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INSTITUTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA
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Influência de fatores endógenos e exógenos na dinâmica populacional de dois pequenos mamíferos em uma área de cerrado denso na Estação Ecológica do Panga (Uberlândia/MG, Brasil)

Rodrigo Cassimiro Rossi

Uberlândia - MG
2021

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

Orientadora: Dra. Natália Oliveira Leiner

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Devido aos crescentes impactos antrópicos causando alterações climáticas e modificando a frequência e intensidade de eventos climáticos extremos, torna-se fundamental entender os fatores que regem as populações naturais. Flutuações populacionais são resultantes dos parâmetros relacionados à taxa de crescimento, como a sobrevivência e recrutamento. Distúrbios ambientais, como incêndios, afetam populações através de efeitos diretos e/ou indiretos. Além dessas variáveis exógenas, fatores endógenos, como a densidade populacional, afetam a regulação das populações. Utilizamos uma série temporal de 9 anos para avaliar os efeitos de fatores endógenos e exógenos nas dinâmicas populacionais de dois pequenos mamíferos (*Gracilinanus agilis* e *Rhipidomys mastacalis*) em uma área de cerrado denso em Uberlândia/MG. Através da estrutura de Royama, identificamos o papel do sistema endógeno (densidade) e de fatores exógenos (chuva, dias frios, dias quentes, NDVI e SOI) na taxa de crescimento anual das populações, verificando se tais fatores exercem efeitos verticais (atuando na sobrevivência e/ou reprodução), laterais (modificando a capacidade de suporte ambiental) ou não lineares (alterando a força da dependência da densidade). Também avaliamos os efeitos atrasados da densidade e de fatores exógenos (chuva, qualidade do habitat, dias frios e fogo) nas taxas de sobrevivência e recrutamento das espécies. Dois incêndios severos e extensos ocorridos durante o período estudado, permitiram que analisássemos o impacto desses distúrbios nos parâmetros demográficos das populações. Os incêndios afetaram indiretamente as populações através da redução na capacidade de suporte, onde nenhuma delas retornou aos padrões de abundância pré-fogo. Detectamos efeitos negativos da densidade (fator endógeno) nas taxas de crescimento das populações, afetando principalmente o recrutamento de machos de *G. agilis* e de machos e fêmeas de *R. mastacalis*, devido aos efeitos negativos da maior competição intraespecífica em altas densidades. Os parâmetros demográficos do marsupial *G. agilis* foram afetados principalmente por sua história de vida semélpara, entretanto, verificamos que a chuva também afetou esta espécie, através dos efeitos verticais na cobertura/qualidade do habitat (medida via NDVI) e no aumento da disponibilidade de recursos, que afetou a sobrevivência e o recrutamento. Em *R. mastacalis* os dias frios no ano anterior exibiram efeitos verticais na taxa de crescimento, enquanto a qualidade do habitat no ano anterior exibiu efeitos positivos na sobrevivência e negativos no recrutamento. Incêndios severos e extensos tiveram fortes efeitos indiretos nas populações. Apesar das semelhanças ecológicas (hábito, dieta), o tempo de resposta e os fatores atuantes foi variável nas espécies, em decorrência das distintas histórias de vida. Dessa forma, ressaltamos a importância de considerar a história de vida e fatores endógenos e exógenos na regulação populacional de pequenos mamíferos, uma vez que os resultados encontrados aqui podem ser encontrados em outras espécies no Cerrado.

Palavras-chave: fogo; parâmetros demográficos; sobrevivência; recrutamento; Didelphidae; Cricetidae; *Gracilinanus agilis*; *Rhipidomys mastacalis*

ABSTRACT

ROSSI, R. C. 2021. Influence of endogenous and exogenous factors on the population dynamics of two small mammals in an area of cerrado denso in the Panga Ecological Station (Uberlândia/MG, Brazil). Master's Thesis in Ecology and Conservation of Natural Resources. Federal University of Uberlândia. Uberlândia-MG, Brazil. 96 p.

