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FILIPA ALEXANDRA DE ABREU PAULOS

COGNIÇÃO ESPACIAL DE *CALLITHRIX JACCHUS* (PRIMATES, CALLITRICHIDAE) EM AMBIENTE DE CAATINGA

Recife – PE

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Tese de doutorado apresentada ao Programa de
Pós-graduação em Etnobiologia e Conservação
da Natureza (UFRPE, UEPB, URCA e UFPE) como
parte dos requisitos para obtenção do título de doutor

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Tese apresentada e aprovada em 08/09/2020

Presidente

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Dr. Paula Braga – UFRPE

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Dr. Daniel Pessoa – UFRN

DEDICATÓRIA

Dedico esta tese à minha família,

e a todos os saguis que acompanhei

EPÍGRAFE

"Only if we understand, can we care.

Only if we care, we will help.

Only if we help, we shall be saved."

- **Jane Goodall**

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SUMÁRIO

Abreu, Filipa Alexandra de (PhD Etnobiologia e Conservação da Natureza) Universidade Federal Rural de Pernambuco. Setembro de 2020. Cognição espacial de *Callithrix jacchus* (Primates, Callitrichidae) em ambiente de Caatinga. Nicola Schiel (Orientadora); Paul Garber e Antonio da Silva Souto (Co-orientadores).

RESUMO

Para aumentar a eficiência na procura por recursos, muitos animais fazem uso de habilidades espaciais. Quando forrageando, os animais podem tanto explorar recursos em pequena escala de espaço (recursos que se encontram dentro do campo de visão) como em larga escala de espaço (recursos fora do campo de visão). Além do uso da memória espacial para recordar a localização espacial de fontes alimentares em pequena escala de espaço, em larga escala de espaço, os animais fazem uso de mapas mentais criados através da representação abstrata do espaço em que navegam (mapa mental baseado em coordenadas ou em rotas). Essa navegação espacial pode ser influenciada por fatores ambientais. Para animais, como primatas, que habitam florestas heterogêneas e consomem recursos com distribuição irregular tanto no espaço como no tempo, a capacidade de integrar informações espaciais, ecológicas e temporais se torna crucial. *Callithrix jacchus* (sagui-comum) são parte de um grupo (Calitriquídeos) especialmente interessantes para estudos nesta temática. Além de possuir uma dieta onívora, com consumo regular de exsudatos, o mesmo ocorre na Caatinga, ambiente com padrões fenológicos assíncronos e baixa disponibilidade de recursos, como frutos carnosos. Dentro deste contexto, o objetivo geral desta tese foi investigar, através de dois estudos, o uso das diferentes habilidades cognitivas espaciais tanto em pequena como em larga escala de espaço deste pequeno primata neotropical. No primeiro estudo montamos um experimento em campo, simulando o forrageio em pequena escala de espaço, em que mudamos a conformação espacial do recurso disponível. Desta forma, pretendemos investigar se saguis-comum fazem uso de sua memória espacial a curto e longo prazo e a sua capacidade de aprender após uma única exposição ao experimento. No segundo estudo investigamos o tipo de representação mental criado pela espécie em larga escala de espaço, através do registro do comportamento e posição espacial de cada animal durante todo o seu período de atividade. Encontramos que, em pequena escala de espaço, os animais mantêm informações espaciais dos locais de alimentação tanto a curto como a longo prazo e se mostraram capazes de aprender a localização espacial de recursos com apenas uma única visita aos mesmos. Verificamos que, quando navegam em larga escala de espaço, os animais usam um mapa mental baseado em rotas, reutilizando segmentos de rota e pontos de mudança de direção. A reutilização de segmentos de rota e pontos de mudança de direção mostrou ser influenciada tanto pela distância a árvores de interesse (alimentação,

dormida e descanso) como pela cobertura vegetal. Em geral, os achados demonstram que saguis-comuns possuem habilidades espaciais que os ajudam a lembrar e regressar a locais de alimentação de forma mais eficiente tanto em pequena como em larga escala de espaço. Estas habilidades em pequena escala de espaço parecem melhorar a busca por recursos dispersos dentro de manchas em ambientes com flutuações na disponibilidade de alimento. Já em larga escala de espaço, o uso de um mapa mental baseado em rotas parece beneficiar estes animais devido ao consumo de exsudatos que apresentam distribuição espacial aglomerada e estão disponíveis durante todo o ano..

Palavras-chave: Semiárido; Saguis-comum; Habilidades espaciais; Navegação espacial

Abreu, Filipa Alexandra de (PhD Etnobiologia e Conservação da Natureza) Federal Rural University of Pernambuco. September 2020. Spatial cognition of *Callithrix jacchus* (PRIMATES, CALLITRICHIDAE) in Caatinga environment. Nicola Schiel (Advisor); Paul Garber e Antonio da Silva Souto (Co-advisors).

ABSTRACT

To increase efficiency in the search for resources, many animals rely on spatial abilities. When foraging, animals can explore resources both in small- (resources within the field of view) and large-scale space (resources outside the field of view). In addition to using spatial memory to recall the spatial location of resources in small-scale space, specifically in large-scale space, animals rely on mental representations created through the abstract representation of the space (coordinate- or route-based mental map) to navigate. Still, this navigation can be influenced by environmental factors. For animals, such as primates, who live in heterogeneous forests and consume resources with irregular distribution both in space and time, the ability to integrate spatial, ecological, and temporal information becomes crucial. *Callithrix jacchus* (common marmoset) appears here as part of a group (Callitrichids) especially interesting for studies on this topic. Besides having an omnivorous diet, with regular consumption of exudates, the same occurs in Caatinga, an environment with asynchronous phenological patterns and low availability of resources, such as fleshy fruits. In this context, we aimed to investigate, through two studies, the different spatial cognitive abilities both in small and large-scale space of this small neotropical primate. In the first study, we set up a field experiment, simulating a small-scale space foraging, in which we changed the spatial conformation of the available resource. We investigated whether common marmosets rely on short- and long-term spatial memory and one-trial learning. In the second study, we investigated the type of mental representation created by the species in large-scale space by recording each animal's behavior and spatial position throughout its activity period. We found that, in small-scale space, animals maintain spatial information on feeding locations both on a short- and long-term basis and can learn the spatial location of resources with just a single visit. When navigating in large-scale space, we found that animals use a route-based mental map, reusing route segments and turning points. The reuse of route segments and turning points was influenced both by distance to sites of interest (feeding, resting, and sleeping sites) and land cover. In general, the findings demonstrate that common marmosets rely on spatial abilities that help them remember and return to feeding places more efficiently both in small- and large-scale space. In small-scale space, these capacities seem to improve the search for dispersed resources in environments with fluctuations of food availability. In large-scale space, using a route-based mental map seems to benefit these

animals due to the consumption of exudates that possess cluster distribution and are available all year round.

INTRODUÇÃO GERAL

1.1 OBJETIVOS E QUESTIONAMENTOS

A pesquisa foi motivada por uma observação anedótica realizada em campo. Enquanto coletava os dados de mestrado relacionados à captura de presas por saguis-comum na Caatinga, me deparei com a capacidade que estes animais tinham de relembrar e voltar ao mesmo local onde tinham encontrado algo de interesse (seja recurso alimentar ou algo que despertasse a sua atenção por algum outro motivo). Assim, durante essa coleta me questionei como isso ocorreria mesmo se os animais não tivessem acesso a pistas visuais ou olfativas. Esta observação levou-nos a questionamentos mais amplos sobre a cognição espacial dos animais, especificamente, questões relacionadas ao modo como os animais navegam e procuram alimento no seu ambiente, haja vista que muitos deles dependem de recursos alimentares que estão distribuídos tanto espacialmente como temporalmente no ambiente.

De maneira geral, a capacidade de um indivíduo recordar informações sobre o meio e manter sua orientação espacial é denominada de cognição espacial (DUKAS, 1999). Por sua vez, a memória espacial é a habilidade de processar e utilizar informações espaciais advindas do meio ambiente (DOLINS; MITCHELL, 2010). Esta habilidade traz diversos benefícios aos animais, uma vez que os ajuda a diminuir o tempo necessário para regressar a pontos geográficos visitados anteriormente, como locais de nidificação e fontes alimentares, ou a evitar locais indesejados, como áreas com presença de predadores (BURNS; THOMSON, 2006; COMBRINK; WARNER; DOWNS, 2017; FAGAN et al., 2013; THORNTON; BOOGERT, 2019). Uma vez que mudanças espaço-temporais afetam a distribuição dos recursos, a procura por alimento se torna bastante complexa (MILTON, 1981; O'DRISCOLL WORMAN; CHAPMAN, 2005; VAN SCHAIK; TERBORGH; WRIGHT, 1993). Asim, um dos maiores desafios enfrentados pelos animais na natureza é localizar potenciais fontes alimentares (CORLETT, 2011) e relembrar e regressar a essas fontes de forma direta (FAGAN et al., 2013). A literatura tem evidenciado que o uso de habilidades espaciais otimiza o sucesso de forrageio dos animais, diminuindo o seu tempo de procura, dispêndio de energia (JANSON, 2019; ROBERTS, 1993) e consequentemente, influenciando positivamente o seu fitness (FAGAN et al., 2013).

Muitos estudos têm examinado como os animais codificam informações espaciais da natureza para navegar, a fim de localizar com sucesso recursos alimentares (por exemplo, insetos: COLLETT, 2009; COLLETT; CHITTKA; COLLETT, 2013; pássaros: GONZÁLEZ-GÓMEZ; VÁSQUEZ, 2006; HEALY; HURLY, 2004; mamíferos: FORTIN, 2003; LAVENEX

et al., 1998; MERKLE; FORTIN; MORALES, 2014; ROBERTS, 1993; VANDER WALL et al., 2008; YI et al., 2016). Especificamente em se tratando de primatas, como os que forrageiam em grupo e habitam florestas heterogêneas, integrar informações espaciais é crucial para otimizar seu sucesso alimentar individual (TEICHROEB; AGUADO, 2016; ZUBERBÜHLER; JANMAAT, 2010). Primatas oferecem uma oportunidade única não só pela sua dieta (consumo de recursos com distribuição irregular no espaço e no tempo, como frutos) como também devido à relação entre cognição espacial e tamanho de cérebro que tem mostrado uma maior capacidade cognitiva espacial em primatas de dietas mais frugívoras (DECASIEN; WILLIAMS; HIGHAM, 2017; GARBER; DOLINS, 2014; MILTON, 1981). Assim, pesquisas com enfoque nas decisões de forrageio em primatas têm tido como objetivo entender como estes animais processam, integram e representam informações espaciais, ecológicas e temporais do ambiente tanto em pequena escala de espaço (ANDREWS, 1988; GARBER; PACIULLI, 1997; GOMES; BICCA-MARQUES, 2012; MACDONALD; AGNES, 1999) como em larga escala de espaço (DI FIORE; SUAREZ, 2007; JANMAAT; BYRNE; ZUBERBÜHLER, 2006a; JANSON, 2016; PORTER; GARBER, 2013).

Enquanto a maioria das pesquisas realizadas em pequena escala de espaço (isto é, dentro de manchas de alimentação: GARBER; DOLINS, 2014) têm procurado entender o uso da memória espacial para regressar a locais previamente visitados pelos animais, estudos em larga escala de espaço (isto é, navegando entre manchas de alimentação: GARBER; DOLINS, 2014) têm focado em como primatas representam espacialmente o ambiente durante a navegação. Em geral, os achados de estudos em pequena escala de espaço apontam que grande parte dos primatas se lembra por breves períodos de tempo (máximo de algumas horas) da localização de fontes alimentares regressando a estas de forma eficiente e direta (sem erros na escolha da localização do recurso) (CUNNINGHAM; JANSON, 2007; GARBER, 1988; GARBER; PACIULLI, 1997; GIBEAULT; MACDONALD, 2000; GOMES; BICCA-MARQUES, 2012; JANMAAT; BYRNE; ZUBERBÜHLER, 2006b; JANSON, 1998; TEICHROEB; CHAPMAN, 2014) no entanto existe pouca literatura mostrando que estes animais têm a capacidade de manter essas informações por longos períodos de tempo (mais de 24 horas) (JANMAAT; BAN; BOESCH, 2013; JANMAAT; CHANCELLOR, 2010; MENDES; CALL, 2014; TUJAGUE; JANSON; LAHITTE, 2015). Por outro lado, estudos em larga escala de espaço têm mostrado que o padrão de navegação mais usado pelos primatas é o de um mapa mental baseado em rotas, indicando que estes animais se guiam através de pontos de referência e tendem a repetir as mesmas rotas diariamente (ASENSIO et al., 2011; DI FIORE; SUAREZ, 2007; ERHART; OVERDORFF, 2008; NOSER; BYRNE, 2007; PRESOTTO et al., 2018;

SCHREIER; GROVE, 2014). Por sua vez, a capacidade de criar atalhos e navegar por rotas não conhecidas (mapa mental baseado em coordenadas) tem sido pouco observado neste grupo de animais (PRESOTTO; IZAR, 2010; NORMAND; BOESCH, 2009).

Calitriquídeos são pequenos primatas neotropicais com ampla distribuição, que habitam ambientes ecologicamente contrastantes, desde florestas tropicais úmidas até ao semiárido. Esta família já demonstrou possuir habilidades cognitivas espaciais, tais como relembrar da posição espacial de um objeto por até 24h em cativeiro (*Callithrix penicillata*: VANNUCHI et al., 2020) ou até mesmo a capacidade de representar mentalmente o espaço através de um mapa topológico (mapa mental baseado em rotas) (*Saguinus fuscicollis weddelli*: PORTER; GARBER, 2013). Contudo, estudos de cognição espacial tanto em pequena como em larga escala de espaço ainda são raros nesta família (BICCA-MARQUES; GARBER, 2005; GARBER, 1988; GARBER; PORTER, 2014; PORTER; GARBER, 2013; VANNUCHI et al., 2020). Os saguis-comum (*Callithrix jacchus*) fazem parte da família e são do gênero *Callithrix* (RYLANDS; DE FARIA, 1993). Estes primatas têm sido o foco de numerosos estudos desde pesquisas de forrageio até pesquisas com foco na sua cognição (DE LA FUENTE et al., 2019, 2014; HUBER; VOELKL, 2009; PESENDORFER et al., 2009; SCHIEL et al., 2010), e recentemente foram apontados como um bom modelo para pesquisas na área cognitiva devido à sua reprodução, comportamento e características neurobiológicas (MILLER, 2017). *Callithrix jacchus* vivem em grupos de até 15 indivíduos, forrageiam em proximidade espacial e sua dieta se baseia em uma gama variada de itens alimentares (insetos, exsudatos, frutas, flores) (SCHIEL; SOUTO, 2017), os quais possuem diferentes distribuições espaciais e temporais. Vivem em dois ambientes completamente distintos tanto em relação à fisionomia e vegetação como ao clima (Mata Atlântica e Caatinga) (GARBER et al., 2019). Estes animais já demonstraram possuir distintas habilidades cognitivas, tais como capacidade de discernir entre quantidades de recursos ou a capacidade de ajustar suas estratégias de forrageio de acordo com o tipo de recurso (HUBER; VOELKL, 2009; SCHIEL et al., 2010; SCHIEL; SOUTO, 2017). Até o momento, os estudos de cognição espacial com a espécie foram apenas realizados em cativeiro, demonstrando que a espécie tem capacidade de usar algumas habilidades espaciais, como relembrar da localização espacial de fontes alimentares por até 1 hora e localizar esses recursos através de pontos de referência (EASTON et al., 2003; MACDONALD et al., 2004; MACDONALD; PANG; GIBEAULT, 1994). Contudo não há evidências do uso da memória espacial em ambiente natural em pequena escala de espaço nem informação sobre a navegação espacial destes pequenos primatas em larga escala de espaço. Assim, além de saguis-comum terem servido como base para os questionamentos da presente tese, apresentam-se também

como excelentes modelos para se estudar em campo aspectos relacionados a habilidades cognitivas espaciais tanto em pequena como em larga escala de espaço.

Desta forma, o objetivo geral da tese foi compreender como saguis-comum, pequenos primatas do Novo Mundo, usam diferentes habilidades cognitivas espaciais para procurar recursos e navegar no seu ambiente. Para isso, abordamos aspectos da memória e aprendizagem espacial em pequena escala de espaço e exploramos como este pequeno primata neotropical navega em seu ambiente em larga escala de espaço através do uso de cognição espacial. Haja vista que os estudos foram desenvolvidos em ambiente semiárido (Caatinga), além de trazer novas informações sobre a cognição espacial de primatas, a tese tem também o intuito de ressaltar importância do uso de habilidades espaciais para a sobrevivência de primatas em um ambiente tão severo como o semiárido brasileiro.

1.2 ESTRATÉGIAS DE PESQUISA

As estratégias de pesquisa da tese seguiram duas abordagens diferentes, mas complementares de forma a abranger o universo de pesquisas em cognição espacial com primatas: estudos experimentais e estudos observacionais em campo.

Estudos de cognição espacial em pequena escala de espaço, são geralmente realizados em condições de cativeiro. Apesar deste tipo de abordagem trazer certas vantagens experimentais (como controle de variáveis ambientais e sociais e a certeza da presença dos animais), os comportamentos mais naturais dos animais em resposta a pressões e/ou variáveis do ambiente natural acabam não sendo comtempladas (CRONIN et al., 2017; TUJAGUE; JANSON; LAHITTE, 2015). Desta forma, pesquisas desenvolvidas no ambiente natural viriam a refletir com maior exatidão a história natural da espécie. Por essa razão, nosso primeiro estudo, relacionado com o uso da memória espacial em pequena escala de espaço, foi realizado através de um experimento em campo, pois além de trazer todas as vantagens de uma pesquisa em meio natural, através da experimentação temos a possibilidade de controlar algumas variáveis que poderiam influenciar os nossos resultados. Com essa abordagem experimental e através de um experimento que consistia em simular uma mancha de forrageio com recursos disponíveis distribuídos espacialmente em que os animais procuravam por alimento em grupo e livremente, conseguimos excluir pistas visuais e olfativas que poderiam interferir nas escolhas dos animais durante esse forrageio (GARBER; PACIULLI, 1997; GOMES; BICCA-MARQUES, 2012; TEICHROEB; CHAPMAN, 2014). Uma vez que não queríamos excluir as pistas sociais durante o forrageio natural da espécie (isto é, pistas que poderiam ser usadas para

localizar o alimento ao invés de pistas espaciais, como por exemplo, a observação de um coespecífico se alimentando em um determinado local), conseguimos controlá-las através do experimento e nos certificar que os resultados se deviam ao uso das habilidades espaciais. Desta forma, controlamos as pistas sociais posteriormente durante as análises estatísticas através de modelos lineares generalizados mistos (BOLKER et al., 2009).

O segundo estudo, que trata da navegação espacial em larga escala de espaço, foi realizado em campo de forma observacional. Esta abordagem foi escolhida seguindo estudos anteriores com perguntas e objetivos que se complementavam aos nossos (por exemplo, DI FIORE; SUAREZ, 2007; JANG et al., 2019; PORTER; GARBER, 2013). Haja vista que o objetivo era verificar como os animais se movem em toda a sua área de uso e como o ambiente com padrões fenológicos assíncronos afetaria a navegação da espécie, escolhemos realizar o estudo de forma observacional. Esta abordagem permite-nos visualizar o comportamento e navegação espacial dos animais sem qualquer intervenção humana. Seguindo o estudo anterior, as variáveis externas que poderiam trazer uma possível confusão foram controladas durante as análises estatísticas através de modelos lineares generalizados mistos (BOLKER et al., 2009).

A escolha dos métodos de observação foi direcionada para as perguntas a serem feitas em cada estudo. No primeiro estudo, optamos por utilizar o método de observação de "todas as ocorrências". Este método nos permitiu registrar todos os comportamentos de todos os animais envolvidos e o mesmo é bastante eficaz quando os animais estão em um local delimitado (no nosso caso, o local do experimento) e conseguimos visualizar todos os animais (MARTIN; BATESON, 2007). Ademais, foi feito uso de duas câmeras fotográficas gravando todo o experimento, para que os comportamentos dos indivíduos pudessem ser revistos e analisados, caso necessário. No segundo estudo optamos por um conjunto de métodos de observação: método animal focal associado ao método de varredura (MARTIN; BATESON, 2007; PORTER; GARBER, 2013). Este conjunto de métodos consistiu em observar por um dia inteiro um único indivíduo registrando o seu comportamento a cada 2 minutos. Este método foi escolhido pois, apesar de saguis-comum forragearem, normalmente, em proximidade espacial (SCHIEL; SOUTO, 2017), o seu pequeno tamanho e rápida movimentação tornaria inviável visualizar e anotar os comportamentos de todos os animais ao mesmo tempo, enquanto se deslocam, podendo levar a dados inexatos. Além disso, este método já foi usado com sucesso em outros estudos com Calitriquídeos (PORTER; GARBER, 2013).

Por fim, para o primeiro estudo decidimos utilizar marcação visual nos animais através de um método de captura bastante utilizado em primatas de pequeno porte (BICCA-MARQUES; GARBER, 2005; GARBER; BICCA-MARQUES; AZEVEDO-LOPES, 2009).

Este método permite capturar todos os membros do grupo de uma vez, anestesiar e colocar um colar de marcação contendo miçangas de diferentes cores e formatos. Optamos pela sua utilização haja vista a necessidade de observar todos os comportamentos e movimentos de todos os indivíduos. Desta forma, conseguimos excluir possíveis erros na identificação dos animais durante o forrageio dentro do experimento. Apesar de ser um método invasivo e estressante para os animais, este método é também o menos impactante haja vista que os todos os procedimentos são realizados no local e os animais são devolvidos ao seu habitat natural o mais depressa possível. Para o segundo estudo, como a observação foi realizada diariamente com apenas um indivíduo, a identificação foi feita através de marcas naturais ou cicatrizes dos animais sem a necessidade de captura (SCHIEL et al., 2008). Contudo, um dos animais ainda tinha os colares de marcação que foram colocados para o estudo anterior.

1.3 ESTRUTURA DA TESE

A presente tese encontra-se dividida em três capítulos que têm como objetivo central trazer informações sobre a capacidade de saguis-comum utilizarem habilidades cognitivas espaciais para localizar e regressar a fontes alimentares no seu ambiente. Enquanto o primeiro capítulo aborda termos e conceitos sobre o tema de cognição espacial e traz o estado da arte do tópico, os outros dois capítulos são pesquisas empíricas que trazem diferentes informações acerca das habilidades espaciais de saguis-comum. Além disso, os capítulos 2 e 3 também foram realizados em diferentes escalas de espaço: pequena e larga escala de espaço. Estas escalas de espaço não se diferenciam pelo tamanho da área que os animais navegam, mas sim em relação ao quanto de acesso visual os animais conseguem ter do seu ambiente e fontes alimentares. Dessa forma, os estudos de cognição espacial em pequena escala de espaço, definem essa escala como a área em que o forrageador consegue visualizar a sua fonte alimentar de diversas perspectivas e direções. Neste caso, estamos nos referindo a um forrageio dentro de uma mancha alimentar, por exemplo, forrageio numa árvore com frutos ou exsudatos. Pelo contrário, larga escala de espaço está relacionada com o forrageio entre manchas alimentares, isto é, dentro da área de uso utilizada pelo animal ou grupo. Nesta escala de espaço, os animais precisam criar e utilizar alguma estratégia navegacional para se deslocarem entre recursos de forma eficiente (GARBER; DOLINS, 2014). Através desta abordagem objetivamos entender como se dá o uso das habilidades espaciais de uma mesma espécie em diferentes escalas de espaço, haja vista que a literatura sugere que os animais podem diferir no uso das suas habilidades cognitivas espaciais em função da escala de espaço em que navegam (DOLINS; MITCHELL, 2010; GARBER; DOLINS, 2014; POUCET, 1993).

Para o primeiro capítulo foi realizada uma revisão sobre o tema geral da tese, cognição espacial, assim como trazer o estado da arte sobre este tópico. Nesse capítulo abordamos aspectos da cognição de animais ressaltando como funcionam os mecanismos de obtenção de informação provenientes do exterior. No decorrer do capítulo, e com foco na cognição espacial (tema da presente tese de doutorado), descrevemos a diferença de estudos realizados em pequena e larga escala de espaço assim como explicamos com maior detalhe os vários tipos de mecanismos existentes para obtenção de informação espacial proveniente do exterior e utilizado por vários animais, inclusive primatas. Por fim, demos ênfase ao domínio morfoclimático onde a presente tese foi desenvolvida assim como ao sujeito de estudo das nossas pesquisas.

O segundo capítulo teve como objetivo principal verificar a capacidade de saguis-comum utilizarem distintas habilidades cognitivas espaciais em pequena escala de espaço. Especificamente, abordamos o uso da memória espacial a curto e a longo prazo de tempo assim como a capacidade de aprendizagem da localização espacial das fontes alimentares com apenas uma visita às mesmas. Estes pequenos primatas neotropicais mostraram conseguir armazenar e posteriormente utilizar informações relativas à localização de fontes alimentares por curtos e longos períodos de tempo. Da mesma forma, observamos que os animais conseguiram regressar ao local onde tinham previamente encontrado alimento, apesar de terem apenas visitado esse local uma única vez. Estes resultados foram discutidos à luz da dieta de espécie e do ambiente semiárido onde os animais habitam. Ainda, os nossos achados levantaram a hipótese, de que estes pequenos primatas poderiam utilizar estratégias de navegação espaciais mais complexas quando navegando entre manchas alimentares ou até mesmo possuir um tipo de memória considerada, por alguns autores, exclusiva de primatas humanos (TULVING, 2005).

No terceiro capítulo abordamos o uso da cognição espacial em larga escala de espaço. Especificamente, queríamos entender se saguis-comum conseguem formar representações mentais do espaço para auxiliar na procura por alimento. Além disso, objetivamos também verificar que fatores ambientais poderiam influenciar na navegação da espécie. Assim, nos propusemos a identificar o tipo de representação mental (mapa mental) usada por saguis-comum durante a navegação em larga escala de espaço e posteriormente verificar a influência das características do ambiente, como vegetação e distribuição de recursos, na navegação da espécie. Existem dois tipos de mapas mentais propostos até ao momento: mapa mental baseado em coordenadas e mapa mental baseado em rotas (GARBER, 2000). O uso de mapas mentais baseados em coordenadas permite aos animais navegar de forma direta entre recursos e criar atalhos para reduzir a distância navegada. Já no mapa mental baseados em rotas, os animais utilizam pontos de referência para modificar a sua trajetória de navegação e não se deslocam

de forma direta entre recursos. Neste mapa mental é comum a reutilização de rotas e pontos de referência (GARBER, 2000). Observamos que saguis-comum navegam em função de um mapa mental baseado em rotas tal como já observado em diversas outras espécies de primatas (DE RAAD; HILL, 2019; DI FIORE; SUAREZ, 2007; PORTER; GARBER, 2013). Contudo, alguns resultados sugeriram a capacidade destes animais formarem representações Euclidianas do ambiente (mapa mental baseado em coordenadas). Em geral, nossos achados levantam a questão da influência da estrutura da vegetação do ambiente na navegação espacial de saguis-comum em larga escala de espaço.

Com isto, podemos concluir que os três capítulos da tese se complementam entre si pelas informações que trazem assim como pela metodologia utilizada (isto é, pelo fato de terem sido realizado tanto em pequena como em larga escala de espaço). Com o segundo capítulo conseguimos mostrar capacidades cognitivas mais simples, como a utilização da memória espacial para localizar itens alimentares dentro de uma mancha de alimentação, enquanto no terceiro capítulo mostramos capacidades cognitivas espaciais mais complexas, nomeadamente, a capacidade de representar mentalmente o espaço e utilizar essa representação mental de forma a navegar mais eficientemente no ambiente. Por fim, os dois capítulos trazem questionamentos acerca do papel do ambiente nas habilidades cognitivas de primatas.

