic, social organization, social mating system.

INTRODUÇÃO GERAL

Os indivíduos de uma população interagem entre si por meio de diferentes comportamentos (como agonístico, afiliativo, corte, acasalamento, cuidado parental), sendo que o conjunto de comportamentos e a frequência de cada tipo de comportamento entre os indivíduos de uma população formam o comportamento social da espécie (Jasso del Toro & Nekaris 2022). Em cada espécie, os comportamentos evoluem quando os benefícios dos mesmos, em termos de sobrevivência e sucesso reprodutivo (habilidade de passar os genes para a próxima geração; Kosova et al. 2010), ultrapassam os custos para os indivíduos; sendo que essa relação custos/benefícios varia de acordo com fatores intrínsecos (individuais e populacionais) e extrínsecos (bióticos e abióticos) (Blumstein et al. 2010; Ha 2010; McGlynn 2010). Assim, estudos sobre espécies em vida livre são cruciais e complementares aos estudos em cativeiro para entender a diversidade dos comportamentos sociais nos animais (Schradin & Pillay 2003; Blumstein et al. 2010; Alberts 2018). Para tal, o estudo das características associadas à forma de crescimento, sobrevivência e reprodução dos organismos ao longo do tempo, conhecida como história de vida (Bednekoff 2019) forma a base para melhor entender as relações sociais entre indivíduos (McPherson & Chenoweth 2012; Székely et al. 2014; Kroeger et al. 2021). Essas relações são descritas por meio do sistema social, que é estruturado pela organização social (se os animais vivem sozinhos, aos pares ou em grupos), estrutura social (como os indivíduos interagem entre si), sistemas de acasalamento (quem acasala com quem) e cuidado parental (quem cuida dos filhotes) (Kappeler 2019). Em populações animais de vida livre, as interações sociais podem ser estudadas por meio das relações espaciais e genéticas entre os indivíduos, uma vez que os mesmos se movimentam no espaço para suprir as suas demandas de sobrevivência e reprodução (Lacey 2000; Nathan 2008). Assim, sob influência direta e/ou indireta dos fatores intrínsecos e extrínsecos, os

indivíduos otimizam seus movimentos frente às diferentes necessidades, maximizando o seu sucesso reprodutivo e moldando a estrutura genética da população (Holyoak et al. 2008; Nathan 2008; Jeltsch et al. 2013).

Nos mamíferos, os movimentos diferem entre os sexos em função das estratégias de história de vida associadas ao sucesso reprodutivo de cada sexo (Greenwood 1980). Enquanto o sucesso dos machos é geralmente determinado diretamente pelo número de cópulas obtidas, de maneira que seus movimentos estão associados aos movimentos das fêmeas (Greenwood 1980), o sucesso das mesmas depende do número e da sobrevivência dos filhotes produzidos, de forma que os movimentos são frequentemente determinados pela distribuição espacial e temporal de recursos alimentares e sítios de nidificação (Emlen & Oring 1977; Ostfeld 1990). Considerando que os movimentos dos machos estão relacionados com a acessibilidade as fêmeas, a organização espacial (tamanho e sobreposição de áreas de vida) das mesmas, assim como a intensidade da competição por parceiras, pode resultar em territorialidade dos machos como garantia de monopolizar o acesso a fêmeas, moldando assim o sistema de acasalamento social da população. Quando os machos monopolizam e copulam exclusivamente com múltiplas fêmeas, as quais copulam com um único macho, ocorre a poliginia (McEachern et al. 2009), que pode ocorrer tanto em espécies sociais como em espécies solitárias. Esse sistema tende a ser favorecido quando os machos conseguem defender o acesso exclusivo a fêmeas durante a época reprodutiva, por meio do aumento de suas áreas de movimento para sobrepor com várias fêmeas (Ostfeld 1990, 2012; Lin et al. 2009). Já a monogamia, em que um único macho e uma única fêmea copulam exclusivamente durante a estação reprodutiva (McEachern et al. 2009) é mais favorecida em populações solitárias em que machos defendem cada fêmea e seu território e ambos os sexos apresentam menor mobilidade. Por outro lado, o acasalamento de machos e fêmeas com múltiplos parceiros na estação

reprodutiva (promiscuidade e poliginandria, McEachern et al. 2009; Skala & Shackelford 2022) é mais provável em populações sociais, dado que esse sistema dificulta a monopolização de parceiros (tanto pelas fêmeas como pelos machos), aumentando as taxas de sobreposição entre as áreas de vida dos sexos (Ostfeld 1990, 2012; Lin et al. 2009). Porém, a organização espacial nem sempre reflete o sistema de acasalamento genético, uma vez que o mesmo depende dos padrões de paternidade, os quais podem sofrer influência da seleção de parceiros reprodutivos antes ou depois da cópula (Dean et al. 2006; Lin et al. 2009). No entanto, de forma geral, em sistemas de acasalamento em que fêmeas copulam com um único macho (monogamia e poliginia) a prole apresenta paternidade única (Zenuto et al. 1999). Em contraste, em fêmeas que copulam com vários machos espera-se que apresentem uma ninhada com paternidade múltipla (poliandria e poliginandria) (Lin et al. 2009; Hauver et al. 2010).

O grau de competição por parceiros em cada um dos sistemas de acasalamento pode moldar a ocorrência e magnitude de diferenças nas características de machos e fêmeas, que é denominado dimorfismo sexual. Nesse sentido, espera-se que em populações com maior proporção de adultos de um dos sexos (i.e. desvio da razão sexual) haja maior competição por parceiros, especialmente entre indivíduos do sexo mais raro (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996), propiciando maior chance de ocorrência de dimorfismo sexual (McPherson & Chenoweth 2012; Székely et al. 2014). Em função da competição comum entre machos por acesso às fêmeas nos mamíferos, machos tendem a investir mais em crescimento do que as fêmeas (McPherson & Chenoweth 2012). Porém, o dimorfismo sexual de tamanho é raro em espécies com baixa intensidade de competição por parceiros, como é o caso de muitas espécies que não apresentam desvios na razão sexual (Cooper et al. 2011).

Os desvios na razão sexual são o resultado de muitos fatores intrínsecos e extrínsecos (Székely et al. 2014), como a sobrevivência e dispersão diferencial dos machos e fêmeas em populações. Entre os mamíferos, geralmente os machos dispersam ainda jovens (i.e. dispersão natal) enquanto as fêmeas se mantêm fiéis aos locais onde nasceram (filopatria) (Greenwood 1980). Tais comportamentos podem resultar em menor probabilidade de sobrevivência dos machos quando comparado às fêmeas, e gerar um desvio da razão sexual em favor do sexo filopátrico. A dispersão natal é considerada uma estratégia para minimizar a competição local por parceiros e recursos entre os indivíduos aparentados do mesmo sexo, assim como para evitar a reprodução entre indivíduos aparentados (i.e. endogamia) (Greenwood 1980). O balanço entre os custos e as vantagens da dispersão variam de acordo com características do ambiente e da população (Mabry et al. 2013), sendo que em populações com alta densidade ou com alto risco de predação, os custos podem ultrapassar os benefícios, podendo forçar ambos os sexos a serem filopátricos (Solomon 2003; Schradin et al. 2020). Nesse caso, a ausência da dispersão ou dispersão tardia pode moldar a evolução da vida em grupo (Burda et al. 2000).

Entender os padrões de movimentos e organização espacial dos mamíferos é crucial não só para o entendimento da história natural das espécies, mas também devido às suas implicações para a estrutura genética das populações, assim como para os padrões de organização social e sistema de acasalamento. Apesar de um número considerável de estudos nessa direção com pequenos mamíferos, há uma lacuna de conhecimento nessa área com relação aos roedores escavadores, especialmente os neotropicais, devido aos seus hábitos crípticos (Adler 2011; Maher & Burger 2011).

Roedores escavadores

Os roedores escavadores são espécies que constroem túneis e galerias subterrâneas, podendo variar quanto à frequência e uso do subsolo e da superfície para realização de atividades de sobrevivência, desenvolvimento e reprodução (Lacey et al. 2000, Burda et al. 2007). Algumas espécies executam suas atividades exclusivamente no subsolo, raramente indo para a superfície, sendo chamados de subterrâneas (Lacey 2000). Por outro lado, as espécies denominadas semi-fossoriais movimentam-se na superfície para procurar alimento, parceiros, novos habitats e defender territórios, enquanto dentro da galeria copulam, cuidam da prole e se defendem de predadores e se abrigam de temperaturas extremas (Kinlaw 1999).

Esses roedores formam um bom modelo de estudo para avaliar o papel do ambiente sobre os movimentos e suas implicações sobre o sistema social e estrutura genética das populações, uma vez que apresentam uma variedade de organizações sociais e sistemas de acasalamentos, os quais variam intra e inter-especificamente em resposta aos diferentes fatores ambientais (predação, recursos alimentares, atributos do solo) e densidades populacionais (Burda et al. 2000; Ebensperger & Blumstein 2006). Esse grupo abrange desde espécies solitárias a eussociais, incluindo sistemas intermediários como colonial, social, comunal e familiar (Burda et al. 2000). As organizações sociais são classificadas ao longo de um *continuum* que envolve o grau de sobreposição espacial entre os indivíduos adultos, o compartilhamento, ou não de galerias e a ocorrência e duração do comportamento cooperativo na galeria, além do sistema de acasalamento (Burda et al. 2000; Lacey 2000). Os indivíduos adultos de populações solitárias e coloniais vivem de forma solitária, em que cada um vive na sua própria galeria, porém os coloniais constroem suas galerias bem próximas umas das outras (Burda et al. 2000). Já em populações comunais, os adultos vivem em grupos, compartilhando a galeria entre si

e podendo cooperar entre si no cuidado com a prole (Burda et al. 2000). Nos sistemas familiar e eussocial, somente uma fêmea no grupo é reprodutiva e os demais indivíduos cooperam nas atividades do grupo (Burda et al. 2000; Lacey 2000). O sistema familiar resulta da dispersão tardia da prole e o eussocial da ausência dessa dispersão (Burda et al. 2000).

Assim, em decorrência da variedade de organizações sociais, os roedores escavadores apresentam diferentes sistemas de acasalamento; poliginia, monogamia e poliginandria (Bennett et al. 2000; Lacey et al. 2000). A poliginia é frequentemente reportada entre os roedores escavadores, e nesse tipo de sistema de acasalamento, geralmente os machos tendem a dispersar, evitando a competição por parceiros, enquanto as fêmeas permanecem na galeria natal ou nas proximidades da mesma (Byrom & Krebs 1999; Bennett et al. 2000; Cutrera 2005). Assim, há uma estrutura de parentesco maior entre as fêmeas nessas populações, isto é, as fêmeas são mais aparentadas entre si do que os machos (Cutrera 2005). A dispersão dos machos à procura de parceiras e de territórios vagos incorre em maior exposição aos predadores (Byrom & Krebs 1999; Busch et al. 2000), especialmente em roedores semi-fossorais que exercem tais atividades na superfície. Além disso, também há um aumento das interações agonísticas em função da competição por parceiras (Byrom & Krebs 1999; Busch et al. 2000). Tais comportamentos tendem a elevar as taxas de mortalidade dos machos, gerando uma razão sexual desviada para fêmeas em algumas espécies escavadoras solitárias (Busch et al. 2000). Porém, populações com razão sexual balanceada também ocorrem nesse grupo (Malizia 1998; Sumner et al. 2003; Santos 2010) enquanto o desvio para machos é raro (Busch et al. 2000).

Estudos envolvendo informações sobre o uso do espaço e genética podem auxiliar no entendimento dos fatores que regem os sistemas sociais (como a evolução da

socialidade, o sistema de acasalamento e os padrões de dispersão) e sua flexibilidade (Adler 2011). Dessa forma, espécies de grupos taxonômicos que apresentam alta diversidade morfológica e distribuição em vários tipos de ambientes funcionam como um bom modelo de estudo nesse sentido (Adler 2011). Um exemplo são roedores da família Echimyidae, uma vez que a família apresenta maior riqueza de espécies entre os roedores Caviomorpha, sendo representada por 90 espécies distribuídas em 23 gêneros, com ocorrência na região Neotropical, desde o Norte da América Central ao Sul da Argentina (Adler 2011; Fabre et al. 2013). Além disso, Echimyidae representa a família com a maior diversidade de adaptações ecomorfológicas entre os roedores histricognatos (grupo de roedores da infraordem Hysrtrricognathi), com gêneros essencialmente arborícolas, terrestres, semi-fossoriais e até mesmo semi-aquáticos, com distribuição desde áreas florestais úmidas (Mata Atlântica e Amazônia) até áreas abertas e secas (Cerrado e Caatinga) (Fabre et al. 2013).

Entre os roedores semi-fossoriais dessa família, destaca-se *Clyomys laticeps*, um roedor de porte médio (180 a 334g) com distribuição nas regiões do Pantanal e Cerrado (Paraguai e Brasil) (Bezerra et al. 2016), hábito noturno (Ferrando & Leiner 2017) e dieta herbívora (Almeida & Galetti 2007). Estudos sobre a estrutura populacional de *C. laticeps* são poucos e inconsistentes, e há pouco conhecimento sobre os padrões de movimentação e sistema social da espécie (Ferrando et al. 2019). Por observações anedóticas, *C. laticeps* tem sido descrito como colonial (Bezerra et al. 2016) ou social (Burda et al. 2000), porém estudos recentes neste sentido com *C. laticeps* indicam um sistema do tipo solitário (Arantes 2011; Ferrando et al. 2019). Ferrando et al. (2019) sugere que a espécie apresenta um sistema de acasalamento do tipo poligínico e que os indivíduos se reproduzem ao longo do ano todo, com proles de um a dois filhotes por vez.

Uma vez que existe uma relação entre características da história de vida, movimentos individuais e as relações sociais, mais especificamente organização social e sistema de acasalamento e consequentemente estrutura social e genética da população, estudos que abordem tanto padrões espaciais quanto genéticos permitem maior compreensão do comportamento social de uma população (Adler 2011), contribuindo para o entendimento da ecologia e biologia das espécies (Adler 2011). Em vista disto, nessa tese serão abordados aspectos da história de vida e dos comportamentos sociais do rato-de-espinho semi-fossorial *Clyomys laticeps* em três capítulos distintos, cada um somente com as citações e referências formatadas conforme as normas das revistas para as quais pretendemos submeter, no intuito de manter um formato geral padrão do documento da tese. O primeiro capítulo está previsto para ser submetido na revista *Mammalian Biology*, o segundo foi submetido na *Journal of Mammalogy* e o terceiro previsto para ser submetido na *Molecular Ecology*. Os estudos foram realizados em uma região de Cerrado, mais especificamente no Parque Estadual da Serra de Caldas Novas (GO, Brasil) (Figura 1, abaixo). O primeiro capítulo explora a dinâmica da população e da escavação de galerias do roedor *C. laticeps*, o segundo, a organização social da espécie por meio das relações espaciais entre os indivíduos e o terceiro explora o sistema de acasalamento genético e a estrutura genética da população.

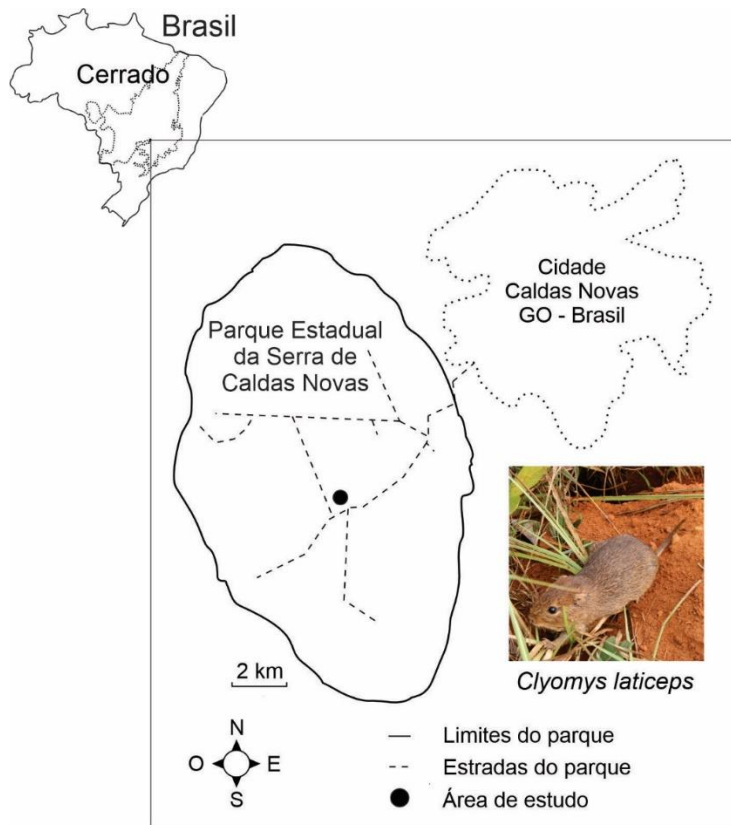


Figura 1. Local de estudo. Parque Estadual da Serra de Caldas Novas, Goiás – Brasil.

CAPÍTULO 1

Intention for submission: Mammalian Biology as Short Communication

(citations and references format according to author guidelines of this journal)

**Population and burrow dynamics of the semi-fossorial rodent *Clyomys laticeps*
(Thomas, 1909) (Rodentia: Echimyidae)**

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ABSTRACT

Describing life-history traits of species contribute to understanding behaviors and population dynamics. For several species, including the ones with cryptic habits as burrowing rodents, most of natural history information is gathered in captivity rather than in free living populations. However, the former does not always mirror the natural condition, while the latter requires greater effort and study time. In order to fill this gap in life-history data for free-living populations of burrowing rodents, this study provides information on population and biological traits as well as burrowing dynamics for the semi-fossorial rodent *Clyomys laticeps* in the Cerrado domain. The species presented a 1:1 sex ratio and a lack of sexual size dimorphism, which probably can reflect the occurrence of a weak competition for mates in the population. Moreover, the individuals were reproductively active throughout the year, which may contribute to the lack of seasonal population fluctuation within a year. Low population density seems to be associated to female monotocy coupled with long gestation length. *Clyomys laticeps*' burrowing activity appears not to be constrained by soil hardness, although the burrow cleaning activity was restricted to the dry season, probably as a strategy to avoid ectoparasites load in the burrow systems.