Due to the increasing anthropogenic impacts that cause climate change and alter the frequency and intensity of extreme climatic events, it is crucial to understand the factors that drive natural populations. Population fluctuations are a result of growth rate parameters such as survival and recruitment. Environmental disturbances, such as fires, affect populations through direct and/or indirect effects. In addition to these exogenous variables, endogenous factors such as population density can also affect the regulation of populations. We used a 9-year time series to evaluate the effects of endogenous and exogenous factors on the population dynamics of two small mammals (*Gracilinanus agilis* and *Rhipidomys mastacalis*) in a cerrado denso area in Uberlândia/MG. Using the Royama framework, we identify the role of the endogenous system (density) and exogenous factors (rainfall, cold days, warm days, NDVI, and SOI) on the population annual growth rate, checking whether these factors exert vertical (acting on survival and/or reproduction), lateral (modifying environmental carrying capacity) or non-linear (changing the strength of density dependence) effects. We also evaluated the delayed effects of density and exogenous factors (rainfall, habitat quality, cold days, and fire) on species survival and recruitment rates. Two severe and extensive fires that occurred during the studied period allowed us to analyze the impact of these disturbances on the demographic parameters of the populations. The fires indirectly affected the populations through a reduction in carrying capacity, where none of them returned to pre-fire abundance patterns. We detected negative effects of density (endogenous factor) on population growth rates, mainly affecting recruitment of *G. agilis* males and *R. mastacalis* males and females, due to the negative effects of increased intraspecific competition at high densities. The demographic parameters of the marsupial *G. agilis* were primarily affected by its semelparous life-history, however, we found that rainfall also affected this species through vertical effects on habitat cover/quality (measured via NDVI) and increased resource availability, which affected survival and recruitment. In *R. mastacalis* cold days in the previous year exhibited vertical effects on the growth rate, while habitat quality in the previous year exhibited positive effects on survival and negative effects on recruitment. Severe and extensive fires had strong indirect effects on populations. Despite ecological similarities (habit, diet), the timing of response and acting factors was variable among species, due to distinct life-histories. Thus, we emphasize the importance of considering life-history and endogenous and exogenous factors in the population regulation of small mammals, since the results found here can be found in other species in the Cerrado.

Keywords: fire; demography parameters; survival; recruitment; Didelphidae; Cricetidae; *Gracilinanus agilis*; *Rhipidomys mastacalis*

INTRODUÇÃO GERAL

Atualmente, as mudanças climáticas são uma das principais ameaças à biodiversidade a nível mundial, além de serem causadoras de impactos socioeconômicos negativos para toda a humanidade (Wheeler e von Braun, 2013; Pecl et al., 2017). O principal fator responsável pelas alterações climáticas é o aumento na emissão dos gases estufa, advindos principalmente do dióxido de carbono (CO_2) proveniente das ações antropogênicas (Farmer e Cook, 2013). Ademais, o aumento da conversão de áreas naturais em ambientes agrícolas e de pastagens também afeta diretamente o clima regional através das modificações no balanço energético e hídrico (Foley et al., 2005). Além do aumento da temperatura média global, outras consequências das mudanças climáticas incluem alterações nos padrões de chuva e na intensidade e frequência de eventos climáticos extremos, tais como incêndios, furacões e períodos de seca (Williams et al., 2003; Vincent et al., 2005; Thibault e Brown, 2008).

O impacto das alterações climáticas em espécies da fauna e flora vem sendo frequentemente estudado, relatando principalmente implicações dessas alterações na distribuição espacial, parâmetros demográficos, densidade, e aspectos morfológicos e fenológicos dos organismos (Parmesan e Yohe, 2003; Lane et al., 2012; Loyola et al., 2012; Pacifici et al., 2017). Características da história de vida, tais como a capacidade de dispersão e as taxas reprodutivas, são constantemente relacionadas como preditoras da sensibilidade e capacidade adaptativa das espécies às mudanças no clima (Angert et al., 2011; Dawson et al., 2011; Santini et al., 2016).