CAPÍTULO 1

(Fundamentação Teórica)

FUNDAMENTAÇÃO TEÓRICA

Cognição

A cognição é definida como o mecanismo neurológico pelo qual o animal adquire, processa e utiliza a informação proveniente do meio ambiente (SHETTLEWORTH, 2010). Existem vários processos mentais ligados à cognição, nomeadamente, aprendizagem, memória, representação mental do espaço, entre outros (DUKAS, 1998). A aprendizagem é definida como sendo a habilidade de adquirir uma representação mental entre um estímulo e um estado ambiental (DUKAS, 2002). Associada à aprendizagem, a memória, que pode ser dividida em memória de curto e longo prazo, refere-se ao armazenamento de informações que foram previamente adquiridas e processadas (DUKAS, 2019). Estes dois tipos de memória diferem uma vez que, tal como o nome indica, a memória de curto prazo é a que recebe informações do exterior, não havendo um armazenamento das mesmas por muito tempo. Já a memória de longo prazo, é a memória que armazena essas mesmas informações e então as processa durante um longo período de tempo. Essas informações podem ser armazenadas de dias, semanas, até à vida total de um indivíduo (REZNIKOVA, 2007).

Assim, a cognição determina os traços comportamentais que afetam a ecologia e evolução dos animais (HUBER; VOELKL, 2009), tais como, comportamento social, forrageio, procura por parceiro sexual, seleção de habitat, entre outros. Mais recentemente, tem se também levantado a hipótese de que fatores ambientais podem influenciar a cognição dos animais. Já a cognição espacial, um dos ramos da cognição, está relacionada com a aquisição, organização e utilização das informações espaciais provenientes do exterior (TOMASSELO; CALL, 1997). A representação mental do espaço, é considerado como um processo bastante complexo, pois envolve vários mecanismos mentais associados, que levam a que o animal adquira e reorganize informação de forma a criar representações cognitivas do ambiente (POUCET, 1993). A cognição espacial, então, viria a possibilitar ao animal maior sucesso na busca e acesso ao alimento e procura de parceiros, bem como na prevenção de possíveis encontros agonísticos e/ou com predadores (DOLINS; MITCHELL, 2010). Portanto, a forma como o animal lida com o espaço e objeto é de extrema importância (TOMASSELO; CALL, 1997).

Cognição espacial em pequena e larga escala de espaço

Estudos que tentam entender como se dá o uso da cognição espacial em animais, principalmente aqueles relacionados à procura e localização de recursos, costumam ser realizados em duas escalas de espaço distintas: pequena escala de espaço e larga escala de

espaço (GARBER; DOLINS, 2010). Pequena escala de espaço é definida como uma área em que o forrageador consegue visualizar vários locais de alimentação e pontos de referência ao mesmo tempo como, por exemplo, a copa de uma árvore. Por outro lado, larga escala de espaço se refere a quando o forrageador não consegue obter múltiplas visões de locais de alimentação ou pontos de referência (GARBER & DOLINS, 2010). Esta escala de espaço é análoga a um animal forrageando entre manchas de alimentação distantes entre si, por exemplo, entre várias árvores alimentares. É importante notar que esta distinção não é feita em função de distância e sim da limitação visual do indivíduo. Por exemplo, para um animal de pequeno porte habitando o semiárido, a área considerada como pequena escala de espaço pode ser de até 1 km. Já para um animal de maior porte habitando a Floresta Amazónia, a área considerada como pequena escala de espaço pode ser bem menor (por exemplo, 300 m) devido à alta densidade de árvores e altura da vegetação o que impossibilita uma visão de longo alcance devido aos obstáculos.

Recentemente, observou-se em algumas espécies que as escalas de espaço podem influenciar na forma como os animais utilizam a cognição espacial durante o forrageio (GARBER; PORTER, 2014; PORTER; GARBER, 2013). Na teoria, essa diferenciação já havia sido proposta em 1993 por POUCET. O autor referiu que, a depender dos estímulos visuais, os animais representam a informação espacial de diferentes formas quando navegam em larga escala de espaço ou quando procuram recursos em pequena escala de espaço. Assim, a cognição espacial parece não ser apenas influenciada pelas diferentes escalas de espaço como também pela distância do seu objetivo e visibilidade do ambiente (GARBER, 2000).

Memória espacial

A maneira como o animal recebe a informação, a processa e a armazena é considerada como memória (DUKAS, 2004). O hipocampo processa as memórias espaciais e é responsável por recordar informação sobre o meio ambiente e auxiliar o indivíduo na sua orientação espacial (DOLINS & MITCHELL, 2010). Esta ajuda os indivíduos a se relembrarem dos locais vitais para a sua sobrevivência como, fontes de alimentação, localização dos predadores e de co-específicos (ROBERTS, 1992). Em animais, a memória espacial parece estar intimamente ligada ao "fitness" dos mesmos (SHETLLEWORTH, 1983). Alguns pesquisadores afirmam que a memória espacial e a teoria do forrageio ótimo estão relacionadas, uma vez que esta tende a minimizar o tempo pela procura de alimento e, maximiza o ganho de energia (ROBERTS, 1992). Assim, estudos que tentam acessar esta memória realizam experimentos em que a

conformação dos alimentos é alterada espacialmente (e.g. PLATT et al., 1996; MACDONALD & AGNES, 1999). Grande parte desses experimentos, realizados em laboratório, apresentam aos animais um labirinto com dois ou mais braços, conhecidos como labirintos radiais, em que um dos braços contem alimento disponível e o(s) outro(s) não (e.g. OLTON et al., 1977; BOND et al., 1981; DIAMOND et al., 1999). Até o momento uma vasta gama de animais mostrou acessar à memória espacial para retornar a locais de alimentação onde estiveram previamente (*Equus caballus*: BARAGLI et al., 2011; *Rattus norvegicus*: BIRD et al., 2003; *Sus scrofa domesticus*: LAUGHLIN; MENDL, 2000; *Eulemur mongoz*, *Lemur catta*, *Propithecus* spp., *Varecia variegata:* ROSATI; RODRIGUEZ; HARE, 2014; SULIKOWSKI; BURKE, 2011; para uma revisão veja LIPP et al., 2001).

A memória espacial pode ser armazenada por curtos e/ou longos períodos de tempo. Enquanto a memória espacial de curto prazo varia de minutos a horas, a memória espacial de longo prazo se relaciona com memórias que duram de dias/semanas até à vida inteira de um indivíduo (BAILEY; BARTSCH; KANDEL, 1996; CORLETT, 2011). A retenção de informações de locais de alimentação por períodos distintos é particularmente crítica para animais que vivem em florestas heterogêneas com recursos de distribuição irregular no espaço e/ou no tempo, uma vez que os desafios são maiores, pois precisam contar com recursos que podem ser renovados rapidamente e/ou com recursos mais estáveis (CORLETT, 2011). Assim, para espécies de animais que vivem em ambientes que possuem em sua dieta recursos com alta flutuação e consomem recursos efêmeros (por exemplo, espécies de árvores de fruta que frutificam e amadurecem rapidamente) seria mais vantajoso usar a memória espacial de curto prazo, haja vista que esses alimentos tendem a ficar disponíveis por curtos períodos. Enquanto memórias de longo prazo são mais úteis em ambientes com recursos estáveis que se mantêm por longos períodos de tempo (por exemplo, exsudatos ou frutas perenes) (JANMAAT; BAN; BOESCH, 2013; SHETTLEWORTH, 2010).

Vários estudos tanto observacionais como experimentais, têm focado em como, especificamente primatas, utilizam a memória espacial a curto prazo para forragear no seu ambiente. Em geral, conclui-se que a maioria das espécies consegue regressar de forma eficiente para locais de alimentação anteriormente explorados por eles (*Pithecia pithecia*: CUNNINGHAM; JANSON, 2007; *Saguinus mystax* e *S. fuscicollis*: GARBER, 1988; *Cebus capucinus*: GARBER; PACIULLI, 1997; *Gorilla gorilla gorilla*: GIBEAULT; MACDONALD, 2000; *S. nigritus* (formerly *C. nigritus*): GOMES; BICCA-MARQUES, 2012; *Alouatta palliata*: HOPKINS, 2016; *Cercocebus atys atys* e *Lophocebus albigena johnstoni*: JANMAAT; BYRNE; ZUBERBÜHLER, 2006b; *Sapajus apella*: JANSON, 1998;

Chlorocebus pygerythrus: TEICHROEB; CHAPMAN, 2014). Contudo, estudos abordando a capacidade dos animais recordarem informações espaciais por mais de 24h são escassos e realizados principalmente em laboratório e com primatas do Velho Mundo (*Pan troglodytes verus*: JANMAAT; BAN; BOESCH, 2013; *Lophocebus albigena johnstonii*: JANMAAT; CHANCELLOR, 2010; *Pan troglodytes*: MENDES; CALL, 2014; *Sapajus libidinosus*: TUJAGUE; JANSON; LAHITTE, 2015). Até o momento sabe-se que algumas destas espécies mantêm por períodos longos as informações espaciais referentes à localização de árvores de alimentação. Por exemplo, MENDES; CALL (2014) observaram que *Pan troglodytes*, em cativeiro, consegue relembrar-se de diferentes localizações de alimento depois de 24h e/ou 3 meses de intervalo. Já CUNNINGHAM (2003) testou, em cativeiro, a capacidade de indivíduos da espécie *Pithecia pithecia* se relembrarem de locais de alimentação já depletados por eles por períodos que variaram de 1 a 120 dias. Apesar da importância da memória espacial tanto a curto como a longo prazo, alguns primatas utilizam simultaneamente pistas sensoriais, como pistas visuais ou olfatórias para localizar alimento (GOMES; BICCA-MARQUES, 2012; TEICHROEB; CHAPMAN, 2014).

Aprendizagem em uma exposição

A habilidade de aprender através de exposições limitadas foi proposta por HARLOW (1949). O autor explica que essa habilidade se dá através de *insights* da situação, em que inicialmente o indivíduo pode levar um tempo a aprender, mas que ao se familiarizar com o problema o animal adquire experiência e, em uma nova situação dentro do mesmo contexto, acaba aprendendo através de exposições limitadas. Desta forma, esta habilidade pode trazer várias vantagens principalmente a animais como primatas que se alimentam de recursos com distintas distribuições espaço-temporais (MILTON, 1981).

Relativamente à procura por fontes alimentares, MILTON (1981) sugeriu que além de primatas poderem ter uma memória de longo prazo, estes animais aprenderiam a localização de fontes alimentares, não através de exposições limitadas como referido anteriormente, mas sim com apenas uma visita às mesmas. Desta forma, além da capacidade de utilizar a memória espacial, os animais se beneficiariam ao memorizar locais de alimentação após uma única visita, haja vista que além dessa habilidade diminuir o tempo e energia gastos durante o forrageio também permitiria que os animais não deixassem de consumir recursos alimentares rapidamente esgotáveis e perecíveis, como é o caso de alguns frutos carnosos (CORLETT, 2011). A habilidade de aprender com uma única exposição pode favorecer também a competição por recursos com seus co-específicos e/ou heteroespecíficos e, consequentemente,

melhorar a eficiência de forrageio do indivíduo (CORLETT, 2011; MILTON, 1981). A capacidade de relembrar a localização espacial de recursos após uma única visita foi demonstrada em primatas do Velho Mundo tanto em pequena escala de espaço (*Pan troglodytes*: MENDES; CALL, 2014) como em larga escala de espaço (*Papio ursinus*: NOSER; BYRNE, 2015). De acordo com NOSER; BYRNE (2015) um macho babuíno selvagem pode relembrar a rentabilidade do alimento, a localização e o intervalo de tempo entre as visitas a determinadas plataformas de alimentação após uma única visita ao local e por períodos de retenção com mais de 2 horas, ajudando-o a manter uma alta taxa de ingestão de recursos a baixo custo. MENDES; CALL (2014), por sua vez, mostraram que *Pan troglodytes*, em cativeiro, conseguia relembrar-se de diferentes localizações de alimento, após apenas uma exposição ao experimento. Em primatas do Novo Mundo, apenas MENZEL; JUNO (1982) observaram, em um experimento não espacial, a aprendizagem de discriminação visual no calitriquídeo *Saguinus fuscicollis*. Contudo, ainda não existem evidências de que um primata do Novo Mundo de vida livre possui a capacidade aprender após uma única exposição em um contexto espacial.

Mapas mentais

Além da memória e aprendizagem espaciais muito estudadas, principalmente em pequena escala de espaço, estudos têm examinado como diferentes táxons incorporam informações como recursos alimentares para regressar a locais específicos em larga escala de espaço (JANSON; BYRNE, 2007; TRAPANESE; MEUNIER; MASI, 2018). Por exemplo, insetos (abelhas e formigas) navegam atualizando a sua posição e distância, uma estratégia chamada de integração de caminho (COLLETT; CHITTKA; COLLETT, 2013; Figura 1C). Aves e alguns mamíferos usam movimentos de caminhada de Lévy ou Brownianos, tipos de navegação randómicas (ATKINSON et al., 2002; BOYER et al., 2006; REYNA-HURTADO et al., 2018; SHAFFER, 2014; VISWANATHAN et al., 1996). Por sua vez, outros mamíferos (por exemplo, ratos, morcegos, elefantes e primatas) podem formar representações abstratas do espaço conhecidas como mapas cognitivos ou mentais (DI FIORE; SUAREZ, 2007; ERHART; OVERDORFF, 2008; GEVA-SAGIV et al., 2015; PORTER; GARBER, 2013; PRESOTTO et al., 2019).

No que diz respeito à navegação espacial em larga escala de espaço em primatas, já foi demonstrado que estes são capazes de representar mentalmente o espaço. Mapas cognitivos ou mentais são representações abstratas do espaço, que advêm da capacidade de receber, processar e organizar informações espaciais (GARBER, 2000). Até o momento, foi

proposto a formação de dois tipos de mapas mentais por primatas: (i) mapa mental baseado em coordenadas (ou mapa Euclidiano, Figura 1A) e (ii) mapa mental baseado em rotas (ou mapa topológico; Figura 1B). No mapa mental baseado em coordenadas, os animais lembram a localização de pontos de interesse específicos na floresta como coordenadas X e Y (distâncias e direções reais) o que lhes permite formar novos atalhos para locais de alimentação, como se houvesse a visualização do ambiente "de cima" (O'KEEFE; NADEL, 1978). Por outro lado, uma navegação baseada em rotas implica uma representação mental de locais e pontos de referência, que servem como pontos de virada (nós) entre rotas. Neste mapa mental, os caminhos podem ser mantidos e os animais podem usar diversas configurações de pontos de referência para se orientarem (por exemplo, ponto único, dois pontos de referência ou vários pontos de referência) (GARBER, 2000; POUCET, 1993). Ainda nesta representação, esses pontos de virada são normalmente escolhidos em função do interesse e/ou necessidade do animal (DI FIORE; SUAREZ, 2007; JOLY; ZIMMERMANN, 2011; NOSER; BYRNE, 2014; PRESOTTO et al., 2018).
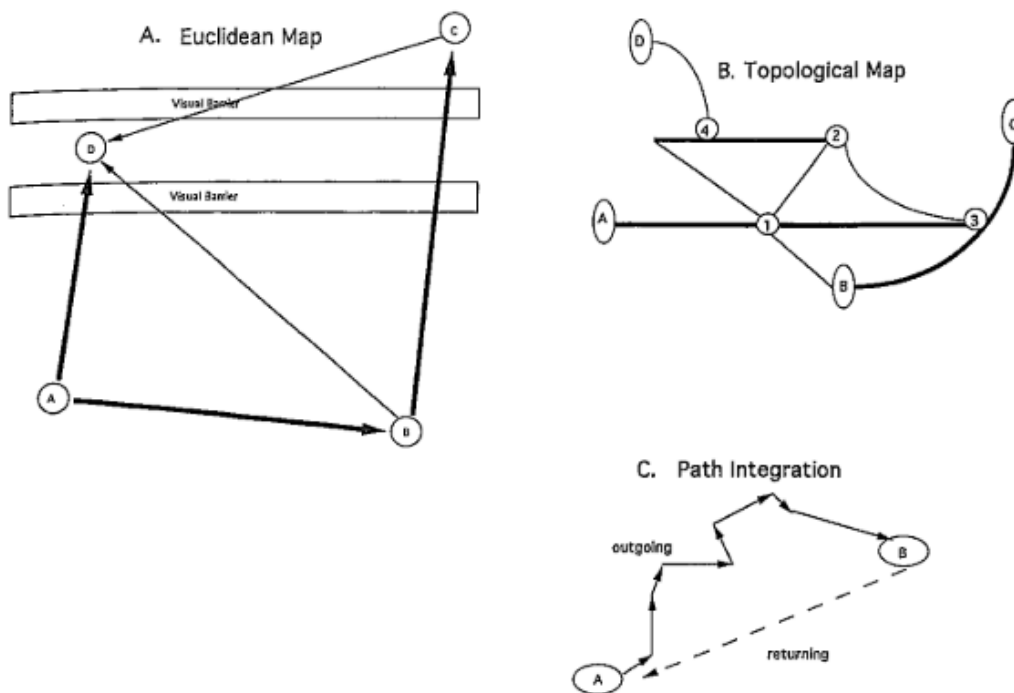
Figura 1 – Formas de representação da informação espacial do ambiente. A) Mapa Euclidiano. As letras A, B, C e D representam locais de alimentação. As linhas em negrito representam as rotas já navegadas pelo animal, enquanto as linhas simples representam atalhos criados pelo forrageador. No caso específico, o forrageador já tendo navegado pelas rotas A-B e A-D, através do mapa euclidiano consegue criar um atalho e navegar diretamente entre B e D, mesmo nunca tendo feito essa rota anteriormente; B) Mapa topológico. As letras

A, B, C e D representam locais de alimentação e os números 1, 2, 3 e 4 representam pontos de mudança de direção onde o forrageador reorienta a sua navegação. Neste tipo de mapa mental, o animal não consegue seguir diretamente de A para C e por isso faz uso de um conjunto de rotas e pontos de mudança de direção já utilizadas por ele; C) Integração de caminho. O forrageador leva em consideração a distância, direção, angulo e velocidade enquanto navega de A para B de forma a que consiga regressar ao ponto de partida através dessas informações (Retirado de Garber, 2000).

Enquanto a navegação baseada na representação de mapas baseados em coordenadas tem sido amplamente comprovada em seres humanos (EPSTEIN et al., 2017; HOWARD et al., 2014; SPIERS, 2012; mas veja WARREN, 2019), existem poucas evidências de que primatas não-humanos tenham capacidade de representar o ambiente desta forma. Até o momento, o uso de mapas mentais baseado em coordenadas foi apenas encontrado em chimpanzés Taî (*Pan troglodytes verus*) (NORMAND; BOESCH, 2009). Os autores relataram a existência da navegação baseada em coordenadas, pois verificaram que os animais foram capazes de reduzir a distância navegada entre os recursos e diminuir a velocidade de navegação ao se aproximar de fontes alimentares. Contudo, as evidências atuais sugerem fortemente que a maioria dos primatas usa um padrão de navegação baseado em rotas quando navegando em larga escala de espaço (ASENSIO et al., 2011; NOSER; BYRNE, 2007; PORTER; GARBER, 2013; SCHREIER; GROVE, 2014). Por exemplo, espécies como o macaco-aranha, o macaco-barrigudo-de-Poeppigii (*Ateles belzebuth* e *Lagothrix poeppigii*) (DI FIORE; SUAREZ, 2007) e o sagui-de-cara-suja (*Saguinus fuscicollis weddelli*) (PORTER; GARBER, 2013) navegam através de um conjunto limitado de rotas e pontos de referência, reutilizando-os com frequência. Da mesma forma, ERHART; OVERDORFF (2008) mostraram que duas espécies de lêmures (*Propithecus edwardsi* e *Eulemur fulvus rufus*) navegam de forma relativamente direta entre recursos pelas mesmas rotas, contudo utilizam a regra do vizinho mais próximo, isto é, visitam árvores em proximidade espacial umas das outras.

Apesar da maioria dos primatas pareça utilizar apenas o mapa mental baseado em rotas durante a navegação, alguns deles também podem alterar seus movimentos entre essa representação mental e o mapa mental baseado em coordenadas. De fato, PRESOTTO; IZAR (2010) mostraram que macacos-prego pretos (*Cebus nigritus*), durante a escassez de recursos de alta qualidade, reutilizam as mesmas rotas. No entanto, eles também foram capazes de criar rotas diferentes para alcançar recursos e revisitar essas fontes alimentares a partir de pontos de partida distintos, apoiando a ideia de consciência euclidiana (mapa mental baseado em

coordenadas) nesses primatas. Navegar usando um mapa mental baseado em coordenadas requer uma organização mental superior, por se tratar de uma forma de navegação mais complexa e flexível. Em contraste, um mapa mental baseado em rotas é mais simples e os animais precisam usar informações adicionais (qualitativas ou visuais) dos pontos de referência (DE RAAD; HILL, 2019; TRAPANESE; MEUNIER; MASI, 2018). Mesmo com diferenças, ambas as representações são vantajosas. De fato, alguns autores argumentam que a navegação em função de rotas pode ser tão eficaz quanto a navegação baseada em coordenadas caso a primeira possua muitos pontos de referência (BYRNE, 2000; JANSON; BYRNE, 2007).

Embora numerosos estudos tenham documentado os movimentos e representações espaciais de primatas em larga escala de espaço (GARBER; DOLINS, 2014; TRAPANESE; MEUNIER; MASI, 2018), apenas uma proporção limitada desses estudos tem sido conduzida com primatas neotropicais (GARBER; HANNON, 1993; PORTER; GARBER, 2013) e todos foram realizados em florestas tropicais úmidas. Como sugerido por PRESOTTO et al. (2019), um ambiente com recursos estáveis e disponíveis na maior parte do ano como o encontrado em florestas tropicais úmidas quando comparado a ambientes semiáridos ou áridos, pode levar primatas a usarem uma navegação topológica. Em contraste, um ambiente semiárido como a Caatinga representaria um novo leque de desafios aos animais, por se tratar de um ambiente cujos recursos se apresentam de forma instável. Neste tipo de cenário relembrar a localização exata das fontes alimentares poderia ser uma vantagem para primatas que exploram recursos em ambientes semiáridos, como a Caatinga, que apresentam escassez de frutos carnosos.

Caatinga

A Caatinga é o único domínio morfoclimático que se encontra restrito ao território brasileiro. A mesma compreende uma área de aproximadamente 800.000 km^2 (WERNECK, 2011), representando 70% da região do Nordeste e 11% do território nacional (ANDRADE-LIMA, 1981). Este ambiente apresenta características climáticas extremas e únicas, como baixa nebulosidade, elevada temperatura média anual, alta radiação solar e, além disso, umidade relativa e precipitações baixas (LEAL; TABARELLI; CARDOSO DA SILVA, 2003). A temperatura média anual varia entre 24 e 28ºC, chegando a máximas de 40ºC, enquanto a precipitação é bastante irregular, reduzida a períodos curtos do ano e varia entre 240 e 1.500 mm por ano (PRADO, 2003).

Considerada como "Floresta Branca" (PRADO, 2003), a Caatinga é composta predominantemente por zonas arbóreas ou arbustivas baixas, possuindo espécies vegetais

decíduas (ARAÚJO; CASTRO; ALBUQUERQUE, 2007). A maioria destas plantas apresentam espinhos, microfilia e características xerofíticas, conseguindo assim sobreviver em períodos longos de estiagem, quando a umidade do solo é extremamente baixa (ALBUQUERQUE et al., 2012; BARBOSA; BARBOSA; LIMA, 2003). A Caatinga possui cerca de 1.500 espécies de plantas diferentes (ALBUQUERQUE et al., 2012), sendo as famílias mais representativas desta região: Fabaceae/Leguminosae, Cactaceae, Bromelacieae, Euphorbaceae (LEAL; TABARELLI; CARDOSO DA SILVA, 2003). Entre estas, as mais representadas e também endêmicas deste ambiente são Fabaceae/Leguminosae (QUEIROZ, 2002) e Cactaceae (TAYLOR; ZAPPI, 2002). No entanto, a composição florística deste ambiente não é uniforme e varia de acordo com o volume de precipitação, com a qualidade dos solos, entre outros fatores (BARBOSA; BARBOSA; LIMA, 2003), podendo ser observadas variações fisionômicas a curtas distâncias (DE AMORIM; SAMPAIO; DE LIMA ARAÚJO, 2005). As características climáticas únicas da Caatinga, fazem com que a presença de frutos ou recursos consumíveis para mamíferos seja bastante escassa durante a maior parte do ano (BARBOSA; BARBOSA; LIMA, 2003; DE AMORIM; SAMPAIO; ARAÚJO, 2009).

Haja vista o interesse crescente neste ambiente e na sua fauna, vários grupos de animais têm sido alvo de muitos estudos, levando a um aumento do seu conhecimento (e.g. ALBUQUERQUE et al., 2012). A Caatinga se apresenta como um especial desafio para os mamíferos pois, ao contrário de roedores do deserto que habitam locais áridos, os mamíferos habitantes da caatinga não possuem adaptações fisiológicas (apenas ajustes comportamentais) para viver neste ambiente tão adverso (STREILEIN, 1982). Isto faz com que passem por grandes desafios no que diz respeito a estresse térmico (DIAZ; OEJA, 1999). Dentro do grupo de mamíferos são conhecidas cerca de 156 espécies que habitam a Caatinga, 12 destas endêmicas do semiárido brasileiro (ALBUQUERQUE et al., 2012; SILVA; LEAL; TABARELLI, 2017). Com relação aos primatas não-humanos, são conhecidas algumas espécies que habitam a Caatinga (e.g. *Callithrix jacchus*, *Callithrix pennicillata*, *Sapajus libidinosus*, *Sapajus flavius*, *Alouatta ululata*) havendo consequentemente, estudos direcionados para a sua ecologia e comportamento nestas condições (ABREU et al., 2016; AMORA; BELTRÃO-MENDES; FERRARI, 2013; DE LA FUENTE et al., 2014; DE MORAES; DA SILVA SOUTO; SCHIEL, 2014; MOURA, 2007; MOURA; LEE, 2004). Contudo, estudos de cognição espacial em primatas habitando ambiente semiárido que poderiam trazer informações relevantes sobre como os animais sobrevivem e forrageiam em locais de condições climáticas únicas, ainda são inexistentes.

Callithrix jacchus

      Callithrix jacchus, popularmente conhecido como sagui-comum ou sagui-de-tufo-branco, é um pequeno primata do Novo Mundo da família Callitrichidae (SCHIEL; SOUTO, 2017). Ocorrem naturalmente no Nordeste do Brasil (SOUSA; PONTES, 2008), possuindo uma grande adaptabilidade a diferentes ambientes podendo ser encontrados desde a Mata Atlântica à Caatinga (MODESTO; BERGALLO, 2008). São animais sociais, vivendo em grupos de 3 a 15 indivíduos, formados por adultos, juvenis e infantes (STEVENSON; RYLANDS, 1988), que podem ou não ser aparentados. Esta espécie possui uma hierarquia social bem definida, possuindo em seu grupo, normalmente um par reprodutor e indivíduos subordinados (DIGBY, 1995), que podem ser ou não filhos do casal. Assim, este pequeno primata neotropical possui uma alta tolerância social (DUNBAR, 1995), uma vez que existe uma cooperação no cuidado parental (FAULKES; ARRUDA; MONTEIRO, 2009). No entanto, havendo uma hierarquia social em grupos desta espécie (DE LA FUENTE et al., 2019), por vezes há comportamentos agonísticos entre os membros do grupo (DIGBY, 1995), principalmente em casos de procura e consumo de recursos alimentares (MICHELS, 1998). Os saguis-comum são onívoros (STEVENSON; RYLANDS, 1988) e a sua dieta é variada, alimentando-se de frutos, folhas, goma, sementes, insetos, aracnídeos, pequenos lagartos, sapos, filhotes e ovos de aves (RYLANDS; DE FARIA, 1993; SOUTO et al., 2007).