Key words: burrowing activity. reproduction, sex ratio, sex dimorphism, soil hardness.

RESUMO

O conhecimento das características da história de vida das espécies permite entender os seus comportamentos e as dinâmicas das populações. Para muitas espécies, incluindo as com hábitos crípticos como os roedores escavadores, grande parte da informação da história natural é obtida em cativeiro, ao invés de populações de vida livre. Estudos em

cativeiro nem sempre refletem as condições naturais dos animais enquanto os de vida livre requerem maior esforço e tempo de pesquisa. Com o objetivo de diminuir a lacuna de conhecimento da história de vida das populações de roedores escavadores de vida livre, este estudo apresenta características populacionais e biológicas assim como informações sobre a dinâmicas de escavação do roedor semi-fossorial *Clyomys laticeps* em uma área de Cerrado. A espécie apresentou uma razão-sexual 1:1 e ausência de dimorfismo sexual de tamanho corporal, o que pode resultar da ocorrência de uma baixa competição por parceiros na população. Ainda, os indivíduos foram reprodutivos ao longo de todo o ano, o que pode contribuir para a ausência de flutuação sazonal na população ao longo do ano. Baixa densidade populacional parece estar associada à geração de um único filhote por ninhada pelas fêmeas. A atividade de escavação do *Clyomys laticeps* parece não ser afetada pela dureza do solo, porém a atividade de limpeza das tocas foi restrita à estação seca, possivelmente como estratégia de evitar acúmulo de ectoparasitas nas galerias.

Palavras-chave: atividade de escavação, dimorfismo sexual, dureza do solo, razão sexual, reprodução

INTRODUCTION

The Echimyidae is the largest family of caviomorph rodents with more than 90 recognized species distributed along several types of environments along the Neotropics (Fabre et al. 2013; Upham et al. 2013). Despite the high species richness in this family, information regarding the species' biology, behavior and ecology is still scarce (Wolff and Sherman 2008; Ebensperger and Hayes 2016a), especially from free-living populations. Most of what is known come from anecdotal information and studies in captivity (Manaf et al. 2003; Patton et al. 2015; Cantano et al. 2021). In both cases, these informations are

important as starting points to provide insights about animal behavior, although extrapolating these observations to natural conditions is limited and should be viewed with caution. To fully understand species' behavior and demography, long-term studies with periodical sampling from free-living populations are required. However, these data are difficult to obtain, especially for species with cryptic habits, like the burrowing rodents, which in the Echimyidae family are represented by four species: *Carterodon sulcidens*, *Clyomys laticeps*, *Euryzygomatomys spinosus* and *Trinomys yonenagae* (Fabre 2013; Tavares et al. 2019).

Burrowing rodents use the underground for many reasons, including thermal buffering from extreme conditions, refuge against predators, storage of food and as safe places to rest and rear their young (Reichman and Smith 1990; Kinlaw 1999). Soil traits, as hardness, mechanical resistance, cohesion and water content, have a direct influence on where and when to dig burrows as well as on the species' social organization, since burrowing implies energetic costs for the animals (Laundré and Reynolds 1993; Ebensperger and Blumstein 2006; Carotenuto et al. 2020). Therefore, variation in burrowing activity patterns may result from environmental and population attributes, such as climate, soil characteristics, predation risk, food availability and parasite load (Butler and Roper 1996; Románach et al. 2006; Ebensperger and Blumstein 2006). As the dynamics of burrow construction mirrors fitness maximization by individuals, the life-history of burrowing animals may be shaped by their digging activities (Ebensperger and Blumstein 2006).

In this sense, we intend to describe some reproductive and demographic traits as well as the burrowing dynamics of the semi-fossorial echimyid *Clyomys laticeps*, which inhabits areas from central Brazil (Cerrado and Pantanal domains) to the Chaco of

Paraguay (Patton et al. 2015; Bezerra et al. 2016). Previous studies described this species as an herbivorous nocturnal rodent of medium size (280 - 334g), with males presenting larger body size than females (Almeida & Galetti 2007; Ferrando & Leiner 2017; Ferrando et al. 2019). Data are still lacking to confirm the solitary behavior suggested in the last studies encompassing genetic diversity (Arantes 2011) and space use patterns (Ferrando et al. 2019). Ferrando et al. (2019) suggest a polygynous mating system and they recorded breeding activity throughout the year with mostly only one offspring per pregnancy. However, data based on parentage analyses are needed to confirm the polygynous mating system.

MATERIALS AND METHODS

Demography and reproduction

We studied a population of *Clyomys laticeps* inhabiting a Cerrado grassland site at Parque Estadual da Serra de Caldas Novas (PESCaN) (17°43'-17°51'S, 48°40'-48°44'W) (Goiás, Brazil), from August 2018 to February 2020. The climate is defined by two seasons: a dry season from April to September and a wet season from October to March (Silva et al. 2008). In this study, the month of October 2019 was included in the dry season, once rainfall started in the end of this month in 2019 (AMAT 2020). Trapping procedures conducted in this study were part of a research project on social behavior of *Clyomys laticeps* (encompassing space use patterns and kinship structure) that was approved by SISBIO (No:62336-2) and Ethics Committee on Use of Animals of the Federal University of Uberlândia, Brazil (No:001/19) and was consistent with the guidelines for animal research provided by the National Advice of Control and Animal Experimentation

(CONCEA/Brazil 176/18) and the American Society of Mammalogists (Sikes et al. 2016).

Clyomys laticeps was bimonthly captured through a capture-mark-recapture design from August 2018 to February 2020, using a 1.7 ha (120 m x 140 m) grid with seven points of reference marked with stakes spaced 20 m apart. Sherman traps (43 x 12.5 x 14.5 cm; Equipos Fauna) were set every 40 m at the marked points of each transect and also in active burrows within this area. This was done because activities of burrowing rodents are strongly associated with their burrow systems and thus enhance the chance of their captures (see Malizia 1998). The traps were baited with a mixture of peanut butter, banana, and oats and checked every morning for ≥ 5 consecutive nights (maximum of 10). Each individual was marked with a numbered ear tag and sex, body mass, age class (young: pup < 100g; juvenile < 200g and adult: > 200g, Ferrando et al. 2019), reproductive status of females (pregnant, lactating, open vagina as a metric of receptiveness for copulation) were recorded. Additionally, to increase sample size and perform analyses of sexual size dimorphism in this species, additional *C. laticeps* individuals were captured using Sherman traps set at the entrance of active burrows located in a nearby grassland site (adjacent to our trapping grid). These traps were set in May and June 2018, February, August and October 2019, and February and August 2020. Trap baiting, individual marking and features of the captured individuals recorded following the same procedures as described before.

Burrow dynamics

All *Clyomys laticeps* burrows (new and old ones) were marked with a numeric code in August 2018. Then, at each of the following trapping sessions (October 2018 to February 2020), newly excavated burrows (different from the pre-existing ones) were recorded and

received their own numeric code to allow a follow-up of burrowing dynamics. Besides new burrows, latrines (feces mounds at the entrance of pre-existing and recently dig burrows), and reactivated burrows (i.e., with evidence of soil removal, feces, and/or dried grass and/or discarded seeds), the last two indicating gallery cleaning activity (Schmid-Holmes et al. 2001), were also recorded within the trapping grid. The trapping grid was divided into 42 sampling units (SU), each consisting of a 400 m² (20 x 20 m) quadrat. In each of these quadrats, measures of soil resistance (hereafter referred to as soil hardness) were based on the number of strokes necessary to penetrate into the first 60 cm of the soil (see Galiano et al. 2014), using a Stolf impact penetrometer with impact mass of 4 kgf. Measures were taken at the center of the sampling unit and at 4 additional points placed 5 m away in the four cardinal directions. These measures were taken in October 2019 (dry season) and February 2020 (wet season), to account for the seasonal difference in hardness of soil.

Mean soil hardness was calculated for each SU, i.e., the sum of all measures (number of strokes) divided per 5 (points of measure within each SU). The new burrows were counted in each SU every other month from October 2018 to February 2020 (N = 9). Then, to estimate the total number of newly excavated burrows in each SU per season, the number of new burrows excavated/SU in each month was pooled according to season

(wet or dry) and divided by the number of months in each season (N= 4 months for the dry season and N = 5 months for the wet season).

Statistical analysis

All the following analyses were made in R version 3.6.3 (R Core Team 2020) and in case of no normal distribution of data, permutation tests were performed with 1,000 iterations. All analyses assumed significance level 95%.

Sex ratio and population size estimates were done using the longitudinal capture-mark-recapture data set (August 2018 – February 2020). The adult sex ratio (ASR) was calculated based on the proportion of males in the adult population (i.e. $ASR = N_{\text{male}} / (N_{\text{male}} + N_{\text{female}})$) (Ancona et al. 2017) and tested for significance with a binomial test. Population size was estimated through the minimum number of individuals known to be alive (MNKA) between intervals (in this study, two months) (Krebs 1966). Moreover, since some rodents present resident and transient behavior, we considered those adults captured only once along the study as transients and those captured more than once as residents (Galindo-Leal 1997; Malizia 1998). Sexual size dimorphism was estimated considering all the adults (except lactating and/or pregnant females) captured during the study. Mean body mass (hereafter body size) of males and females was compared with t-test. Permutation paired t-test were performed using the function “paired.perm.test” from the package “broman” (Broman 2021) to compare the mean number of new burrows/SU as well as the mean soil hardness/SU between seasons. Moreover, linear regressions (through permutations) were performed to test the effect of soil hardness/SU on the mean number of new burrows/SU, separately for each season (wet and dry). The test was

performed using the function “lm()” from the package “lmPerm” that allows permutation test for linear models (Wheeler & Torchiano 2016).

RESULTS

Demography and reproduction

A total of 53 individuals were captured (females: 18 adults and 15 youngs; males: 10 adults and 10 youngs) and the total sampling effort was > 5,908 trap-night within an 11 ha area. From these individuals, 22 were captured in the longitudinal dataset (i.e, bimonthly trapping sessions) (adults: 15 = 7 males and 8 females; youngs: 7 = 5 females and 2 males) obtained from 4,344 of > 5,908 trap-night . Seven of the adults were classified as residents (2 males and 5 females) ($\bar{x}$ = 299.25 and $\bar{x}$ = 277.4 g, respectively), being captured for longer than 5 months in the trapping grid, whereas the remaining ones were captured only once and thus classified as transient individuals (5 males and 3 females) ($\bar{x}$ = 282.8 g and $\bar{x}$ = 258.3 g, respectively). The estimated number of individuals per month in 1.7 ha (from December 2018 on) varied from 6 – 9 (all individuals), 2 – 8 (adults only) and 5 – 7 (resident adults only), suggesting low density according to Adler (2011) in the studied population. From December 2018 onwards, all residents were captured and remained inside the trapping grid; hence, their numbers remained constant until February 2020, lacking any seasonal fluctuations (Fig. 1). Transients and young individuals accounted for small and regular variations in population size throughout the study period (Fig. 1). The proportion of males in the adult population

was 0.5, indicating that sex-ratio was not significantly different from 1:1 (binomial test $P = 1$).

Mean body mass of *Clyomys laticeps* was $\bar{x} = 291.88 \pm SD 38.34$ g and for adult males was $\bar{x} = 300.73 \pm SD 38.89$ g, which did not differ from females mean body mass ($\bar{x} = 284.93 \pm 37.84$ g) (t test: $t = -1.02$; $P = 0.3188$). The leaner (and probably the youngest) individual captured had 47 g (female) and the heaviest ones weighed 360 g (non-reproductive female) and 356 g (male). We have evidence that males may live more than four years in nature, as we captured an adult male in a previous study in April 2016, and again in August 2019. Pregnant females ($N = 6$), as well as youngs (pup and juveniles; $N = 25$), were captured along the study period, regardless from season (Table 1), thus reinforcing the suggestion that *C. laticeps* presents aseasonal, year-round reproduction made by Ferrando et al. (2019). There were two females which had their body mass registered before and after giving birth within the same trapping session. One lost 40 g and the other 65 g. Based on kinship data, we were able to identify the mother of three different litters, indicating that a same female may produce young at least three times a year (see F1 and F3; Table 2). Each of the studied females produced only a single young per pregnancy, suggesting monotoccy in *C. laticeps*. We were able to observe two pregnancies for a same female within seven months (see F3 in Table 2; December 2018 and August 2019) with a probable another one within that time interval when the offspring captured in December 2019 was possibly born. Moreover, the minimum interval between births (seven months) was observed for female F3 (Table 2).

Burrow dynamics

Despite higher mean soil hardness in the dry season (Permutation of paired t-test: $N = 42$; $t = 40.28$; $P < 0.001$ - dry season: $\bar{x} = 14.46$; $SD \pm 1.582$, wet season: $\bar{x} = 4.933$; $SD \pm$

0.766), the number of newly excavated burrows was similar between the wet ($N = 219$) and dry ($N = 152$) seasons (Permutation of paired t-test: $N = 42$; $t = -0.55$; $P = 0.586$ - dry season: $\bar{x} = 0.90$; $SD \pm 0.857$, wet season: $\bar{x} = 1.042$; $SD \pm 1.384$). Indeed, the mean number of new burrows was not associated to mean soil hardness in neither seasons (Regression by permutation: dry season: $F = 2.16$; $P = 0.15$; $R^2 = 0.051$; and wet season: $F = 0.96$; $P = 0.33$; $R^2 = 0.023$). Latrines were only identified during the dry season, mostly in recently dig burrows (except for one, which was present in a two-month old burrow) corresponding to 4.6 % of the new burrows from the dry season ($N = 7$). Burrow cleaning were also only identified during the dry season ($N = 8$).

DISCUSSION

The population of *Clyomys laticeps* studied in Parque Estadual da Serra de Caldas Novas (GO, Brazil) presented a 1:1 sex ratio, and a lack of sexual size dimorphism. Moreover, the individuals were reproductively active throughout the year with females being monotocous and apparently being able to give birth three times a year. Adult males may live more than four years in nature, and could be identified as residents and transients. Additionally, monthly population density was low, lacking seasonal fluctuations within the year. Regarding burrow dynamics, *C. laticeps* constantly dig new burrows, regardless of season or soil hardness, although burrow cleaning activities were concentrated in the dry season.

Adult sex ratio (ASR) is the result of several ecological and genetic factors (Székely et al. 2014), and the observed ratios may be one of the mechanisms shaping mating systems and sexual selection patterns among mammals (Clutton-Brock and Iason 1986). As predicted for most mammals, *C. laticeps* presented a balanced (1:1) sex ratio,

although females were more frequently captured than males due to site fidelity of the former (Ferrando et al. 2019). The lack of biased sex ratio in the studied population may reflect similar survival probabilities, as both sexes disperse in the population (Ferrando et al. in prep.), although this idea needs further testing. Genetic basis may also account for a balanced sex-ratio (Fisher's principle - 1930) in the studied population, and this ratio may predict the intensity of mating competition (Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996; McEachern et al. 2009).

Sexual dimorphism may manifest as differences in anatomical and physiological features, like body size, horns, and fur color, between males and females (McPherson and Chenoweth 2012). Distinct growth trajectories and sexual selection may account for sexual dimorphism; thus these differences are usually closely linked to the mating behavior of species (McPherson & Chenoweth 2012). Previous studies have already discussed that sexual monomorphism may evolve in species presenting soft intra-sexual mate competition, as selective pressures for increased body size may not translate into increased reproductive success (Cooper et al. 2011). Although sexual dimorphism is common among most mammals (Linderfors et al. 2007), it seems absent or rare within echimyid species (Maher & Burger 2016). Indeed, previous studies have found sexual monomorphism in body size or cranial size and shape for semi-fossorial, terrestrial and arboreal species of this family (Monteiro et al. 1999; Bezerra & Oliveira 2010; Raidan et al. 2019), suggesting that this pattern might be phylogenetically conserved among echimyids. As previously demonstrated for craniodental measures (Bezerra & Oliveira 2010), *Clyomys laticeps* appears to follow the same pattern as the other echimyid rodents, although Ferrando et al. (2019) previously suggested male-biased size dimorphism in the same population of *C. laticeps* studied here. The identification of dimorphism between sexes in Ferrando et al. (2019) may result from the small sample size coupled with the

inclusion of all females (regardless of their reproductive status) in the analyses, factors that were not an issue in the present study. Irrespective of the causes of sexual monomorphism in this species, this pattern may shape species' mating systems (McEachern et al. 2009). Similar body size can impair the monopolization of females by males, favoring a condition where females could mate with several males (Cooper et al. 2011); this pattern is corroborated by molecular data, which evidenced that most males and females shared their partners (Ferrando et al. in prep.). Copulation with more than one individual of the opposite sex may also be favored by the occurrence of transient adults, especially for females with residency behavior as in *C. laticeps* (Ferrando et al. 2019).

Reproductive patterns constitute important aspects of a species life-history and population dynamics. Most caviomorphs, including the echimyids, produce small litters; in many cases ranging from 1 to 3 (Tang-Martínez and Congdon 2016). Although the production of a single young (monotocy) is rare among rodents, especially within solitary species, it seems associated to the production of precocial newborns (Lukas and Clutton-Brock 2020). This seems to be the case for *C. laticeps*, since its newborns are precocial (Freitas 2013; Ferrando et al. 2019) as several caviomorphs which seem to trade-off offspring number x size. Accompanied by these life-history attributes, echimyids usually present long gestation length (close to 100 days – Roberts et al. 1988), which probably occur in the studied *C. laticeps* population, as evidenced by one of the females (i.e. F3) in this study that apparently was able to give birth two times and get pregnant again within seven months. Monotocy and the constant year-round breeding activity of *C. laticeps*, as already demonstrated by (Ferrando et al. 2019) may account for the relative constant population size throughout the year in the studied population. Monotocy may be one of the explanations of the low density of adults (residents and transients) observed in the

studied population. Regarding survival, we have evidence that adults may live for more than 4 years in nature, in agreement to the observed for *Proechimys semispinosus* in the wild (3 to 5 years – Oaks et al. 2008); nevertheless, larger sample size and longer study time are necessary to discuss *C. laticeps* lifespan.