Uma vez que a mudança climática é um distúrbio comprovado e cada vez mais comum em virtude das ações antropogênicas, torna-se extremamente necessário entendermos o impacto de tais mudanças na biodiversidade e nos serviços ecossistêmicos, uma vez que tal compreensão pode nos auxiliar no planejamento de estratégias de conservação mitigatórias (Stenseth et al., 2002; Yang e Rudolf, 2010). Nesse sentido, uma importante ferramenta são os estudos de longa duração, também chamados de séries temporais, que avaliam os processos estruturadores dos sistemas investigados (Strayer et al., 1986; Klein, 1997). Além de diagnosticar a estrutura e os causadores da variação na série de dados, essa abordagem também possibilita fazer previsões acerca das possíveis modificações no sistema estudado (Shumway e Stoffer, 2006). A base para criação de dados e estudos de séries temporais é oriunda dos monitoramentos, realizados a partir de observações ao longo de intervalos de tempo regulares (Hobbie et al., 2003).

Estudos de monitoramento frequentemente são realizados na ecologia populacional, a fim de encontrar as possíveis causas de variação da dinâmica populacional (Gentile et al., 2012). O principal parâmetro responsável por causar flutuações na abundância de indivíduos de uma população é a taxa de crescimento populacional (Sibly e Hone, 2002). Entretanto, esse parâmetro varia conforme dois parâmetros demográficos básicos: sobrevivência, que representa os indivíduos que não emigraram e permanecem vivos na população, e recrutamento, que representa a fração de indivíduos que ingressou na população, seja através de nascimentos ou imigração (Korpimäki et al., 2004). As causas responsáveis pela variação na sobrevivência e recrutamento, e consequentemente na taxa de crescimento populacional, são os fatores dependentes da densidade (ou endógenos) e os independentes da densidade (exógenos) (Royama, 1992).

Existe uma crescente linha de pesquisa na ecologia que busca investigar a importância relativa dos fatores endógenos e exógenos na dinâmica populacional (por exemplo White, 2001; Hixon et al., 2002; Goswami et al., 2011). Os fatores endógenos afetam e são afetados pela população através de um sistema de retroalimentação, envolvendo interações bióticas como a competição intraespecífica por recursos, a predação e o parasitismo (Berryman, 1999). Essas interações fazem o sistema endógeno operar em dependência da densidade direta ou tardia (Sinclair e Pech, 1996). Já os fatores exógenos geram modificações diretas ou indiretas na população, mas não são afetados por ela, sendo representados pelas condições climáticas, ambientais, distúrbios e catástrofes (Royama, 1992; Berryman, 1999). Os efeitos diretos ocorrem através da mortalidade de indivíduos, enquanto os efeitos indiretos ocorrem através de alterações na disponibilidade de recursos, competidores e predadores, sendo identificados na população em um tempo posterior à ação exógena (Berryman et al., 1987). Para avaliar como os efeitos exógenos afetam a dinâmica populacional, Royama (1992) os categorizou de acordo com sua forma de atuação, a saber: efeito vertical, gera mudanças na reprodução e sobrevivência; efeito lateral, modifica a capacidade de suporte do ambiente; e efeito não-linear, afeta a força da dependência da densidade. Embora tenha sido muito debatido o papel de fatores endógenos e exógenos na dinâmica populacional (Krebs, 2002; Berryman, 2004), atualmente há um consenso de que ambos interagem na regulação das populações (Turchin, 1995; Coulson et al., 2005; Krebs, 2013).