      Estudos focando na cognição destes primatas em cativeiro são extensos (BUGNYAR; HUBER, 1997; CALDWELL; WHITEN, 2003, 2004; DE SOUSA et al., 2001; HUBER; VOELKL, 2009; MACDONALD et al., 2004; MENDES; HUBER, 2004; SPINELLI et al., 2004) comparativamente a estudos em campo que são mais escassos (GUNHOLD et al., 2014; HALSEY; BEZERRA; SOUTO, 2006; PESENDORFER et al., 2009; SCHIEL et al., 2010). Ainda, estudos focando especificamente na cognição espacial destes animais em ambiente selvagem são inexistentes. Relativamente à memória espacial desta espécie, estudos realizados em cativeiro demonstram que estes utilizam a memória para regressar a fontes alimentares previamente descobertas (i.e., estratégia de "win-stay") e que podiam localizar recursos espacialmente através do uso de pontos de referência (EASTON et al., 2003; MACDONALD et al., 2004; MACDONALD; PANG; GIBEAULT, 1994; STEVENS; HALLINAN; HAUSER, 2005). Por sua vez, com um experimento simples em labirinto em que os animais tiveram que escolher entre dois locais (um com recompensa alimentar e outro sem recompensa alimentar), EASTON et al. (2003) descobriram que os animais eram capazes de lembrar corretamente a localização espacial com os recursos alimentares após curtos intervalos de retenção (1 h). No entanto, todos os trabalhos supracitados foram realizados em laboratório e com um número

reduzido de indivíduos. Até ao momento não se sabe se, em um contexto de forrageio na natureza em pequena escala de espaço, essa espécie usa a memória espacial de curto e longo prazo para localizar fontes de alimento ou mesmo se consegue aprender e memorizar a localização espacial desses recursos após uma única visita (aprendizagem espacial em uma exposição). Da mesma forma, apesar de os saguis-comum terem sido recentemente considerados excelentes modelos na pesquisa cognitiva (MILLER, 2017), nada se sabe sobre suas decisões de navegação ou sua cognição espacial em larga escala de espaço.

CAPÍTULO 2

(artigo publicado na *Primates*)

ORIGINAL ARTICLE

Wild common marmosets (*Callithrix jacchus*) employ spatial cognitive abilities to improve their food search and consumption: an experimental approach in small-scale space

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Abstract
The ability of an animal to integrate and retain spatial information of resources often depends on the spatial memory and the speed at which this memory crystallizes. These become especially important once foragers reach their target area. However, very little is known about how wild common marmosets encode spatial information when feeding rewards are near to each other in a small-scale space. With this in mind, we performed field experiments to test foraging decisions related to a small-scale space setting. Specifically, we tested the (i) short- and (ii) long-term spatial memory, as well as (iii) the ability to remember the spatial location of resources after a single visit (one-trial spatial learning). The study was conducted with four groups of wild common marmosets (*Callithrix jacchus*) living in a semiarid Caatinga environment. We observed that individuals were able to retain spatial information of food sources on both a short- and long-term basis and to learn the spatial location of these resources after a single visit. We suggest that such abilities during foraging can improve the search for scattered resources with fluctuations of food availability. Presumably, this would be particularly advantageous in Caatinga, with its vegetation exhibiting asynchronous phenological patterns. Altogether, our results demonstrate that common marmosets employ all three studied spatial cognitive abilities to improve their food search and consumption.

Keywords Caatinga · Foraging decisions · Short-term spatial memory · Long-term spatial memory · One-trial spatial learning

Introduction

The ability to rely on memory to locate and remember stable productive feeding sites is a powerful tool for many foragers (Fagan et al. 2013). While the distribution and availability of feeding sites change over time and space, the ability to integrate and retain such changes depends on both the animals' spatial (Corlett 2011) and temporal memories (Milton 1981; Tsalyuk et al. 2019). Whereas spatial memories help animals to choose where to explore resources, temporal memories help them to decide when to return to resource locations

(Garber 2000). Thus, once a forager reaches a specific feeding site in a small-scale space [i.e., an area in which individuals can have several views of the feeding spots from distinct directions and perspectives (Garber and Dolins 2010, 2014)], it faces within-patch foraging decisions. However, regardless of the spatial scale where animals forage (large- or small-scale space: Garber and Dolins 2014), individuals can use two types of spatiotemporal memory (Bailey et al. 1996; Corlett 2011): short-term spatial memory, which can go from minutes to hours, and long-term spatial memory, which includes memories lasting from days/weeks to even a lifetime (Bailey et al. 1996; Corlett 2011).

For animals, such as primates, living in environments featuring highly fluctuating resources and consuming from ephemeral food sources (e.g., fruits from synchronous trees or insects), it would be more advantageous to rely on short-term spatial memory, given that these foods tend to be available for short periods of time. On the other hand, long-term spatial memory would be more useful in environments with stable resources that last for long periods of time

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or are available all year round such as perennial leaves or fruits from asynchronous trees (Shettleworth 2010; Janmaat et al. 2013). To date, most studies with wild primates have focused on the use of short-term spatial memories and concluded that these animals can remember the spatial location of resources (experimental studies: *Saguinus mystax*: Garber and Dolins 1996; *Cebus capucinus*: Garber and Paciulli 1997; *Saguinus oedipus oedipus*: Dolins 2009; *S. nigritus* (formerly *C. nigritus*): Gomes and Bicca-Marques 2012; observational studies: *Chlorocebus pygerythrus*: Teichroeb and Chapman 2014; *Alouatta palliata*: Hopkins 2016). Regarding long-term spatial abilities, only a few studies have demonstrated that non-human primates can store spatial information for periods longer than 24 h (observational studies: *Pan troglodytes verus*: Janmaat et al. 2013; experimental studies: *Leontopithecus rosalia* and *Callithrix kuhli*: Platt et al. 1996; *Pan troglodytes*: Mendes and Call 2014; *Sapajus cay*: Tujague et al. 2015). In the meantime, most available data on small-scale foraging of New World primates in the wild are focused on short-term spatial memory (Tujague et al. 2015). On the other hand, studies attempting to understand whether these primates are able to remember the location of feeding sites after long periods of time or if they possess temporal knowledge of resources are still scarce and carried out only in captivity (*Callicebus moloch* and *Saimiri sciureus*: Andrews 1988; *Leontopithecus rosalia* and *Callithrix kuhli*: Platt et al. 1996; *Sapajus cay*: Tujague et al. 2015; *Callithrix penicillata*: Vannuchi et al. 2020; but see Tujague and Janson 2017; Trapanese et al. 2018 for a review of spatiotemporal studies).

Along with spatial memory, the ability to memorize a feeding patch after one single visit (i.e., one-trial learning: Harlow 1949) could also be of advantage. This ability can be important, for example, when foraging on quickly depletable and perishable food resources (e.g., young leaves or ripe fruits: Janmaat et al. 2016) in a feeding patch. This quick spatial learning can make the individual more efficient than others (conspecific or heterospecific individuals) in competitive situations (Milton 1981; Corlett 2011). The ability to remember the spatial position of resources in small-scale space after a single visit has so far been demonstrated only in chimpanzees (*Pan troglodytes*: Mendes and Call 2014). The authors observed that captive chimpanzees remember different food locations after 24 h with only one exposure to the experiment. Although Menzel and Juno (1982) also observed, in a non-spatial experiment, one-trial visual discrimination learning in *Saguinus fuscicollis*, there is no information on whether a free-living New World primate would exhibit one-trial learning in a spatial foraging context.

Common marmosets (*Callithrix jacchus*) are small callitrichines that rely on both ephemeral resources (such as insects, fruits from synchronous trees, and birds' eggs) and stable resources (e.g., exudates) (Souto et al. 2007; Abreu et al.

2016), and inhabit two types of environments with contrasting ecological conditions (Rylands and de Faria 1993; Garber et al. 2019). Cognitively, this species has shown to be capable of waiting for longer to obtain greater food rewards (self-control: Stevens et al. 2005), discern among different amounts of available resources (Stevens et al. 2007), and even maintain their own preferences in foraging tasks (habit formation: Pesendorfer et al. 2009). In addition, through a field experiment ('push or pull' box), Gunhold et al. (2014) demonstrated the remarkable memory of these primates as they were able to remember the way they used the 'push or pull' box after a 2-year-gap without the exposure to the apparatus. Studies carried out in 1994 and 2004 by MacDonald et al. demonstrate that common marmosets use spatial memory accurately, often adopting the "win-stay" strategy (i.e., returning to places where they had previously found food), and that they could locate resources spatially through the use of landmarks, respectively. In turn, with a simple T-maze experiment in which animals had to choose between two sites (one with a food reward and the other without), Easton et al. (2003) found that marmosets were able to correctly remember the spatial location with the food resources after short retention intervals (1 h). However, so far it is unknown whether, in a foraging context in the wild, this species can rely on spatiotemporal memory (short- and long-term spatial memory) to locate food sources, or even whether these primates can learn and recall the spatial location of these resources after a single visit (one-trial spatial learning).

Here we investigated the spatial abilities of wild common marmosets in a small-scale space. For wild common marmosets living in a Caatinga environment, small-scale space could represent an exudate or cacti tree or an area with an aggregated set of food sources, such as bromeliads. We carried out a set of field experiments with four platforms close together by changing the spatial location and presentation times of food rewards to test the animals' (i) short- and long-term memory for spatial information and (ii) their ability to retain spatial information from feeding sites after a single visit (one-trial spatial learning). We hypothesized that if common marmosets are capable of encoding the spatial location of a food reward in a short- and long-term basis, then they should accurately find the feeding rewards more than expected by chance. Additionally, if they are capable of one-trial spatial learning, we would expect that they will find accurately the feeding rewards after only one exposure to the correct choice.

Methods

Study area and subjects

The study was carried out at the Baracuhy Biological Field Station (7°31′42″S–36°17′50″W), an area of Caatinga

located in the state of Paraíba, northeast Brazil. The study site features high temperatures and low precipitation, and the native vegetation is that typical of the semi-arid region, consisting mainly of short vegetation and xerophytic formations (Nascimento and Alves 2008). The area features plenty of thorny vegetation and scattered trees with a density of about 4.5 individuals per hectare (De la Fuente et al. 2014).

In this study, we observed four common marmosets' groups (ALG, COQ, VAC, PRI: average number of individuals per group = 5 ± 1 SD) composed of adult females and males, juveniles and infants (Table 1). We classified the animals as infant (≤ 4 months), juvenile (5–11 months), subadult (12–15 months), or adult (> 15 months) (Garber et al. 2019). Age categories were based on body and genital lengths, body mass and teeth eruptions, or through knowledge of their birth dates. Due to expulsion and emigration events, the number of individuals per group decreased throughout the study. The animals under study were habituated to the presence of researchers, as they have been included in field observational studies since 2012 (De la Fuente et al. 2014; Abreu et al. 2016). Study subjects were individually identified based on natural marks and scars (Abreu et al. 2019), or through marking collars (De la Fuente et al. 2019). In our analyses, we use only subadults/adults ($N = 20$; age ≥ 12 months: Garber et al. 2019), given that both spatial and foraging capacities are not yet fully developed in primate infants and juveniles (Lacreuse et al. 2005; Schiel et al. 2010).

Experimental design and data collection

To simulate food search in small-scale space, we built a feeding station in the home range of each group. Each feeding station consisted of four visually identical 1.1-m-high platforms, with a 50 × 50-cm surface area, in a quadrangular arrangement, 2.5-m apart from each other (Garber and Dolins 1996). The animals had similar access to all platforms and could only access it through trees or the ground (not directly from one to another) (for more details see De la Fuente et al. 2019). We placed a two-compartment plastic container with small banana slices (± 3 g) at the top of each platform. To ensure that the olfactory cues were equal, all the containers were provided with food. However, only one of the containers had side openings to make the resource

accessible to the animals. The other three containers had only small side holes to prevent the animals from accessing the food (Fig. 1). Thus, during the experimental sets, we had only one accessible container. In order to exclude visual cues, we placed side curtains and opaque paper on top of each container. We provided the same amount of food in all containers regardless of their accessibility.

Before the systematic data collection, we habituated the animals to the experimental station for 5 months (about 10 days/month). At first, we offered whole bananas on the top of each platform in order to familiarize the animals to the platforms. Later, we offered banana slices inside each container on the top of all platforms so that the animals could learn to take the food out of the containers. Finally, we included the side curtains and opaque paper. The habituation period was considered completed after all individuals could
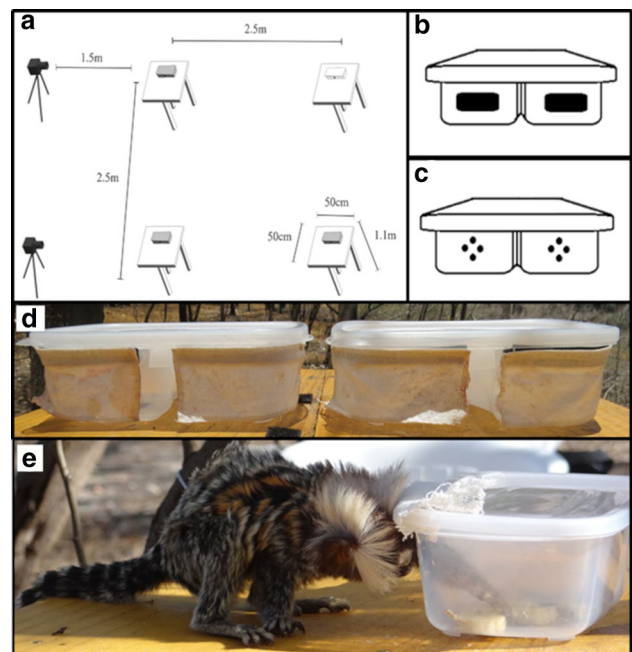
Fig. 1 **a** Schematic design of the experimental setting (the *black boxes* represent the inaccessible containers and the *white box* the accessible container); **b** accessible container; **c** inaccessible container; **d** Container with opaque paper and side curtains used in the experiment; **e** Common marmoset (Veruska from ALG group) reaching out for the food reward from the accessible container (Image: María Fernanda De la Fuente)

Table 1 Group's composition of *Callithrix jacchus* at the beginning of the study

Age (in months)	ALG ♀	ALG ♂	COQ ♀	COQ ♂	VAC ♀	VAC ♂	PRI ♀	PRI ♂
Infant (1–4)	–	–	–	–	–	–	–	2[a]
Juvenile (5–11)	–	–	–	1[a]	–	–	–	–
Subadult/adult (≥ 12)	5	1	1	3	1	4	4	1

[a]Individuals not included in the analyses

successfully remove food from the container. During the habituation period, we offered for each group an average of four whole bananas (cut into slices), which is more than the animals could eat, irrespective of the group. After the animals left the experimental station, we counted the number of slices consumed and calculated for each group, the amount of banana slices that were used during the two experimental sets. We collected systematic data during August and September 2015 (Groups ALG and COQ), and during May and June 2016 (Groups VAC and PRI). Data were collected by four trained and experienced observers (De la Fuente et al. 2019). We used two cameras (Canon PowerShot SX50 HS) in each feeding station to aid the observations. Once data collection was completed, all videos were reviewed and re-analyzed by the first author for increased accuracy. We used the 'all-occurrences' sampling method (Martin and Bateson 2007) to collect systematic data of all individuals. We recorded the order the animals arrived at the experimental station, and the correct and incorrect choices.

To test our hypotheses, we exposed the animals to the experiment using two sets of time intervals. First (experimental set I), the animals were exposed to the experiment every 4½ h for 10 consecutive days during their activity period (6 a.m., 10:30 a.m. and 3 p.m.); then, we allowed an interval of 11 days and repeated the same experiment (experimental set II) at the same time intervals for 10 consecutive days. The 4½-h retention interval between each trial was set according to the available literature on short-term memory information, while the 11-day interval was set according to information available on long-term memory (*Leontopithecus rosalia* and *Callithrix kuhli*: Platt et al. 1996; *Gorilla gorilla gorilla*: Schwartz et al. 2002; *Pan troglodytes*: Mendes and Call 2014; *Sapajus cay*: Tujague et al. 2015). Times 6 a.m. and 3 p.m. were selected because they correspond to the daily forage peaks of these animals (De la Fuente et al. 2014); while 10:30 a.m. was chosen to have equal intervals between trials. At the beginning of each experimental set, the reward platform with the accessible container was chosen randomly and was not the same between the two experimental sets. Once the location of the reward platform was established, it was kept constant throughout each experimental set.

Upon completion of the experiment, and to make sure that the animals did not use external cues to locate food (e.g., tree or platform shapes) instead of spatial abilities, we performed a control test. To this end, we used two of the study groups (VAC and COQ: seven individuals in total) for 5 days and performed three trials per day, for a total of 15 trials for each group observed. In this test, the spatial position of the accessible container was randomly changed in all trials. The amount of resources offered was enough to satisfy all members of the group. The observation method and the data collected were the same as those previously described.

For the analyses of this study, we considered a 'visit' whenever an animal inspected the container or took food out of it, whether or not the food was consumed (adapted from Garber and Dolins 1996; Garber and Paciulli 1997). Correct and incorrect choices were based on the animals' visits to the platforms. The visit of an individual to a platform with accessible food was regarded as a correct choice; if an animal visited a platform with inaccessible food, this choice was considered incorrect (Garber and Dolins 1996; Garber and Paciulli 1997). Given that this study was part of a broad project that addressed different aspects of the ecology and behavior of common marmosets, we offered different amounts of food in each experimental set. During the experimental set I, we provided enough food to satisfy all individuals in the group and, after the 11-day interval, in the experimental set II, we provided half the amount required to feed the entire group (for more details see De la Fuente et al. 2019).

Data analyses

Because the aim of this study was not to verify the influence of the amount of resource on the spatial abilities of the species, we examined whether the difference in the amount of food offered influenced the correct and incorrect choices made by the animals. To do so, we used the *G*-test of independence (Mcdonald 2014) and we found that the experimental sets were independent, that is, the amount of resources provided did not influence the number of correct and incorrect choices ($G = 0.78$, $df = 1$, $p = 0.37$), thus, we combined the data from the two experimental sets to test our hypotheses.

In order to test the first hypothesis, we used Monte Carlo simulations (Robert and Casella 2010) to determine if the proportion of correct choices observed was higher than those expected at random (null hypothesis: the capacity of the animals to remember the spatial location of the platform with accessible food is not higher than what is expected at random). To test short-term spatial memory (4½-h retention interval), we excluded the first trial of each experimental set and analyzed the following 14 trials (the analysis was performed by pooling together experimental sets I and II). We excluded the first trial from the analysis, as it was the first exposure of the animals to that spatial arrangement, thus being of no use for testing short-term spatial memory (Gomes and Bicca-Marques 2012). The proportion of correct choices observed for each individual during each trial was calculated on the basis of the first four visits to the platforms or on the number of visits it took to choose the platform with accessible food (if they succeeded before the fourth visit) per trial. For example, if the animal reached the correct platform on its first visit, the proportion would be $1/1 = 1$, while if the animal visited the correct platform on

its third visit, the proportion would be $1/3 = 0.33$. Revisits were considered as valid visits (e.g., assuming that platform 4 (P4) had accessible food, if a marmoset visited P1, P2, and P3 and then returned to P1, they would be counted as four visits without finding food, thus the calculated proportion would be $0/4 = 0$). The Monte Carlo method allowed us to reproduce a scenario similar to the experiment in order to calculate the proportion expected by chance. We simulated that in the first visit, animals were exposed to a total of four platforms given that they could reach the experimental site from any direction or angle. In order to be more conservative, in the subsequent visits we excluded the platform where the animal was (or had been), and the animals could choose the accessible platform between three platforms. The distribution of proportions expected by chance (null hypothesis) was produced through 5000 Monte Carlo simulations, and then we estimated the probability of occurrence (*p* value) of the proportion of correct choices observed (one-tailed test) in the scenario generated (Robert and Casella 2010). In order to test long-term spatial memory (11-day retention interval), we analyzed only the proportion of correct choices in the first trial of experimental set II to verify if the animals had the capacity of remembering the spatial position of the platform featuring the container with accessible food in the previous experimental set (experimental set I). In this analysis, the calculation of the proportions of correct choices observed and those expected by chance was carried out according to the procedure described above, which was followed by the same randomization procedure conducted through Monte Carlo simulations (see above).

For our second hypothesis (one-trial spatial learning), we analyzed only the first visit of the animals in the first two trials of experimental set I and II. This procedure was adopted because, if the animals do learn after a single exposure to the experiment, we expect that, in the second trial, their first visit will be to the platform with accessible food. We used a generalized linear mixed model (GLMM) with binomial distribution to verify whether the choice of the animals was influenced by the trials. The choice of each animal (correct or incorrect) was included as a response variable and the trials (trial 1 and 2) as a predictor variable. We input the animal ID, order of arrival at the experiment (social cues) and experimental set (I and II) as random variables. The use of GLMM allowed us to account for temporal pseudoreplication (the repeated measurement from the same individual in the two trials) (Baayen et al. 2008). We verified the significance of the predictor by using the *Anova* function in the R Stats package and compared the full model with the null model containing only the random variables. When the comparison attained a significant level, we chose the full model. This selection was performed through the R lme4 package (Bates et al. 2015). We also performed a binomial

test only on the first visit of the second trial for the two experimental sets (the analysis was carried out clustering experimental set I and II) in order to verify whether or not, in this trial (trial 2), the animals visited the platform with accessible food (number of correct choices) more than what was expected by chance (one platform with accessible food in four existing platforms: 0.25 chance level).

Finally, to ensure that any effect observed in our results was not driven by external factors (visual cues from the environment or social cues), we performed two post tests. In order to investigate the use of environmental visual cues that the animals could be using to locate the platform with accessible food, we performed a binomial test on the data collected during the control test. This test verified whether the correct choices of the animals were higher than those expected by chance for that control test (0.25). We observed that, in the control test, the animals did not make more correct choices than those expected by chance, suggesting that they were not using external visual cues (proportion of correct choices: 0.33; $p = 0.08$).

Additionally, to verify if testing the animals in groups had affected their performance during the experimental sets, we first confirmed that different animals arrived first to the experiment between trials and then, performed a *G*-test of independence (Mcdonald 2014) to evaluate if the number of correct and incorrect choices of the animals was influenced by social cues. Social cues were considered to be the order of arrival of each animal at the experimental station (i.e., if an animal was the first to arrive we considered that this animal did not have access to social cues because it was alone in the experimental station and made its choice regardless of the presence of other members of the group. On the other hand, all the animals that reached the experimental station after the arrival of one or more individual(s) were considered to have access to social cues. In fact, their choices could have been based on the group members already present in the experimental station). However, our analysis showed that there was no influence of social cues on the animals' choices (correct choices with social cues = 77%, correct choices without social cues = 78%, $G = 0.16$, $df = 1$, $p = 0.7$). Note that our aim with this analysis was not to exclude social cues. Instead, we wanted to ensure that animals' choices were performed by spatial memory rather than visual cues from other animals. Finally, during the trials, two individuals could visit at the same time the same container. However, at each 20 to 25 visits, this event happened only two times. We want to highlight that this did not change the behavior of the animals or the ability to obtain/consume the food in the container, given that the animals used to take out the food very quickly and then went to consume it in a nearby tree. Throughout the analyses, we considered significance at $p \leq 0.05$. All data were analyzed in the R environment, version 3.5.2 (R Core Team 2018).

Results

We observed that, after the short retention intervals (4½ h), common marmosets showed a performance above that expected by chance, as their visits to the platform with accessible food was significantly higher than random, indicating that they remembered the spatial location of the resource ($N_{attempts} = 462$; observed proportion of correct choices = 0.79, simulated proportion of correct choices = 0.30; $p < 0.0001$). Similarly, the animals retained information on the spatial location of the resource after an interval of 11 days, since in the first trial of experimental set II, the performance of the animals was above expectation by chance. In fact, they returned to the platform that contained accessible food in the previous experimental set ($N_{attempts} = 19$, observed proportion of correct choices = 0.74, simulated proportion of correct choices = 0.31; $p < 0.0001$).

As for one-trial learning, we observed that the choices of the individuals were influenced by the trials of the experimental sets, as the animals chose the platform with accessible food (correct choices) more often in trial 2 than in trial 1 ($X^2 = 17.45$; $df = 1$; $p < 0.001$; Fig. 2). When we tested if, in the second trial, the animals reached out for the platform with accessible food more than expected at random we found that the correct choices were also higher than expected by chance in the second exposure to the experimental sets (trial 2: $N_{correct\ choices} = 19$; $N_{attempts} = 40$; $p = 0.002$; Fig. 2).
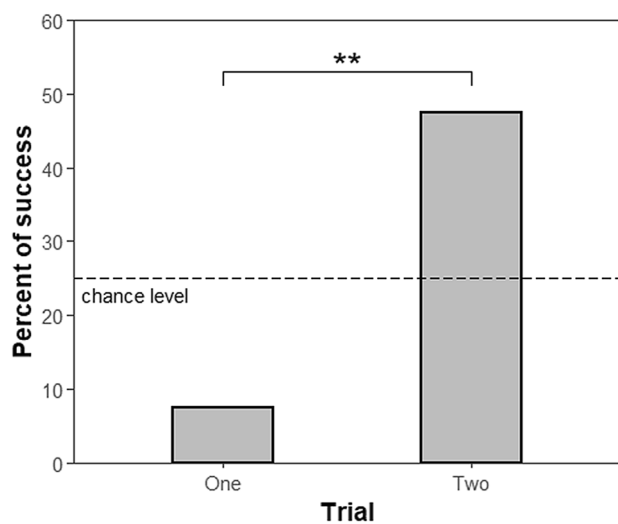

Fig. 2 Comparison of percent of success (number of correct choices divided by the number of attempts made by all individuals) between the two first trials (1 e 2). The *dashed black line* represents the chance level (one platform with accessible food in four existing platforms: 25%, i.e., percent of success if the animals do not rely on spatial memory to locate feeding platforms). **$p \leq 0.001$

Discussion

In this study, we investigated short- and long-term spatial memory capacities and the ability of one-trial spatial learning in wild common marmosets through a field experiment. We observed that after changing the available feeding site, the animals successfully returned to it in both short- and long-term intervals, thus supporting our first hypothesis. In addition, we found that common marmosets are capable of one-trial spatial learning within a foraging context, as they successfully revisit the available feeding site after just one exposure, which is in line with our second hypothesis.

The findings regarding the spatial memory of common marmosets in a small-scale space reveal that the accuracy of the short-term spatial memory observed in the present study (79% of correct choices), besides matching what has already been observed in captive studies carried out with this species (~ 85%: MacDonald et al. 1994, 2004; ~ 80%: Easton et al. 2003), seems to be similar to the one found in other callitrichines (e.g., Captive study: *Callithrix kuhli* (~ 79%): Platt et al. 1996; *Callithrix penicillata* (~ 84%): Vannuchi et al. 2020; Field study: *Saguinus imperator* (~ 75%): Bicca-Marques and Garber 2005). Interestingly, the results of our study with regard to long-term spatial memory accuracy (74% of correct choices) were also similar to previous studies conducted on Wied's black-tufted-ear marmosets and golden lion tamarins (24-h retention intervals: Platt et al. 1996), capuchin monkeys (Tujague et al. 2015) and chimpanzees (Mendes and Call 2014) in captivity. The similarity among these results may be due to the more omnivorous diet shared by these species (e.g., chimpanzees: Hladik 1977; golden lion tamarins: Raboy and Dietz 2004; Wied's black-tufted-ear marmosets: Raboy et al. 2008; capuchin monkeys: Izar et al. 2012; common marmosets: Schiel and Souto 2017). Along this line, diet has been identified as one of the precursors for the development of primate brain size, as it is associated with the use of spatial abilities (DeCasien et al. 2017; Powell et al. 2017). Milton (1981) and Tujague and Janson (2017) argue that, associated to diet, another selective factor that can trigger the development of spatial capacities is the spatiotemporal distribution of resources in heterogeneous forests. Thus, retaining spatial information of food sources for short and/or long periods of time is evidence for a cognitive ability necessary for foraging efficiency and success.