Among burrowing animals, digging is an essential behavior, contributing to individual survival and population social systems (Bennett and Faulkes 2000; Ebensperger 2001). Some burrowing rodents concentrate building on their subterranean tunnels during the rainy season, as a strategy to minimize energy expenditure due to reduced soil hardness in this period (Romañach et al. 2006). Apparently, soil hardness was not an ecological constraint for burrow construction in the studied *C. laticeps* population. Luchesi et al. (2022) studied several parameters of burrow system architecture of *C. laticeps* in Itirapina Ecological Station (SP, Brazil), and similar to our findings, they did not find seasonal effects on the number of burrow openings, although the maximum depth of the burrow systems varied seasonally (Luchesi et al. 2022). The authors suggest that *C. laticeps* excavate deeper during the dry season, irrespective of soil hardness, as a strategy to overcome the high temperatures and look for cooler and more humid environments than the top soil layers (Luchesi et al. 2022). In our study, the number of new burrows did not change with season, but burrow cleaning restricted to the dry season may reflect a modification in the underground burrow system architecture in this period (Šumbera et al. 2003). Conversely, burrow cleaning may be a strategy to avoid accumulation of ectoparasites, by discarding the fecal matter, debris and dried grass (Schmid-Holmes et al. 2001). Several burrowing rodents were reported to avoid ectoparasites, either by switching from one nest chamber to another (Roper et al. 2002, Šklíba et al. 2008) or by cleaning burrows (Schmid-Holmes et al. 2001). Ectoparasites' prevalence and abundance normally peak in response to the higher nutritional and water

stresses during the dry season (Buchholz and Dick 2017; Shilereyo et al. 2022), and we observed a higher number of individuals infected with lice, fleas and mites during this period at the study site. Therefore, burrow cleaning behavior may be associated with a strategy to avoid accumulation of ectoparasites within the subterranean tunnels. Pitfall trapping at the study site (PESCaN) found fleas exclusively close to *C. laticeps* burrows (Lamberto & Leiner 2019) which gives more support for the possible parasite avoidance behavior, although further studies are needed to support this affirmative.

The description of life-history traits and burrowing dynamics of caviomorph rodents are restricted to a few species, and most studies were performed in captivity or including museum specimens (Patton et al. 2015; Ebensperger and Hayes 2016a; Tavares et al. 2019). Nevertheless, studies of populations in the wild are essential to understand the evolution of species' behavior and are complementary to those in captivity. In this way, the present study contributes to the knowledge of the diverse, although poorly studied, echimyid natural-history. The data presented here, regarding reproductive patterns, demographic traits, and burrowing dynamics, may provide insights into the forces driving the evolution of natural and sexual selection patterns, mating and social systems, and behavioral strategies of individuals within a population (McPherson and Chenoweth 2012; Ebensperger and Hayes 2016b). Future studies should compare life-history and burrowing attributes among echimyid rodents, exploring the role of phylogeny and ecological factors on the existent diversity.

ACKNOWLEDGMENTS

We would like to thank Neto J. E. and its family, for receiving us at their home, so we could do the first field trips. Ferrando M. A. and Röpke U. O. for lending us their car, so

we could travel to the study site. Ferrando E. M. R., Rodrigues F. O., Toledo V. B., Bomfim P. M. S., Melo F. S. for helping in the field trips, especially Queiroga D. S., Figueiredo C. P. G., de Oliveira M. M. and Rossi R. C. for helping during the long nights of telemetry in the field. Szabó M. P. J. and its lab students for lending us the capture traps and improve the field procedures of animal manipulation. as well as Wendling B. for lending us the stolf impact penetrometer. We are greatfull to all the people who help to with the genetic study. Our thanks to the Secretaria Estadual de Meio Ambiente e Desenvolvimento Sustentável de Goiás (SEMAD) for logistical support. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 and by Conselho Nacional de Desenvolvimento Científico (CNPq - PELD 403733/2012-0 and 442603/2014-2).

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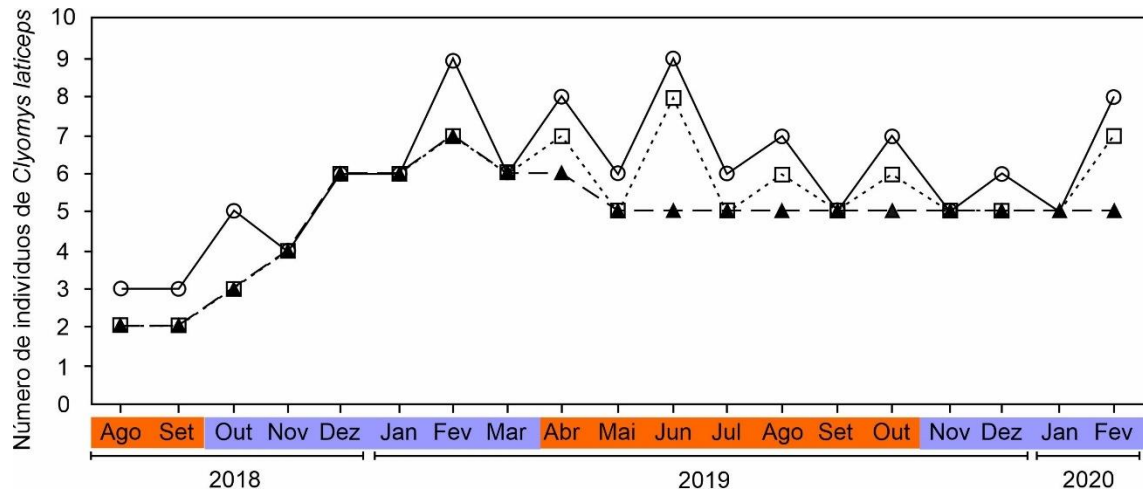


Figure 1. Estimates of the number of *Clyomys laticeps* on a 1.7 ha grid at Parque Estadual da Serra de Caldas Novas (Goiás, Brazil) showing the minimum number of animals known to be alive (MNKA) estimate. Open circle: all individuals captured, regardless of age class. Open square: only adults. Filled triangle: residents adults (present ≥ 5 months in the study site). Orange: dry season. Blue: wet season.

Table 1. Pregnant females identified by numbers and number of youngs (P = pup: < 100 g and J = juveniles < 200 g) of *Clyomys latieps* captured throughout the study (2018 – 2020) at Parque Estadual da Serra de Caldas Novas (GO - Brazil). Pregnant females and number of youngs columns are independent of each other.

Year/month	Pregnant females			Number of youngs		
	2018	2019	2020	2018	2019	2020
Jan.						
Feb.		F5			2 P 1 J	2 P 1 J
Mar.			F2			1 P
Apr.					1 P	
May				2 J		
Jun.		F1				
Jul.				1 J		
Aug.		F1 F3 F6			3 P 3 J	1 P 1 J
Sept.						
Oct.	F3	F4		1 P	1 P 3 J	
Nov.						
Dec.	F3				1 J	

Table 2. Three females of *Clyomys laticeps* at Parque Estadual da Serra de Caldas Novas (GO - Brazil) that were captured pregnant and youngs identified as their offsprings through parentage analysis. m.F = mother female x; o.f = offspring from the mother x; NC = not captured; NP = not pregnant; P = pregnant; ns = No capture session; Values = body mass (g).

Years/ Months	Years									
	2019		2020		2019		2018		2019	
	m.F1	o.F1	m.F1	o.F1	m.F2	o.F2	m.F3	o.F3	m.F3	o.F3
Jan.	ns		ns		ns		ns		ns	
Feb.	NP 265		NP 300		NP 302		NC		NP 312	135
Mar.	ns		NP 300	109	NP 302		ns		NP 312	
Apr.	NP 262		NC		NP 212	99	NC		NP 316	
May	ns		ns		ns		ns		ns	
Jun.	P 271		NC		NP 291		ns		NC	
Jul.	ns		ns		ns		NP 312		ns	
Aug.	P 284		NP 278	94	NP 289		NC		P 328	
Set.	ns		ns				ns		ns	
Oct.	NP 257	91	ns		NP 243		P 290	105	NP 303	
Nov.	ns		ns				ns		ns	
Dec.	NC		ns		NC		P 383		NP 354	179

CAPÍTULO 2

Submitted: Journal of Mammalogy

(citations and references format according to author guidelines of this journal)

Spatial and social organization of the burrowing rodent *Clyomys laticeps* (Thomas, 1909)

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ABSTRACT

Burrowing rodents display diverse patterns of social organization, ranging from solitary to group living. Differences in social organization are often inferred from patterns of space use, particularly differences in the degree to which individual home ranges overlap. Here, we characterize patterns of space use in a poorly studied species of burrow-dwelling echimyid rodent, *Clyomys laticeps*. Specifically, we use radiotelemetry studies of a free-living population in Parque Estadual da Serra de Caldas Novas (Goiás, Brazil) to evaluate previous, apparently contradictory reports suggesting that this species is both solitary and social. A total of 20 adult (12 female, 8 male) *C. laticeps* were monitored via telemetry during two consecutive cycles of annual wet and dry seasons. The resulting data indicate that although overlap of individual home ranges was common, co-occurrence of adults in time and space was rare and was limited to male-female pairs, a pattern that is most

consistent with a solitary lifestyle in which individuals occupy distinct burrow systems. Neither sex nor season affected spatial overlap; this outcome is consistent with evidence suggesting that reproduction in this species occurs throughout the year. Although home ranges for males were larger than those for females, areas occupied by both males and females overlapped with multiple opposite-sex individuals, making it difficult to determine from spatial data whether the study population was polygynous or polygynandrous. While genetic data are needed to characterize fully the mating system of these animals, our analyses provide the first detailed information regarding spatial relationships in *C. laticeps*, thereby allowing more accurate placement of this species within a larger, comparative behavioral framework and facilitating efforts to identify the factors contributing to social diversity among burrow-dwelling rodents.

Key words: burrowing rodents, Echimyidae, spatial relationships, social organization, mating system.

RESUMO

Roedores escavadores apresentam uma gama de padrões de organização social, desde uma vida solitária até em grupo. As diferenças nas organizações sociais são frequentemente descritas através dos padrões de uso do espaço, especialmente nas diferenças no grau de sobreposição entre os indivíduos. Nesse estudo, nós caracterizamos padrões de uso do espaço da espécie semi-fossorial pouco estudada, *Clyomys laticeps* com o uso da radiotelemetria em uma população de vida livre no Parque Estadual da Serra de Caldas Novas (Goiás, Brasil) afim de avaliar as observações anteriores descrevendo essa espécie como solitária e social. Um total de 20 adultos (12 fêmeas, 8 machos) de *C. laticeps* foram monitorados por telemetria durante duas estações de seca e chuvosa. Os

resultados indicaram que embora a sobreposição da área de vida dos indivíduos foi frequente, a co-ocorrência entre os adultos no tempo e espaço foi rara e limitada entre pares macho-fêmea, um padrão que é mais consistente com o hábito de vida solitário em que os indivíduos ocupam diferentes galerias subterrâneas. Sexo e estação não influenciaram nos padrões espaciais de sobreposição, reforçando a evidência de uma reprodução ao longo do ano todo nessa espécie. Embora a área de vida dos machos foi maior em relação a das fêmeas, áreas ocupadas por ambos os sexos se sobrepuseram a vários indivíduos do sexo oposto, tornando difícil determinar a partir de dados espaciais se a população do estudo é poligínica ou poliginândrica. Enquanto dados genéticos são necessários para a caracterização do sistema de acasalamento desses animais, esse estudo descreve pela primeira vez, de forma detalhada, as relações espaciais de *C. laticeps*, permitindo dessa forma, uma colocação mais precisa dessa espécie dentro de uma estrutura comportamental comparativa maior, facilitando os esforços de identificação dos fatores que contribuem para a diversidade social entre os roedores escavadores.

Palavras-chave: Echimyidae, organização espacial, relações espaciais, roedores escavadores, sistema de acasalamento.

INTRODUCTION

The spatial distribution of animals within a population can generate important insights into a species' social organization and mating system (Smith and Ivins 1983; Geffen et al. 1996; Maher and Burger 2011; VanderWaal et al. 2014; Kappeler 2019). For example, the degree of overlap among home ranges belonging to different individuals can be used to characterize a species as solitary or social (Lacey 2000; Graw et al. 2019). At

the same time, spatial relationships between males and females can be used to estimate the number of potential reproductive partners per individual, thereby allowing inferences about the social and possibly the genetic mating system (McEachern et al. 2009; Lin et al. 2009). Describing these aspects of a species' behavior is critical, given that mating systems and social organization are directly linked to evolutionarily important aspects of the demographic and genetic structures of natural populations (Schradin et al. 2018; Kappeler 2019).

Many species of rodents use underground burrows, with the degree of specialization for burrow dwellings ranging from truly subterranean to semi-fossorial lifestyles (Nevo 1979, Kinlaw 1999, Beca et al. 2021). While taxa identified as subterranean perform almost all activities underground and only rarely emerge on the surface (Lacey et al. 2000), taxa characterized as semi-fossorial use burrows for critical functions (e.g., nesting, escape from predators) but spend a considerable proportion of time above ground foraging and, in some cases, interacting with conspecifics (Kinlaw 1999; Ojeda et al. 2013). Because these animals cannot be observed directly when underground, the social organizations and mating systems of burrowing rodents are often characterized based on analyses of spatial overlap among individuals (Lacey 2000, Steinwald et al. 2013; Amaya et al. 2021). For example, species in which adults display little or no overlap with conspecifics are typically described as solitary (Mares et al. 1997; Cooper and Randall 2007; Amaya et al. 2021), whereas those displaying extensive and persistent overlap (i.e., burrow sharing) are often identified as group living (Sobrero et al. 2014; Lacey et al. 2019; O'Brien et al. 2020). Regarding mating system, spatial overlap that is restricted to male-female pairs is frequently interpreted as evidence for social monogamy (McEachern et al. 2009; Lin et al. 2009), whereas spatial overlap and burrow

sharing among multiple adults of one or both sexes are considered indicative of polygamy (McEachern et al. 2009; Lin et al. 2009).

The Echimyidae is a morphologically and ecologically diverse family of caviomorph rodents that is widely distributed in Central and South America (Fabre et al. 2013; Herrera 2016). Four members of this family (*Euryzygomatomys russatus*, *Clyomys laticeps*, *Carterodon sulcidens*, *Trinomys yonenagae*) are burrow-dwelling (Fabre et al. 2016; Tavares et al. 2019). Three of these species are part of a monophyletic sub-clade consisting of *Euryzygomatomys*, *Clyomys* and *Trinomys*; in contrast, the position of *Carterodon* within the family remains uncertain (Fabre et al. 2016; Tavares et al. 2019). Despite multiple comparative analyses of social organization in burrowing caviomorphs (Lacey and Ebensperger 2007; Maher and Burger 2011), few studies have examined the social behavior of burrowing echimyids (Adler 2011). Indeed, detailed behavioral data are available only for *T. yonenagae*. This species is endemic to sand dunes along the São Francisco River in northeastern Brazil (Luchesi et al. 2019), where it lives in cohesive social groups, members of which behave amicably toward each other and display a polygynandrous mating system (De Freitas et al. 2010; Santos and Lacey 2011).

In comparison, relatively little is known regarding the behavioral biology of *C. laticeps*. This nocturnal and herbivorous species occurs in the Pantanal and Cerrado biomes of central Brazil and eastern Paraguay (Patton et al. 2015; Bezerra et al. 2016; Ferrando and Leiner 2017). Although anecdotal information has led to the characterization of *C. laticeps* as social (Burda et al. 2000), mark-recapture and spool-and-line tracking studies as well as analyses of population-level genetic diversity have been interpreted as evidence that this species is solitary (Arantes 2011; Ferrando et al. 2019). To reconcile these seemingly contradictory descriptions, we used radiotelemetry to generate detailed information regarding spatial relationships among adult *C. laticeps*,

thereby allowing more robust inferences regarding the social organization and mating system of this species. Specifically, we sought to determine if patterns of spatial overlap among adults were more consistent with those expected for solitary versus group-living species of burrowing rodents (Lacey 2000). Based on our preliminary observations in the field, we predicted that persistent burrow sharing among adults would be rare and that overlap of adult home ranges would be minimal, as expected if *C. laticeps* is largely solitary. Our analyses provide the first detailed characterization of the social organization of this species and generate potential new insights into the ecological factors associated with behavioral convergence and divergence among burrow-dwelling rodents.

MATERIALS AND METHODS

Study area

Fieldwork was conducted in Parque Estadual da Serra de Caldas Novas (PESCaN) (17°43'-17°51'S, 48°40'-48°44'W) in Goiás, Brazil. Located in the Cerrado biome, this park encompasses approximately 12,315 ha containing a mosaic of forest, savannah, and grassland habitats, each of which is associated with a distinct soil type (Eiten 1978; SEMAD 2020). The study site consisted of an ~ 11 ha area located in grassland habitat referred to as “cerrado campo sujo”, which is characterized by a sparse distribution of shrubs intermixed with herbaceous plants (Ribeiro and Walter 1998; Fig. 1). The mean estimated density of *C. laticeps* in this habitat is ~ 4 adults/ha (C. Ferrando, pers. obs.), which is low based on comparative data from other echimyids (Adler 2011). Population density was calculated based on monthly estimates of the minimum number of adults alive on a 1.7 ha subsection of the study site from December 2018 to February 2020;

monthly estimates of density were then averaged to produce a mean estimated density for the study population.