For the common marmoset, the combination of both types of spatial memory (short- and long-term) in a small-scale space can be particularly advantageous and adaptive. Populations of this species successful inhabits contrasting environments such as the dry Caatinga and the humid Atlantic

Forest (De la Fuente et al. 2014; Garber et al. 2019), which offer different types of resources with distinct phenological patterns and spatial distributions. Furthermore, common marmosets are known for their omnivorous diet (Souto et al. 2007), which results in foraging on a diverse range of food items (e.g., exudates, fruits, insects). For instance, short-term memory would be useful when the animals are searching for invertebrates and/or small vertebrates in an aggregated set of food sources (e.g., bromeliads), or to forage on the sporadic fruits of the cacti *Pilosocereus gounellei* (Quirino 2006; Gomes et al. 2017) in the Caatinga (Abreu et al. 2016). Additionally, short-term spatial memory could also improve marmosets return to particular exudate holes in specific trees, as it happens with Wied's marmosets (Platt et al. 1996). On the other hand, spatial information that is retained for weeks or months could help the animals make better use of cashews fruits (*Anacardium occidentale*) in the Atlantic Forest. In fact, although cashew trees have well-defined fruiting peaks, it represents a source of resources throughout the year, since not only fruit can be obtained from it but also the exudate, which is available all year round (Pontes and Soares 2005; da Silva et al. 2019). Hence, retaining short- and long-term spatial information would help the animals return to exudate trees and their specific exudate holes (one of the main food sources for this species) both in the Atlantic Forest and in the Caatinga (Francisco et al. 2014; Abreu et al. 2016).

The results also corroborated our second hypothesis, indicating that the common marmoset has the ability to remember the spatial location of food sources after a single visit (one-trial spatial learning). One-trial spatial learning in primates during foraging may led to the optimization of the search for patchy resources (Kushwaha et al. 2011). This ability would be valuable for common marmosets living in the Caatinga, a region that presents asynchronous phenological patterns, that is, trees with different fruiting and flowering periods (Araújo et al. 2007; Albuquerque et al. 2012). Quirino (2006) found that, despite the cacti *Pilosocereus gounellei* (xique-xique) flowering at various times of the year and the cacti *Cereus jamacaru* (mandacaru) exhibiting a semi-annual fruiting pattern, their reproductive structures (flowers/fruit) are only available for a short time and limited by predation by herbivores and rapid ripening. The characteristics of these two cactus species (seasonal fruiting/flowering associated with low and rapid food availability), used as food sources by common marmosets in the Caatinga environment (Abreu et al. 2016), require that these animals quickly learn the location of flowers and/or ripe fruit in order to avoid the loss of resources to competition. There were few studies conducted providing evidence that primates are capable of one-trial spatial learning, and studies that demonstrated such capacity were conducted only on Old World primates (captive study: Mendes and Call 2014; field study:

Noser and Byrne 2015). For this reason, the question related to the ability of primates to remember specific events of their past after limited exposure, such as the spatial location of feeding sites, is still controversial and inconclusive (where, when, what, (WWW) memory: Schwartz and Evans 2001; but see: Tulving 2005); and, by contrast, our study provides insight into these questions by presenting the ability of common marmosets to retain spatial information (where) for long periods of time and after only one exposure.

Overall, our data revealed that common marmosets have accurate spatiotemporal cognitive abilities that probably improve their search and acquisition of food resources when feeding on rewards in small-scale space. At this point, it should be mentioned that our findings on the well-developed spatial abilities in this species, associated with other factors (e.g., general diet, gummivory, manual dexterity: Abreu et al. 2016; Garber et al. 2019; De la Fuente et al. 2019), might represent an additional trigger for the successful radiation of these primates, helping them inhabit challenging environments such as the Caatinga (Schiel and Souto 2017). Furthermore, the findings of the present study also raise the question about the presence of episodic-like memory (WWW-memory) in this small New World primate. This type of memory is characterized as the ability to remember past personal events for long periods of time and recalling information on where (e.g., spatial location of the feeding tree), what (e.g., type of food) and when (e.g., time of day the feeding tree was visited) it occurred (Crystal 2010). Its presence has already been suggested in some New and Old World primates (e.g., Hampton et al. 2005; Bourjade et al. 2012; Janmaat et al. 2012; Tujague and Janson 2017). For this reason, it is important to study these kinds of questions in future studies, as this species has become a promising model in cognitive research (Miller 2017). Moreover, it would be interesting to investigate how common marmosets encode spatial and temporal information in large-scale space (i.e., navigating between resources), as Poucet (1993) suggested that primates may represent this information differently in both scales of space. The present study also serves as a viable model for studying spatial abilities in wild primates, to better and more deeply examine the cognitive flexibility with which nonhuman animals adapt their spatial cognitive responses to resource availability in differing habitats.

by Ethics Committee for Animal Use of the Federal Rural University of Pernambuco (license n°144/2014) and SISBio (license n°46770/1). In addition, the study has complied with the ethical standards in the treatment of their animals of University of Illinois for Animal Research (IACUC n°14263). The research adhered to the guidelines laid down by EC guide for animal experiments and Brazilian laws.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All procedures performed involving animals were in accordance with Brazilian laws for the use of wild animals in research and were approved by Ethics Committee for Animal Use of the Federal Rural University of Pernambuco (license n° 144/2014) and SISBio (license n°46770/1). In addition, the study has complied with the ethical standards in the treatment of their animals of University of Illinois for Animal Research (IACUC n°14263).

References

Abreu F, De la Fuente MFC, Schiel N, Souto A (2016) Feeding ecology and behavioral adjustments: flexibility of a small neotropical primate (*Callithrix jacchus*) to survive in a semiarid environment. Mammal Res 61:221–229. https://doi.org/10.1007/s13364-016-0262-4

Abreu F, Souto A, Bonci DMO, Montavani V, Pessoa DMA, Schiel N (2019) Detection of insect prey by wild common marmosets: the effect of color vision. Am J Primatol. https://doi.org/10.1002/ajp.22963

Albuquerque UP, Araújo EDL, El-Deir ACA et al (2012) Caatinga revisited: ecology and conservation of an important seasonal dry forest. Sci World J. https://doi.org/10.1100/2012/205182

Andrews MW (1988) Selection of food sites by *Callicebus moloch* and *Saimiri sciureus* under spatially and temporally varying food distribution. Learn Motiv 19:254–268. https://doi.org/10.1016/0023-9690(88)90004-5

Araújo EDL, Castro CC, Albuquerque UP (2007) Dynamics of Brazilian Caatinga—a review concerning the plants, environment and people. Funct Ecosyst Communities 1:15–28

Baayen RH, Davidson DJ, Bates DM (2008) Mixed-effects modeling with crossed random effects for subjects and items. J Mem Lang 59:390–412. https://doi.org/10.1016/j.jml.2007.12.005

Bailey C, Bartsch D, Kandel E (1996) Toward a molecular definition of long-term memory storage. Proc Natl Acad Sci USA 93:13445–13452

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Bicca-Marques JC, Garber PA (2005) Use of social and ecological information in tamarin foraging decisions. Int J Primatol 26:1321–1344. https://doi.org/10.1007/s10764-005-8855-9

Bourjade M, Thierry B, Call J, Dufour V (2012) Are monkeys able to plan for future exchange? Anim Cogn 15:783–795. https://doi.org/10.1007/s10071-012-0502-1

Corlett RT (2011) How to be a frugivore (in a changing world). Acta Oecol 37:674–681. https://doi.org/10.1016/j.actao.2011.01.005

Crystal JD (2010) Episodic-like memory in animals. Behav Brain Res 215:235–243. https://doi.org/10.1016/j.bbr.2010.03.005

da Silva PO, Menino GCO, Reys P, Sá JL, Soares MP, Silva FG (2019) Phenology of *Anacardium occidentale* (Anacardiaceae) and relationship with climatic factors. Floresta 49:69–78. https://doi.org/10.5380/rf.v49i1.56310

De la Fuente MF, Schiel N, Bicca-Marques JC, Caselli CB, Souto A, Garber PA (2019) Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (*Callithrix jacchus*). Am J Primatol. https://doi.org/10.1002/ajp.22964

De la Fuente MFC, Souto A, Sampaio MB, Schiel N (2014) Behavioral adjustments by a small neotropical primate (*Callithrix jacchus*) in a semiarid caatinga environment. Sci World J. https://doi.org/10.1155/2014/326524

DeCasien AR, Williams SA, Higham JP (2017) Primate brain size is predicted by diet but not sociality. Nat Ecol Evol 1:1–7. https://doi.org/10.1038/s41559-017-0112

Dolins FL (2009) Captive cotton-top tamarins' (*Saguinus oedipus oedipus*) use of landmarks to localize hidden food items. Am J Primatol 71:316–323. https://doi.org/10.1002/ajp.20654

Easton A, Parker K, Derrington AM, Parker A (2003) Behaviour of marmoset monkeys in a T-maze: comparison with rats and macaque monkeys on a spatial delayed non-match to sample task. Exp Brain Res 150:114–116. https://doi.org/10.1007/s00221-003-1409-5

Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G, LaDage L, Schlägel UE, Tang W, Papastamatiou YP, Forester J, Mueller T (2013) Spatial memory and animal movement. Ecol Lett 16:1316–1329. https://doi.org/10.1111/ele.12165

Francisco TM, Couto DR, Zanuncio JC, Serrão JE, Silva IDO, Boere V (2014) Vegetable exudates as food for *Callithrix* spp. (Callitrichidae): exploratory patterns. PLoS ONE 9:1–7. https://doi.org/10.1371/journal.pone.0112321

Garber PA (2000) The ecology of group movement: evidence for the use of spatial, temporal, and social information in some primate foragers. In: Boinski S, Garber PA (eds) On the move. How and why animals travel in groups, Chicago. University of Chicago Press, Chicago, pp 261–298

Garber PA, Caselli CB, McKenney AC, Abreu F, De la Fuente MFC, Araújo A, Arruda MDF, Souto A, Schiel N, Bicca-Marques JC (2019) Trait variation and trait stability in common marmosets (*Callithrix jacchus*) inhabiting ecologically distinct habitats in northeastern Brazil. Am J Primatol. https://doi.org/10.1002/ajp.23018

Garber PA, Dolins F (1996) Testing learning paradigms in the field. In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive radiations of neotropical primates. Springer US, Boston, pp 201–216

Garber PA, Dolins FL (2010) Examining spatial cognitive strategies in small-scale space and large-scale space in tamarin monkeys. In: Dolins FL, Mitchell RW (eds) Spatial cognition, spatial perception: mapping the self and space, 1st edn. Cambridge University Press, Cambridge, p 581

Garber PA, Dolins FL (2014) Primate spatial strategies and cognition: introduction to this special issue. Am J Primatol 76:393–398. https://doi.org/10.1002/ajp.22257

Garber PA, Paciulli LM (1997) Experimental field study of spatial memory and learning in wild capuchin monkeys (*Cebus capucinus*). Folia Primatol 68:236–253. https://doi.org/10.1159/000157250

Gomes DF, Bicca-Marques JCJC (2012) Capuchin monkeys (*Cebus nigritus*) use spatial and visual information during within-patch foraging. Am J Primatol 74:58–67. https://doi.org/10.1002/ajp.21009

Gomes VGN, Meiado MV, Quirino ZGM, de Araujo HFP, Machado IC (2017) Synchronous fruiting and common seed dispersers of two endemic columnar cacti in the Caatinga, a dry forest in Brazil. Plant Ecol 218:1325–1338. https://doi.org/10.1007/s11258-017-0771-5

Gunhold T, Massen JJM, Schiel N, Souto A, Bugnyar T (2014) Memory, transmission and persistence of alternative foraging techniques in wild common marmosets. Anim Behav 91:79–91. https://doi.org/10.1016/j.anbehav.2014.02.023

Hampton RR, Hampstead BM, Murray EA (2005) Rhesus monkeys (*Macaca mulatta*) demonstrate robust memory for what and where, but not when, in an open-field test of memory. Learn Motiv 36:245–259. https://doi.org/10.1016/j.lmot.2005.02.004

Harlow HF (1949) The formation of learning sets. Psychol Rev 56:51–65

Hladik CM (1977) Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In: Clutton-Brock TH (ed) Primate ecology: studies of feeding and ranging behavior in lemurs, monkey and apes. Academic Press, London, pp 81–501

Hopkins ME (2016) Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. Anim Cogn 19:387–403. https://doi.org/10.1007/s10071-015-0941-6

Izar P, Verderane MP, Peternelli-dos-Santos L, Mendonça-Furtado O, Presotto A, Tokuda M, Visalberghi E, Fragaszy D (2012) Flexible and conservative features of social systems in tufted capuchin monkeys: comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. Am J Primatol 74:315–331. https://doi.org/10.1002/ajp.20968

Janmaat KRL, Chapman CA, Meijer R, Zuberbühler K (2012) The use of fruiting synchrony by foraging mangabey monkeys: a "simple tool" to find fruit. Anim Cogn 15:83–96. https://doi.org/10.1007/s10071-011-0435-0

Janmaat KRL, Ban SD, Boesch C (2013) Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Anim Behav 86:1183–1205. https://doi.org/10.1016/j.anbehav.2013.09.021

Janmaat KRL, Boesch C, Byrne R, Chapman CA, Bi ZBG, Head JS, Robbins MM, Wrangham RW, Polansky L (2016) Spatio-temporal complexity of chimpanzee food: How cognitive adaptations can counteract the ephemeral nature of ripe fruit. Am J Primatol 78:626–645. https://doi.org/10.1002/ajp.22527

Kushwaha CP, Tripathi SK, Tripathi BD, Singh KP (2011) Patterns of tree phenological diversity in dry tropics. Acta Ecol Sin 31:179–185. https://doi.org/10.1016/j.chnaes.2011.04.003

Lacreuse A, Kim CB, Rosene DL, Killiany RJ, Moss MB, Moore TL, Chennareddi L, Herndon JG (2005) Sex, age, and training modulate spatial memory in the rhesus monkey (*Macaca mulatta*). Behav Neurosci 119:118–126. https://doi.org/10.1037/0735-7044.119.1.118

MacDonald SE, Pang JC, Gibeault S (1994) Marmoset (*Callithrix jacchus jacchus*) spatial memory in a foraging task: win-stay versus win-shift strategies. J Comp Psychol 108:328–334. https://doi.org/10.1037/0735-7036.108.4.328

MacDonald SE, Spetch ML, Kelly DM, Cheng K (2004) Strategies in landmark use by children, adults, and marmoset monkeys. Learn Motiv 35:322–347. https://doi.org/10.1016/j.lmot.2004.03.002

Martin P, Bateson P (2007) Measuring behavior: an introductory guide, 3rd edn. Cambridge University Press, Cambridge

Mcdonald JH (2014) Handbook of biological statistics, 3rd edn. Sparky House Publishing, Baltimore

Mendes N, Call J (2014) Chimpanzees form long-term memories for food locations after limited exposure. Am J Primatol 76:485–495. https://doi.org/10.1002/ajp.22248

Menzel EW, Juno C (1982) Marmosets (*Saguinus fuscicollis*): Are Learning Sets Learned? Science 217:750–752. https://doi.org/10.1126/science.217.4561.750

Miller CT (2017) Why marmosets? Dev Neurobiol 77:237–243. https://doi.org/10.1002/dneu.22483

Milton K (1981) Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. Am Anthropol 83:534–548

Nascimento SS, Alves JJA (2008) Ecoclimatologia do cariri paraibano. Rev Geográfica Acadêmica 2:28–41

Noser R, Byrne RW (2015) Wild chacma baboons (*Papio ursinus*) remember single foraging episodes. Anim Cogn 18:921–929. https://doi.org/10.1007/s10071-015-0862-4

Pesendorfer MB, Gunhold T, Schiel N, Souto A, Huber L, Range F (2009) The maintenance of traditions in marmosets: individual habit, not social conformity? A field experiment. PLoS ONE. https://doi.org/10.1371/journal.pone.0004472

Platt ML, Brannon EM, Briese TL, French JA (1996) Differences in feeding ecology predict differences in performance between golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhli*) on spatial and visual memory tasks. Anim Learn Behav 24:384–393. https://doi.org/10.3758/BF03199010

Pontes ARM, Soares ML (2005) Sleeping sites of common marmosets (*Callithrix jacchus*) in defaunated urban forest fragments: a strategy to maximize food intake. J Zool 266:55–63. https://doi.org/10.1017/S095283690500662X

Poucet B (1993) Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. Psychol Rev 100:163–182. https://doi.org/10.1037/0033-295X.100.2.163

Powell LE, Isler K, Barton RA (2017) Re-evaluating the link between brain size and behavioural ecology in primates. Proc Biol Sci 284:20171765. https://doi.org/10.1098/rspb.2017.1765

Quirino ZGM (2006) Fenologia, síndromes de polinização e dispersão e recursos florais de uma comunidade de caatinga no cariri paraibano. Universidade Federal de Pernambuco, Tesis

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Raboy BE, Canale GR, Dietz JM (2008) Ecology of *Callithrix kuhlii* and a review of eastern Brazilian marmosets. Int J Primatol 29:449–467. https://doi.org/10.1007/s10764-008-9249-6

Raboy BE, Dietz JM (2004) Diet, foraging, and use of space in wild golden-headed lion tamarins. Am J Primatol 63:1–15. https://doi.org/10.1002/ajp.20032

Robert C, Casella G (2010) Introduction Monte Carlo methods with R. Springer, New York

Rylands AB, de Faria DS (1993) Habitats, feeding ecology, and home range size in the genus Callithrix. In: Rylands AB (ed) Marmosets and tamarins: systematics, behavior, and ecology. Oxford University Press, UK, pp 262–272

Schiel N, Souto A (2017) The common marmoset: an overview of its natural history, ecology and behavior. Dev Neurobiol 77:244–262. https://doi.org/10.1002/dneu.22458

Schiel N, Souto A, Huber L, Bezerra BM (2010) Hunting strategies in wild common marmosets are prey and age dependent. Am J Primatol 72:1039–1046. https://doi.org/10.1002/ajp.20860

Schwartz BL, Colon MR, Sanchez IC, Rodriguez I, Evans S (2002) Single-trial learning of "what" and "who" information in a gorilla

(*Gorilla gorilla gorilla*): implications for episodic memory. Anim Cogn 5:85–90. https://doi.org/10.1007/s10071-002-0132-0

Schwartz BL, Evans S (2001) Episodic memory in primates. Am J Primatol 55:71–85. https://doi.org/10.1002/ajp.1041

Shettleworth SJ (2010) Cognition, evolution and behavior, 2nd edn. Oxford University Press, USA

Souto A, Bezerra BM, Schiel N, Huber L (2007) Saltatory search in free-living *Callithrix jacchus*: environmental and age influences. Int J Primatol 28:881–893. https://doi.org/10.1007/s10764-007-9165-1

Stevens JR, Hallinan EV, Hauser MD (2005) The ecology and evolution of patience in two New World monkeys. Biol Lett 1:223–226. https://doi.org/10.1098/rsbl.2004.0285

Stevens JR, Wood JN, Hauser MD (2007) When quantity trumps number: discrimination experiments in cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*). Anim Cogn 10:429–437. https://doi.org/10.1007/s10071-007-0081-8

Teichroeb JA, Chapman CA (2014) Sensory information and associative cues used in food detection by wild vervet monkeys. Anim Cogn 17:517–528. https://doi.org/10.1007/s10071-013-0683-2

Trapanese C, Meunier H, Masi S (2018) What, where and when: spatial foraging decisions in primates. Biol Rev. https://doi.org/10.1111/brv.12462

Tsalyuk M, Kilian W, Reineking B, Getz WM (2019) Temporal variation in resource selection of African elephants follows long-term variability in resource availability. Ecol Monogr 89:1–19. https://doi.org/10.1002/ecm.1348

Tujague MP, Janson CH (2017) Foraging cognition in Neotropical primates: Integrating studies from the wild and from captivity. In: Kowalewski MM, Oklander LI (eds) Primatology in Argentina, III edn. Sociedad Argentina para Estudio de los Mamíferos SAREM, Buenos Aires, pp 151–170

Tujague MP, Janson CH, Lahitte HB (2015) Long-term spatial memory and learning set formation in captive capuchin monkeys (*Cebus libidinosus = Sapajus cay*). Int J Primatol 36:1067–1085. https://doi.org/10.1007/s10764-015-9878-5

Tulving E (2005) Episodic memory and autonoesis: uniquely human? In: Terrace HS, Metfalfe J (eds) The missing link in cognition: origins of self-reflective consciousness. Oxford University Press, Oxford, pp 3–56

Vannuchi CRS, Costa CS, de Jesus FM et al (2020) Sex, diurnal variation and retention interval differently affect performance of marmoset monkeys in a recognition memory task for object location. Behav Brain Res 379:112334. https://doi.org/10.1016/j.bbr.2019.112334

CAPÍTULO 3

(artigo publicado na *Animal Cognition*)

ORIGINAL PAPER

Navigating in a challenging semiarid environment: the use of a route-based mental map by a small-bodied neotropical primate

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Abstract

To increase efficiency in the search for resources, many animals rely on their spatial abilities. Specifically, primates have been reported to use mostly topological and rarely Euclidean maps when navigating in large-scale space. Here, we aimed to investigate if the navigation of wild common marmosets inhabiting a semiarid environment is consistent with a topological representation and how environmental factors affect navigation. We collected 497 h of direct behavioral and GPS information on a group of marmosets using a 2-min instantaneous focal animal sampling technique. We found that our study group reused not only long-route segments (mean of 1007 m) but entire daily routes, a pattern that is not commonly seen in primates. The most frequently reused route segments were the ones closer to feeding sites, distant to resting sites, and in areas sparse in tree vegetation. We also identified a total of 56 clustered direction change points indicating that the group modified their direction of travel. These changes in direction were influenced by their close proximity to resting and feeding sites. Despite our small sample size, the obtained results are important and consistent with the contention that common marmosets navigate using a topological map that seems to benefit these animals in response to the exploitation of clustered exudate trees. Based on our findings, we hypothesize that the Caatinga landscape imposes physical restrictions in our group's navigation such as gaps in vegetation, small trees and xerophytic plants. This study, based on preliminary evidence, raises the question of whether navigation patterns are an intrinsic characteristic of a species or are ecologically dependent and change according to the environment.

Keywords *Callithrix jacchus* · Cognitive maps · Spatial cognition · Animal movement · Route network · Change-point test

Introduction

Wild animals are constantly challenged to locate, remember, and return to productive feeding sites (Corlett 2011; Fagan et al. 2013; Riotte-Lambert and Matthiopoulos 2020). From sensory cues to sophisticated spatial skills, animals have developed a mosaic of strategies to successfully navigate and encode spatial relationships (Gould 2004; Spiegel and Crofoot 2016; Fagan et al. 2017). Moreover, movement patterns in wild animals are typically characterized by a combination of within-patch movement, in which food resources are visible from different perspectives and angles, and travel to out-of-sight resources (i.e. between patch movements) (Porter and Garber 2013; Garber and Porter 2014). Such differences in information availability (i.e. visual cues) while traveling have been suggested to trigger the emergence of different mechanisms to navigate (*Diomedea exulans*:Viswanathan et al. 1996; *Canis adustus*: Atkinson et al. 2002; *Chiropotes sagulatus:* Shaffer 2014; *Selasphorus rufus*: Pritchard et al.

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2018; *Dendrobates auratus*: Liu et al. 2019; *Loxodonta africana*: Presotto et al. 2019; *Rousettus aegyptiacus*: Fenton 2020; *Cataglyphis fortis*: Ronacher 2020; see Collett et al. 2013 and Geva-Sagiv et al. 2015 for reviews of navigation in insects, bats, and rats). One of these mechanisms is related to the ability to form mental representations to acquire, store and encode different information from the environment (Trapanese et al. 2018), and thus, navigate relying on cognitive maps (Dolins and Mitchell 2010).

Tolman (1948) first postulated that animal movements were likely supported by internal mental representations of space, acquired through experience—so-called cognitive maps. Subsequent neurological research reinforced Tolman's claims by revealing the existence of specialized neurons in the hippocampus and entorhinal cortex (O'Keefe and Nadel 1978; McNaughton et al. 2006; Moser et al. 2008). Cognitive maps have been hypothesized to represent the external world: (1) based on coordinates (hereafter coordinate-based mental map, Poucet 1993), and (2) based on routes (hereafter route-based mental map, Garber 2000). Animals that navigate using a coordinate-based mental map are able to compute the most direct route between points even if this route has not been previously traveled, which can lead to new shortcuts (Tolman 1948; Byrne 1979). In contrast, animals that navigate using a route-based mental map are expected to (1) reuse the same set of specific sites and/or landmarks to make directional decisions, which leads to patterns of navigation that often result in reusing the same routes (Garber 2000) or (2) create new routes relying on old route segments, from a network map which integrates many routes (Byrne 2000). Consequently, animals using route-based mental maps do not show the capacity to travel directly between distant points (Garber 2000).

Among animals that use cognitive maps as a mechanism to navigate in large-scale space, primates have gained increasing interest due to the combination of their relatively large brains and temporal and spatial distributions of their food resources (Janmaat et al. 2016; Trapanese et al. 2018, 2019). To date, research has found evidence associated with coordinate-based cognitive maps in capuchin monkeys (*Sapajus nigritus*, formerly *Cebus nigritus*: Presotto and Izar 2010), western gorillas (*Gorilla gorilla*: Salmi et al. 2020), chimpanzees (*Pan troglodytes*: Normand and Boesch 2009) and human primates (*Homo sapiens*: Lee et al. 2012; Howard et al. 2014; Epstein et al. 2017). However, more recently, Warren (2019) has proposed the use of a cognitive graph (or labeled graph) by humans, similar to topological maps constructed using a detailed metric system (Byrne 1979; Foo et al. 2005; Warren et al. 2017; Warren 2019; Ericson and Warren 2020). On the other hand, current evidence strongly suggests that most wild primates rely on a route-based mental map to navigate (*Pongo pygmaeus*: Mackinnon 1974; *Ateles belzebuth* and *Lagothrix poeppigii*: Di Fiore

and Suarez 2007; *Papio ursinus*: Noser and Byrne 2007b; *Propithecus edwardsi* and *Eulemur fulvus rufus*: Erhart and Overdorff 2008; *Alouatta palliata*: Hopkins 2011; *Saguinus fuscicollis weddelli*: Porter and Garber 2013; *Papio hamadryas*: Schreier and Grove 2014; *Papio ursinus*: de Raad and Hill 2019). Additionally, some authors also have argued that both types of cognitive maps can be used, depending on environmental factors (Valero and Byrne 2007; Presotto and Izar 2010; Presotto et al. 2018).

Even though both types of cognitive maps can support efficient navigation, coordinate-based maps are more cognitive demanding than route-based maps because of the increasing environmental information that the animal is required to memorize (Trapanese et al. 2018; de Raad and Hill 2019). In turn, the movement patterns supported by coordinate-based maps are more flexible and complex than those of animals using a route-based map (Bennett 1996). Apart from the influence of cognitive ability in the development of mental maps, studies have also shown that resource distribution and forest structure strongly affect primate movement decisions (Valero and Byrne 2007; Di Fiore and Suarez 2007; Presotto and Izar 2010). For example, Presotto et al. (2019) suggest that an environment with constant resource availability may induce primates to use topological navigation. In fact, some authors have argued that the repeated use of routes may act to connect sites with a higher density of feeding trees (Mackinnon 1974; Milton 1981, 2000; de Guinea et al. 2019) and help monitor future feeding sites (Di Fiore and Suarez 2007; Porter and Garber 2013). Moreover, route repetition seems to be greater in areas of the forest with higher canopy cover (Hopkins 2016; de Guinea et al. 2019) and/or in higher parts of the forest (de Guinea et al. 2019), facilitating the visual access to resources. Moreover, visual access over the landscape has been reported to be highly relevant in directional decision-making and to re-orient travel routes in animals using a route-based map (Noser and Byrne 2014; Presotto et al. 2018). While clustered directional changes have been found to concur with feeding sites in a wide range of primate populations (Valero and Byrne 2007; Di Fiore and Suarez 2007; Asensio et al. 2011; Joly and Zimmermann 2011; Presotto et al. 2018), on some species there is a clear association between clustered directional changes, emergent trees and mountain ridges as well (Di Fiore and Suarez 2007; Gregory et al. 2014; Presotto et al. 2018). Increasing visual access over the terrain favors the detection of landmarks providing additional information to decide where to go next in wild primates relying on a route-based map (De Raad and Hill 2019).

Callitrichines are small-bodied Neotropical primates with a wide geographic distribution, occurring in environments with diverse ecotones and different resource availabilities (Ford et al. 2009; Buckner et al. 2015; Schiel and Souto

2017). Although they have been the subject of an increasing number of studies on cognition (Oh et al. 2019; Burkart and van Schaik 2020; Masilkova et al. 2020) and, more specifically, on spatial cognition (Garber and Dolins 1996, 2010; Huber and Voelkl 2009; Abreu et al. 2020; Vannuchi et al. 2020), as far as we know, only *Leontocebus weddelli*, *Leontocebus nigrifrons*, and *Saguinus mystax* have had their spatial navigation and cognitive maps studied in large-scale space in the wild (e.g. Garber 1988, 1989; Garber and Hannon 1993; Porter and Garber 2013). The authors observed that these wild species navigated using a route-based mental map characterized by a specific set of routes and salient points (landmarks), where the animals adjusted and re-oriented their travel direction (Porter and Garber 2013). However, these studies were conducted in the Amazon rainforest. To the best of our knowledge, less is known concerning how primates inhabiting a semiarid environment, where vegetation is sparse and primary productivity is low, navigate. According to Fagan et al. (2013), in landscapes with moderate complexity (e.g. with limited spatiotemporal predictability of resources), relying on spatial memory brings greater benefits to the animals such as increased fitness. Compared to rainforests, semiarid environments (such as Caatinga) can be considered as a moderate landscape and could help us to understand how non-human primates navigate under a range of different patterns of resource availability. Based on this, we sought to investigate large-scale spatial navigation in free-living common marmosets in a semiarid environment (Caatinga) to test if this small-bodied New World primate navigates through a route-based or a coordinate-based mental map.

Common marmosets inhabit both the Caatinga and the Atlantic Forest, live and forage in cohesive groups (Stevenson and Rylands 1988; Schiel and Huber 2006), consume a wide variety of resources (insects, fruits, nectar, vertebrates, and exudates; Schiel and Souto 2017), including the regular consumption of exudates (Abreu et al. 2016). Although marmosets have recently been considered excellent models in cognitive research (Miller 2017; Schiel and Souto 2017), nothing is known about their navigation decisions or their spatial cognition in large-scale space. In a small-scale space, captive common marmosets have already proven capable of remembering the location of eight feeding sites and locating resources using visible reference points in the room (MacDonald et al. 1994, 2004). Field experiments with feeding platforms have shown that they also use short- ($4^1/_2$ h) and long-term (11 days) spatial memory to forage in the wild (Abreu et al. 2020).

Given that most primates travel using topological navigation (Trapanese et al. 2018) and that exudates (a stationary and renewable resource available throughout the year) are a significant component of the diet in common marmosets (Amora et al. 2013; Abreu et al. 2016; Schiel and Souto

2017), we assumed the spatial movements of common marmosets to be associated with route-based navigation (topological). Therefore, we predict that marmosets navigate: (P1) using a limited set of reused route segments; and (P2) make directional decisions at the same locations. In addition, we predict (P3) that marmosets do not navigate in straight lines between sites of interest, even after having previously visited those sites. Environmental factors (e.g. keystone food resources, food availability and terrain characteristics: Presotto et al. 2018; Trapanese et al. 2018) and physical characteristics of the environment (e.g. gaps in the tree canopy, small trees, sparse vegetation) can have a strong influence on navigation in arboreal animals. Based on this, we assumed that both the reuse of route segments and the distribution of direction change points would be associated with the locations of commonly used resources and forest structure, such as feeding trees and/or vegetation cover. Therefore, we expected to observe (P4) a higher reuse of route segments near sites of interest; as well as (P5) a higher reuse of route segments in densely vegetated areas. We also predicted that (P6) clustered direction change points would be in close proximity to sites of interest as well as (P7) in areas sparse in tree vegetation.

Methods

Study area and animals

The study was conducted at Baracuhy Biological Field Station (BBFS) (S 7° 31′ 42″—W 36° 17′ 50″) in the state of Paraíba, Northeast Brazil. The Station has three houses and fences which are surrounded by a 400-ha primary and secondary forest. This region is located in the Paraiba Cariri and is characterized by a typical semiarid vegetation (Nascimento and Alves 2008). It is a shrubby Caatinga and, for this reason, it has low, deciduous, xerophytic (thorny) and scattered vegetation (Leal et al. 2003; De la Fuente et al. 2014; Fig. 1). The study area has an average canopy height of 3.55 m and a low tree density with 4.46 individuals per hectare (De la Fuente et al. 2014). Moreover, BBFS is located in one of the regions with the lowest rainfall (average: 336 mm/year in the last 86 years) of the whole semi-arid region of Brazil (Nascimento and Alves 2008). The rainy season usually occurs from February to July (average rainfall: 46.9 mm [min: 0.00 mm and max: 226.1 mm]), while the dry season extends from August to January (average rainfall: 9.93 mm [min: 0.00 mm and max: 115.6 mm]) (Nascimento and Alves 2008; Medeiros et al. 2012). However, over the past 9 years, the region has experienced a severe drought (INMET). The temperatures at the study site are high, reaching an average of 29.1 °C in the rainy months (min: 19.3 °C and max:

Fig. 1 a Study site at the Baracuhy Biological Field Station and **b** a group of Caatinga living common marmosets (pictures: Souto, A.)

32.3 °C) and an average of 31.3 °C in the dry months (min: 15.8 °C and max: 35.2 °C) (De la Fuente et al. 2014; Abreu et al. 2016; Garber et al. 2019).

We observed and followed a group of six wild common marmosets (*Callithrix jacchus*): one adult female, two adult males, one juvenile male and two infants of unidentified sex. The group size is representative of the study area and did not change during the study period (mean group size of 6 animals: Caselli et al. 2018; Abreu et al. 2019, 2020; Garber et al. 2019; De la Fuente et al. 2019). Following the methodology of previous studies of spatial cognition, we observed the navigation patterns of a single group of animals (Porter and Garber 2013; Presotto et al. 2018; Salmi et al. 2020). Two of the three adults (1 female and 1 male) were marked during previous studies and were fitted with collars of different colored beads for better identification (Garber et al. 2019; De la Fuente et al. 2019; Abreu et al. 2020). The other adult male and the juvenile male were identified based on body size, natural marks and/or scars (Schiel et al. 2008).

Data collection

The study was conducted between February and April 2018, for a total of 46 consecutive days of behavioral data collection. We were unable to follow the group throughout the day for 6 days out of 46 and, on these days, we collected behavioral data for only half a day. Our sampling effort amounted to a total of 552 h, which included 497 h of direct observation. Observations were carried out from the time the group left their sleeping site in the morning (~5 a.m.) until they returned to the sleeping site in the evening (~5 p.m.) (De la Fuente et al. 2014). The animals were observed using a 2-min focal instantaneous sampling technique (each 2-min interval is called Instantaneous Activity Record, IAR) (Martin and Bateson 2007; Porter and Garber 2013; Garber and Porter 2014). At the beginning of each day, we randomly chose the focal animal and recorded its behavior for the entire day. If we lost sight of the focal animal for an interval longer than 4 min (2 IAR), the next adult on the right became the new focal animal and was followed for the rest of the day. Each adult contributed with a similar number of observations at the end of the study (~15 daily observations per individual). We only collected behavioral data from adults since both the cognitive abilities and the foraging capacity of juveniles and infants are not yet fully developed (Lacreuse et al. 2005; Schiel et al. 2010).

In each interval of instantaneous activity record (IAR, i.e. every 2 min), we recorded: (1) the activity of the focal animal (feeding, foraging, resting, traveling, social interactions, etc.) (for behavioral definitions, see Table S1) and (2) the location (by GPS, Garmin Gpsmap 64) of the focal animal. When the animals were feeding or foraging, we also recorded the type of food consumed or foraged. Before the beginning of data collection, we measured and verified the accuracy of the GPS instrument used. For that, we recorded 20 GPS points, with an interval of 10 s between them, in 9 different locations and on different days, chosen at random. Thus, by analyzing a total of 180 geographical points we achieved an error of 1.8 m (DRMS) (Drosos and Malesios 2012). Since the error was very small, we assume that it did not influence our analyses.

For the present study, we defined a feeding site as a tree or area where the focal animal engaged in (1) feeding, (2) foraging or (3) feeding + foraging behaviors for two or more IARs (Instantaneous Activity Records). We used a cut-off time of 4 min (2 IARs) following other studies (Valero and Byrne 2007; Porter and Garber 2013). The feeding sites could be, for example, the crown of a tree, a single cactus or a group of bromeliads. Once they were considered as feeding sites, these locations were marked, numbered with a pull-tight seal, and their GPS location and food type recorded. The identification of the plant species fed on was performed in the field with the help of field manuals and a

virtual herbarium (Reflora—Virtual Herbarium) or, later, through expert consultation (Dr. André Borba, Dr. André Souza, and Msc. Wesley Cordeiro, all botanists). Sites where we observed consumption of mobile prey (insects and/or small vertebrates) were not included in our analysis. When the focal animal rested for more than 20 min (10 IAR), we considered the site as a resting site and performed the above-mentioned procedures (excluding the record of the type of food). On the other hand, we considered a sleeping site to be the location where the animals stayed overnight. It should be emphasized that the same site could be classified as a feeding, resting and sleeping site, depending on the activity of the animals. To observe sample sufficiency, we performed a cumulative curve with the data collected from the visited feeding sites. We verified that the cumulative curve flattens near day 16, indicating that our group decreased the visit to new feeding sites (Fig. S1, Supplementary Material).

To estimate 'visibility distance' or line of sight for our environment (Janmaat et al. 2006, 2013a, b) and to determine the visibility between sequential sites of interest, we used a protocol based on navigation studies in large-scale space conducted on baboons (Noser and Byrne 2007a, b, 2015). The method consisted of installing a 50×20 cm opaque pink rectangular board next to the feeding, resting, and sleeping sites, close to the height at which the animals normally traveled, and then checking whether we could see this board at the site of interest from the location of the marmosets prior to traveling to that target site (previous site of interest). The board color was chosen according to the fruit with the strongest color consumed by the marmosets in the Caatinga environment, which is a magenta cactus fruit (Abreu et al. 2016). The procedure was performed at the end of the behavioral data collection and according to the sites of interest visited each day. So, for example, if during day 1, animals traveled to the sites of interest A–B–C we placed the board at site B and checked if we could see it from site A, then placed the board at site C to check if we could see it from site B. If the next day, the group visited a different sequence of sites of interest we changed the procedure accordingly. This choice was based on the fact that the visual acuity of marmosets (~ 30 cycles/degree) and humans (~ 50 cycles/degree) is similar (Mitchell and Leopold 2015).

Analyses

First, we calculated the size of the area used by the group of common marmosets under study in hectares with the Minimum Convex Polygon method (MCP method: Hayne 1949) using 95% of the points (Powell 2000). To investigate whether common marmosets navigate through a topological map we defined a number of navigation components, such as daily route, route segments and direction change points. Daily routes (hereafter routes) were

created based on the GPS daily point locations. Each day was a set of GPS points starting and ending at the sleeping sites. The route segments were considered as segments of the entire daily route (vector line) repeated between every two months and had a mean length equal to 1007 m (SD: 481 m, min: 9.5 m and max: 1805 m) with a minimum width of 2 and a maximum of 65 m. To determine whether animals reuse routes segments frequently (Prediction 1 of H1), we applied the method adopted by Presotto et al. (2019). This method consists of splitting the data into daily points, and then creating the line vector route over each day. Points and lines were created using ArcGIS 10.6.1. We then applied the Habitual Route Analysis Method tool (HRAM) to determine the location of habitual routes. HRAM isolates each recorded route (entire day travel) and outlines a buffer distance around the route. The size of the buffer is estimated as the the visual detection distance of the study species, which was averaged as 13 ± 11 m for the marmosets. To be more conservative with our analyses, we decided to use a buffer size of 20 m in our analysis. Subsequently, HRAM overlays onto the buffer generated for each route, all other routes to determine which segments of the routes were repeatedly used. The tool excludes routes within the same month to avoid repetition based on food distribution within that specific month (Presotto and Izar 2010). In this study, we compared all the routes day by day. So, if the monkeys revisited a specific location on March 1st and then repeated the segment on March 15th, this segment was excluded. The result is all the repeated routes or route segments that fell within the 20 m buffer distance, in all the daily routes. We checked for backtracking and, although backtracking appeared among the used trees, we did not find backtracking in the most reused routes (Fig. S2, supplementary material). The backtrackings occurring among and between the reused resource trees and repeated route segments. These segments were counted as repeated even if they came from different directions within a small-scale movement. We did not analyze these small-scale repeated segments separately but instead included them in the route network map.

Next, we detected locations within routes in which the animals engaged in significant directional changes (hereafter "change points" or "CPs") using the Change Point Test developed by Byrne et al. (2009). These CPs were identified using the CPT analysis proposed by Byrne et al. (2009). This procedure allows to find objective directional changes in the daily routes. We applied the CPT on all 46 daily routes, from dawn—when the animals woke up, until dusk—when they went to sleep. This test verifies if two vectors (each one represented by two consecutive GPS points) are aligned with each other. If the vectors are not aligned, the test assumes that a change of direction has occurred. This analysis required us to set a number of variables, such as q

and α (for more details on CPT analysis, see Byrne et al. 2009). In our case, we tested variable values between $q = 1$ and $q = 6$, but we discarded values of $q = 1$ and $q = 2$, which were too weak to show the marmosets' changes of direction, as well as values from $q = 4$ to $q = 6$, which on the contrary were too sensitive. Our q value was set at 3, and the alpha level at $p < 0.05$.

After the CPs were selected by the CPT, we classified them into clustered CPs and dispersed CPs. This division was made according to their spatial position across the landscape and not in relation to the deviation angle. Clustered CPs were grouped in the landscape regardless of whether the animals change their cardinal direction of travel by a minimum of 60°. Dispersed CPs occurred scattered along the routes, regardless of the value of the angle because the animals seemed to maintain the same course of travel when using the same route segment. We plotted all CPs in Arc-GIS 10.6.1 and identified the two groups (clustered CPs vs. dispersed CPs) both visually and by means of cluster and outlier analysis (Anselin Local *Moran*'s I statistics). First, we identified visually aggregated groups of CPs and then we performed the analysis, leading to a division of 8 aggregated CP groups. To be included in groups, the CPs were 20 m maximum from each other. In each group, we selected a random point and created a buffer of 20 m from each CP randomly chosen. All the CPs outside the 20 m buffer were considered dispersed. Moreover, through the last analysis, we clustered the points based on their correlation, which, in our study, was defined as the Euclidean distance between CPs. After that, we counted the number of GPS points inside the 20 m buffers and we obtained the percentage of use of clustered CPs. All the remaining GPS points used were included as dispersed CPs and divided by the total number of GPS points used by the animals to obtain the percentage use of dispersed CPs. With those values, we performed an exact binomial test to verify if the use of these points was greater than expected at random (P2 of H1).

To calculate 'path straightness', we first broke the daily route into travel bouts. The travel bouts for this analysis were defined according to the stops made by the marmosets at sequential sites of interest (feeding, resting, and sleeping sites) that could not be visually detected by marmosets (more than 20 m distance in a straight line between them). For each travel bout, we calculated: (1) the actual distance traveled by the animals, (2) the distance in a straight line, and (3) the path straightness (distance in a straight line divided by the actual traveled distance). An index close to 1 indicates that the animals navigated in a straight line between the sites of interest.

We also determined the land cover of our study site using remote sensing. We classified the dense forested vegetation and areas of sparse tree vegetation using Landsat 8 imagery at 30 m resolution. The Landsat image

(LC08_L1TP_215065_20170825_01_T1) was acquired from the United States Geological Survey (USGS). We used an unsupervised (ISODATA) pixel-based classification in ERDAS (Hexagon) and a maximum probability algorithm. This approach clusters the values of surface reflectance of the image pixels based on statistical analysis. The ISO-DATA algorithm iteratively calculates class means in the images and groups them using minimum distance techniques (Lillesand et al. 2015). The iterations then recalculate the means and reclassifies the pixels according to their new means. Results returned four classes of vegetation (forest, mixed forest, grassland, and built areas). Forest and mixed forest were grouped into the dense forested vegetation category because both represent areas with tree canopy cover, while the predominance of grassland with sparse trees and built areas were classified in the sparse tree vegetation category due to their low forested areas and gaps in the canopy. Therefore, we used this classification and adopted the dense forested and sparse tree vegetation area categories (Fig. 4). We validated our classification by comparing the categories using field data and high-resolution image classification on Google Earth. We did not include the terrain slope because the group home range area is mostly flat and the freely available data (Digital Elevation Model—ASTER—NASA) resolution did not show slope differences in the area.

Statistical analysis

Next, we used a series of Generalized Linear Models (GLM) and Generalized Mixed Linear Models (GLMM). First, to investigate whether common marmosets maintained a constant path straightness as they visited the sites of interest (Prediction 3 of H1), we performed a Generalized Linear Mixed Model using Template Model Builder ("*glmmTMB*") with a betabinomial distribution and a logit link function. We set path straightness as a dependent variable, the number of visits made by the group to each site of interest as an explanatory variable, and the ID of the visited sites and the straight line distance in between the starting and ending locations of each travel bout as random factors. We excluded from the analysis all sites that were revisited only once and twice during the study, as these visits may have been occasional and non-targeted.

To investigate if the reuse of route segments is associated with some environmental factor, we added both the distance to the sites of interest and the land cover as variables. Thus, to evaluate predictions 4 and 5 of our second hypothesis, we used a Generalized Linear Model (GLM) with a Poisson distribution and a log link function, with the number of times that each habitual route segment was used set as dependent variable, and four explanatory variables: (a) distance to feeding sites, (b) distance to resting sites, (c) distance to sleeping sites and (d) land cover. According to the data obtained (see

results), we carried out an a posteriori analysis to determine the distribution of the angles of approach to certain resting sites. To this end, we employed a parametric Rao's spacing test for each of these sites. We only included resting sites with more than 10 visits. This test assesses whether the approach angles are evenly distributed (null hypothesis) or whether they show some specific direction and have been used in other spatial cognition studies (Luehrs et al. 2009; de Raad and Hill 2019). Moreover, Rao's spacing test is powerful with small sample sizes, and when the data have multimodal distributions (Landler et al. 2019, 2020). We also performed a Rayleigh test to increase the confidence of our analyses.

Lastly, to verify the impact of environmental factors (Predictions 6 and 7 of H2) on CPs distribution, we implemented a Generalized Linear Model (GLM) with a binomial distribution and a logit link function. To do so, we set clustered CPs/dispersed CPs as dependent variable (with clustered CPs being equal to 1 and dispersed CPs being equal to 0). We also included four explanatory variables in the model: (a) distance to feeding sites, (b) distance to resting sites, (c) distance to sleeping sites, and (d) land cover. In all the above models, we first compared the complete model with the null model using the *Anova* function in the R Stats package (likelihood ratio test). If the two models differed significantly, we checked the significance of the predictor variables and adjusted our model by sequentially removing the variables that showed no significant impact (for full details of statistical analyses see "*R Markdown*" in Supplementary Material). This selection was made through the R *Lme4* package (Bates et al. 2015). All statistical analyses were performed in R environment, version 3.6.2 (R Core Team 2019), and in Excel (Microsoft Corporation). The other spatial data were analyzed in ArcGIS 10.6.1. The level of significance was set at 5%.

Results

Throughout the study period, the group's main activity was resting (IAR records: 5253; 36%), followed by foraging (IAR records: 5228; 35%) and feeding (IAR records: 1674; 11%). Social interactions and traveling accounted for 11% (IAR records: 1605) and 7% (IAR records: 995), respectively. We estimated the group's home range size as 7.31 ha (95% of the points). During the 46 days of observation, the animals traveled an average daily distance of 1048 m $\pm$ 446 m (min.: 70 m and max.: 1805 m) and visited a total of 36 individual feeding sites (excluding insects and vertebrate feeding/foraging sites). Among these, 11 were fruit feeding sites, 7 were used to consume exudates and 13 were used to forage and/or eat flowers or nectar. In the five remaining sites, the animals consumed both fruit and exudates. During the study period,
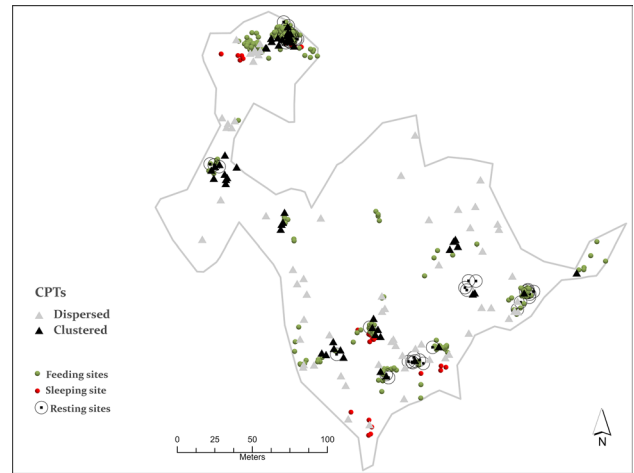

Fig. 2 Home range during the study period with clustered and dispersed CPs and sleeping, feeding, and resting sites

common marmosets also used 12 resting sites and 5 sleeping sites (Fig. 2).

Twenty-three individual feeding sites were visited repeatedly by the animals at least once a week throughout the study period, whereas flower and nectar feeding sites were visited over the course of 3 weeks (in the remaining 6 weeks of observation these sites were not visited). The marmosets exploited seven different plant species as feeding sites: 17 specimens of *Prosopis juliflora* (47.2%; mesquite), 11 specimens of *Manihot carthagenensis* (30.5%; cassava), 3 specimens of *Pilosocereus pachycladus* (8.3%; blue columnar cactus), 2 specimens of *Jatropha mollissima* (5.6%; known in Brazil as "pinhão-bravo"), 1 specimen of *Pilosocereus gounelli* (2.8%; commonly known as "xique-xique"), 1 specimen of *Croton heliotropiifolius* (2.8%; popularly known as "velame" or "marmeleiro"), and 1 specimen of *Mimosa tenuiflora* (2.8%; black jurema).

As expected in our first and second predictions (P1 and P2), we identified 43 route segments that were reused between 20 and 43 times (Fig. 3). The mean length of travel route segments was 1007 $\pm$ 481 m. Using the CPT (Change Point Test), we also observed a total number of 121 direction change points (CPs). Among these, 56 were clustered CPs, while 65 were dispersed CPs (Fig. 2). The percentage of clustered CPs usage (this is, the number of GPS points found inside the 20 m buffers divided by the total GPS points used) was 71.5%. Dispersed CPs accounted for 28.5%. We also observed that the clustered CPs were used more than expected at random (use ratio: 0.71; $p < 0.0001$), while no significant difference was found in the dispersed CPs (use ratio: 0.28; $p =$ ns).

When we analyzed the data for our third prediction (P3), we found that the path straightness between the sites of interest was 0.51, ranging from 0.05 to 1 ($N = 193$ route
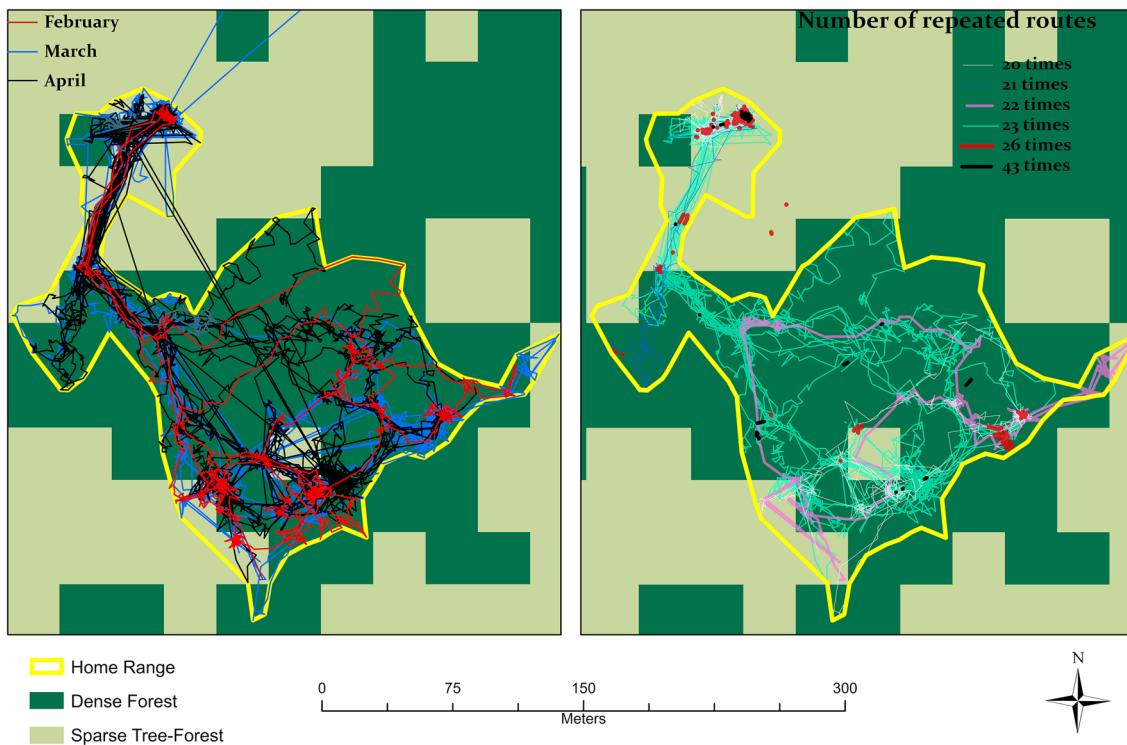
Fig. 3 Route network map showing the repeated route segments traveled by common marmosets during the study period with examples of dense and sparse tree-forest areas
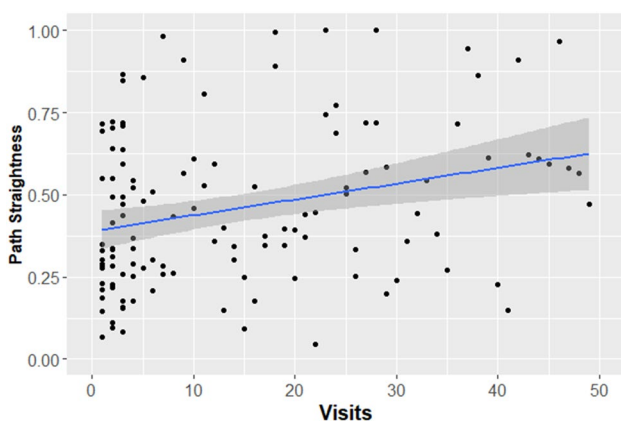

Fig. 4 Relationship between consecutive visits to sites of interest and the path straightness. The points represent the ID of the sites visited and the blue line represents the regression line between these two variables. The confidence interval is represented by the gray area

segments), and that the path straightness increased as the primates revisited each site over time ($N = 122$, $Z = 2.99$, Odds ratio $= 1.00$, $p = 0.003$; Fig. 4). The more times a site was visited the more direct was the route taken to that site.

Regarding predictions P4 and P5 of our second hypothesis, we found that the best model to predict the reuse of route segments included all variables (comparison with the null model: $X^2 = 97.653$, $p < 0.0001$; Table 1). Relative to resting sites, we found that the shorter the distance from sites, the less likely the animals were to reuse the same route segment (mean distance from route segments used $\geq 43 = 54.80$ m). For feeding and sleeping sites, we observed that route segment reuse increased due to their proximity to these sites (mean distance of feeding sites from route segments used $\geq 43 = 0.63$ m; mean distance of sleeping sites from route segments used $\geq 43 = 7.29$ m). The group also showed greater route segment reuse in sparse tree vegetation areas when compared to areas of dense forested vegetation. The model explained only 13% of the variation ($R^2 = 0.13$). To better understand the influence of resting sites on the reuse of route segments, we performed a Rao's spacing test and a Rayleigh test (see "Statistical analysis"). We found that approach angles were randomly distributed in the two most visited resting sites (Rao's test: Resting site 02: $N = 34$, $U = 131$, $p = $ ns; Resting site 05: $N = 10$, $U = 116$, $p = $ ns; Fig. 5; Rayleigh test: Resting site 02, $p = $ ns; Resting site 05, $p = $ ns).