The climate at the study site is defined by two seasons: a dry season from April to September and a wet season from October to March (Silva et al. 2008). Data were collected from February 2019 - February 2020; during this period, the mean monthly temperature ranged from 19 °C to 27 °C in the dry seasons and from 23 °C to 27 °C in the wet seasons. Total monthly rainfall varied from 0 to 250 mm, with mean monthly values of 32.0 mm during the dry seasons versus 77.0 mm during the wet seasons (AMAT 2020). Although the seasons in the Cerrado are generally temporally consistent, 2019 was unusual in that rainfall did not start until the middle of October, compared to a more typical start in the middle of September (AMAT 2020). For that reason, October 2019 was considered part of the dry season for this study.

Animal capture and marking

During each sampling period (February 2019, August 2019, October 2019, February 2020), *C. laticeps* were captured using Sherman traps (43 x 12.5 x 14.5 cm; Equipos Fauna) baited with a mixture of peanut butter, banana and oats. Because this species is nocturnal, traps were opened at dusk and closed shortly after sunrise the next morning. Traps were set at active burrow entrances, as identified based on signs of recent rodent activity (e.g., freshly excavated soil, undisturbed footprints, remnants of freshly consumed fruits, fresh fecal pellets); each burrow entrance was trapped for 5 to 8 consecutive nights. To capture potential transient animals (e.g., males moving between burrow systems, Ferrando et al. 2019), baited traps were also randomly placed throughout the study area. Because the number of active burrows and their locations varied over the course of the study, both the total number of traps set and the size of the area trapped

varied among sampling periods; the number of traps set ranged from 100 to 130 per night and the size of the area monitored ranged from 3.3 to 5.2 ha per sampling period. Areas trapped during different sampling periods overlapped at least partially, in order to ensure population continuity in space.

Captured animals were individually marked with a numbered metal ear tag (Zootech ZT 900 modelo1) placed in the left pinna. The sex and body mass of each animal were recorded; mass was used to determine the relative age of each individual (pups < 100 g; juveniles 100-200 g; adults > 200 g; Ferrando et al. 2019). For adult females, reproductive status was determined based on the appearance of the external genitalia (open vagina = sexually receptive), the ability to palpate fetuses (pregnant), and the presence of enlarged mammae (lactating). Because the testes of adult males remain abdominal (Ferrando et al. 2019), reproductive status could not be determined for members of this sex. All procedures involving live animals were consistent with the National Advice of Control and Animal Experimentation (CONCEA/Brazil) and the guidelines of the American Society of Mammalogists (Sikes et al. 2016) and had been approved by the Ethics Committee on Use of Animals at the Federal University of Uberlândia, Brazil (permit number: 176/18). Permission to trap and to handle *C. laticeps* was issued by SISBIO/ICMBio (Permit Number: 62336-2).

Radiotelemetry data

Radiotelemetry was used to monitor animal locations during each of the four sampling periods. Two of these periods occurred during the wet season (February 2019 and February 2020) and two occurred during the dry season (August 2019 and October 2019). During each sampling period, all adults captured were fitted with radio-transmitters (TXC-009CZ transmitters, Telenax Wildlife Telemetry, Playa del Carmen, México) that

were affixed using plastic cable ties as collars. Each transmitter weighed ~ 6 g, which is $< 5\%$ of adult body mass (Sikes et al. 2016). Collared individuals were released at the point of capture, after which the animals were located using a 3-element hand-held Yagi antenna and an RX-600 receiver (Telenax Wildlife Telemetry, Playa del Carmen, México). The location of each individual was determined following the “homing in” method (Freegard 2009). In brief, we followed the radio signal for each individual until we identified the location at which that signal was strongest, after which that position in the habitat was recorded with a GPS unit (e-Trex 20x Garmin, accuracy ~ 3 m). Localities of all collared individuals were determined every two hours during both the daytime and the nighttime (00:00 to 23:59); during each sampling period, all collared individuals were monitored simultaneously (i.e., same days and times) to allow detection of potential instances of co-occurrence (see below). Telemetry data were collected over five consecutive days, resulting in 60 data points per individual per sampling period. At the end of each period, we attempted to recapture all animals so that their radio collars could be removed.

Home range characterization

To estimate home range sizes and patterns of spatial overlap for radiocollared animals, we generated 50% and 95% Autocorrelated Kernel Density Estimators (AKDE, Fleming et al. 2015) for each individual using the “ctmm” package (Calabrese et al. 2016) as implemented in R version 3.6.3 (R Core Team 2020) and RStudio version 1.3.1073 (RStudio Team 2020). While other commonly used methods of home range construction such as Minimum Convex Polygons (Mohr 1947) and Kernel Density estimators (Worton 1989) assume that individual localities are independent and identically distributed (Fleming et al. 2015), AKDE takes into account potential autocorrelation among localities

for the same animal, thereby providing what is expected to be a more realistic depiction of an individual's home range and pattern of space use (Fleming et al. 2015).

Prior to generating AKDEs, telemetry data from each animal were subjected to a variogram analysis and a non-Markovian maximum likelihood estimation of autocorrelation (Calabrese et al. 2016) to identify the most appropriate model of each individual's movements. Once the best model had been selected, the "akde" function was applied to the fitted model to allow home range estimation (Fleming et al. 2015; Calabrese et al. 2016). This method of home range estimation can only be conducted when animals display range residency behavior (i.e., restriction of movement to a subset of the habitat; Calabrese et al. 2016). Thus, only individuals for whom telemetry data could be fitted to a range-resident model of movement, such as the independent identically distributed IID, Ornstein-Uhlenbeck (OU), or OU-Foraging (OUF) models, were included in our AKDE analyses (Calabrese et al. 2016).

To explore potential predictors of home range overlap, we first examined variation in home range size among members of the study population. To do this, we constructed a Generalized Linear Model (GLM) based on a gamma distribution, with estimated home range size (AKDE 95%) as the response variable and season (wet, dry) and sex as fixed effects. Although our analyses focused on AKDE estimators, estimates of home range size based on MCP and KDE methods are presented in Supplementary Data S1 to facilitate comparisons between this and other studies of space use in burrow-dwelling rodents.

Home range overlaps

Overlap of home ranges was quantified for all possible pairwise combinations of individuals monitored during the same data collection period. Because *C. laticeps* were present at relatively low density on our study site (see below), lack of overlap between some pairs of animals may have resulted simply from limited opportunities for those individuals to encounter one another. To minimize the effects of this potential demographic confound, we used a neighborhood criterion to exclude pairs of individuals for which spatial overlap was unlikely due to their distribution on the study site. Specifically, we calculated the maximum distance recorded between each pair of individuals that were tracked simultaneously and that displayed non-zero home range overlap (see below). Distances were calculated using the Pythagorean theorem, with GPS coordinates for fixes in UTM format. We then calculated the mean maximum distance for each dyad type (male-male, male-female, female-female) and set this value as the dyad-specific threshold for inclusion in analyses of spatial overlap. Pairs of individuals for whom the maximum distance detected was greater than the mean value for their dyad type were excluded from subsequent analyses of spatial overlap; use of the maximum distance for this criterion was conservative in that it excluded pairs of animals for whom actual spatial overlap was likely to be rare.

Once the final subset of individuals for analysis had been determined, overlap of home ranges was estimated in QGIS 3.14 based on the intersection of AKDE polygons (i.e. absolute overlap area), with separate measures of overlap generated for 50% and 95% polygons. Since the overlap between individuals areas may not be symmetric, we calculated the percent overlap from the perspective of each animal included in a pairwise comparison. Consistent with analyses of home range size, estimates of absolute area

overlap and percent pairwise overlap based on MCP and KDE methods are presented in Supplementary Data S2.

To facilitate comparisons with other studies, we also calculated the index of home range overlap for each pair of animals following the procedure in Winner et al. (2018), as implemented in *ctmmweb* (Calabrese et al. 2021). Standard estimates of home range overlap are calculated from the area of the intersection between two ranges; in contrast, Winner's index is based on the estimated volume of the intersection between pairs of three-dimensional density utilization distributions such as AKDE polygons. Thus, Winner's index values approaching zero indicate little overlap or overlap of areas seldom used by members of a pair, while values approaching 1 indicate substantial home range overlap or overlap of areas that are frequently used by a pair of individuals. Unlike other overlap metrics, values for this index include confidence intervals that can be used to assess the uncertainty associated with estimates of overlap (Winner et al. 2018).

To explore potential predictors of home range overlap, we constructed GLMs based on binomial distribution, with dyad type (MF, FF, MM for overlap index; MF, FM, FF, MM for pairwise overlap) and season (wet, dry) as fixed effects. Separate models were constructed with (1) home range overlap index values and (2) values for percent pairwise overlap (AKDE 95%) as response variables. The same pairs of individuals (i.e. those that met the neighborhood criterion) were used in both models; the limited number of pairs examined precluded the inclusion of interaction terms in either model. Values for percent pairwise overlap may not have been symmetric and thus, for that analysis, we parsed dyads into four types: FF (percentage of females' home range overlapped by other females), MM (percentage of males' home range overlapped by other males), FM (percentage of males' home range overlapped by females) and MF (percentage of females' home range overlapped by males). For each measure of home range overlap,

the best fit model was determined based on the Akaike Information Criterion (AIC). Overlap of core areas (50% AKDEs) was not examined statistically due to the limited number of pairs ($N = 14\%$ of potential pairwise combinations) for which overlap was detected using this metric.

Co-occurrence of individuals

Because social interactions require that individuals be present at the same location at the same point in time, we evaluated the number of co-occurrence events between each pair of animals for which overlap of 95% AKDE polygons was detected. Specifically, we calculated pairwise distances between the localities recorded for all individuals for which radio fixes were recorded simultaneously (i.e., same day and time). Distances were calculated as described above. Individuals were said to co-occur if they were located ≤ 3 m from each other during the same fix; this distance was chosen because it corresponds to the mean error for the GPS localities recorded during this study. We then calculated the percentage of fixes at which each individual co-occurred with an animal of the same or the opposite sex.

Statistical analysis.

All analyses were conducted in R version 3.6.3 (R Core Team, 2020). Standard two-sample tests were performed using the permutation test with 1,000 randomizations with the package “broman” (Broman 2021). Throughout the text, means are reported $\pm$ one standard deviation.

RESULTS

Across all sampling periods (> 1,899 traps nights), a total of 25 (16 female, 9 male) adult *C. laticeps* were captured, of which 20 (12 females, 8 males) were monitored via telemetry. The remaining five adults were captured after data collection had ended, during additional trapping conducted to remove radio collars from members of the study population. Capture of these uncollared animals indicates that not all adults in the population were monitored via telemetry, which may have implications for estimates of home range overlap and co-occurrence (below). The number of radiocollared adults of each sex monitored per sampling period is shown in Fig. 2.

Most individuals were tracked during only one data collection period; two individuals (one male, one female) were tracked during two consecutive periods (dry and subsequent wet season) and three individuals (two females, one male) were tracked during three consecutive periods (two wet seasons plus the intervening dry season). To avoid pseudoreplication, only one home range per individual was included in our analyses of home range size; for animals monitored during more than one data collection period, only the home range estimated for the first data collection period was examined. Visual inspection of the data revealed that the home range size for one male monitored during the 2019 dry season was conspicuously larger than those for other animals; because the inclusion of this individual (M2 in Fig. 2; Supplementary Data S3) affected the selection of best-fit models (Aguinis et al. 2013), this animal was excluded from analyses of home range size. In contrast, the exclusion of this individual from analyses of home range overlap did not affect model outcomes and thus this animal was retained in our analyses of spatial overlap. For those individuals that overlapped spatially with the same conspecific(s) during more than one data collection period, only data from the first period were included in our analyses of home range overlap.

Home range size

Overall, mean home range size based on 95% AKDEs was 0.4 ± 0.5 ha (N = 19 animals). The best-fit GLM identified by our analyses (AICc Weight = 0.77; Table 1) included sex as a predictor of home range size. Consistent with this outcome, mean home range size for males (0.8 ± 0.6 ha, N = 7) was significantly greater than that for females (0.2 ± 0.2 ha, N = 12; Permutation t-test: $t = 3.05$; $P = 0.002$; Fig. 2). Similarly, the best-fit model identified for 50% AKDEs included sex as a predictor variable (AICc Weight = 0.67, Table 1); again, mean home range size for males (0.1 ± 0.1 ha, N = 7 males) was significantly greater than that for females (0.04 ± 0.05 ha, N = 12 females; Permutation t-test: $t = 2.78$; $P = 0.01$; Table 1, Supplementary Data S3). In contrast, neither season nor the interaction between sex and season were included in the best-fit model for either estimator (95% or 50% AKDEs) of home range size.

Home range overlaps

After applying the neighborhood criterion developed for each dyad type, 29 different pairs of individuals (14 MF pairs, 8 FF pairs, 7 MM pairs) were included in our analyses of home range overlap. Based on this data set, the absolute area of overlap between a pair of individuals was greater for 95% AKDEs compared to 50% AKDEs (Permutation of paired t-test: N = 29; $t = 2.1$; $P < 0.01$). Consistent with this finding, only 4 (13.8%) of the 29 pairs (3 MF, 1 MM) whose 95% AKDE home ranges overlapped also displayed overlap of 50% AKDE homes ranges, suggesting that most spatial overlap occurred near the periphery of individual home ranges.

Overall, mean percent pairwise overlap of 95% AKDEs was $21.2 \pm 30.2\%$ (N = 58 dyads composed of 10 females and 7 males). Mean percent overlap was greatest for

MF dyads ($39.6 \pm 36.6\%$, $N = 14$ dyads containing 4 females and 5 males), followed by MM dyads ($24.1 \pm 30.7\%$, $N = 14$ dyads containing 5 different males) and FM dyads ($12.6 \pm 21.6\%$, $N = 14$ dyads containing 4 females and 4 males), with overlap being least for FF dyads ($10.2 \pm 23.9\%$, $N = 16$ dyads containing 9 females). The best-fit model for percent pairwise overlap was the null model (AICc Weight = 0.61; Table 2), indicating that neither sex nor season were significant predictors of spatial overlap among individuals.

When home range overlap was assessed using Winner's index, the mean pairwise index value across all individuals was 0.2 ± 0.2 ($CI = 0.1-0.5$; $N = 29$ pairs containing 10 females and 7 males). Mean values were greatest for MM dyads (0.3 ± 0.2 ; $CI = 0.1-0.7$; $N = 7$ dyads containing 5 males), followed by MF dyads (0.2 ± 0.2 ; $CI = 0.1-0.5$; $N = 14$ dyads containing 10 females and 7 males), with FF dyads displaying the least mean overlap (0.1 ± 0.1 ; $CI = 0.03-0.4$; $N = 8$ dyads containing 9 females). The best-fit GLM for overlap index values was again the null model ($\Delta AICc > 2$; AICc Weight = 0.69; Table 2), indicating that neither dyad type or season were significant predictors of this metric of overlap between individuals.

Spatial relationships among adults

Individual males overlapped spatially with multiple females and vice versa (Fig. 2). After application of our neighborhood criterion, only two (11.7%) of the 17 animals (10 females, 7 males) for whom 95% AKDE home ranges were estimated failed to display any overlap with other adults. Although an additional five animals (17.6%) overlapped with just one conspecific, the majority of individuals monitored (70.5%) overlapped spatially with at least two different animals. The mean number of conspecifics overlapped

was 3.3 ± 2.4 (range = 0-8, N = 17). Nine females and five males were included in analyses of same-sex dyads, with seven females and six males included in analyses of opposite-sex dyads. Each male home range overlapped with that of at least one other male, with a mean of 2.4 ± 1.1 (range = 1-4, N = 5) overlapping males per individual. Among females, five (55.5%) of nine females overlapped with at least one other adult female; the mean number of overlapping females per individual was 0.7 ± 0.8 (range = 0-2, N = 9). When spatial overlap of opposite-sex adults was considered, the mean number of overlapping females per male home range was 1.6 ± 0.6 (range = 1-3, N = 6 males); the mean number of overlapping males per female home range was 1.8 ± 1.5 (range = 0-4, N = 7 females).

Co-occurrence of individuals.

Co-occurrence in space and time was examined for 21 pairs of individuals (February 2019: N = 9 pairs; August 2019: N = 8 pairs; October 2019: N = 1 pair; February 2020: N = 3 pairs) for which simultaneous radio fixes were obtained. Of the 1,260 distinct fixes (60 radio fixes per pair) recorded for these animals, only four (0.3%; N = 4 pairs of individuals) involved the co-occurrence of different adults. No more than two adults were detected at the same location at the same point in time; all examples of co-occurrence involved a male-female pair.

DISCUSSION

Our results reveal that although adult *C. laticeps* in Parque Estadual da Serra de Caldas Novas engaged in regular spatial overlap, multiple adults did not occupy the same burrow system. Indeed, while overlap of individual home ranges was detected for most adults

monitored, co-occurrence of individuals in space and time was rare and was limited to four male-female dyads. The extent of overlap between pairs of individuals did not vary with sex or season in which data were collected. Moreover, comparisons of results based on 95% versus 50% AKDEs indicated that overlap was largely restricted to the periphery of individual home ranges. Collectively, these findings suggest that although overlap of home ranges is common, patterns of space use by adults in the study population are not consistent with those for group living species of burrow-dwelling rodents (Lacey 2000; O'Brien et al. 2021). Instead, these results appear to reflect a colonial organization, in which generally solitary individuals live in close proximity to one another, leading to overlap of the areas occupied by different animals (Burda et al. 2000).

The short duration of this study combined with the limited number of animals monitored via telemetry may have resulted in a tendency for our data to underestimate the full extent of spatial overlap and co-occurrence by members of the study population. The capture of unmarked animals at the end of some sampling periods also suggests that we may have underestimated spatial overlap among adults. Collectively, these factors may have biased our interpretation of the spatial data in favor of a solitary social organization. Although we cannot exclude this possibility, several observations suggest that neither collection of additional data nor inclusion of unmarked individuals would have altered our overall conclusion that *C. laticeps* is generally solitary. First, only five uncollared adults were captured during this study, suggesting that a relatively limited number of individuals was not included in our data set. Second, capture localities for uncollared animals were generally associated with burrow systems other than those where radiocollared individuals were captured, thus reducing the likelihood of significant spatial overlap between collared and uncollared animals. Third, a more intensive capture-mark-recapture study conducted on a 1.7 ha subset of the study site from December 2018 to

February 2021 (C. Ferrando, pers. obs.) confirms the low population density reported here; this information supports the assertion that only a few individuals were missed in our analyses while also suggesting that low density may contribute to a generally solitary lifestyle (Kristen et al. 2008; Schradin et al. 2020). Finally, although failure to capture all individuals in a population is common in studies of free-living rodents, analyses of spatial relationships in other burrow-dwelling species have detected evidence of group-living even when not all animals were monitored (e.g., tuco-tucos: Lacey et al. 2019; O'Brien et al. 2020, degus: Ebensperger et al. 2004). Collectively, these observations suggest that although sampling of our study population was not complete, our failure to monitor all individuals is unlikely to have affected our overall characterization of spatial relationships among these animals.

Shared versus exclusive use of home ranges. – Our analyses revealed that overlap of individual home ranges was smallest between pairs of females, with overlap being greater for both male-male and male-female dyads. Areas of exclusive use are typically expected to encompass critical resources (Burt 1943, Kaufmann 1962) and thus the variation in spatial relationships detected here may reflect differences in the resources that are of greatest value to each sex. In particular, while the distribution of females may be driven primarily by food resources, the distribution of males may be driven by females (Emlen and Oring 1977; Davies 1991). Active defense of exclusive areas has been reported for females in multiple species of burrowing rodents (Festa-Bianchet and Boag 1982; Ims 1987; Travis and Slobodchikoff 1993; Vom Saal et al. 1995; Shier and Randall 2004), raising the possibility that female *C. laticeps* also actively defend the exclusive portions of their home ranges. Fresh wounds and scars have been observed on males in our study population (C. Ferrando, pers. obs.), providing indirect evidence of aggressive encounters

among members of this sex. Additional studies are needed to assess the role of aggressive interactions in maintaining spatial relationships in *C. laticeps*, including potential intersexual differences in the resources associated with such interactions.

Mating system of Clyomys laticeps. – Previous studies of *C. laticeps* suggest that these animals are characterized by a polygynous mating system (Ferrando et al. 2019). This inference is based on observations indicating that home ranges for males are typically larger than those for females (Ferrando et al. 2019), which may reflect efforts by males to gain access to multiple breeding females (McEachern et al. 2009; Lin et al. 2009). Although this pattern has been reported for other polygynous species of rodents (Cooper and Randall 2007; Adler 2011), it may also characterize polygynandrous systems in which both males and females mate with multiple members of the opposite sex (McEachern et al. 2009). With regard to home range overlap, both males and females in polygynandrous species may visit the areas occupied by potential mates (Steinwald et al. 2013), leading to the expectation that patterns of overlap should be more symmetric than those in polygynous systems. Actual patterns of overlap, however, vary greatly among polygynous species (Davies 1991) and both polygyny and polygynandry have been reported for other species of burrow-dwelling rodents (Winters & Waser 2003; Santos & Lacey 2010; 2011; Bergeron et al. 2011; Steinwald et al. 2013; Ebensperger et al. 2019), suggesting that either system is possible in our study population. Thus, although spatial data can provide insights into reproductive relationships, genetic analyses of parentage and kinship are needed to accurately characterize the mating system of our study population.

Social organization of Clyomys laticeps. – Previous studies have provided contradictory information regarding the social organization of *C. laticeps*. For example, Burda et al. (2000) described this species as social, which these authors defined as multiple adults sharing the same burrow system. Bezerra et al. (2016) characterized the animals as colonial, indicating that burrow systems and thus their inhabitants tend to be clustered within the habitat. Neither study included quantitative information regarding spatial or social relationships, making it challenging to evaluate these descriptions of the behavior of in *C. laticeps*. In contrast, analyses of population-level patterns of genetic variability in habitat similar to our study site (Arantes 2011) have been used to suggest that *C. laticeps* is solitary; this interpretation was also applied to spool-and-line tracking data for animals at our study site (Ferrando et al. 2019). The telemetry data examined here provided no evidence of regular burrow sharing and revealed few instances of spatial and temporal co-occurrence by adults, leading us to conclude that the animals tend to be solitary. Our findings are similar to those reported for other solitary, semi-fossorial species of rodents (*Arvicola terrestris*; Potapov et al. 2004; *Pedetes capensis*; Peinke and Brown 2005; *Dipodomys merriami insularis*; Vázquez and Alvarez-Castañeda 2011), lending support to our interpretation of the social organization of *C. laticeps*. Future studies conducted over larger spatial scales should help to clarify how individual- and population-level spatial relationships intersect to shape the social organization of this species.

Comparisons with other burrow-dwelling rodents. – Social organization varies greatly among burrowing rodents, ranging from species in which both sexes are solitary to species in which members of both sexes routinely share burrow systems (Ebensperger and Blumstein 2006; Randall 2007). Our analyses suggest that *C. laticeps* is characterized

by an intermediate organization in which individuals are not entirely solitary but adults do not live in spatially cohesive groups. Accordingly, the social organization of our study animals most closely resembles that of burrow-dwelling species such as the giant kangaroo rat (*Dipodomys ingens*: Cooper and Randall 2007) or Heermann's kangaroo rat (*D. heermanni arenae*: Shier and Randall 2004), in which a burrow system is occupied by only a single adult but spatial overlap (and hence presumably social interactions) among neighboring animals are relatively common. Ecological factors thought to influence the degree of sociality in these animals include predation pressures, the distribution of food resources, and the costs of burrowing; the relative importance of these factors is expected to vary across species, contributing to observed differences in social organization (Ebensperger and Blumstein 2006; Smorkatcheva and Lukhtanov 2014). To date, *Trinomys yonenagae* and *C. laticeps* are the only burrow-dwelling echimyids that have been studied with regard to social organization and mating system. Despite their phylogenetic proximity (Fabre et al. 2013), they differ with respect to social organization, with the former species having been described as group living (Santos and Lacey 2011). Future studies will explore the interplay of ecological factors and phylogenetic history in shaping social diversity within the Echimyidae and, more generally, all burrow-dwelling rodents.

ACKNOWLEDGMENTS

We would like to thank Neto J. E. and its family, for receiving us at their home, so we could do the first field trips. Ferrando M. A. and Röpke U. O. for lending us their car, so we could travel to the study site. Ferrando E. M. R., Rodrigues F. O., Toledo V. B., Bomfim P. M. S., Melo F. S. for helping in the field trips, especially Queiroga D. S.,

Figueiredo C. P. G., de Oliveira M. M. and Rossi R. C. for helping during the long nights of telemetry in the field. Szabó M. P. J. and its lab students for lending us the capture traps and improve the field procedures of animal manipulation. We also thank the Movement Ecology Group (Unesp Rio Claro/LEEC) for always being willing to help us with the spatial analyses. Our thanks to the Secretaria Estadual de Meio Ambiente e Desenvolvimento Sustentável de Goiás (SEMAD) for logistical support. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 and by Conselho Nacional de Desenvolvimento Científico (CNPq - PELD 403733/2012-0 and 442603/2014-2).

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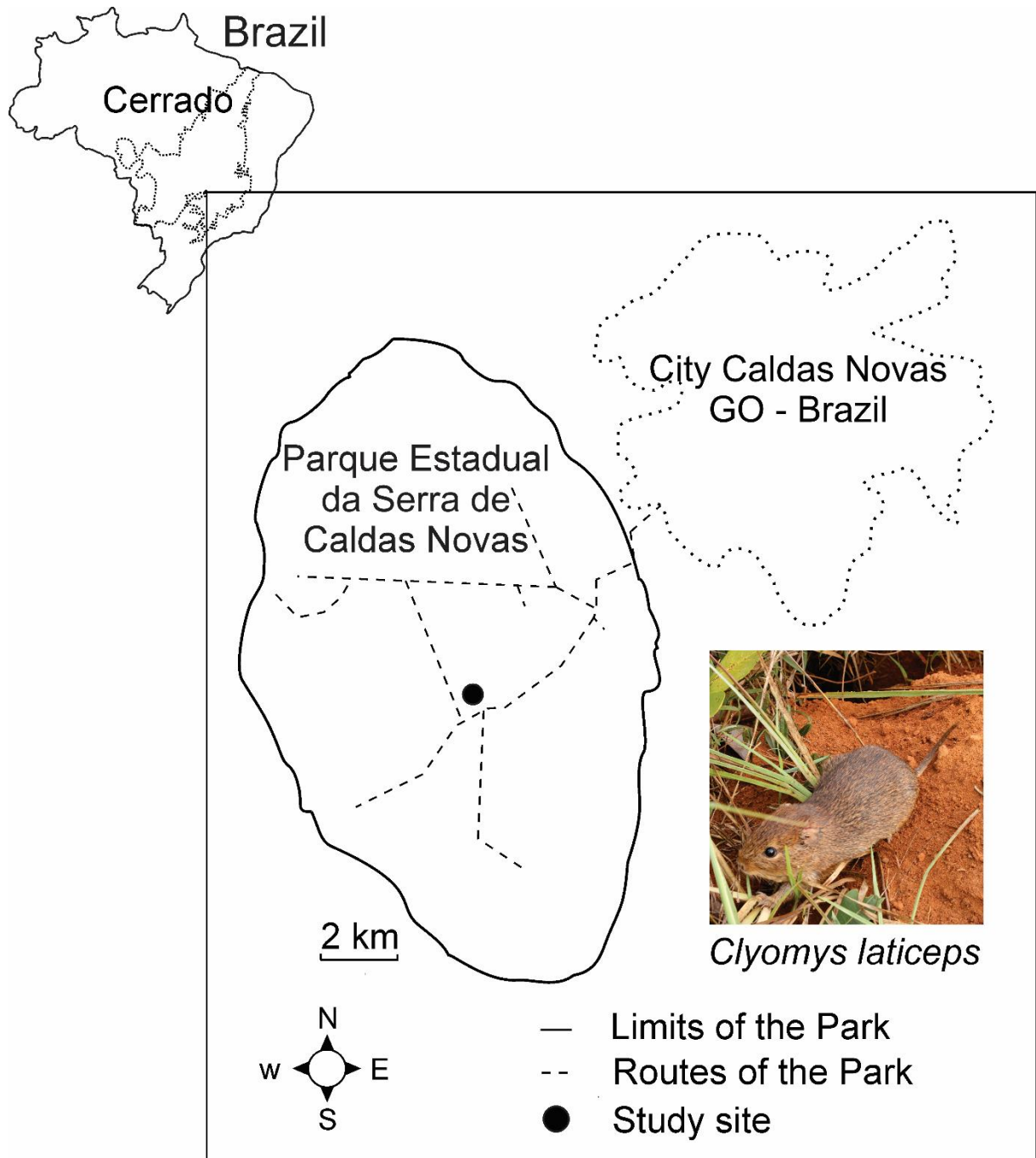


Figure 1. Map of Parque Estadual da Serra de Caldas Novas (PESCaN) in Goiás, Brazil ($17^{\circ}43'-17^{\circ}51'S$, $48^{\circ}40'-48^{\circ}44'W$). The location of the study site for *Clyomys laticeps* is indicated with a black dot. The site is located in the Cerrado biome in central Brazil.

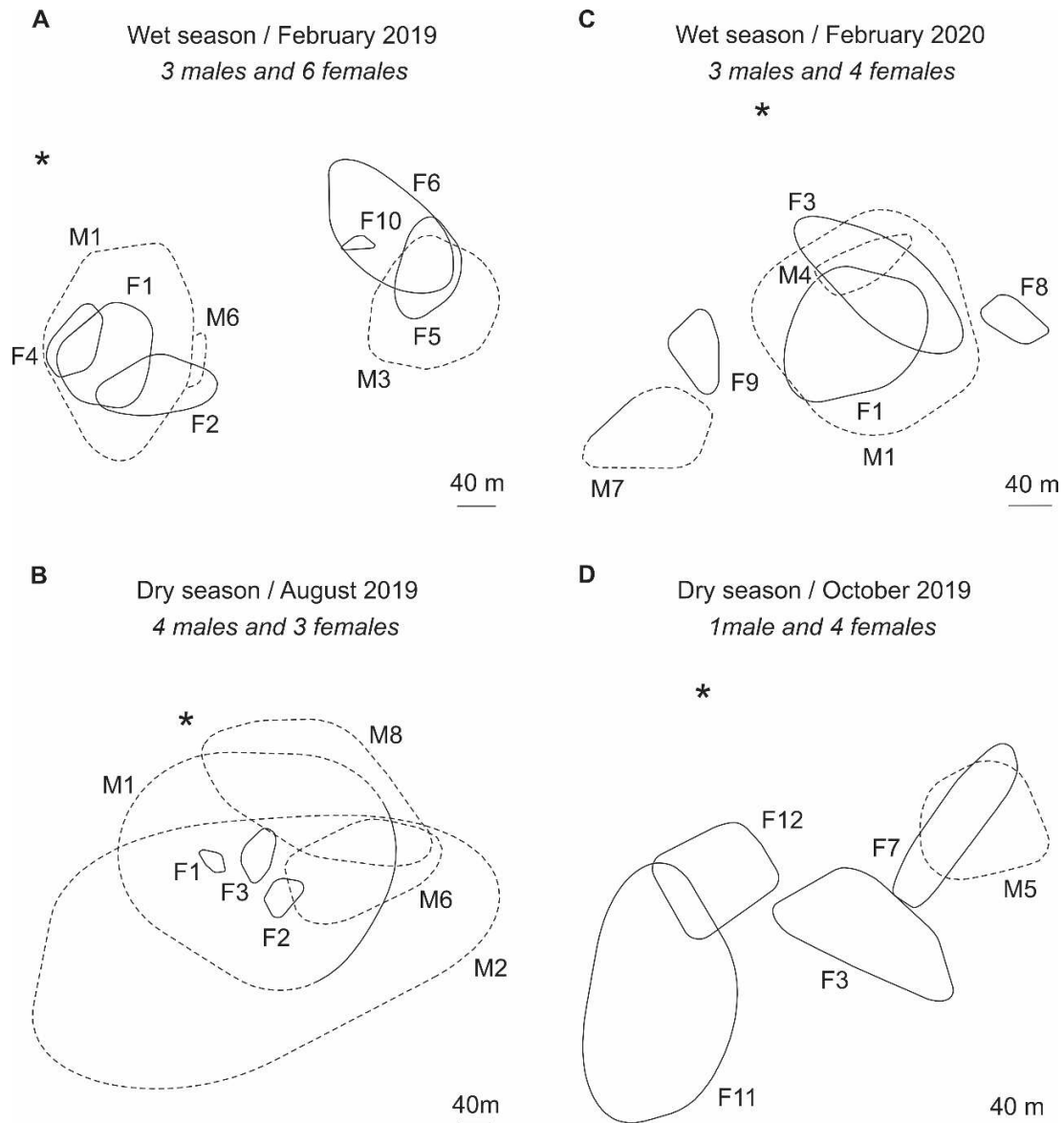


Figure 2. Plots of individual home ranges (100% AKDEs) for 12 adult female and 8 adult male *C. laticeps* monitored using radiotelemetry in Parque Estadual da Serra de Caldas Novas, Goiás, Brazil; 100% AKDEs are shown to facilitate visualization of the locations of smaller home ranges. Telemetry data were collected during four different sampling periods: (A) February 2019, (B) August 2019, (C) February 2020 and (D) October 2019. Sample sizes for each sampling period (number of adults monitored via telemetry) are indicated in the figure. Dotted lines denote the boundaries of male (M) home ranges; solid lines denote the boundaries of female (F) home ranges. The asterisk (*) indicates the location of a spatial reference point that was used during all sampling periods.

Table 1. Results of GLMs used to examine the effects of sex and season (wet or dry) on home range size. Sizes were determined based on 95% and 50% AKDE analyses of telemetry data obtained from 20 adult *C. laticeps* studied in Parque Estadual da Serra de Caldas Novas, Goiás, Brazil. Models were ranked according to Akaike's information criterion corrected for small samples (AICc, Burnham and Anderson 2002); models with the smallest AIC scores ($\Delta \text{AICc} \leq 2$; indicated in bold) were identified as the best-fit suite of predictors for home range size.

Factors (models)	K		AICc		ΔAICc		AICc Weight	
	95%	50%	95%	50%	95%	50%	95%	50%
Sex	3	3	353.75	294.48	0.00	0.00	0.77	0.67
Sex + Season	4	4	356.97	297.73	3.22	3.26	0.15	0.13
Null Model	3	2	362.62	297.72	8.87	3.24	0.13	0.13
Sex*Season	5	5	360.62	300.70	6.45	6.22	0.03	0.03
Season	2	3	359.92	300.48	6.17	6.00	0.04	0.03

Table 2. Results of GLMs used to examine the effects of dyad and season (wet or dry) values of home range overlap. Home ranges were based on 95% AKDEs constructed from telemetry data obtained from 19 *C. laticeps* monitored in Parque Estadual da Serra de Caldas Novas, Goiás, Brazil. Separate models were constructed with percent overlap and values of Winner's overlap index as response variables. Models were ranked according to Akaike's information criterion corrected for small samples (AICc, Burnham and Anderson 2002); models with the smallest AIC scores ($\Delta AICc \leq 2$; indicated in bold) were identified as the best-fit suite of predictors of the extent of overlap among individual home ranges.