Finally, for our final predictions (P6 and P7), we found that the best model to predict CPs distribution only included the distance to sites of interest (comparison with the full model: $X^2 = 0.14875$, $p = 0.6997$; Table 2). The likelihood of finding CP clusters appeared to be higher in the vicinity of feeding (mean distance 4.11 m $\pm$ 5.20 m) and resting

Table 1 Parameters of the GLM analysis on the influence of environmental factors on the reuse of route segments

	Estimate	Std. error	CI$_{lower}$	CI$_{upper}$	p value
(Intercept)	3.629	0.040	3.551	3.708	0.000
Sleeping site distance	−0.001	0.000	−0.002	−0.001	0.000
Resting site distance	0.001	0.000	0.000	0.001	0.000
Feeding site distance	−0.008	0.002	−0.014	−0.004	0.000
Land cover [non-dense areas]	0.115	0.036	0.044	0.184	0.001

The table includes estimated regression parameters, standard errors, t and p values for each one of the significant variables
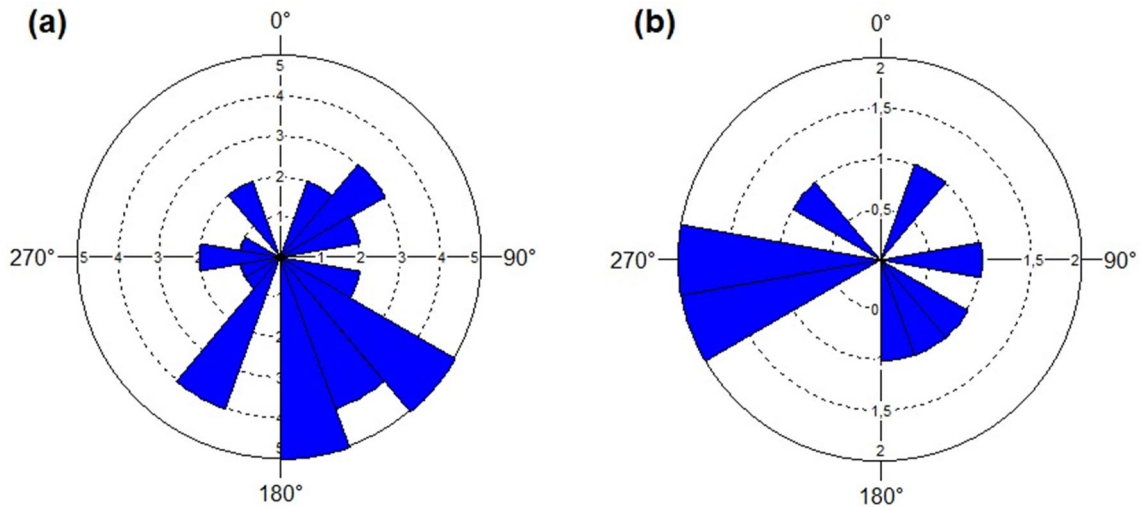

Fig. 5 Distribution of the approach angles in two of the most visited resting sites by the group: **a** resting site 02 and **b** Resting site 05. The numbers inside the plot represent the observations within each bar

Table 2 Parameters of the GLM analysis on the influence of environmental factors on the distribution of CPs

	Estimate	Std. error	CI$_{lower}$	CI$_{upper}$	p value	Odds ratio
(Intercept)	1.126	0.378	0.411	1.906	0.003	–
Sleeping tree distance	0.030	0.010	0.011	0.052	0.004	1.030
Resting tree distance	−0.083	0.022	−0.130	−0.041	0.000	1.086
Feeding tree distance	−0.151	0.045	−0.249	−0.069	0.000	1.162
Land cover [non-dense areas]	0.201	0.522	−0.825	1.236	0.699	1.222

The table includes estimated regression parameters, standard errors, t and p values and effect sizes for each one of the significant variables

sites (mean distance 10.38 m ± 14.80 m). In contrast, the likelihood of observing clustered CPs was higher away from sleeping sites (mean distance 35.61 ± 35.42 m). Overall, our model explained 63% of the total variation ($R^2 = 0.63$).

Discussion

Here we aimed to investigate if wild common marmosets use a topological map when navigating in large-scale space. As expected by our first and second predictions, marmosets repeated both route segments and CPs several times throughout the study. This pattern has been observed not only in other primate species (*Nasalis larvatus*: Boonratana 2000; *Alouatta palliata*: Garber and Jelinek 2006; *Ateles belzebuth* and *Lagothrix poeppigii*: Di Fiore and Suarez 2007; *Leontocebus weddelli*: Porter and Garber 2013; *Sapajus libidinosos*: Presotto et al. 2018; *Papio ursinus*: Noser and Byrne 2007a, b) but also in other animals (*Melophorus bagoti*: Wehner et al. 2006; *Apis mellifera*: Kheradmand et al. 2018; *Loxodonta africana*: Presotto et al. 2019; *Eptesicus fuscus*: Yu et al. 2019).

Our group repeated not only long-route segments, but entire daily routes. In common marmosets, which are characterized by a gumivorous–insectivorous–frugivorous diet (Schiel and Souto 2017), in which exudates can represent up to 70% of feeding time (Rylands 1984; Stevenson and Rylands 1988; Amora et al. 2013), the repetitive use of routes may enable individuals to relocate commonly used feeding sites. As suggested by Riotte-Lambert and Matthiopoulus (2020) environmental predictability can lead to the use of a routine pattern of movement behavior. Since exudate trees tend to have a clustered distribution in the Atlantic Forest (Thompson et al. 2013), and possibly in Caatinga, and are available during all months of the year, our findings that the marmosets revisited the same limited number of exudate trees daily over a 3-month period, are consistent with route-based foraging. Furthermore, not only does gumivory require the animals to chew into the bark and then return several hours later to consume the newly produced exudate, efficient use of this resource requires that the marmosets repeatedly return to the same exudate sites over an extended period (Stevenson and Rylands 1988; Schiel and Souto 2017). As a result, the reuse of route segments increases the likelihood of returning to the same set of feeding sites (Poucet 1993; Di Fiore and Suarez 2007). Moreover, our results on CPs suggest that animals remember clustered CPs and use them repeatedly as decision-making points. These CPs are likely located in areas with salient points/landmarks where the group adjusts its trajectory to target sites of interest, as they show a high percentage of use (~70%) when compared to dispersed CPs (Garber 2000; Porter and Garber 2013; Presotto et al. 2018). The use of landmark cues to efficiently travel between sites of interest was also reported in various animal species (e.g. *Leontocebus weddelli*: Porter and Garber 2013; *Papio ursinus*: Noser and Byrne 2014; *Apis mellifera:* Kheradmand et al. 2018; *Selasphorus rufus*: Pritchard et al. 2018). Our findings support the hypothesis that common marmosets navigate using a route-based mental map that includes the re-use of habitual route segments, as well as directional decision points (clustered CPs), based on perceived landmarks from the environment.

In addition, even though marmosets tended to deviate from a straight line when traveling to out-of-sight locations, such deviation decreased with an increasing number of visits to revisited sites. While previous research has highlighted primates' ability to systematically travel in a linear (Valero and Byrne 2007; Normand and Boesch 2009) or non-linear fashion (Porter and Garber 2013), here we report novel evidence indicating a primates' ability to enhance their spatial performance over time. A possible explanation for our finding would be the use of visual clues due to the sparse vegetation of the study site. However, recurring visits and familiarity with the environment seem to be a more plausible explanation, since they may have triggered

the improvement of navigation skills that served to reduce the traveled distance. In fact, these factors have been shown to positively affect some components of spatial navigation in other species (e.g. *Alouatta palliata* and *Ateles geoffroyi*: Milton 1981; *Saguinus mystax* and *Leontocebus nigrifrons*: Garber 1989; *Papio ursinus*: Noser and Byrne 2007b; *Cervus elaphus*: Wolf et al. 2009; *Homo sapiens*: Jang et al. 2019; *Loxodonta africana*: Presotto et al. 2019; for a review see: Spiegel and Crofoot 2016). These results may indicate that our study group can improve their navigation strategies as they revisit sites of interest, having the ability to change references using landmarks (visual cues) and to remember the exact location of certain sites of interest. For mammals inhabiting semi-arid environments, travel can be challenging due to heat and water stress (Streilein 1982). This environment presents high temperatures throughout the day and during many months of the year. In response to heat and water stressors, common marmosets have been shown to adjust their behavior, such as reducing their activities and increased resting during high temperatures (De la Fuente et al. 2014). Furthermore, Garber et al. (2019) also showed that Caatinga common marmosets possess a high surface area to body mass ratio compared to Atlantic Forest common marmosets. Thus, the capacity to reduce the distance travel with an increasing number of visits to revisited sites could reduce energy expenditure during navigation and consequently, heat stress.

As assumed by the second hypothesis, we observed that environmental factors affected both the reuse of route segments and the distribution of CPs. First, we noted that the reuse of route segments by the group was affected both by the distance to the sites of interest and by land cover. Frequent reuse of route segments in the vicinity of feeding sites was already expected because, according to the literature, primates tend to reuse a higher number of routes in close proximity to feeding sites or in locations with higher density of these trees (Di Fiore and Suarez 2007; Presotto et al. 2018; de Guinea et al. 2019). Similarly, the reuse of route segments was more frequent as the monkeys approached a sleeping site, suggesting that these locations are incorporated into the common marmosets' mental map, possibly because these sites are often exudate trees. Moreover, most studies have not observed the influence of resting sites on the reuse of route segments. Due to the Caatingas adverse characteristics, these sites can be of great importance for common marmosets, which rest during the hot hours of the day (De la Fuente et al. 2014). Contrary to our expectations, we observed that the closer the group was to a resting site, the less the group reused the same route segment. To gain a better understanding of this pattern, we evaluated the approach angles to the most frequently visited resting sites. Although the group reused routes, it seems that when the group approached a resting site, the animals used different

route segments to arrive at the site (the angles were uniformly distributed around each resting site). This result may indicate an ability to recall the spatial location of some specific sites through a coordinate system (Poucet 1993; Milton 2000; Normand and Boesch 2009; de Raad and Hill 2019; Fenton 2020). However, since resting trees were also used as exudate feeding sites, it is more likely that once the animals were in sighting distance, they managed to compute the most direct travel route. Nevertheless, it should be emphasized that although significant, the effects of the above factors on the reuse of route segments were low.

Among the environmental factors that affect the reuse of route segments, we found that land cover had the greatest influence. That is, the monkeys reused more route segments in areas of sparse trees vegetation compared to areas of dense forested vegetation. This result was not expected and is in contrast to findings from earlier studies (Hopkins 2011; de Guinea et al. 2019). For example, McLean et al. (2016) documented that arboreal primates (*Alouatta palliata*, *Ateles geoffroyi* and *Cebus capucinus*) avoided traveling in open areas. However, it is important to mention that these studies were conducted in rainforests with continuous canopy cover, different from the canopy cover in semiarid environments. In common marmosets, navigation in areas with higher tree density would allow for both an increase in direct travel routes as well as a larger number of route choices during traveling and in avoiding potential airborne (e.g. hawks) and terrestrial (e.g. snakes) predators. However, our results suggest that landscape features associated with a more open and shrubby Caatinga habitat with scattered small trees (Leal et al. 2003; De la Fuente et al. 2014) may have influenced navigation or limited the choice of travel routes, particularly in areas of sparse tree vegetation. It is important to highlight the fact that this is one of a small number of studies to examine a primate's cognitive map in a semiarid environment (e.g. Sigg and Stolba 1981; Schreier and Grove 2010, 2014). In a different environment, for example the Atlantic Forest of Brazil which is characterized by a more continuous forest cover, marmosets might rely less on routes to navigate.

Finally, data on the change of direction points (CPs) were based only on the distance to sites of interest. In our group, the clustered CPs were adjacent to feeding sites, reinforcing both the importance of these trees for navigation decisions and previous observations from other studies on primates (Valero and Byrne 2007; Asensio et al. 2011; Joly and Zimmermann 2011). We also found that the animals did not change direction near sleeping sites. Since these sites are usually located at the borders of the group's home range, and visited only at dawn and dusk, we might not expect to find decision-making sites in these areas. However, clustered CPs were observed near resting sites. Studies show that in many animals, navigation decisions are more likely to occur

during brief periods of inactivity (such as resting) (for a review see: Petit and Bon 2010). In our study, the group remained inactive for periods ranging from 20 to 182 min at resting sites (~ 36% of the total observation time, similar to previous research at the study site, Abreu et al. 2016). In and around these sites the animals also engaged in social interactions such as grooming and playing. Furthermore, most resting sites were exudate trees, *Prosopis juliflora*, which, in general, has been reported in other field sites to have a height and diameter greater than the majority of Caatinga vegetation (Pegado et al. 2006; De Oliveira et al. 2012; De la Fuente et al. 2014). Due to its physical characteristics, common marmosets could be using these sites as visual landmarks to re-orient their travel directions. Thus, resting sites could be important decision-making locations.

Overall, our findings indicate that wild common marmosets use a route-based mental map (topological) to navigate in large-scale space. However, since our data sample is small, it must be interpreted carefully. The set of our findings (such as the combination of navigation through a route network system and taking detours to some sites of interest) can be considered as evidence of a cognitive graph (labeled graph) as proposed by Warren (2019). However, we do not have sufficient data to test such a hypothesis. Meanwhile, the decrease in the distance traveled to certain sites of interest with consecutive visits, and the approach to these sites from different angles may also highlight the possibility that these monkeys possess some kind of Euclidean awareness (Poucet 1993; Garber 2000; Normand and Boesch 2009; Presotto and Izar 2010). While there is growing evidence that virtually all non-human primates rely on topological maps when foraging (Trapanese et al. 2018), indicating that this ability may be related to phylogeny, some authors have proposed that the use of different forms of cognitive maps may be ecologically dependent (Byrne 1979; Normand and Boesch 2009; Presotto and Izar 2010). These authors suggest that contrasting environments with different vegetation patterns as well as differences in resource availability could induce both human and non-human primates to construct different mental representations. In fact, Normand and Boesch (2009) explained the use of a Euclidean representation of *Pan troglodytes verus* based on the ecosystem where these animals were studied, while contradictory findings were reported for this same species in Rwanda (Green et al. 2020) and the Ivory Coast (Janmaat et al. 2013a, b, 2016).

In this sense, some of our findings pose the hypothesis that the peculiarities of the Caatinga landscape (such as gaps in vegetation and small trees and xerophytes Leal et al. 2003; Araújo et al. 2007) and, specifically, the characteristics of our study area (see Fig. 3), may impose physical restrictions on marmoset navigation. In fact, we observed that the reuse of route segments was higher in areas of sparse tree vegetation compared to areas of dense forested vegetation

and that the daily movement of the group usually occurred via the same route, between the northern and southern edges of their home range (see Fig. 2). In addition, the majority of exudate trees exploited by the marmosets were located at the northern and southern ends of the group home range. Therefore, the topological navigation pattern we found may not be related to the vegetation pattern, but rather to the distribution of this resource. Apart from being able to visit exudate trees regularly and daily, this type of navigation would also help animals monitor other feeding trees along their common daily routes. Thus, it remains to be understood whether the observed navigation pattern is common to this species and unaffected by the environment in which the animals live, or whether the physical limitations of the semiarid environment have shaped the travel patterns of the marmosets in a way that does not favor the use of other navigational strategies. For the purpose of a comparative analysis, it would be interesting to apply the method used in this study to common marmosets inhabiting the Atlantic Forest and increase our data sample in both environments (for one full annual cycle). Such an approach would help answer these questions and gather additional information concerning the effects of environmental factors on spatial navigation.

Author contributions PAG and FA conceived the study and discussed the methodological approach with ASS and NS. FA collected the data. AP and FA analyzed the data. PAG wishes to thank Chrissie, Sara, Jenni, and Dax for their support. All authors wrote and reviewed the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest There are no conflicts of interest. The manuscript has not been published previously and is not under consideration for publication elsewhere.

Ethics approval The study was not invasive and was conducted in accordance with the Brazilian law, having been approved by the Ethics Committee for the Use of Animals of the Federal Rural University of Pernambuco (CEUA License No. 144/2014) and SISBio (License No. 46770/1).

References

Abreu F, De la Fuente MFC, Schiel N, Souto A (2016) Feeding ecology and behavioral adjustments: flexibility of a small neotropical primate (*Callithrix jacchus*) to survive in a semiarid environment. Mammal Res 61:221–229. https://doi.org/10.1007/s13364-016-0262-4

Abreu F, Souto A, Bonci DMO et al (2019) Detection of insect prey by wild common marmosets: the effect of color vision. Am J Primatol. https://doi.org/10.1002/ajp.22963

Abreu F, Souto A, Schiel N (2020) Wild common marmosets (*Callithrix jacchus*) employ spatial cognitive abilities to improve their food search and consumption: an experimental approach in small-scale space. Primates. https://doi.org/10.1007/s10329-020-00826-1

Amora TD, Beltrão-Mendes R, Ferrari SF (2013) Use of alternative plant resources by common marmosets (*Callithrix jacchus*) in the semi-arid Caatinga Scrub forests of Northeastern Brazil. Am J Primatol 75:333–341. https://doi.org/10.1002/ajp.22110

Araújo EDL, De CCC, Albuquerque UP (2007) Dynamics of Brazilian Caatinga–a review concerning the plants, environment and people. Funct Ecosyst Communities 1:15–28. https://doi.org/10.1111/1365-2745.12712

Asensio N, Brockelman WY, Malaivijitnond S, Reichard UH (2011) Gibbon travel paths are goal oriented. Anim Cogn 14:395–405. https://doi.org/10.1007/s10071-010-0374-1

Atkinson RPD, Rhodes CJ, Macdonald DW, Anderson RM (2002) Scale-free dynamics in the movement patterns of jackals. Oikos 98:134–140. https://doi.org/10.1034/j.1600-0706.2002.980114.x

Ban SD, Boesch C, N'Guessan A et al (2016) Taï chimpanzees change their travel direction for rare feeding trees providing fatty fruits. Anim Behav 118:135–147. https://doi.org/10.1016/j.anbehav.2016.05.014

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Bennett ATD (1996) Do animals have cognitive maps? J Exp Biol 199:219–224

Boonratana R (2000) Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, Northern Borneo. Int J Primatol 21:239–248. https://doi.org/10.1023/A:1005496004129

Buckner JC, Lynch Alfaro JW, Rylands AB, Alfaro ME (2015) Biogeography of the marmosets and tamarins (Callitrichidae). Mol Phylogenet Evol 82:413–425. https://doi.org/10.1016/j.ympev.2014.04.031

Burkart JM, van Schaik CP (2020) Marmoset prosociality is intentional. Anim Cogn 23:581–594. https://doi.org/10.1007/s10071-020-01363-6

Byrne RW (1979) Memory for urban geography. Q J Exp Psychol 31:147–154

Byrne RW (2000) How monkeys find their way. Leadership, coordination, and cognitive maps of African baboons. In: Boinski S, Garber PA (eds) On the move: How and why animals travel in groups. University of Chicago Press, Chicago, pp 491–518

Byrne RW, Noser R, Bates LA, Jupp PE (2009) How did they get here from there? Detecting changes of direction in terrestrial ranging. Anim Behav 77:619–631. https://doi.org/10.1016/j.anbehav.2008.11.014

Caselli CB, Ayres PHB, Castro SCN et al (2018) The role of extragroup encounters in a Neotropical, cooperative breeding primate, the common marmoset: a field playback experiment. Anim Behav 136:137–146. https://doi.org/10.1016/j.anbehav.2017.12.009

Collett M, Chittka L, Collett TS (2013) Spatial memory in insect navigation. Curr Biol 23:R789–R800. https://doi.org/10.1016/j.cub.2013.07.020

Corlett RT (2011) How to be a frugivore (in a changing world). Acta Oecologica 37:674–681. https://doi.org/10.1016/j.actao.2011.01.005

de Raad AL, Hill RA (2019) Topological spatial representation in wild chacma baboons (*Papio ursinus*). Anim Cogn 22:397–412. https://doi.org/10.1007/s10071-019-01253-6

de Guinea M, Estrada A, Nekaris KA, Van Belle S (2019) Arboreal navigation and route selection: energetic implications associated with tree monitoring and landscape attributes in a Neotropical primate. Mov Ecol 7:39

De la Fuente MFC, Souto A, Sampaio MB, Schiel N (2014) Behavioral adjustments by a small neotropical primate (*Callithrix jacchus*) in a semiarid caatinga environment. Sci World J. https://doi.org/10.1155/2014/326524

De la Fuente MF, Schiel N, Bicca-Marques JC et al (2019) Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (*Callithrix jacchus*). Am J Primatol. https://doi.org/10.1002/ajp.22964

De Oliveira LSB, De Andrade LA, Fabricante JR, Gonçalves GS (2012) Structure of a *Prosopis juliflora* (Sw.) DC. population established in a temporary riverbed in the Microregion of Cariri in the State of Paraiba. Semin Agrar 33:1769–1778. https://doi.org/10.5433/1679-0359.2012v33n5p1769

Di Fiore A, Suarez SA (2007) Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. Anim Cogn 10:317–329. https://doi.org/10.1007/s.10071-006-0067-y

Dolins FL, Mitchell RW (2010) Spatial cognition, spatial perception: mapping the self and space, 1st edn. Cambridge University Press, Cambridge

Drosos BK, Malesios C (2012) Measuring the accuracy and precision of the garmin GPS positioning in forested areas: a case study in taxiarchis-vrastama university forest. J Environ Sci Eng B. https://doi.org/10.17265/2162-5263/2012.04.015

Epstein RA, Patai EZ, Julian JB, Spiers HJ (2017) The cognitive map in humans: Spatial navigation and beyond. Nat Neurosci 20:1504–1513. https://doi.org/10.1038/nn.4656

Erhart EM, Overdorff DJ (2008) Spatial memory during foraging in prosimian primates: *Propithecus edwardsi* and *Eulemur fulvus rufus*. FOLIA Primatol 79:185–196. https://doi.org/10.1159/000112911

Ericson JD, Warren WH (2020) Probing the invariant structure of spatial knowledge: support for the cognitive graph hypothesis. Cognition 200:104276. https://doi.org/10.1016/j.cognition.2020.104276

Fagan WF, Lewis MA, Auger-Méthé M et al (2013) Spatial memory and animal movement. Ecol Lett 16:1316–1329. https://doi.org/10.1111/ele.12165

Fagan WF, Gurarie E, Bewick S et al (2017) Perceptual ranges, information gathering, and foraging success in dynamic landscapes. Am Nat 189:474–489. https://doi.org/10.1086/691099

Fenton BM (2020) Bats navigate with cognitive maps. Science (80–) 369:142

Foo P, Warren WH, Duchon A, Tarr MJ (2005) Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. J Exp Psychol Learn Mem Cogn 31:195–215. https://doi.org/10.1037/0278-7393.31.2.195

Ford SM, Porter LM, Davis LC (2009) The smallest anthropoids, 1st edn. Springer, Boston

Garber PA (1988) Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. Biotropica 20:100–106. https://doi.org/10.2307/2388181

Garber PA (1989) Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. Am J Primatol 19:203–216. https://doi.org/10.1002/ajp.1350190403

Garber PA (2000) The ecology of group movement: evidence for the use of spatial, temporal, and social information in some primate foragers. In: Boinski S, Garber PA (eds) On the move. How and why animals travel in groups. University of Chicago Press, Chicago, pp 261–298

Garber PA, Dolins F (1996) Testing learning paradigms in the field. In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive radiations of neotropical primates. Springer, Boston, pp 201–216

Garber PA, Dolins FL (2010) Examining spatial cognitive strategies in small-scale space and large-scale space in tamarin monkeys. In: Dolins FL, Mitchell RW (eds) Spatial cognition, spatial perception: mapping the self and space, 1st edn. Cambridge University Press, Cambridge, p 581

Garber PA, Dolins FL (2014) Primate spatial strategies and cognition: introduction to this special issue. Am J Primatol 76:393–398. https://doi.org/10.1002/ajp.22257

Garber PA, Hannon B (1993) Modeling monkeys: a comparison of computer-generated and naturally occurring foraging patterns in two species of neotropical primates. Int J Primatol 14:827–852. https://doi.org/10.1007/BF02220255

Garber PA, Jelinek PE (2006) Travel Patterns and Spatial Mapping in Nicaraguan Mantled Howler Monkeys (*Alouatta palliata*). New Perspect Study Mesoamerican Primates. https://doi.org/10.1007/0-387-25872-8_14

Garber PA, Porter LM (2014) Navigating in small-scale space: the role of landmarks and resource monitoring in understanding saddleback tamarin travel. Am J Primatol 76:447–459. https://doi.org/10.1002/ajp.22196

Garber PA, Caselli CB, McKenney AC et al (2019) Trait variation and trait stability in common marmosets (*Callithrix jacchus*) inhabiting ecologically distinct habitats in northeastern Brazil. Am J Primatol. https://doi.org/10.1002/ajp.23018

Gregory T, Mullett A, Norconk MA (2014) Strategies for navigating large areas: A GIS spatial ecology analysis of the bearded saki monkey, chiropotes sagulatus, in suriname. Am J Primatol 76:586–595. https://doi.org/10.1002/ajp.22251

Geva-Sagiv M, Las L, Yovel Y, Ulanovsky N (2015) Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. Nat Rev Neurosci 16:94–108. https://doi.org/10.1038/nrn3888

Gould JL (2004) Animal navigation. Curr Biol 14:221–224. https://doi.org/10.1016/j.cub.2004.02.049

Green SJ, Boruff BJ, Bonnell TR, Grueter CC (2020) Chimpanzees use least-cost routes to out-of-sight goals. Curr Biol. https://doi.org/10.1016/j.cub.2020.08.076

Hayne DW (1949) Calculation of size of home range. J Mammal 30:1–18

Hopkins ME (2011) Mantled howler (*Alouatta palliata*) arboreal pathway networks: relative impacts of resource availability and forest structure. Int J Primatol 32:238–258. https://doi.org/10.1007/s10764-010-9464-9

Hopkins ME (2016) Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. Anim Cogn 19:387–403. https://doi.org/10.1007/s10071-015-0941-6

Howard LR, Javadi AH, Yu Y et al (2014) The hippocampus and entorhinal cortex encode the path and euclidean distances to goals during navigation. Curr Biol 24:1331–1340. https://doi.org/10.1016/j.cub.2014.05.001

Huber L, Voelkl B (2009) Social and physical cognition in marmosets and tamarins. The smallest anthropoids. Springer, Boston, pp 183–201

INMET (2020) Instituto Nacional de Meteorologia. Ministério da Agricultura, Pecuária e Abastecimento/MAPA. 3° Distrito de Meteorologia. https://portal.inmet.gov.br/

Jang H, Boesch C, Mundry R et al (2019) Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. Sci Rep. https://doi.org/10.1038/s41598-019-47247-9

Janmaat KRL, Byrne RW, Zuberbühler K (2006) Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. Anim Behav 72:797–807. https://doi.org/10.1016/j.anbehav.2005.12.009

Janmaat KRL, Ban SD, Boesch C (2013a) Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Anim Behav 86:1183–1205. https://doi.org/10.1016/j.anbehav.2013.09.021

Janmaat KRL, Ban SD, Boesch C (2013b) Tai chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. Anim Cogn 16:851–860. https://doi.org/10.1007/s10071-013-0617-z

Janmaat KRL, Boesch C, Byrne R et al (2016) Spatio-temporal complexity of chimpanzee food: How cognitive adaptations can counteract the ephemeral nature of ripe fruit. Am J Primatol 78:626–645. https://doi.org/10.1002/ajp.22527