Factors (models)	K		AICc		$\Delta AICc$		AICc Weight	
			Index	Overlap %	Index	Overlap %	Index	Overlap %
null model	1	1	25	53.35	0.00	0.00	0.69	0.61
Season	2	2	27.5	55.53	2.5	2.18	0.20	0.21
Dyad	3	4	28.9	56.28	3.9	2.93	0.10	0.14
Dyad + season	4	5	32.08	58.71	7.1	5.36	0.02	0.04

Supplementary Data S1. Mean values for home range size for 20 adult *C. laticeps* monitored via telemetry in Parque Estadual da Serra de Caldas Novas, Goiás, Brazil. Telemetry data were collected during four sampling periods completed between February 2019 and February 2020. Home ranges were estimated using 95% Minimum Convex Polygons (MCPs) (Mohr 1947) and the Kernel Density Estimator (KDE) (Worton 1989), as implemented in the “adehabitatHR” package (Calenge 2006) in R version 3.6.3 (R Core Team, 2020) and RStudio version 1.3.1073 (RStudio Team, 2020). For KDE estimates, we used the bivariate normal fixed-kernel method. The smoothing parameter h_{ref} was estimated for each individual ($h_{ref} \bar{x} = 9.16 \pm SD = 7.47$ m) and the mean reference value was assumed for construction of KDE homes.

	Home Range Size	Home Range Size
	KDE ha (95%)	MCP ha (95%)
Population (N = 20)	0.6 ± 0.3	0.3 ± 0.6
Male (N = 8)	0.6 ± 0.3	0.6 ± 0.8
Female (N = 12)	0.3 ± 0.09	0.08 ± 0.04

Supplementary Data S2. Mean values for area of overlap and percent pairwise overlap of home ranges for 20 adult *C. laticeps* monitored via telemetry in Parque Estadual da Serra de Caldas Novas, Goiás, Brazil. Telemetry data were collected during four sampling periods completed between February 2019 and February 2020. Home ranges were estimated using 95% Minimum Convex Polygons (MCPs) (Mohr 1947) and the Kernel Density Estimator (KDE) (Worton 1989), as implemented in the “adehabitatHR” package (Calenge 2006) in R version 3.6.3 (R Core Team, 2020) and RStudio version 1.3.1073 (RStudio Team, 2020). For KDE estimates, we used the bivariate normal fixed-kernel method. The smoothing parameter h_{ref} was estimated for each individual ($h_{ref} \bar{x} = 9.16 \pm SD = 7.47$ m) and the mean reference value was assumed for construction of KDE homes. Pairwise estimates of percent overlap for home ranges based on MCP and KDE estimators were generated from the area of intersection between home ranges; the area of intersection was calculated using the “gIntesection” function in the package “rgeos” (Bivand and Rundel 2020). For analyses of home range overlap, pairs of individuals were placed in one of the following categories of dyads: male-female (MF), female-female (FF), and male-male (MM). Because overlap may not be symmetric, MF dyads were defined as the % of a male’s home range that overlapped with a given female; FM dyads were defined as the converse, meaning the % of a female’s home range that overlapped with a given male. In all cases, N represents the number of individuals included in a given analysis (*next page*)

Absolute area of overlap (ha)			Percent pairwise overlap (%)		
Dyad	KDE (95%)	MCP (95%)	Dyad	KDE (95%)	MCP (95%)
Population	0.06 ± 0.09	0.01 ± 0.03	Population	13.1 ± 19.9	9.1 ± 22.5
N = 29	N = 18	N = 9	N = 58	N = 30	N = 18
MF	0.11 ± 0.0	0.03 ± 0.05	MF	22 ± 26.5	23 ± 35.2
N = 14	N = 8	N = 7	N = 14	N = 8	N = 7
FF	0.03 ± 0.03	0	FM	15.5 ± 23.7	11.7 ± 22.6
N = 8	N = 4	N = 0	N = 14	N = 8	N = 7
MM	0.04 ± 0.05	0.04 ± 0.007	FF	7.8 ± 10.2	0
N = 7	N = 6	N = 2	N = 16	N = 8	N = 0
			MM	7.9 ± 14	3.2 ± 10.9
			N = 14	N = 6	N = 4

Supplementary Data S3. Movement parameters and home range sizes for individual C. laticeps monitored via telemetry in Parque Estadual da Serra de Caldas Novas, Goiás, Brazil. Animals were tracked during four different periods representing two wet and two dry seasons: February 2019 (wet), August 2019 (dry), February 2020 (wet) and August 2020 (dry). For all individuals tracked, the best-fit movement model was one of the range-resident models (see Calabrese et al. 2016), although four individuals were characterized by DOF area less than 5, indicating greater uncertainty in the estimated home range areas for these animals. Asterisks (*) indicate animals for which DOF < 5. For each individual, estimates of home range size are shown based on 95% AKDE and 50% AKDE analyses.

Season / ID	Best Model Selected	DOF area	DOF bandwidth	AKDE ha (95%)	AKDE ha (95% CI)	AKDE ha (50%)	AKDE ha (50% CI)
Wet 2019							
F1	OU isotropic	19.04	28.14	0.45	(0.27 - 0.67)	0.12	(0.07 – 0.18)
F2_2	OU anisotropic	6.3	10.045	0.29	(0.11 - 0.56)	0.07	(0.02 – 0.13)
F4	OU anisotropic	20.07	31.19	0.15	(0.09 - 0.22)	0.04	(0.02 - 0.06)
F5	OU anisotropic	4.21*	5.19	0.28	(0.08 - 0.62)	0.07	(0.02 – 0.16)
F6	OU anisotropic	4.25*	5.48	0.63	(0.18 - 1.37)	0.16	(0.04 – 0.34)
F10	IID anisotropic	59.75	60	0.006	(0.005- 0.008)	0.001	(0.0009 - 0.001)
M1	OU anisotropic	28.64	41.65	1.31	(0.87 - 1.84)	0.20	(0.13 – 0.28)
M3	OU isotropic	29.29	42.84	0.79	(0.53 - 1.11)	0.17	(0.12 – 0.24)
M6	OU anisotropic	17.13	27.58	0.03	(0.02 - 0.05)	0.005	(0.003 – 0.007)
Dry 2019 Aug.							
F1_2	IID anisotropic	12.92	60	0.02	(0.01 - 0.04)	0.003	(0.002 – 0.004)

F3	OU anisotropic	22.22	34.22	0.10	(0.06 - 0.15)	0.01	(0.008 – 0.02)
M1_2	OU isotropic	5.12	6.69	4.52	(1.49 - 9.19)	1.23	(0.41 – 2.51)
M2	OUF anisotropic	5.073	5.917	8.26	(2.71 - 16.85)	1.93	(0.63 – 3.94)
M6	OU anisotropic	16.86	28.03	0.96	(0.56 - 1.48)	0.18	(0.10 – 0.27)
M8	OU anisotropic	18.54	29.96	1.94	(1.16 - 2.92)	0.36	(0.21 – 0.54)
Dry 2019 Oct.							
F2	OU anisotropic	34.44	46.09	0.06	(0.04 - 0.08)	0.01	(0.01 – 0.02)
F3_2	OU anisotropic	21.09	36.97	0.23	(0.14 - 0.34)	0.03	(0.02 – 0.05)
F7	OU anisotropic	19.21	35.04	0.15	(0.09 - 0.23)	0.02	(0.01 – 0.03)
F11	OU anisotropic	3.89*	5.19	0.61	(0.16 - 1.35)	0.15	(0.04 – 0.34)
F12	OU isotropic	43.34	51.40	0.13	(0.09 - 0.17)	0.01	(0.008 – 0.01)
M5	OU isotropic	11.3	17.04	0.23	(0.11 - 0.39)	0.06	(0.03 – 0.09)
Wet 2020							
F1_3	OU anisotropic	5.97	8.03	0.66	(0.24 - 1.28)	0.17	(0.06 – 0.32)
F3_3	OU anisotropic	5.88	7.39	0.56	(0.20 - 1.09)	0.14	(0.05 – 0.28)
F8	OU anisotropic	13.29	25.45	0.07	(0.04 - 0.12)	0.01	(0.007 – 0.02)
F9	OU anisotropic	15.13	27.85	0.11	(0.06 - 0.17)	0.01	(0.009 – 0.02)
M1_3	OU isotropic	20.63	31.12	1.71	(1.06 - 2.53)	0.46	(0.28 – 0.68)
M4	OU anisotropic	9.67	15.99	0.12	(0.06 - 0.21)	0.28	(0.01 – 0.05)
M7	OU anisotropic	27.49	38.77	0.33	(0.22 - 0.47)	0.06	(0.04 – 0.09)

CAPÍTULO 3

Intention for submission: Molecular Ecology

(citations and references format according to author guidelines of this journal)

Mating system and genetic structure of the solitary burrowing rodent *Clyomys laticeps* (Thomas, 1909)

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ABSTRACT

The degree of gene sharing among individuals in a population can provide valuable knowledge about animal behavioral strategies, such as of dispersal patterns and mating system. Understanding these components of animal social systems may help unraveling the mechanisms behind these behavioral strategies. Molecular techniques are especially useful to generate insights into dispersal patterns and mating systems of burrowing species, which are difficult to observe as the echimyid rodent *Clyomys laticeps*. In this sense, we intended to describe the genetic structure of a *C. laticeps* population, and test the following predictions: *C. laticeps* presents 1) a polygynandrous mating system with females having offsprings with different males, and 2) male-biased natal dispersal. Consequently, there is a 3) greater genetic structure among females than males and, 4) low inbreeding in the studied population. Fifty-three free-living *C. laticeps* were captured at Parque Estadual da Serra de Caldas Novas (GO, Brazil) between May 2018 and February 2020 and genotyped for 10 microsatellites. Genetic structure and kinship were estimated indicating that males and females of *C. laticeps* mated nonexclusively with one or multiple partners, structuring a mating system similar to a polygynandrous one. Both sexes presented natal dispersal, leading to a lack of sex-biased kin structure in the studied

population. We suggest that *C. laticeps* males could be dispersing to reduce kin competition for mates, while females may disperse to escape resource (food and burrow) competition. Moreover, dispersal and polygynandry seem to contribute to the low levels of inbreeding registered in *C. laticeps*.

Key words: Echimyidae; kinship structure; natal dispersal; polygynandry; semi-fossorial.

RESUMO

O grau de compartilhamento de genes entre indivíduos de uma população pode revelar informações relevantes sobre as estratégias de comportamento dos animais, como; de padrões de dispersão e sistema de acasalamento. A compreensão desses componentes do sistema social em animais pode ajudar a entender os mecanismos que regem essas estratégias comportamentais. Técnicas moleculares são especialmente úteis para o entendimento dos padrões de dispersão e sistemas de acasalamento de espécies que vivem no subterrâneo, as quais são difíceis de serem capturadas e observadas como o roedor equimídeo *Clyomys laticeps*. Nesse sentido, nosso objetivo foi descrever a estrutura genética de uma população de *C. laticeps* e testar as seguintes hipóteses: *C. laticeps* apresenta: 1) um sistema de acasalamento poliginândrico com fêmeas com filhotes de diferentes machos, e 2) dispersão natal desviada para machos. Consequentemente, ocorre 3) maior estrutura genética entre as fêmeas do que entre os machos e, 4) baixa endogamia na população estudada. Cinquenta e três *C. laticeps* de vida livre foram capturados no Parque Estadual da Serra de Caldas Novas (GO, Brasil) entre maio 2018 e fevereiro 2020 e genotipados. A estrutura genética a parentesco foram estimados e indicaram que os machos e as fêmeas de *C. laticeps* acasalaram com um ou mais parceiros de forma não

exclusiva, ou seja, compartilhando-os com outros indivíduos do mesmo sexo, configurando um sistema de acasalamento similar ao poliginândrico. Ambos os sexos apresentam dispersão natal, gerando ausência de estrutura de parentesco desviada para um dos sexos. Acreditamos que os machos de *C. laticeps* podem estar dispersando para reduzir a competição por parceiras com seus aparentados, enquanto as fêmeas podem estar dispersando para evitar competição por recurso (alimento e tocas). Ainda, a dispersão e a poliginandria parecem contribuir para os baixos níveis de endogamia observados em *C. laticeps*.

Palavras-chave: dispersão natal, Echimyidae; estrutura de parentesco, poliginandria, semi-fossorial

INTRODUCTION

Animal genetic mating systems vary in the number of reproductive partners per individual, ranging from monogamy (pair-bonding and single litter paternity) to polygynandry (multiple partners per individual and multiple litter paternity) in which there is no monopolization of partners by one of the sexes (Clutton-Brock 1989; Dobson *et al.* 2018). It mirrors the sex-specific mating strategies of the individuals of each sex for maximizing reproductive success (Trivers 1972; Emlen & Oring 1977; Waterman 2007), thus reflecting the result of sexual selection and contributing to genetic structure of populations (Ross 2001). Until recently, studies on mating systems in mammals have focused on males and overlook female strategies (Waterman 2007), following the sexual selection theory of females being the limiting sex and males competing for access to them (Trivers 1972; Shuster 2009). Consequently, most mammals have been described as

polygynous, where males monopolize and mate with multiple females, the latter mating with a single male (Clutton-Brock 1989; McEachern *et al.* 2009; Lin *et al.* 2009). However, genetic research has been unraveling multiple mating by females in previously polygynous described species, indicating that polygynandry is probably more common than previously thought (Spencer *et al.* 1998; Kitchen *et al.* 2006; Waterman 2007; Pérez-González *et al.* 2014). Thus, shedding light on species' mating systems and understanding the mechanisms driving their evolution is a key question in animal behavior and population ecology.

In mammals, animals that live in groups have been commonly described as polygynandrous, most likely via the improved access to mates as a consequence of nest sharing among adults (Santos & Lacey 2011; Ebensperger *et al.* 2019). Although fewer studies explored mating systems of solitary mammals (McEachern *et al.* 2009; Patzenhauerová *et al.* 2010), evidence suggesting the occurrence of polygynandry has increased with the advent of molecular techniques (Waterman 2007; McEachern *et al.* 2009). Apparently, features of population, such as density and kinship among individuals within an area, environmental attributes and species life-history shape the evolution of polygynandry among solitary species (Rychlik 1998; Randall *et al.* 2002; Winters & Waser 2003; Endries & Adler 2005). For example, in high density populations, individuals are spatially close to each other, promoting great overlap among them and increasing the costs of territory defense, thus leading to polygynandry (Dobson 1984). Moreover, a polygynandrous behavior may also be favored in animals with year-round reproduction living in areas where resources are available throughout the year (Rychlik 1998). Finally, multi-mating behavior may be a strategy to reduce relatedness between

mates when individuals do not engage in long distance dispersal, remaining in their natal site even after dispersal from natal nests (Winters & Waser 2003).

Social organization and mating system are frequently affected by dispersal patterns, presumably as an adaptive strategy to avoid competition for mates, food and/or to avoid inbreeding (Greenwood 1980; Dobson 1982). Natal dispersal has a critical role in shaping the genetic variation and promoting gene flow in natural populations (Cushman & Lewis 2010; Li & Kokko 2018), since dispersal results in the redistribution of organisms and their genes. Depending on which sex disperses, there will be differences in the kinship structure of males and females at breeding areas (Walker *et al.* 2008). In solitary, polygynous or polygynandrous mammals, natal dispersal is usually male-biased. Males disperse more frequently and further than females, resulting in populations with greater kinship structure among females than among males (Costello *et al.* 2008; Quaglietta *et al.* 2013). Thus, dispersal, as well as multiple partners breeding systems, are mechanisms that reduce inbreeding levels within a population by decreasing the chance of males and females reproducing with genetically incompatible mates (Long *et al.* 2008; Michalczyk *et al.* 2021; Liu *et al.* 2013).

Social behavior is poorly studied in the largest family of caviomorph rodents (Echimyidae) (Fabre *et al.* 2013; Herrera 2016). Indeed, social organization data are available for only 17 echimyids, ten of them described as solitary (Ebensperger & Hayes 2016), and mating system in this group ranges from monogamy to polygyny and polygynandry (Adler 2011). In some of these species, social and mating behaviors vary in response to environmental and demographic conditions such as population density or food distribution (Adler 2011; Maher & Burger 2011). In most cases, information on social behavior has been inferred solely from spatial data (Adler 2011). While such data reveal social interactions among individuals over limited time frames, they may not

capture information over longer time scales needed to understand movement of genetic materials. As a result, studies of the population genetic structure are also required (Hughes 1998).

Molecular techniques are especially useful to generate insights into dispersal patterns and mating systems of species, especially the burrower ones which are difficult to observe (Adler 2011; Santos & Lacey 2011; Ebensperger *et al.* 2019). Within echimyids, *Clyomys laticeps* is a burrowing, more specifically semi-fossorial, rodent distributed throughout the Pantanal and Cerrado regions of Paraguay and Brazil (Bezerra *et al.* 2016). Recent studies suggest a solitary habit, with individuals occupying exclusive burrow systems (Arantes 2011; Ferrando *et al.* 2019, Ferrando *et al.* In prep.). Moreover, spatial data obtained at Parque Estadual da Serra de Caldas Novas (GO-Brazil) indicate that males could mate with several females and vice-versa (Ferrando *et al.* 2019, Ferrando *et al.* In prep). However, genetic data are needed to confirm the interpretation of the mating systems of this population.

Therefore, the present study aims to unravel kinship relations within a population of *C. laticeps* to understand some of its social behavior. Based on the existing literature and spatial data obtained for this solitary burrowing rodent, we predict a 1) a polygynandrous mating system with female having offsprings with different males, and 2) male-biased natal dispersal. Consequently, there is a 3) greater genetic structure among females than males and, 4) low inbreeding in the studied population. Collectively, this information will provide the first detailed characterization of the social and genetic structures of *C. laticeps*, thereby providing the foundation for future studies aimed at identifying the extrinsic and intrinsic afactors associated with behavioral convergence and divergence among echimyid rodents.

MATERIALS AND METHODS

Study site and sampling

Free-living *Clyomys laticeps* were captured in grassland Cerrado habitat in Parque Estadual da Serra de Caldas Novas (PESCaN) in Goiás, Brazil (17°43'-17°51'S, 48°40'-48°44'W). A total of 12 field trips were carried out between May 2018 and February 2020 (every two months, except for May and June 2018) with a sampling effort of > 5,908 trap-nights. The project was approved by SISBIO (No:62336-2) and Ethics Committee on Use of Animals of the Federal University of Uberlândia, Brazil (No:001/19) and is consistent with the guidelines for animal research provided by the National Advice of Control and Animal Experimentation (CONCEA/Brazil 176/18) and the American Society of Mammalogists (Sikes *et al.* 2016).

Individuals were captured within an area measuring 200 m x 550 m. The animals were captured using Sherman traps (43 x 12.5 x 14.5 cm; Equipos Fauna) set at the entrances of active burrows (i.e., with signs of recent activity, such as soil removal, footprints, freshly consumed fruits, and fresh feces of *C. laticeps*) during ≥ 5 (maximum of 10) consecutive nights. Traps were baited with a mixture of peanut butter, banana, and oats and checked every morning. Captured individuals were marked with a numbered ear tag and the sex, body mass, and age class of each animal was estimated (adult: > 200 g, juvenile: > 100 g and pup: < 100 g; *et al.* 2019). For females, reproductive activity was determined by visual inspection of the genitalia, presence of swollen mammae and palpation of embryos. The location(s) of each individual captured was recorded with a GPS unit. Before releasing the individuals at the same point of capture, a small sliver of ear tissue (2mm from one ear pinna) (Santos 2010; Davis *et al.* 2015) was collected for

each individual, regardless of their age class, and preserved in EtOH 99.8% for genetic analysis.

Genotyping

Genetic analyses were conducted in the Laboratorio de Evolución at the Facultad de Ciencias, Universidad de la República (Montevideo, Uruguay). DNA was extracted from the ear samples of 56 *C. laticeps* individuals, following the modified protocol from Miller *et al.* (1988) and its concentration was quantified using nanodrop (NANODROP LITE Spectrophotometer, Thermo Scientific). After extraction, 1 µl of DNA and 1 µl of each primer were diluted in 500 and 10 µl, respectively, in distilled water. Genotyping was performed using ten microsatellite loci described previously for *C. bishopi* (Cbi 06, Cbi 07, Cbi 08, Cbi 11, Cbi 12, Cbi 14, Cbi 15, Cbi 16, Cbi 17, Cbi 18; Arantes *et al.* 2012) (Macrogen). The forward primer of each primer pair was labeled with a fluorescent dye (6-FAM or HEX). The loci were amplified using polymerase chain reactions (PCRs), consisting of 5 µl of GoTaq® Hot Start Master Mix (Promega), 2 µl of genomic DNA, 1 µl of each pair of primer (e.g. 0.5 µl Cbi 12 forward + 0.5 µl Cbi 12 reverse) and 2 µl of distilled water. In the case of the primers Cbi 6 and Cbi 11, only 1 µl of distilled water was used, since they were able to be mixed and amplify together since the PCR conditions were the same for both and they greatly differentiate in number of nucleotides. The PCR conditions were optimized from Arantes *et al.* (2012) for *Clyomys laticeps* and the final annealing temperatures are given in Table 1. PCR cycling conditions included 2 min of initial denaturation at 94°C followed by 35 cycles of the following: 20 s at 94 °C, 20 s of annealing at the appropriate temperature for each locus (Table 1), 20 s at 72°C to amplify the microsatellite fragments, finishing with 4 min at 72 °C. In the case

of primer Cbi7, two annealing temperatures were necessary; 64 °C and 63 °C in this sequence and with 10 and 25 cycles, respectively (Table 1).

All the PCR products were electrophoresed on polyacrylamide gels for 20 min at 170V, and visualized in silver staining using the modified protocol of Sanguinetti *et al.* (1994). The size of PCR products was estimated visually via comparison with a 100bp DNA size standard (RAINBOW Bioron). Successful amplifications were analyzed by electrophoresis on an ABI 3130 Genetic Analyzer housed in the Unidad de Biología Molecular of the Institut Pasteur (Montevideo, Uruguay). A LIZ600 size standard was included in all lanes. The fragment sizes were determined and genotypes were assigned using the Peak Scanner Software v1 software (Applied Biosystems).

Analysis

Genetic summary statistics

To calculate standard measures of genetic diversity such as the number of alleles per locus (N_a), and observed and expected heterozygosities (H_o and H_e), GenAlex 6.51 software (Peakall and Smouse, 2012) was used. The genotypes were tested for departures from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) at each locus within the population using GENEPOP on the web version 4.0 (Raymond & Rousset 1995), with significance levels set at $\alpha < 0.05$ with a Bonferroni correction for multiple tests (Rice 1989). For these tests, we did a probability test using Markov chain parameters, in which the dememorization number, number of batches and iterations per batch were 1,000, 100 and 1,000, respectively. Moreover, all loci were checked for null alleles with the Microchecker software (van Oosterhout *et al.* 2004). The mean polymorphic information content (PIC) was estimated with the use of the Cervus 3.0 software

(Marshall *et al.* 1998; Kalinowski *et al.* 2007). After HWE and LD tests, and identity analysis using Cervus was performed to ensure each sample corresponded to a unique individual and it revealed an exact match between two females, and fuzzy matches between three females (they shared five to seven loci, thus indicating that they probably were all the same individual). Thus, these five females were considered as two, based on genetic and captured data that reinforced our decision.. FSTAT 2.9.4 (Peakall & Smouse 2006, 2012) was used to calculate the inbreeding coefficient of the population (F_{IS}) (Goudet 2003), which varies from -1 to +1 (excess and deficit of heterozygotes in the population, i.e., exogamy and endogamy, respectively). The P-value for F_{IS} within samples was based on 160 randomizations. For this analysis only adult individuals were included, since they already dispersed from their natal home.

Population genetic structure and dispersal pattern

Considering only *C. laticeps* adults, an analysis of spatial genetic structure (SGS) was carried out in GenAlEx 6.5 (Peakall & Smouse 2006, 2012), which calculates an autocorrelation coefficient r . GenAlEx constructs spatial autocorrelograms based on pairwise geographic and genetic distance matrices, thus providing a measure of genetic similarity between pairs of individuals whose geographic distance falls within a specified distance class, represented by the autocorrelation coefficient r . Positive or negative r values indicate non-random genetic structure, while $r = 0$ means that there is a random distribution of genotypes in space. We generated autocorrelograms assuming even distance classes. Test for heterogeneity was used for the overall correlogram significance (α of 1% - Banks & Peakall, 2012) and for each distance class by random permutations (= 9999 permutations/test). We examined spatial autocorrelation using 145 m as the

standard distance class because it corresponds to the closest value to average neighborhood distance among adults in the studied population (161 m) (C. P. R. Ferrando, pers. comm.), thus contemplating the minimum and maximum distance between the studied individuals.

For the geographic matrix, each individual was assigned as a single geographic point in space. Since some individuals were captured more than once and tracked with telemetry, their single geographic point was defined as the mean value of all their radio fixes (different X and Y GPS coordinates, in UTM format), thus providing a more accurate geographic point in space. Finally, we failed to compare the genetic and geographic distance between sexes, due to small sample size.

Moreover, the mean values of relatedness among dyads of adults (male-male, male-female, female-female) of a population can contribute to natal dispersal pattern understanding, e.g. sex-biased dispersal leads to a higher mean value of relatedness to the philopatric sex, while both sex dispersal or philopatry leads to mean value of relatedness close to 0 or 1, respectively. The pairwise genetic relatedness, i.e. coefficient of relatedness (r), among *Clyomys laticeps* adults was estimated using the maximum likelihood algorithm in ML-RELATE (Kalinowski *et al.* 2006). ML-RELATE was selected because it employs a maximum likelihood approach and accommodates null alleles (when present) by estimating relatedness or relationship (Kalinowski *et al.* 2006). The coefficients of relatedness (r) ranges from 0 (not related) to 1 (highly related). Mean relatedness of each dyad type was compared through PERMANOVA (2,000 permutations/test) using package “permuco” (Frossard & Renaud 2021) once relatedness did not follow normal distribution.

For analysis of sex-biased dispersal using FSTAT (Goudet *et al.* 2002) based on the mean of AIC (mAIC), only adult individuals were considered for the same reason as

for the endogamy test (previous described). The assignment index (AI) calculates the likelihood of finding a particular genotype in the population from which it was sampled, after correcting for population differences (AIC) (Favre *et al.* 1997). The AIC are distributed around a mean of zero, with immigrants and residents presenting negative and positive AIC values, respectively (Favre *et al.* 1997). Hence, the more philopatric sex tends to display higher mean AIC (positive values) compared to the dispersing sex (Favre *et al.* 1997). The significance of sex-specific differences in the mean values of AIC was determined using 1,000 randomizations.

Parentage assignment

We used the software COLONY v. 2.0 (Jones & Wang 2010) to assign paternity and maternity to all offspring captured. The software assumes loci in Hardy-Weinberg and linkage equilibrium and employs a likelihood approach, thus accommodating genotyping errors in parentage assignments (Jones & Wang 2010). By performing pedigree reconstruction, COLONY allows 1) parentage assignment from the candidate mothers and fathers, 2) assignment of parents to those offspring whose parents were not sampled, and 3) clustering (half-)siblings sharing the same, non-genotyped parent. In addition, COLONY uses a full-pedigree likelihood approach over the entire pedigree configuration, in which parentage and sibships are inferred jointly and assigned with probabilities (Jones & Wang 2010).

Because *C. laticeps* individuals mate and reproduce throughout the year (Ferrando *et al.* 2019), all captured individuals were pooled in a single analysis, with adults being assigned as parents and pups and juveniles assigned as offspring. Actually, individuals in juvenile age were seldom recaptured more than once, indicating that they probably

disperse from the natal burrow system before becoming adults. COLONY was run under a non-restrictive criterion considering a polygamous system for both sexes, without inbreeding ($F_{IS} = -0.019$, this study) and clone. Analyses to calculate the assignment probabilities for parentage and sib-ship were performed according to the full likelihood method, with a single run of medium length and error rate of 0.01. The random number seed was 1000 and the probability of a father or mother within the candidates was assumed as 0.85 and 0.90, respectively. We assumed as the parentage result that described in the best pedigree configuration output.

Moreover, we estimated the approximate time of birth of each pup based on sequential pup recaptures until the juvenile age class and their changes in body mass over two months (growth rate). This data enabled visualization of pups born at the same time or within a small time frame, thus allowing inferences about whether those pups born from a same female and together, shared paternity or not.

RESULTS

Genetic summary statistics

We genotyped all 53 individuals of *C. laticeps* (females: 18 adults and 15 young; males: 11 adults and 9 young). using the 10 loci. Comparisons of observed and expected heterozygosities revealed significant deviations from Hardy-Weinberg expectations in locus Cbi 15 (Table 1) and evidence of linkage disequilibrium was detected for the pairs Cbi 11 and Cbi 06 ($P \leq 0.005$, after Bonferroni correction). The locus Cbi 15 was therefore excluded from the analysis as well as locus Cbi 11, since it had less number of alleles than Cbi 06, thus remaining 8 loci for testing the study's hypotheses. As for the presence of null alleles, there was evidence in the locus Cbi 06, however, it was not

required to be excluded since nowadays software deals with the presence of different types of errors in loci. The average of genetic diversity for all 10 loci was $H_o = 0.74 \pm 0.12$ and $H_e = 0.74 \pm 0.13$, number of alleles $N_a = 8.8 \pm 4.24$ (Table 1) and of $PIC = 0.71$. After removing two loci the average of genetic diversity for all 8 loci remained used in the analysis was $H_o = 0.73 \pm 0.14$ and $H_e = 0.72 \pm 0.14$, number of alleles $N_a = 8.12 \pm 4.12$ and $PIC = 0.71$. Finally, the *C. laticeps* population presented a mean $F_{IS} = -0.019$ which wasn't statistically significant (Bonferroni correction: $P > 0.006$), indicating no evidence of endogamy.

Population genetic structure and dispersal pattern

To evaluate population genetic structure, the adults ($N = 29$) were represented by 18 females and 11 males. The spatial genetic structure, the maximum distance between adults was 577 m, thus the sample size of pairs of individuals of the first (145 m), second (290 m), third (435 m) and fourth (580 m) distance classes were, 141, 174, 71 and 20, respectively. The correlogram was not statistically significant ($P = 0.046$). Regarding each distance class, none of them presented significant autocorrelation (145 m: $r = 0.021$, $P = 0.033$; 290 m: $r = -0.009$, $P = 0.823$; 435 m: $r = -0.011$, $P = 0.729$; and 580 m: $r = -0.036$, $P = 0.861$), providing no evidence of spatial genetic structure in the studied population. The mean population pairwise measures of relatedness was $\bar{x} = 0.06 \pm SD = 0.10$ ($N = 406$ pairs, and it did not differ between dyad types (PERMANOVA: $F_{2,403} = 0.894$, $P = 0.404$ – MM, $\bar{x} = 0.05 \pm SD = 0.11$, $N = 55$; FF $\bar{x} = 0.05 \pm SD = 0.09$, $N = 153$, and FM $\bar{x} = 0.06 \pm SD = 0.10$, $N = 198$). Regarding dispersal pattern, there was no indication of sex-biased dispersal in the population, as A_{Ic} mean did not significantly differ between adult females ($A_{Ic} = -0.05$) and males ($A_{Ic} = 0.082$) ($P = 0.577$).

Parentage assignment

COLONY attributed 11 different males and 15 females as parents to the 25 captured pups and juveniles. Based on the mean growth rate estimated for every two months (34 g), it was possible to identify five females (33 %) sharing paternity of their litter at the same time (i.e. three females with one male and the other two with another male), while only one female (6 %) had a litter composed of two pups, each belonging to a different male. Most of the females were identified to give birth to only one individual at a time (93 %; N = 14), indicating that *C. laticeps* presents a monotocy breeding.

Thus, as *C. laticeps* is mainly monotocus (singleton births) and has a non-seasonal reproduction (Ferrando et al. 2019), leads to higher level of complexity regarding its mating system characterization, since we cannot rely on the most common references for mating system classification used (i.e. litter paternity pattern or number of partners per breeding season). Thus, in the case of this work, we classified the mating system based on number of partners each individual had during the study period.

Only two pairs (8%) (N = 25) were monogamous (i.e. a single male and a single female mate exclusively). Moreover, there was only one polygynous (one male mating with two females) and none polyandrous mating. Thus, 73% of males (N = 8) and 87% of females (N = 13) had no exclusive partners, sharing them with the conspecifics of the same sex. Within males, 46% mated with 2 to 4 females and 25% of the females with 2 to 4 males. However, there was no significant difference in the mean number of mates ($\bar{x} = 1.6 \pm SD = 1$) between females ($\bar{x} = 1.4 \pm SD = 0.8$) and males $\bar{x} = 1.9 \pm SD = 1.2$) (Permutation t-test: $t = 1.27$; $P = 0.279$; N = 13). COLONY indicated that 18% (N = 2) of the males (N = 11) mated more than once with a same female, while 20% (N = 3) of the females (N = 15) mated with the same male, and only one female mated exclusively

with a male more than one sequential occasions (i.e. three occasions), regardless of the monogamous pairs.

DISCUSSION

Our results of a free-living population of *Clyomys laticeps* indicated that males and females mated nonexclusively with one or multiple partners, configuring a mating system with absence of monopolization of partners by one of the sexes, as polygynandry. Regarding dispersal, our results failed to provide evidence supporting male-biased dispersal as in most mammals. Actually, both sexes presented natal dispersal, leading to a lack of genetic and kinship structure among males or females. Moreover, dispersal and polygynandry seem to contribute to the low levels of inbreeding registered in *C. laticeps*.

Previous studies with *C. laticeps* suggested a polygynous or either polygynandrous mating system, based on daily home range size patterns and spatial overlap data, respectively (Ferrando *et al.* 2019; Ferrando *et al.* In prep.). The genetic data provided evidence of monogamous, polygynous and polygynandrous mating systems within the studied population. Mixed patterns of mating systems have already been reported in mammals, including solitary burrowing rodents (Roemer *et al.* 2001; Kitchen *et al.* 2006; McEachern 2009; Patzenhauerová *et al.* 2010; Bergeron *et al.* 2011; Ebensperger *et al.* 2019). Although multiple matings occurred in only 46% of the males and 25% of the females, most individuals shared their reproductive partners with other individuals of the same sex (73% of the males and 87% of the females), suggesting that polygynandry is the most common mating system in the studied population, thus reinforcing the spatial overlap data.

Although polygynandry is more likely to occur in social and/or high density populations (Endries & Adler 2005; Ebensperger *et al.* 2019), we found evidence of this mating system despite *C. laticeps* solitary behavior and low population density (Ferrando *et al.* In prep.). Indeed, in some solitary species, some level of low density may facilitate extra pair copulation when males are not able to effectively monopolize multiple females (Waterman 2007; McEachern *et al.* 2009). This appears to be the case in the population studied, in which some males and females mated more than once with the same partner, but they also presented extra-pair copulations. These mating patterns resemble the ones previously described in eastern chipmunks (*Tamias striatus*), which presents a type of polygyny and extra-pair polyandry (Bergeron *et al.* 2011), and the giant kangaroo rat (*Dipodomys ingens*), in which males attempt to defend/monopolize females but sometimes without success, occurring polygynandry (Randall 2002). Hence, it appears that while *C. laticeps* males try to monopolize breeding partners and may be successful in a few cases, females engage in multiple and extra-pair copulations. Indeed, along a telemetry study in the same population, we observed that males do not seem to present their own burrows, but instead wander around burrows throughout the day, visiting several female burrow systems. This behavior seems to reflect their attempts to maximize the number of breeding partners and consequently their reproductive success (Clutton-Brock 1989). Additionally, the year-round, asynchronous reproduction by *C. laticeps* could (Ferrando *et al.* 2019), as well as the sexual monomorphism in the species (Ferrando *et al.* in prep.), may be factors contributing to impair female monopolization by males and consequently favor female multiple mating (Emlen & Oring 1977; Clutton-Brock & Parker 1992; Waterman 1998; Schulte-Hostedde *et al.* 2004; Cooper *et al.* 2011), however, this assumption need to be tested in future studies.