Joly M, Zimmermann E (2011) Do solitary foraging nocturnal mammals plan their routes? Biol Lett 7:638–640. https://doi.org/10.1098/rsbl.2011.0258

Kheradmand B, Cassano J, Gray S, Nieh JC (2018) Influence of visual targets and landmarks on honey bee foraging and waggle dancing. Insect Sci 27:349–360. https://doi.org/10.1017/CBO9781107415324.004

Lacreuse A, Kim CB, Rosene DL et al (2005) Sex, age, and training modulate spatial memory in the rhesus monkey (*Macaca mulatta*). Behav Neurosci 119:118–126. https://doi.org/10.1037/0735-7044.119.1.118

Landler L, Ruxton GD, Malkemper EP (2019) Circular statistics meets practical limitations: a simulation-based Rao's spacing test for non-continuous data. Mov Ecol. https://doi.org/10.1186/s40462-019-0160-x

Landler L, Ruxton GD, Malkemper EP (2020) Model selection versus traditional hypothesis testing in circular statistics: a simulation study. Biol Open 9:9–12. https://doi.org/10.1242/bio.049866

Leal IR, Tabarelli M, Cardoso da Silva JM (2003) Ecologia e Conservação da, Caatinga. Universitária da UFPE, Recife

Lee SA, Sovrano VA, Spelke ES (2012) Navigation as a source of geometric knowledge: young children's use of length, angle, distance, and direction in a reorientation task. Cognition 123:144–161. https://doi.org/10.1016/j.cognition.2011.12.015

Lillesand T, Kiefer RW, Chipman J (2015) Remote sensing and image interpretation. Wiley, Hoboken

Liu Y, Day LB, Summers K, Burmeister SS (2019) A cognitive map in a poison frog. J Exp Biol. https://doi.org/10.1242/jeb.197467

Luehrs M-L, Dammhahn M, Kappeler PM, Fichtel C (2009) Spatial memory in the grey mouse lemur (*Microcebus murinus*). Anim Cogn 12:599–609. https://doi.org/10.1007/s10071-009-0219-y

MacDonald SE, Pang JC, Gibeault S (1994) Marmoset (*Callithrix jacchus jacchus*) spatial memory in a foraging task: win-stay versus win-shift strategies. J Comp Psychol 108:328–334. https://doi.org/10.1037/0735-7036.108.4.328

MacDonald SE, Spetch ML, Kelly DM, Cheng K (2004) Strategies in landmark use by children, adults, and marmoset monkeys. Learn Motiv 35:322–347. https://doi.org/10.1016/j.lmot.2004.03.002

Mackinnon J (1974) The behaviour and ecology of wild orangutans (*Pongo pygmaeus*). Anim Behav 22:3–74. https://doi.org/10.1016/S0003-3472(74)80054-0

Martin P, Bateson P (2007) Measuring behavior: an introductory guide, 3rd edn. Cambridge University Press, Cambridge

Masilkova M, Weiss A, Šlipogor V, Konecná M (2020) Comparative assessment of behaviorally derived personality structures in golden-handed tamarins (*Saguinus midas*), cotton-top tamarins (*Saguinus oedipus*), and common marmosets (*Callithrix jacchus*). J Comp Psychol. https://doi.org/10.1037/com0000226

McLean KA, Trainor AM, Asner GP et al (2016) Movement patterns of three arboreal primates in a Neotropical moist forest explained by LiDAR-estimated canopy structure. Landsc Ecol 31:1849–1862. https://doi.org/10.1007/s10980-016-0367-9

McNaughton BL, Battaglia FP, Jensen O et al (2006) Path integration and the neural basis of the "cognitive map." Nat Rev Neurosci 7:663–678. https://doi.org/10.1038/nrn1932

Medeiros RM, Brito JIB, Borges CK (2012) Análise Hidroclimático do Município de Cabaceiras, PB. Rev Bras Geogr Física 05:1174–1190

Miller CT (2017) Why marmosets? Dev Neurobiol 77:237–243. https://doi.org/10.1002/dneu.22483

Milton K (1981) Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. Am Anthropol 83:534–548

Milton K (2000) Quo vadis? Tactics of food search and group movement in primates and other animals. In: Boinsky S, Garber PA (eds) On the move: How and why animals travel in groups. University of Chicago Press, Chicago, p 811

Mitchell JF, Leopold DA (2015) The marmoset monkey as a model for visual neuroscience. Neurosci Res 93:20–46. https://doi.org/10.1016/j.neures.2015.01.008

Moser EI, Kropff E, Moser MB (2008) Place cells, grid cells, and the brain's spatial representation system. Annu Rev Neurosci 31:69–89. https://doi.org/10.1146/annurev.neuro.31.061307.090723

Nascimento SS, Alves JJA (2008) Ecoclimatologia do cariri paraibano. Rev Geográfica Acadêmica 2:28–41

Normand E, Boesch C (2009) Sophisticated Euclidean maps in forest chimpanzees. Anim Behav 77:1195–1201. https://doi.org/10.1016/j.anbehav.2009.01.025

Noser R, Byrne RW (2007a) Mental maps in chacma baboons (*Papio ursinus*): using inter-group encounters as a natural experiment. Anim Cogn 10:331–340. https://doi.org/10.1007/s10071-006-0068-x

Noser R, Byrne RW (2007b) Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. Anim Behav 73:257–266. https://doi.org/10.1016/j.anbehav.2006.04.012

Noser R, Byrne RW (2014) Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. Am J Primatol 76:399–409. https://doi.org/10.1002/ajp.22181

Noser R, Byrne RW (2015) Wild chacma baboons (*Papio ursinus*) remember single foraging episodes. Anim Cogn 18:921–929. https://doi.org/10.1007/s10071-015-0862-4

O'Keefe J, Nadel L (1978) The hippocampus as a cognitive map. Oxford University Press, Oxford

Oh J, Šlipogor V, Tecumseh Fitch W (2019) Artificial visual stimuli for animal experiments: an experimental evaluation in a prey capture context with common marmosets (*Callithrix jacchus*). J Comp Psychol 133:72–80. https://doi.org/10.1037/com0000129

Pegado CMA, De Andrade LA, Félix LP, Pereira IM (2006) Efeitos da invasão biológica de algaroba - *Prosopis juliflora* (Sw.) DC. sobre a composição e a estrutura do estrato arbustivo-arbóreo da caatinga no Município de Monteiro, PB. Brasil Acta Bot Brasilica 20:887–898. https://doi.org/10.1590/S0102-33062006000400013

Petit O, Bon R (2010) Decision-making processes: the case of collective movements. Behav Process 84:635–647. https://doi.org/10.1016/j.beproc.2010.04.009

Porter LM, Garber PA (2013) Foraging and spatial memory in wild Weddell's Saddleback Tamarins (*Saguinus fuscicollis weddelli*) when moving between distant and out-of-sight goals. Int J Primatol 34:30–48. https://doi.org/10.1007/s10764-012-9644-x

Poucet B (1993) Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. Psychol Rev 100:163–182. https://doi.org/10.1037/0033-295X.100.2.163

Powell RA (2000) Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, pp 65–103

Presotto A, Izar P (2010) Spatial reference of black capuchin monkeys in Brazilian Atlantic Forest: egocentric or allocentric? Anim Behav 80:125–132. https://doi.org/10.1016/j.anbehav.2010.04.009

Presotto A, Verderane MP, Biondi L et al (2018) Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. Anim Cogn 21:1–13. https://doi.org/10.1007/s10071-018-1176-0

Presotto A, Fayrer-Hosken R, Curry C, Madden M (2019) Spatial mapping shows that some African elephants use cognitive maps to navigate the core but not the periphery of their home ranges. Anim Cogn 22:251–263. https://doi.org/10.1007/s10071-019-01242-9

Pritchard DJ, Hurly TA, Healy SD (2018) Wild hummingbirds require a consistent view of landmarks to pinpoint a goal location. Anim Behav 137:83–94. https://doi.org/10.1016/j.anbehav.2018.01.014

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Riotte-Lambert L, Matthiopoulos J (2020) Environmental predictability as a cause and consequence of animal movement. Trends Ecol Evol 35:163–174. https://doi.org/10.1016/j.tree.2019.09.009

Ronacher B (2020) Path integration in a three-dimensional world: the case of desert ants. J Comp Physiol A Neuroethol Sensory Neural Behav Physiol. https://doi.org/10.1007/s00359-020-01401-1

Rylands AB (1984) Exudate-eating and tree-gouging by marmosets (Callitrichidae, Primates). Trop Rain For Leeds Symp 155–168

Salmi R, Presotto A, Scarry CJ et al (2020) Spatial cognition in western gorillas (*Gorilla gorilla*): an analysis of distance, linearity, and speed of travel routes. Anim Cogn. https://doi.org/10.1007/s10071-020-01358-3

Schiel N, Souto A (2017) The common marmoset: an overview of its natural history, ecology and behavior. Dev Neurobiol 77:244–262. https://doi.org/10.1002/dneu.22458

Schiel N, Souto A, Bezerra BM, Huber L (2008) A stress-free method of identifying common marmosets (*Callithrix jacchus*) in the wild. In: Ferrari SF, Rimoli J (eds) A Primatologia no Brasil. Sociedade Brasileira de Primatologia, Biologia Geral e Experimental–UFS. A, pp 147–153

Schiel N, Souto A, Huber L, Bezerra BM (2010) Hunting strategies in wild common marmosets are prey and age dependent. Am J Primatol 72:1039–1046. https://doi.org/10.1002/ajp.20860

Schreier AL, Grove M (2010) Ranging patterns of hamadryas baboons: random walk analyses. Anim Behav 80:75–87. https://doi.org/10.1016/j.anbehav.2010.04.002

Schreier AL, Grove M (2014) Recurrent patterning in the daily foraging routes of Hamadryas Baboons (*Papio hamadryas*): spatial memory in large- scale versus small- scale space. Am J Primatol 435:421–435. https://doi.org/10.1002/ajp.22192

Shaffer CA (2014) Spatial foraging in free ranging bearded sakis: traveling salesmen or Lévy walkers? Am J Primatol 76:472–484. https://doi.org/10.1002/ajp.22227

Sigg H, Stolba A (1981) Home range and daily March in a Hamandryas Baboon Troop. Folia Primatol 36:40–75

Spiegel O, Crofoot MC (2016) The feedback between where we go and what we know—information shapes movement, but movement also impacts information acquisition. Curr Opin Behav Sci 12:90–96. https://doi.org/10.1016/j.cobeha.2016.09.009

Stevenson MF, Rylands AB (1988) The marmosets, genus Callithrix. In: Coimbrafilho A, Mittermeier R, Rylands AB, Fonseca G (eds) Ecology and behavior of neotropical primates, vol 2, 2nd edn. World Wildlife Fund, Washington, p 612

Streilein KE (1982) Ecology of small mammals in the semiarid Brazilian Caatinga. II. Water relations. Ann Carnegie Museum 51:109–126

Thompson CL, Robl NJ, de Oliveira Melo LC et al (2013) Spatial distribution and exploitation of trees gouged by common marmosets (*Callithrix jacchus*). Int J Primatol 34:65–85. https://doi.org/10.1007/s10764-012-9647-7

Tolman EC (1948) Cognitive maps in rats and men. Psychol Rev 55:189–208. https://doi.org/10.4324/9780203789155-11

Trapanese C, Meunier H, Masi S (2018) What, where and when: spatial foraging decisions in primates. Biol Rev. https://doi.org/10.1111/brv.12462

Trapanese C, Robira B, Tonachella G et al (2019) Where and what? Frugivory is associated with more efficient foraging in three semi-free ranging primate species. R Soc Open Sci. https://doi.org/10.1098/rsos.181722

Valero A, Byrne RW (2007) Spider monkey ranging patterns in Mexican subtropical forest: Do travel routes reflect planning? Anim Cogn 10:305–315. https://doi.org/10.1007/s10071-006-0066-z

Vannuchi CRS, Costa CS, de Jesus FM et al (2020) Sex, diurnal variation and retention interval differently affect performance of marmoset monkeys in a recognition memory task for object location. Elsevier B.V, Amsterdam

Viswanathan GM, Afanasyev V, Buldyrev SV et al (1996) Lévy flight search patterns of wandering albatrosses. Nature 381:413–415

Warren WH (2019) Non-Euclidean navigation. J Exp Biol. https://doi.org/10.1242/jeb.187971

Warren WH, Rothman DB, Schnapp BH, Ericson JD (2017) Wormholes in virtual space: from cognitive maps to cognitive graphs. Cognition 166:152–163. https://doi.org/10.1016/j.cognition.2017.05.020

Wehner R, Boyer M, Loertscher F et al (2006) Ant navigation: one-way routes rather than maps. Curr Biol 16:75–79. https://doi.org/10.1016/j.cub.2005.11.035

Wolf M, Frair J, Merrill E, Turchin P (2009) The attraction of the known: The importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. Ecography (Cop) 32:401–410. https://doi.org/10.1111/j.1600-0587.2008.05626.x

Yu C, Luo J, Wohlgemuth M, Moss CF (2019) Echolocating bats inspect and discriminate landmark features to guide navigation. J Exp Biol. https://doi.org/10.1242/jeb.191965

CAPÍTULO 4

(considerações finais)

CONSIDERAÇÕES FINAIS

4.1 PRINCIPAIS CONCLUSÕES

Em geral, observamos que saguis-comum fazem uso de habilidades cognitivas espaciais para procurar e regressar a fontes alimentares tanto em pequena como em larga escala de espaço. Em pequena escala de espaço, os animais têm a capacidade de manter informações espaciais de locais de importância alimentar tanto a curto como a longo prazo e que possuem a habilidade de aprender a localização espacial de fontes alimentares após as terem visitado apenas uma vez. Estas habilidades parecem melhorar a busca por recursos dispersos dentro de manchas em ambientes com flutuações na disponibilidade de alimento. Já em larga escala de espaço, observamos que a espécie possuí uma navegação baseada em rotas, isto é, navega repetindo normalmente os mesmos caminhos e reutiliza, frequentemente, os mesmos locais como pontos de mudança de direção. Observamos também que esta repetição de segmentos de rota e de pontos de mudança de direção parece ser influenciada por fatores ambientais, tais como distância das fontes alimentares e densidade de vegetação do ambiente. Em larga escala de espaço, o uso de um mapa mental baseado em rotas parece beneficiar estes animais devido ao consumo de exsudatos que apresentam distribuição espacial aglomerada e estão disponíveis durante todo o ano. Desta forma, para localizar recursos no ambiente, saguis-comum parecem fazer uso de mapas mentais baseados em rotas e uma vez forrageando dentro de manchas alimentares o uso da memória de curto e longo prazo torna o seu forrageio mais eficiente.

Além disso, ao longo dos dois capítulos ressaltamos a importância do ambiente no uso das habilidades espaciais de saguis-comum. É previsto, teoricamente, que o ambiente exerça forte influência sobre o uso de habilidades cognitivas espaciais em primatas, com ambientes mais "desafiadores" sendo os que mais moldam essas habilidades (ROSATI, 2017). Contudo, a dificuldade de definir o que é um ambiente "desafiador" torna difícil comparações empíricas. Apesar da tese não contribuir empiricamente para "Hipótese da Inteligência Ecológica" citada anteriormente, haja vista que não foi realizada nenhuma comparação entre biomas, a mesma ressalta fortemente a influência do ambiente na navegação espacial dos saguis-comum e levanta questionamentos sobre o papel do mesmo na cognição espacial de primatas. Até ao momento, vários pesquisadores sugerem que a forma como os animais navegam no ambiente é influenciado apenas pela filogenia, e por essa razão, a grande maioria dos primatas não-humanos navega em função de um mapa baseado em rotas.

4.2 CONTRIBUIÇÕES TEÓRICAS/METODOLÓGICAS DA TESE

Relativamente às contribuições teóricas, podemos concluir que nos nossos dois estudos observamos uma grande influência do ambiente na cognição espacial de saguis-comum. Esta influência do ambiente gera questionamentos acerca da pressão exercida pelas variáveis ambientais e pode contribuir para o melhor entendimento da "Hipótese da Inteligência Ecológica". Ainda, podemos afirmar que a tese contribuiu para examinar de forma mais profunda a flexibilidade cognitiva de primatas não humanos e entender como estes adaptam as suas respostas cognitivas espaciais à disponibilidade de recursos alimentares em diferentes contextos.

Ao realizarmos estudos experimentais de campo mostramos a importância da observação de animais selvagens e de como podemos contornar metodologicamente as variáveis externas de possível influência nesses estudos. Com a presente tese, reforçamos também a importância de coletar dados comportamentais, principalmente de cognição espacial, em indivíduos selvagens. Ainda, metodologicamente com a nossa pesquisa reforçamos a importância e vantagens de usar saguis-comum como modelos para estudos de cognição, algo já ressaltado por alguns autores como MILLER (2017). Estes pequenos primatas além da sua fácil habituação à presença humana possuem também uma ampla distribuição e dieta variada além de uma cognição física e social bastante desenvolvida (SCHIEL; SOUTO, 2017). Por fim, a presente tese pode contribuir também para a conservação de primatas não-humanos. Por exemplo, os resultados obtidos no terceiro capítulo, isto é, a informação de onde se situam espacialmente os segmentos de rotas e locais de mudança de direção mais usados pelos animais, poderão ser usados para se decidir onde devem ser criados os corredores ecológicos de forma a permitir o deslocamento de animais entre áreas isoladas. Apesar de saguis-comum não estarem ameaçados de extinção, a metodologia usada no terceiro capítulo da presente tese de doutorado pode ser de suma importância para espécies de primatas ameaçadas ou criticamente ameaçadas.

4.3 PRINCIPAIS LIMITAÇÕES DO ESTUDO

Relativamente ao segundo capítulo da tese, podemos afirmar que realizar experimentos de campo com foco em cognição espacial podem trazer tanto vantagens como desvantagens. As vantagens foram enumeradas nos capítulos anteriores. Contudo, algumas desvantagens e consequentemente, limitações de pesquisas experimentais em campo são: (1) impossibilidade de controlar todas as variáveis que podem interferir nos resultados, por exemplo, informações sociais; (2) pouco controle sobre os sujeitos de estudo que, por serem de vida livre, podem ou

não estar dispostos a participar do experimento; (3) investimento de material e mão de obra, o que pode levar a uma redução no tempo de estudo e consequentemente a uma redução do tamanho amostral.

O terceiro capítulo, que focou em investigar o tipo de navegação espacial usado por saguis-comum em larga escala de espaço, teve algumas limitações que se relacionam principalmente com a dificuldade de seguir os animais durante todo o seu período de atividade haja vista que são primatas pequenos e rápidos e que navegam principalmente entre as copas das árvores. Além disso, para realizar este tipo de estudos, se torna necessário um tempo amplo de habituação dos animais ao pesquisador assim como a necessidade de se identificar individualmente cada animal, o que demanda não só paciência (uma vez que quando não-habituados os animais fogem) como também um grande esforço físico. Esta limitação fica ainda mais evidente em estudos de campo observacionais em que é necessária uma grande proximidade sujeito de estudo-pesquisador e consequentemente uma excelente habituação, como foi o caso da pesquisa aqui supracitada pela necessidade de registrar a localização espacial dos animais.

4.4 PROPOSTAS DE INVESTIGAÇÕES FUTURAS

Com o desenvolvimento e resultados encontrados nos dois estudos (segundo e terceiro capítulo) surgiram algumas questões e possíveis propostas para investigações futuras. Sugerimos, por exemplo, que o experimento realizado no segundo capítulo seja reproduzido em larga escala de espaço e que sejam observadas e coletadas as mesmas variáveis. Além disso, seria interessante a comparação do uso de mapas mentais por saguis-comum também em diferentes escalas de espaço. O terceiro capítulo, por sua vez, ressaltou a possível influência do ambiente na navegação espacial de saguis-comum. Este achado levanta questionamentos sobre o efeito de variáveis ambientais que poderiam ser avaliadas em estudos posteriores.

4.5 ORÇAMENTO

Custos estimados do segundo capítulo da tese

Este estudo que focou no uso de diferentes habilidades espaciais em pequena escala de espaço por saguis-comum foi desenvolvido no interstício de janeiro de 2015 a novembro de 2016 sendo financiado pela Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) através de uma bolsa de doutorado atribuída à aluna Filipa Alexandra de Abreu Paulos

e pelo Programa Professor Visitante do Exterior (PVE/CAPES No: 88881.064998/2014-01) sob coordenação da Professora Dra. Nicola Schiel.

As despesas referentes ao desenvolvimento do segundo capítulo da tese incluem compra de material de campo, contratação de terceiros para montagem do material de campo, combustível ou passagem de ônibus para deslocamento da estudante para o local de coleta e alimentação. Num total de cerca de 120 dias de estudo (incluindo preparação e montagem do experimento, habituação dos animais e coleta de dados) foram gastos cerca de 7.940,00 reais. Esse valor inclui 2.500,00 reais para a compra de material para montagem do experimento, 800,00 reais pagos a terceiros para montagem do experimento, 2.400,00 reais de deslocamento (combustível ou compra de passagens) e 2.240,00 reais para custos de alimentação e gastos associados. Incluindo a bolsa de doutorado atribuída à aluna durante o tempo do estudo (8.800,00 reais), o valor total foi de 16.740,00 reais. Assim, o investimento diário para a coleta dos dados do segundo capítulo foi de 139,50 reais. Já o investimento para coleta de dados em cada uma das sessões (3 sessões diárias) foi de 46,50 reais. É importante ressaltar que como mencionado acima, o presente estudo esteve inserido em um projeto maior que tinha como objetivo abordar diferentes aspectos da ecologia e cognição de saguis-comum. Esse projeto teve financiamento de 142.200,00 reais e teve duração de dois anos (esforço de campo de cerca de 470 dias).

Custos estimados do terceiro capítulo da tese

O terceiro capítulo da tese (navegação espacial em larga escala de espaço) foi desenvolvido de janeiro a abril de 2018. O mesmo também foi financiado pela Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) por meio de uma bolsa de doutorado atribuída à aluna Filipa Alexandra de Abreu Paulos e pelo Programa Professor Visitante do Exterior (PVE/CAPES No: 88881.064998/2014-01) sob coordenação da Professora Dra. Nicola Schiel.

As despesas do terceiro capítulo da tese incluem as passagens de ônibus ou combustível de carro, alimentação e gastos associados e compra de material tanto permanente como usado em campo. O estudo teve duração de 72 dias em que foi gasto um total de 2.495,00 reais que incluiu 915,00 reais de alimentação e gastos de alojamento, 350,00 reais de gastos de combustível e passagens terrestres e 1230,00 reais de compra de material a ser usado durante a coleta de dados. Aliado a esse gasto, ainda teve o pagamento de uma bolsa de doutorado que referente aos dias de trabalho de campo somou 5.133,33 reais. O investimento total para o

desenvolvimento e elaboração do estudo foi de 7.628,33 reais. Desta forma, uma coleta de dados diária (12h) para observar saguis-comum durante todo o período de atividade deu investimento diário de 105,94 reais. O valor mencionado não inclui despesas de taxonomistas ou ajudantes de campo uma vez que essa ajuda foi voluntária.

4.6 REFERÊNCIAS BIBLIOGRÁFICAS

ALBUQUERQUE, U. P. et al. Caatinga revisited: Ecology and conservation of an important seasonal dry forest. **The Scientific World Journal**, v. 2012, 2012.

AMORA, T. D.; BELTRÃO-MENDES, R.; FERRARI, S. F. Use of Alternative Plant Resources by Common Marmosets (*Callithrix jacchus*) in the Semi-Arid Caatinga Scrub Forests of Northeastern Brazil. **American Journal of Primatology**, v. 75, n. 4, p. 333–341, 2013.

ANDRADE-LIMA, D. The caatingas dominium. **Revista Brasileira de Botânica**, v. 4, p. 149–163, 1981.

ANDREWS, M. W. Selection of food sites by Callicebus moloch and Saimiri sciureus under spatially and temporally varying food distribution. **Learning and Motivation**, v. 19, n. 3, p. 254–268, 1988.

ARAÚJO, E. D. L.; CASTRO, C. C. DE; ALBUQUERQUE, U. P. Dynamics of brazilian Caatinga – A review concerning the plants, environment and people. **Functional Ecosystems and Communities**, v. 1, n. 1, p. 15–28, 2007.

ASENSIO, N. et al. Gibbon travel paths are goal oriented. **Animal Cognition**, v. 14, n. 3, p. 395–405, 2011.

ATKINSON, R. P. D. et al. Scale-free dynamics in the movement patterns of jackals. **Oikos**, v. 98, n. 1, p. 134–140, 2002.

BAILEY, C.; BARTSCH, D.; KANDEL, E. Toward a molecular definition of long-term memory storage. **Proc. Natl. Acad. Sci. USA**, v. 93, n. November, p. 13445–13452, 1996.

BARAGLI, P. et al. Encoding the Object Position for Assessment of Short Term Spatial Memory in Horses (*Equus caballus*). **International Journal of Comparative Psychology**, v. 24, n. June 2016, p. 284–291, 2011.

BARBOSA, D. C. A.; BARBOSA, M. C. A.; LIMA, L. C. M. Fenologia de espécies lenhosas da Caatinga. In: LEAL, I. R.; TABARELLI, M.; CARDOSO DA SILVA, J. M. (Eds.). . **Ecologia e Conservação da Caatinga**. 2 Ed. ed. [s.l.] Ed. Universitária da UFPE, 2003. p. 657–693.

BICCA-MARQUES, J. C.; GARBER, P. A. Use of social and ecological information in tamarin foraging decisions. **International Journal of Primatology**, v. 26, n. 6, p. 1321–1344, 2005.

BIRD, L. R. et al. Spatial Memory for Food Hidden by Rats (*Rattus norvegicus*) on the Radial Maze: Studies of Memory for Where, What, and When. **Journal of Comparative Psychology**, v. 117, n. 2, p. 176–187, 2003.

BOLKER, B. M. et al. Generalized linear mixed models: a practical guide for ecology and evolution. **Trends in Ecology and Evolution**, v. 24, n. 3, p. 127–135, 2009.

BOYER, D. et al. Scale-free foraging by primates emerges from their interaction with a complex environment. **Proceedings of the Royal Society B: Biological Sciences**, v. 273, n. 1595, p. 1743–1750, 2006.

BUGNYAR, T.; HUBER, L. Push or pull: An experimental study on imitation in marmosets. **Animal Behaviour**, v. 54, n. 4, p. 817–831, 1997.

BURNS, J. G.; THOMSON, J. D. A test of spatial memory and movement patterns of bumblebees at multiple spatial and temporal scales. **Behavioral Ecology**, v. 17, n. 1, p. 48–55, 2006.

BYRNE, R. W. Evolution of Primate Cognition. **COGNITIVE SCIENCE Vol**, v. 24, n. 3, p. 543–570, 2000.

CALDWELL, C. A.; WHITEN, A. Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. **Animal Behaviour**, v. 65, n. 6, p. 1085–1092, 2003.

CALDWELL, C. A.; WHITEN, A. Testing for social learning and imitation in common marmosets, *Callithrix jacchus*, using an artificial fruit. **Animal Cognition**, v. 7, n. 2, p. 77–85, 2004.

COLLETT, M. Spatial memories in insects. **Current Biology**, v. 19, n. 24, p. 1103–1108, 2009.

COLLETT, M.; CHITTKA, L.; COLLETT, T. S. Spatial memory in insect navigation. **Current Biology**, v. 23, n. 17, p. 789–800, 2013.

COMBRINK, X.; WARNER, J. K.; DOWNS, C. T. Nest-site selection, nesting behaviour and

spatial ecology of female Nile crocodiles (*Crocodylus niloticus*) in South Africa. **Behavioural Processes**, v. 135, n. September 2017, p. 101–112, 2017.

CORLETT, R. T. How to be a frugivore (in a changing world). **Acta Oecologica**, v. 37, n. 6, SI, p. 674–681, 2011.

CRONIN, K. A. et al. Studying primate cognition in a social setting to improve validity and welfare: a literature review highlighting successful approaches. **PeerJ**, v. 5, p. e3649, 2017.

CUNNINGHAM, E.; JANSON, C. H. Integrating information about location and value of resources by white-faced saki monkeys (*Pithecia pithecia*). **ANIMAL COGNITION**, v. 10, n. 3, p. 293–304, jul. 2007.

DE AMORIM, I. L.; SAMPAIO, E. V. S. B.; ARAÃ°JO, E. L. Phenology of woody species in the caatinga of SeridÃ³, RN, Brazil. **Fenologia de espÃ©cies lenhosas da caatinga do SeridÃ³, RN**, v. 33, n. 3, p. 491–499, 2009.

DE AMORIM, I. L.; SAMPAIO, E. V. S. B.; DE LIMA ARAÚJO, E. Flora e estrutura da vegetação arbustivo-arbórea de uma área de caatinga do Seridó, RN, Brasil. **Acta Botanica Brasilica**, v. 19, n. 3, p. 615–623, 2005.

DE LA FUENTE, M. F. et al. Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (*Callithrix jacchus*). **American Journal of Primatology**, n. August 2018, p. e22964, 27 fev. 2019.

DE LA FUENTE, M. F. C. et al. Behavioral adjustments by a small neotropical primate (*Callithrix jacchus*) in a semiarid caatinga environment. **Scientific World Journal**, v. 2014, 2014.

DE MORAES, B. L. C.; DA SILVA SOUTO, A.; SCHIEL, N. Adaptability in stone tool use by wild capuchin monkeys (*Sapajus libidinosus*). **American Journal of Primatology**, v. 76, n. 10, p. 967–977, 2014.

DE RAAD, A. L.; HILL, R. A. Topological spatial representation in wild chacma baboons (*Papio ursinus*). **Animal Cognition**, v. 22, n. 3, p. 397–412, 2019.

DE SOUSA, M. B. et al. Hand preference study in marmosets (*Callithrix jacchus*) using food reaching tests. **Primates**, v. 42, n. 1, p. 57–66, 2001.

DECASIEN, A. R.; WILLIAMS, S. A.; HIGHAM, J. P. Primate brain size is predicted by diet but not sociality. **Nature Ecology and Evolution**, v. 1, n. 5, p. 1–7, 2017.

DI FIORE, A.; SUAREZ, S. A. Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. **ANIMAL COGNITION**, v. 10, n. 3, p. 317–329, jul. 2007.

DIGBY, L. J. Social organization in a wild population of *Callithrix jacchus*: II. Intragroup social behavior. **Primates**, v. 36, n. 3, p. 361–375, 1995.

DOLINS, F. L.; MITCHELL, R. W. Linking spatial cognition and spatial perception. **Spatial Perception, Spatial Cognition: Mapping the Self and Space**, p. 1–10, 2010.

DUKAS, R. **Cognitive ecology: The evolutionary ecology information processing and decision making.** [s.l.] University Chicago Press, 1998.

DUKAS, R. Costs of memory: Ideas and predictions. **Journal of Theoretical Biology**, v. 197, n. 1, p. 41–50, 1999.

DUKAS, R. Behavioural and ecological consequences of limited attention. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 357, n. 1427, p. 1539–1547, 2002.

DUKAS, R. Animal expertise: mechanisms, ecology and evolution. **Animal Behaviour**, v. 147, p. 199–210, 2019.

DUNBAR, R. I. M. The mating system of callitrichid primates: I. Conditions for the coevolution of pair bonding and twinning. **Animal Behaviour**, v. 50, n. 4, p. 1057–1070, 1995.

EASTON, A. et al. Behaviour of marmoset monkeys in a T-maze: Comparison with rats and macaque monkeys on a spatial delayed non-match to sample task. **Experimental Brain Research**, v. 150, n. 1, p. 114–116, 2003.

EPSTEIN, R. A. et al. The cognitive map in humans: Spatial navigation and beyond. **Nature Neuroscience**, v. 20, n. 11, p. 1504–1513, 2017.

ERHART, E. M.; OVERDORFF, D. J. Spatial memory during foraging in prosimian primates: Propithecus edwardsi and Eulemur fulvus rufus. **FOLIA PRIMATOLOGICA**, v. 79, n. 4, p. 185–196, 2008.

FAGAN, W. F. et al. Spatial memory and animal movement. **Ecology Letters**, v. 16, n. 10, p. 1316–1329, 2013.

FAULKES, C. G.; ARRUDA, M. D.; MONTEIRO, M. A. O. Genetic structure within and among populations of the common marmosets, *Callithrix jacchus*: implications for cooperative

breeding. In: FORD, S. M.; PETER, L. M.; DAVIS, L. C. (Eds.). . **The smallest anthropoids: the marmoset/callimico radiation**. New York, NY: Springer, 2009. p. 103–117.

FORTIN, D. Searching behavior and use of sampling information by free-ranging bison (Bos bison). **Behavioral Ecology and Sociobiology**, v. 54, n. 2, p. 194–203, 2003.

GARBER, P. A. Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. **Source: Biotropica**, v. 20, n. 2, p. 100–106, 1988.

GARBER, P. A. The ecology of group movement: evidence for the use of spatial, temporal, and social information in some primate foragers. In: BOINSKI, S.; GARBER, P. A. (Eds.). . **On the move. How and why animals travel in groups**. Chicago ed. [s.l.] University of Chicago Press, 2000. p. 261–298.

GARBER, P. A. et al. Trait variation and trait stability in common marmosets (*Callithrix jacchus)* inhabiting ecologically distinct habitats in northeastern Brazil. **American Journal of Primatology**, n. April, p. e23018, 2019.

GARBER, P. A.; BICCA-MARQUES, J. C. J. C.; AZEVEDO-LOPES, M. A. **Primate Cognition: Integrating Social and Ecological Information in Decision-Making**. New York, NY: Springer New York, 2009.

GARBER, P. A.; DOLINS, F. L. Examining spatial cognitive strategies in small-scale space and large-scale space in tamarin monkeys. In: DOLINS, F. L.; MITCHELL, R. W. (Eds.). . **Spatial cognition, spatial perception: mapping the self and space**. 1. ed. Cambridge: Cambridge University Press, 2010. p. 581.

GARBER, P. A.; DOLINS, F. L. Primate spatial strategies and cognition: Introduction to this special issue. **American Journal of Primatology**, v. 76, n. 5, p. 393–398, 2014.

GARBER, P. A.; HANNON, B. Modeling Monkeys: A Comparison of Computer-Generated and Naturally Occurring Foraging Patterns in Two Species of Neotropical Primates. **INTERNATIONAL JOURNAL OF PRIMATOLOGY**, v. 14, n. 6, p. 827–852, 1993.

GARBER, P. A.; PACIULLI, L. M. Experimental field study of spatial memory and learning in wild capuchin monkeys (*Cebus capucinus*). **Folia Primatologica**, v. 68, n. 3–5, p. 236–253, 1997.

GARBER, P. A.; PORTER, L. M. Navigating in Small-Scale Space: The Role of Landmarks

and Resource Monitoring in Understanding Saddleback Tamarin Travel. **AMERICAN JOURNAL OF PRIMATOLOGY**, v. 76, n. 5, p. 447–459, 2014.

GEVA-SAGIV, M. et al. Spatial cognition in bats and rats: From sensory acquisition to multiscale maps and navigation. **Nature Reviews Neuroscience**, v. 16, n. 2, p. 94–108, 2015.

GIBEAULT, S.; MACDONALD, S. E. Spatial memory and foraging competition in captive western lowland gorillas (*Gorilla gorilla gorilla*). **Primates**, v. 41, n. 2, p. 147–160, 2000.

GOMES, D. F.; BICCA-MARQUES, J. C. J. C. Capuchin monkeys (*Cebus nigritus*) use spatial and visual information during within-patch foraging. **AMERICAN JOURNAL OF PRIMATOLOGY**, v. 74, n. 1, p. 58–67, jan. 2012.

GONZÁLEZ-GÓMEZ, P. L.; VÁSQUEZ, R. A. A field study of spatial memory in green-backed firecrown hummingbirds (*Sephanoides sephaniodes*). **Ethology**, v. 112, n. 8, p. 790–795, 2006.

GUNHOLD, T. et al. Memory, transmission and persistence of alternative foraging techniques in wild common marmosets. **Animal Behaviour**, v. 91, p. 79–91, 2014.

HALSEY, L. G.; BEZERRA, B. M.; SOUTO, A. S. Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? **Animal Cognition**, v. 9, n. 3, p. 229–233, 2006.

HARLOW, H. F. The formation of learning sets. **Psychological Review**, v. 56, n. 1, p. 51–65, 1949.

HEALY, S. D.; HURLY, T. A. Spatial learning and memory in birds. **Brain, Behavior and Evolution**, v. 63, n. 4, p. 211–220, 2004.

HOPKINS, M. E. Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. **ANIMAL COGNITION**, v. 19, n. 2, p. 387–403, mar. 2016.

HOWARD, L. R. et al. The hippocampus and entorhinal cortex encode the path and euclidean distances to goals during navigation. **Current Biology**, v. 24, n. 12, p. 1331–1340, 2014.

HUBER, L.; VOELKL, B. Social and Physical Cognition in Marmosets and Tamarins. In: **The Smallest Anthropoids**. Boston, MA: Springer US, 2009. p. 183–201.

JANG, H. et al. Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. **Scientific Reports**, v. 9, n. 1, 2019.

JANMAAT, K. R. L.; BAN, S. D.; BOESCH, C. Chimpanzees use long-term spatial memory

to monitor large fruit trees and remember feeding experiences across seasons. **ANIMAL BEHAVIOUR**, v. 86, n. 6, p. 1183–1205, 2013.

JANMAAT, K. R. L.; BYRNE, R. W.; ZUBERBÜHLER, K. Primates Take Weather into Account when Searching for Fruits. **Current Biology**, v. 16, n. 12, p. 1232–1237, 2006a.

JANMAAT, K. R. L.; BYRNE, R. W.; ZUBERBÜHLER, K. Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. **ANIMAL BEHAVIOUR**, v. 72, n. 4, p. 797–807, 2006b.

JANMAAT, K. R. L.; CHANCELLOR, R. L. Exploring new areas: How important is long-term spatial memory for mangabey (*Lophocebus albigena johnstonii*) foraging efficiency? **International Journal of Primatology**, v. 31, n. 5, p. 863–886, 2010.

JANSON, C. H. Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. **Animal Behaviour**, v. 55, n. 5, p. 1229–1243, 1998.

JANSON, C. H. Capuchins, space, time and memory: an experimental test of what-where-when memory in wild monkeys. **Proceedings of the Royal Society B: Biological Sciences**, v. 283, p. 20161432, 2016.

JANSON, C. H. Foraging benefits of ecological cognition in fruit-eating primates: Results from field experiments and computer simulations. **Frontiers in Ecology and Evolution**, v. 7, n. APR, p. 1–8, 2019.

JANSON, C. H.; BYRNE, R. What wild primates know about resources: opening up the black box. **ANIMAL COGNITION**, v. 10, n. 3, p. 357–367, jul. 2007.

JOLY, M.; ZIMMERMANN, E. Do solitary foraging nocturnal mammals plan their routes? **Biology Letters**, v. 7, n. 4, p. 638–640, 2011.

LAVENEX, P. et al. Spatial versus nonspatial relational learning in free-ranging fox squirrels (Sciurus niger). **Journal of Comparative Psychology**, v. 112, n. 2, p. 127–136, 1998.

LEAL, I. R.; TABARELLI, M.; CARDOSO DA SILVA, J. M. **Ecologia e Conservação da Caatinga**. Recife: Ed. Universitária da UFPE, 2003.

LIPP, H. P. et al. A large outdoor radial maze for comparative studies in birds and mammals. **Neuroscience and Biobehavioral Reviews**, v. 25, n. 1, p. 83–99, 2001.

MACDONALD, S. E. et al. Strategies in landmark use by children, adults, and marmoset monkeys. **Learning and Motivation**, v. 35, n. 4, p. 322–347, 2004.

MACDONALD, S. E.; AGNES, M. M. Orangutan (*Pongo pygmaeus abelii*) Spatial Memory and Behavior in a Foraging Task. **Journal of Comparative Psychology**, v. 113, n. 2, p. 213–217, 1999.

MACDONALD, S. E.; PANG, J. C.; GIBEAULT, S. Marmoset (*Callithrix jacchus jacchus*) spatial memory in a foraging task: win-stay versus win-shift strategies. **Journal of comparative psychology**, v. 108, n. 4, p. 328–334, 1994.

MARTIN, P.; BATESON, P. **Measuring behavior: an introductory guide**. 3. ed. Cambridge: Cambridge University Press, 2007.

MENDES, N.; CALL, J. Chimpanzees form long-term memories for food locations after limited exposure. **American Journal of Primatology**, v. 76, n. 5, p. 485–495, 2014.

MENDES, N.; HUBER, L. Object Permanence in Common Marmosets (*Callithrix jacchus*). **Journal of Comparative Psychology**, v. 118, n. 1, p. 103–112, 2004.

MENZEL, E. W.; JUNO, C. Marmosets (*Saguinus fuscicollis*): Are Learning Sets Learned? **Science**, v. 217, n. August, p. 750–752, 1982.

MERKLE, J. A.; FORTIN, D.; MORALES, J. M. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. **Ecology Letters**, v. 17, n. 8, p. 924–931, ago. 2014.

MICHELS, A. M. Sex differences in food acquisition and aggression in captive common marmosets (*Callithrix jacchus*). **Primates**, v. 39, n. 4, p. 549–556, 1998.

MILLER, C. T. Why marmosets? **Developmental Neurobiology**, v. 77, n. 3, p. 237–243, 2017.

MILTON, K. **Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental developmentAmerican Anthropologist**, 1981. Disponível em: <http://doi.wiley.com/10.1525/aa.1981.83.3.02a00020%5Cnpapers3://publication/doi/10.1525/aa.1981.83.3.02a00020>

MODESTO, T.; BERGALLO, H. Ambientes diferentes, diferentes gastos do tempo entre atividades: o caso de dois grupos mistos do exótico Callithrix spp. na Ilha Grande, RJ, Brasil. **Neotropical Biology and Conservation**, v. 3, n. 3, p. 112–118, 2008.

MOURA, A. C. D. A. Primate group size and abundance in the Caatinga dry forest, northeastern Brazil. **International Journal of Primatology**, v. 28, n. 6, p. 1279–1297, 2007.

MOURA, A. C. D. A.; LEE, P. C. Capuchin stone tool use in Caatinga dry forest. **Science**, v. 306, n. 5703, p. 1909, 2004.

NORMAND, E.; BOESCH, C. Sophisticated Euclidean maps in forest chimpanzees. **ANIMAL BEHAVIOUR**, v. 77, n. 5, p. 1195–1201, 2009.

NOSER, R.; BYRNE, R. W. Mental maps in chacma baboons (*Papio ursinus*): using inter-group encounters as a natural experiment. **ANIMAL COGNITION**, v. 10, n. 3, p. 331–340, jul. 2007.

NOSER, R.; BYRNE, R. W. Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. **American Journal of Primatology**, v. 76, n. 5, p. 399–409, 2014.

NOSER, R.; BYRNE, R. W. Wild chacma baboons (*Papio ursinus*) remember single foraging episodes. **Animal Cognition**, v. 18, n. 4, p. 921–929, 2015.

O'KEEFE, J.; NADEL, L. **The hippocampus as a cognitive map**. [s.l.] Oxford University Press, 1978.

PESENDORFER, M. B. et al. The maintenance of traditions in marmosets: Individual habit, not social conformity? A field experiment. **PLoS ONE**, v. 4, n. 2, 2009.

PORTER, L. M.; GARBER, P. A. Foraging and Spatial Memory in Wild Weddell's Saddleback Tamarins (*Saguinus fuscicollis weddelli*) When Moving Between Distant and Out-of-Sight Goals. **INTERNATIONAL JOURNAL OF PRIMATOLOGY**, v. 34, n. 1, p. 30–48, 2013.

POUCET, B. Spatial Cognitive Maps in Animals: New Hypotheses on Their Structure and Neural Mechanisms. **Psychological Review**, v. 100, n. 2, p. 163–182, 1993.

PRADO, D. As caatingas da América do Sul. In: LEAL, I. R.; TABARELLI, M.; CARDOSO DA SILVA, J. M. (Eds.). . **Ecologia e Conservação da Caatinga Recife**. Recife: Ed. Universitária da UFPE, 2003. v. 1p. 3–74.

PRESOTTO, A. et al. Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. **Animal Cognition**, v. 21, n. 3, p. 1–13, 2018.

PRESOTTO, A. et al. Spatial mapping shows that some African elephants use cognitive maps to navigate the core but not the periphery of their home ranges. **Animal Cognition**, v. 22, n. 2, p. 251–263, 2019.

PRESOTTO, A.; IZAR, P. Spatial reference of black capuchin monkeys in Brazilian Atlantic Forest: Egocentric or allocentric? **Animal Behaviour**, v. 80, n. 1, p. 125–132, 2010.

QUEIROZ, L. P. Distribuição das espécies de Leguminoseae na caatinga. In: SAMPAIO, E. V. S. B. et al. (Eds.). . **Vegetação e flora das caatingas**. Recife/PE: APNE / CNIP, 2002. p. 141–153.

REYNA-HURTADO, R. et al. Primates adjust movement strategies due to changing food availability. **Behavioral Ecology**, v. 29, n. March, p. 368–376, 2018.

REZNIKOVA, Z. **Animal intelligence: From individual to social cognition.** [s.l.] Cambridge University Press, 2007.

ROBERTS, W. A. Foraging by rats on a radial maze: learning, memory and decision rules. In: GORMEZANO, I.; WASSERMAN, E. A. (Eds.). . **learning and memory: The behavioral and biological substrates**. New York: Psychology Press, 1993. p. 415.

ROSATI, A. G. Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. **Trends in Cognitive Sciences**, v. 21, n. 9, p. 1–12, 2017.

ROSATI, A. G.; RODRIGUEZ, K.; HARE, B. The ecology of spatial memory in four lemur species. **ANIMAL COGNITION**, v. 17, n. 4, p. 947–961, jul. 2014.

RYLANDS, A. B.; DE FARIA, D. S. Habitats, feeding ecology, and home range size in the genus Callithrix. In: RYLANDS, A. B. (Ed.). . **Marmosets and tamarins: Systematics, behavior, and ecology**. [s.l.] Oxford University Press, 1993. p. 262–272.

SCHIEL, N. et al. A stress-free method of identifying common marmosets (*Callithrix jacchus*) in the wild. In: FERRARI, S. F.; RIMOLI, J. (Eds.). . **A Primatologia no Brasil**. [s.l.] Sociedade Brasileira de Primatologia, Biologia Geral e Experimental – UFS. A, 2008. v. 9p. 147–153.

SCHIEL, N. et al. Hunting strategies in wild common marmosets are prey and age dependent. **American Journal of Primatology**, v. 72, n. 12, p. 1039–1046, 2010.

SCHIEL, N.; SOUTO, A. The common marmoset: An overview of its natural history, ecology and behavior. **Developmental Neurobiology**, v. 77, n. 3, p. 244–262, 2017.

SCHREIER, A. L.; GROVE, M. Recurrent Patterning in the Daily Foraging Routes of Hamadryas Baboons (*Papio hamadryas*): Spatial Memory in Large - Scale Versus Small - Scale

Space. **American Journal of Primatology**, v. 435, n. July 2013, p. 421–435, 2014.

SHAFFER, C. A. Spatial foraging in free ranging bearded sakis: Traveling salesmen or Lévy walkers? **American Journal of Primatology**, v. 76, n. 5, p. 472–484, 2014.

SHETTLEWORTH, S. J. **Cognition, evolution and behavior**. 2. ed. USA: Oxford University Press, 2010.

SILVA, J. M. C.; LEAL, I. R.; TABARELLI, M. **Caatinga: The Largest Tropical Dry Forest Region in South America**. [s.l.] Springer, 2017.

SOUSA, M. B. C.; PONTES, M. C. Variação temporal diurna de comportamentos afiliativos de sagui comum machos vivendo em ambiente natural. **Zoociências**, v. 10, n. 1, p. 7–12, 2008.

SOUTO, A. et al. Saltatory search in free-living *Callithrix jacchus*: Environmental and age influences. **International Journal of Primatology**, v. 28, n. 4, p. 881–893, 2007.

SPIERS, H. J. Hippocampal Formation. In: RAMACHANDRAN, V. S. (Ed.). . **Encyclopedia of Human Behavior**. 2. ed. [s.l.] Academic Press, 2012. v. 2p. 297–304.

SPINELLI, S. et al. Performance of the marmoset monkey on computerized tasks of attention and working memory. **Cognitive Brain Research**, v. 19, n. 2, p. 123–137, 2004.

STEVENS, J. R.; HALLINAN, E. V.; HAUSER, M. D. The ecology and evolution of patience in two New World monkeys. **Biology Letters**, v. 1, n. 2, p. 223–226, 2005.

STEVENSON, M. F.; RYLANDS, A. B. The marmosets, genus Callithrix. In: COIMBRA FILHO, A. et al. (Eds.). . **Ecology and behavior of neotropical primates, vol. 2**. 2. ed. [s.l.] Washington, DC: World Wildlife Fund., 1988. p. 612.

STREILEIN, K. E. Ecology ofsmall mammals in the semiarid brazilian Caatinga. II. Water relations. **Annals of Carnegie Museum**, v. 51, n. 6, p. 109–126, 1982.

SULIKOWSKI, D.; BURKE, D. Movement and memory : Different cognitive strategies are used to search for resources with different natural distributions Movement and memory : different cognitive strategies are used to search for resources with different natural distributions. v. 65, n. APRIL, p. 621–631, 2011.

TAYLOR, N. P.; ZAPPI, D. Distribuição das espécies de Cactaceae na caatinga. In: SAMPAIO, E. V. S. B. et al. (Eds.). . **Vegetação e flora das caatingas.** Recife/PE: APNE / CNIP, 2002. p. 123–125.

TEICHROEB, J. A.; AGUADO, W. D. Foraging vervet monkeys optimize travel distance when

alone but prioritize high-reward food sites when in competition. **Animal Behaviour**, v. 115, p. 1–10, 2016.

TEICHROEB, J. A.; CHAPMAN, C. A. Sensory information and associative cues used in food detection by wild vervet monkeys. **Animal Cognition**, v. 17, n. 3, p. 517–528, 2014.

THORNTON, A.; BOOGERT, N. J. Animal Cognition: The Benefits of Remembering. **Current Biology**, v. 29, n. 9, p. R324–R327, 2019.

TOMASSELO, M.; CALL, J. Space and objects. In: TOMASSELO, M.; CALL, J. (Eds.). . **Primate cognition**. New York, NY: Oxford University Press, 1997. p. 27–56.

TRAPANESE, C.; MEUNIER, H.; MASI, S. What, where and when: spatial foraging decisions in primates. **Biological Reviews**, v. 9, 2018.

TUJAGUE, M. P.; JANSON, C. H.; LAHITTE, H. B. Long-term spatial memory and learning set formation in captive capuchin monkeys (*Cebus libidinosus = Sapajus cay*). **International Journal of Primatology**, v. 36, n. 6, p. 1067–1085, 2015.

TULVING, E. Episodic memory and autonoesis: Uniquely human? In: TERRACE, H. S.; METFALFE, J. (Eds.). . **The Missing Link in Cognition: Origins of Self-Reflective Consciousness**. Oxford: Oxford University Press, 2005. v. 84p. 3–56.

VANDER WALL, S. B. et al. Do yellow-pine chipmunks prefer to recover their own caches. **Western North American Naturalist**, v. 68, n. 3, p. 319–323, 2008.

VANNUCHI, C. R. S. et al. **Sex, diurnal variation and retention interval differently affect performance of marmoset monkeys in a recognition memory task for object location**. [s.l.] Elsevier B.V., 2020. v. 379

VISWANATHAN, G. M. et al. **Lévy flight search patterns of wandering albatrossesNature**Nature, , 1996.

WARREN, W. H. Non-Euclidean navigation. **The Journal of Experimental Biology**, v. 222, n. Suppl 1, p. jeb187971, 2019.

WERNECK, F. P. The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. **Quaternary Science Reviews**, v. 30, n. 13–14, p. 1630–1648, 2011.

YI, X. et al. The use of spatial memory for cache management by a scatter-hoarding rodent.

Behavioral Ecology and Sociobiology, v. 70, n. 9, p. 1527–1534, 2016.

ZUBERBÜHLER, K.; JANMAAT, K. R. L. Foraging cognition in nonhuman primates. In: MICHAEL PLATT; GHAZANFAR, A. (Eds.). . **Primate Neuroethology**. Oxford Uni ed. [s.l: s.n.]. p. 64–83.
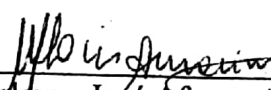
ANEXO 1

(autorizações legais)

Universidade Federal Rural de Pernambuco
Rua Dom Manoel de Medeiros, s/n,
Dois Irmãos - CEP: 52171-900 - Recife/PE

UFRPE

Comissão de ética no uso de animais - CEUA

Licença para o uso de animais em experimentação e/ou ensino

O Comitê de ética no uso de animais CEUA da Universidade Federal Rural de Pernambuco, no uso de suas atribuições, autoriza a execução do projeto descriminado abaixo. O presente projeto também se encontra de acordo com as normas vigentes no Brasil, especialmente a Lei 11794/2008.

Número da licença	144/2014
Número do processo	23082.023966/2014
Data de emissão da licença	09 de Dezembro de 2014
Título do Projeto	Testando a habilidade de primatas selvagens em integrar informações sociais e ecológicas em tomada de decisões: ecologia cognitiva, forrageio social e comportamento cooperativo em saguis comuns.
Finalidade (Ensino, Pesquisa, Extensão)	Pesquisa
Responsável pela execução do projeto	Nicola Schiel
Colaboradores	Antônio da Silva Souto; Júlio César Bicca-Marques; Maria Fernanda de La Fuente; Paul A. Garber; Cory Miller.
Tipo de animal e quantidade total autorizada	Primata não-humano; total de 25 animais.

Profª. Dra. Marleyne José Afonso Accioly Lins Amorim
(Presidente da CEUA-UFRPE)

Prof. Dr. Marleyne Am
Coordenadora CEUA

Ministério do Meio Ambiente - MMA
Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 46770-2	Data da Emissão: 26/11/2015 11:45	Data para Revalidação*: 25/12/2016

* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: Nicola Schiel	CPF: 893.835.914-04

Título do Projeto: Testando a habilidade de primatas selvagens em integrar informações sociais e ecológicas em tomada de decisões: ecologia cognitiva, forrageio social e comportamento cooperativo em saguis comuns

Nome da Instituição : UNIVERSIDADE FEDERAL RURAL DE PE	CNPJ: 24.416.174/0001-06

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Coleta de fezes e pelos	01/2015	02/2015
2	Marcação dos animais	01/2015	02/2015
3	Coleta de dados comportamentais	01/2015	09/2016

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
2	Esta autorização NÃO exime o pesquisador titular e os membros da sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
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4	A autorização para envio ao exterior de material biológico não consignado deverá ser requerida por meio do endereço eletrônico www.ibama.gov.br (Serviços on-line - Licença para importação ou exportação de flora e fauna - CITES e não CITES).
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7	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.
8	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.

Outras ressalvas

1	Os membros estrangeiros da equipe: Paul Alan Garber, que possui o vínculo de Programa de professor visitante na Universidade Federal Rural de Pernambuco; Cory Miller, que possui o vínculo de Programas de intercâmbio científico, firmado entre instituição de ensino; E Maria Fernanda de la Fuente Castellón que possui vínculo de visto permanente. Dispensados de autorização do Ministério da Ciência, Tecnologia e Inovação.

Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Antonio da Silva Souto	Pesquisador	375.429.234-04	2053984 SSP/PE-PE	Brasileira
2	Maria Fernanda de la Fuente Castellón	Médica Veterinária	011.175.771-12	V740235-M DIREX/DPF-	Estrangeira
3	Paul Alan Garber	Pesquisador		056461856 US governm-ES	Estrangeira
4	Júlio César Bicca Marques	Pesquisador	389.518.000-91	1024626341 SSP-PC-RS	Brasileira

Código de autenticação: 59463796

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