Females have been assumed as passive participants in male copulation attempts, as their reproductive success was mainly associated to offspring production and survival (Solomon & Keane 2007; Waterman 2007). However, females can also engage in multiple mates, whenever the benefits of this strategy overcome the costs for them (Jennions & Petrie 2000; Wolff & Macdonald 2004; Simmons 2005). Multi-male mating (MMM) may present several benefits: 1) decreases the risks of infanticide, through paternity uncertainty, 2) contributes to female mate choice, through sperm competition and inbreeding avoidance, and 3) increases litter size and the fitness and genetic diversity of offspring (Jennions & Petrie 2000; Wolff & Macdonald 2004; Simmons 2005). As *C. laticeps* frequently produces a single young (monotocy), extra-pair copulations by females are probably not related to a strategy for paternity uncertainty to counter infanticide, to increase the litter size or genetic diversity. However, since exceptions already were registered in mammals (Wolff & Macdonald 2004), they should not be overlooked in future studies in *C. laticeps*. Ultimately, MMM has been reported as a strategy to avoid inbreeding (Michalczyk *et al.* 2011), which was suggested for some burrowing rodents (Winters & Waser 2003; Bergeron *et al.* 2011; Liu *et al.* 2013). Although future studies should investigate the mechanisms driving this behavior among *C. laticeps* females, our results suggest that polygynandry may contribute to the low levels of inbreeding found in the studied population.

Multiple factors, working alone or simultaneously, can affect an individuals' decision to disperse or remain philopatric (Lawson Handley & Perrin 2007). Among mammals, males commonly disperse and females remain philopatric (Greenwood 1980; Lawson Handley & Perrin 2007), producing differences in kinship among males versus females in breeding areas (Lacey 2016). Usually, the degree of sociality determines the magnitude of sex-biased dispersal (Greenwood 1980), with the strongest male-biased

dispersal among polygynous, social mammals (Smale *et al.* 1997; Devillard *et al.* 2004), although a bias towards male dispersal may also occur among solitary, polygynous rodents (Lawson Handley & Perrin. 2007). In the studied population, both males and females disperse from their natal site (study area), which is an uncommon pattern among mammals (Lawson Handley & Perrin 2007). However, a few mammals present contrasting patterns, as female-biased dispersal (Walker *et al.* 2008), lack of dispersal (Winters & Waser 2007) and dispersal performed by both sexes (Sarno *et al.* 2003). There are three most studied selective pressures that favor dispersal 1) resource availability, 2) kin competition avoidance and 3) inbreeding avoidance (Perrin & Mazalov 2000). Hence, dispersal by both sexes is expected when local competition equally affects males and females, as long as female fitness is limited by extrinsic factors (breeding resources) (Perrin & Mazalov 2000). *Clyomys laticeps* males could be dispersing to reduce kin competition for mates, while females may disperse to escape resource (food and burrow) competition. Irrespective of the mechanisms driving dispersal, this behavior precludes differences in kinship structure between sexes, at least on a local scale, and promotes inbreeding avoidance in the studied population. However, we cannot exclude the possibility that differences between the sexes occur on a greater spatial scale, regarding dispersal distance (Lawson Handley & Perrin 2007), especially when we take into account that males are more vagile than females (Ferrando *et al.* 2019). Hence, future studies should provide more detailed information on dispersal patterns of *C. laticeps* and investigate the selective pressures determining these patterns.

Our study reinforces how molecular data can be a useful tool to unravel several aspects of animal social behavior, as demonstrated by this first detailed characterization of the social and genetic structures of *C. laticeps*. Overall, a polygynandrous mating system coupled with natal dispersal by both sexes could have implications for *C. laticeps*

population persistence at the study site, despite its low density and small litter size (singleton). Indeed, both behaviors may increase genetic diversity and minimize the risks of inbreeding depression in the population. The Echimyidae offers a good model taxon to test hypotheses about the evolution and implications of mating and dispersal strategies for mammalian population genetic structure, as this group represents the most speciose and ecologically diverse family of Caviomorpha (Fabre *et al.* 2013), and display a wide array of context-dependent mating systems (Herrera 2016). However, so far, to our knowledge, detailed information (genetic and spatial data) about social system among burrow-dwelling echimyids has only been described for the semi-fossorial rodent *Trinomys yonenagae*. It presents male-biased dispersal and lives in kin groups, in which relatedness among adult females is greater than that among adult males or male-female pairs (Santos 2010; Santos & Lacey 2011). Regarding the mating system, *T. yonenagae* converges with *C. laticeps*, as both present a polygynandrous behavior (Santos 2010; Santos & Lacey 2011). In this way, future studies about the genetic structure of echimyid species are needed to build up the diversity of social behavior in this group and to understand the drivers behind this diversity.

ACKNOWLEDGEMENTS

We would like to thank J. E. Neto and its family, for receiving us at their home, so we could do the first field trips. M. A. Ferrando and U. O. Röpke for lending us their car, so we could finish our study. E. M. R. Ferrando, F. O. Rodrigues, V. B. Toledo, P. M. S. Bomfim, F. S. Melo for helping in the field trips, especially D. S. Queiroga, C. P. G. Figueiredo, M. M. de Oliveira and R. C. Rossi for spending also the long nights in the field. M. P. J. Szabó and its lab students for lending us the capture traps and to improve the field study. We also thank C. Biondo and G. Schmaedecke for introducing us how to

use genetic analysis programs. We thank all the people that contributed to the crowdfunding “O preço da genética” that made it possible to cover the genetic costs of this study. Moreover, E. P. Lessa to allow us to use the infrastructure of his laboratory (Laboratorio de Evolución – Universidad de la Republica, Uruguay) as well as P. E. A. M. de Oliveira for all the bureaucracies required for the internship process. We also thank the Secretaria Estadual de Meio Ambiente e Desenvolvimento Sustentável de Goiás (SEMAD) for logistical support. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. This study has also the financial support of Conselho Nacional de Desenvolvimento Científico (CNPq - PELD 403733/2012-0 and 442603/2014-2).

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Table 1. The genetic diversity found in *Clyomys laticeps* at Parque Estadual da Serra de Caldas Novas (GO, Brazil) for 10 microsatellite loci . Ta: Annealing temperature used (°C); Allele size range = PCR product size (bp); Na = n° of different alleles; Ho = observed heterozygosity; He = expected heterozygosity; H-W *P-value* = *P-value* of Hardy-Weinberg equilibrium. In bold, significant values after Bonferroni correction (≤ 0.006).

Locus	Fluorescent Dye	Ta (°C)	Allele size range (bp)	Na	Ho	He	H-W <i>P-value</i>
Cbi06	FAM	60	148 - 270	15	0.755	0.860	0.0512
Cbi07	FAM	64 & 63	260 - 280	8	0.736	0.812	0.0132
Cbi08	HEX	54	179 - 213	12	0.868	0.875	0.1638
Cbi11	FAM	60	132 - 172	6	0.491	0.558	0.1078
Cbi12	FAM	60	76 - 120	4	0.830	0.650	0.1074
Cbi14	FAM	54	142 - 162	8	0.774	0.806	0.7400
Cbi15	HEX	58	123 - 163	15	0.792	0.841	0.0021
Cbi16	FAM	57	200 - 244	11	0.887	0.867	0.7321
Cbi17	FAM	58	171 – 183	4	0.698	0.641	0.8667
Cbi18	HEX	57	221 - 235	5	0.585	0.556	0.8563

DISCUSSÃO GERAL E CONCLUSÕES

Estudos sobre aspectos da história de vida assim como do sistema social das espécies contribuem para melhor entender as suas estratégias comportamentais e reprodutivas no ambiente em que vivem (Blumstein et al. 2010; Clutton-Brock 2021). Tais estratégias refletem um balanço energético, visando maximizar sucesso reprodutivo sem incorrer em custos excessivos associados aos seus comportamentos (Ha 2010; McGlynn 2010). No presente estudo, aspectos da história de vida, padrões espaciais e dados genéticos revelaram que indivíduos de uma população de vida livre do roedor semi-fossorial *Clyomys laticeps* apresentam comportamento solitário (provável colonial) e sistema de acasalamento poliginândrico em uma área de campo sujo de Cerrado. A co-ocorrência entre os indivíduos de *C. laticeps* foi rara e limitada entre macho – fêmea e a sobreposição espacial restrita à periferia das áreas de vida, indicando um hábito de vida solitário em que cada galeria subterrânea é ocupada por um único indivíduo adulto, corroborando estudos anteriores (Arantes 2011, Ferrando et al. 2019). Tanto machos quanto fêmeas copularam com múltiplos parceiros, compartilhando tais parceiros entre si, indicando um sistema poliginândrico na população estudada.

A organização social nos roedores escavadores é resultado de um processo multifatorial em que risco de predação, distribuição e qualidade do alimento, atributos do solo e densidade populacional podem atuar como fatores relevantes (Lacey 2000; Ebenpserger 2001; Ebenpserger & Blumstein 2006). Apesar de não termos testado diretamente o efeito destes fatores sobre a evolução e manutenção do sistema social encontrado em *C. laticeps*, dados de história natural nos fornecem pistas sobre a atuação dos mesmos e indicam linhas de pesquisa futuras para compreender quais mecanismos podem ser responsáveis pelo comportamento solitário nessa espécie. Um possível

mecanismo que merece atenção, em estudos detalhados no futuro, diz respeito ao papel das propriedades do solo, em especial a dureza, conforme já demonstrado para outros roedores escavadores (Ebensperger & Bozinovic 2000; Ebensperger & Blumstein 2006). Os animais procuram viver em grupo quando o custo energético per capita da construção de galerias subterrâneas é muito alto em virtude da dureza do solo, afetando assim negativamente o sucesso reprodutivo de cada indivíduo (Ebensperger & Bozinovic 2000; Ebensperger & Blumstein 2006). Na população estudada, o aumento da dureza do solo não influenciou a atividade de escavação de novas tocas por *C. laticeps*, indicando que a dureza do solo não é um fator limitante para a construção das galerias e que os atributos do solo na área estudada possibilitam uma vida solitária. Porém, uma vez que *C. laticeps* apresenta ampla distribuição geográfica (Patton et al. 2015; Bezerra et al. 2016), estudos específicos sobre o efeito das características do solo sobre a organização social de *C. laticeps* são necessários e oportunos.

A vida solitária tende a ser favorecida em contextos de baixo risco de predação e distribuição homogênea do recurso, dado que a defesa dos predadores e do alimento são energeticamente dispensáveis (Alexander 1974; Slobodchikoff 1984; Schradin 2006). Porém, dentro do sistema estudado, não foi possível avaliar a pressão de predação ou a disponibilidade, distribuição e qualidade dos alimentos consumidos sobre os roedores. Ferrando et al. (2019) não observou mudança no uso do espaço pelo *C. laticeps* em relação à variação da oferta de frutos da palmeira *Allagoptera campestris* na mesma área de estudo e sugere que os indivíduos variam na proporção dos itens alimentares consumidos ao longo do ano, uma vez que apresentam uma dieta herbívora ampla (contendo raízes, frutos, sementes e gramíneas - Almeida & Galetti 2007; Ferrando et al. 2019). Dessa forma, em conjunto com a evidência de uma reprodução durante o ano todo em *C. laticeps* (Ferrando et al. 2019; presente estudo), supomos que o alimento não seja

um fator limitante que poderia favorecer a tolerância de uma vida em grupo. No entanto, se esse princípio ocorre em *C. laticeps* requer estudos direcionados avaliando a dieta ao longo do tempo.

De acordo com a hipótese do habitat saturado, altas densidades populacionais limitam a oferta de territórios vagos, aumentando a proporção de filhotes que se mantêm filopátricos, levando os indivíduos a formarem grupos sociais (Kristen et al. 2008; Schradin et al. 2020). No sentido contrário, a baixa densidade populacional observada em *C. laticeps* parece estruturar uma vida solitária na espécie, uma vez que favorece a dispersão natal de ambos os sexos, conforme registrado pela alta diversidade genética e ausência de estrutura de parentesco para um dos sexos no estudo. A dispersão natal tanto dos machos quanto das fêmeas na população estudada indica que os benefícios dessa estratégia, tais como redução da competição por parceiros, alimento e abrigo, superam os custos associados a dispersão (Martinig et al. 2020), como risco de predação, escassez de alimento e competição. A dispersão natal do local de estudo, junto à produção de um filhote por ninhada, eventualmente dois (Ferrando et al. 2019, presente estudo) pode estar refletindo a mesma probabilidade de sobrevivência para ambos os sexos, contribuindo para uma razão sexual de adultos 1:1, como esperada em mamíferos (Jennions et al. 2017).

Os padrões de movimento dos indivíduos de *C. laticeps* sugerem inicialmente um sistema de acasalamento polígino (Bond & Wolff 1999; Cooper & Randall 2007; Harris & Leitner 2004), dado que machos se movimentaram por áreas maiores do que as fêmeas durante todo o ano, enquanto as fêmeas se mantiveram fiéis ao sítio, restringindo suas atividades nas proximidades da sua galeria, em resposta ao constante cuidado com os seus filhotes (Ferrando et al. 2019; presente estudo). Porém, dados de sobreposição no uso espaço e a aplicação de ferramentas moleculares apontaram um sistema poliginândrico

em *C. laticeps* já que houve grande sobreposição espacial entre os sexos e evidências de cópulas com múltiplos parceiros. A razão 1:1 junto à baixa densidade em *C. laticeps* parecem beneficiar o sistema poliginândrico identificado no presente estudo, uma vez que a competição por acesso aos parceiros deve ser reduzida em função do equilíbrio no número de indivíduos de cada sexo (Székely et al. 2014). Além disso, a provável ineficiência na monopolização das fêmeas pelos machos de *C. laticeps* pode estar permitindo que as fêmeas copulem tanto com machos residentes quanto com transientes (indivíduos que se deslocam pelo habitat antes de estabelecer sua área de residência - Lacey 2000).

Autores sugerem que a poliginandria pode ser mais comum em espécies que apresentam monomorfismo sexual (Schulte-Hostedde et al. 2004; Cooper et al. 2011), uma vez o nível de dimorfismo sexual em tamanho pode estar associada à pressão da competição intrasexual por parceiros (Darwin 1871; Andersson 1994). Dessa forma, a ausência de dimorfismo sexual de tamanho em *C. laticeps* pode ser um fator que contribui na incapacidade dos machos de monopolizar parceiras reprodutivas, de forma que o tamanho corporal não funciona como um atributo sexual secundário vantajoso na espécie (Cooper et al. 2011). O acasalamento com múltiplos machos oferece benefícios às fêmeas (Wolff & McDonalds 2004), tais como o impedimento de infanticídio pelos machos, por meio da confusão de paternidade (Jennions & Petrie 2000; Wolff & McDonalds 2004). Além disso, o acasalamento com múltiplos parceiros pode resultar em maior diversidade genética dos filhotes, aumentando assim a chance de sobrevivência dos mesmos e consequentemente o sucesso reprodutivo das fêmeas (Jennions & Petrie 2000; Wolff & McDonalds 2004). Porém, qual(ais) o(s) benefício(s) que as fêmeas de *C. laticeps* apresentam ao acasalar com vários machos ainda precisa ser investigado em estudos futuros. Mesmo assim, a poliginandria, assim como a dispersão de ambos os sexos na

população estudada contribuem para a alta diversidade genética, assim como um baixo nível de endogamia registrado nesse estudo, indicando que ambas as estratégias são vantajosas por minimizar os riscos da depressão endogâmica na população estudada.

Dados de história de vida, padrões espaciais e genéticos obtidos nesse estudo mostram a importância de se trabalhar com ferramentas complementares para se entender o comportamento social das espécies. Dados moleculares vêm sendo um recurso relevante que ajuda a elucidar os processos que moldam a estrutura genética de uma população, como por exemplo sistema de acasalamento e fluxo gênico (Winters & Waser 2003; Walker et al. 2008; Estes-Zumpf et al. 2010). A maior parte dos trabalhos envolvendo comportamento social foi obtida somente a partir de dados espaciais, como no caso dos roedores equimídeos (Adler 2011). Porém, estudos mais recentes com mamíferos têm revelado divergências em relação ao sistema de acasalamento obtido com dados genéticos e espaciais (Waterman 2007; McEachern *et al.* 2009). Dessa forma, esse estudo contribui na redução da lacuna de conhecimento sobre sistema social da família Echimyidae, os quais permanecem escassos (Herrera 2016) e muitas vezes inconsistentes (Adler 2011), e aumenta o conhecimento sobre a socialidade em roedores caviomorfos (Hayes et al. 2011).

Uma vez que o sucesso reprodutivo impulsiona a evolução, o entendimento dos padrões comportamentais das espécies é relevante para estudos comparativos que permitem identificar os fatores que promovem a evolução convergente e divergente dos comportamentos entre linhagens, especialmente em grupos altamente diversos como os roedores caviomorfos (com 246 espécies), que apresentam diferentes especializações ecomorfológicas e ocorrem ao longo de vários tipos de habitats (Ojeda & Novillo 2016). Apesar do seu potencial para estudos comparativos, informações sobre o sistema social

dos membros desse grupo estão restritos a apenas 32% das espécies, o que já sugerem uma diversidade expressiva no grupo (Herrera 2016).

Pesquisas sobre comportamento social são cruciais para entender o surgimento da diversidade animal, seja taxonômica, genética, ecomorfológica ou funcional, uma vez este comportamento é resultado de um processo multifatorial e implica na geração de filhotes com características adaptativas (Blumstein et al. 2010; Hager 2010). Múltiplos fatores, especialmente os atributos intrínsecos observados em *C. laticeps*, foram discutidos nesse estudo como possíveis modeladores da vida solitária e poliginândrica na espécie. Porém, sugerimos que estudos direcionados e comparativos sejam feitos no futuro para esclarecer os mecanismos (tanto intrínsecos quanto extrínsecos) que moldam o sistema solitário na espécie, a qual é um bom modelo de estudo nesse sentido uma vez que tem uma ampla distribuição geográfica, vivendo sob diferentes condições ambientais (Patton et al. 2015, Bezerra et al. 2016). Acreditamos que as informações desse trabalho contribuirão para questões intrigantes sobre os fatores que promovem convergência e divergência na evolução social dos roedores caviomorfos assim como dos roedores escavadores.

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