Os pequenos mamíferos são um excelente modelo de estudo para investigar os fatores que regulam a dinâmica das populações, uma vez que eles apresentam populações com grande flutuação na abundância, expectativa de vida curta e maior facilidade de realizar captura e monitoramento (Mares e Ernest, 1995; Krebs, 2013). Além disso, esse grupo desempenha um importante papel na dinâmica e fluxo de energia nos ecossistemas em que ocorrem, atuando em processos de sucessão ecológica, predação e dispersão de sementes, controle de populações de insetos, transmissão e reservatório de doenças, além de serem predados por outros animais (Brewer e Rejmánek, 1999; Dickman, 1999; Azevedo et al., 2006; DeMattia et al., 2006; Varela et al., 2008; Keesing et al., 2009; Lessa e Costa, 2010; Camargo et al., 2017).

Estudos analisando a regulação populacional de pequenos mamíferos indicam que os parâmetros demográficos dessas populações, como a sobrevivência e o recrutamento, são afetados por interações complexas entre a densidade populacional e as variáveis independentes da densidade (Julliard et al., 1999; Ekerholm et al., 2001; Wang et al., 2001; Morrison e Hik, 2007). No geral, a densidade afeta negativamente a taxa de crescimento populacional, através da diminuição da sobrevivência e recrutamento dos indivíduos (por exemplo Ostfeld et al., 1993; Reed e Slade, 2008; Ferreira et al., 2015). Em relação aos fatores exógenos, distúrbios ambientais, como furacões, inundações, incêndios e períodos de seca, podem exercer efeitos diretos ou indiretos na sobrevivência e reprodução, seja por seu efeito instantâneo ou subsequente (Kelt et al., 2005; Mendonça et al. 2015; Dhawan et al. 2018; Mason-Romo et al. 2018). Por outro lado, as variáveis climáticas (locais ou de larga escala) exercem efeitos na disponibilidade de recursos, impactando assim indiretamente a taxa de crescimento populacional (Bergallo e Magnusson, 1999; Lima et al., 1999; Madsen e Shine, 1999; Gentile et al., 2004; Mendel et al., 2008). Dessa forma, a interação entre efeitos dependentes e independentes de densidade (distúrbios, clima e ambiente) ocasiona uma série de impactos nas populações de pequenos mamíferos, como extinções locais, surtos populacionais, mudanças nos padrões de dominância e estrutura das comunidades, e perda de diversidade funcional (Ernest et al., 2000; Lima et al., 2008; Bateman et al., 2012; Mason-Romo et al., 2018).

Sistema de estudo

Pouca atenção foi dada quanto ao papel da manutenção dos ecossistemas naturais na redução dos riscos associados às mudanças climáticas e na regulação do clima local (Pielke et al., 2011). Apesar disso, já foi demonstrado que ambientes naturais, como florestas, campos, e recifes de coral, desempenham uma importante proteção contra os riscos das mudanças climáticas (Bradshaw et al., 2007; Ferrario et al., 2014). As savanas tropicais, além de possuírem um alto grau de biodiversidade e endemismo de espécies, são extremamente importantes no sistema climático da Terra, sendo responsáveis por 21% da evapotranspiração global (Miralles et al., 2011). Entretanto, as savanas têm sido um dos biomas que mais sofrem com as ações antrópicas, especialmente em decorrência da supressão da vegetação nativa (Fehlenberg et al., 2017).

O Cerrado é a maior savana neotropical, compreendendo 25% do Brasil e algumas regiões do Paraguai e Bolívia (Olson et al., 2001). Uma de suas principais características é a forte sazonalidade da precipitação, sendo classificada de acordo com o tipo climático AW (tropical com inverno seco) de acordo com a classificação climática de Köppen (Woodward, 2009). Dessa forma, há uma predominância de altas temperaturas durante todo o ano, enquanto há uma estação chuvosa no verão e uma seca no inverno (Peel et al., 2007). A sazonalidade da chuva impacta na produtividade da vegetação, de forma que o aumento das chuvas no verão gera um aumento na produtividade primária, estimulando o crescimento da vegetação e a produção de frutos (Franco, 2002). Assim como em outras savanas, o fogo é um importante determinante da composição, abundância e estrutura da vegetação (Walter e Breckle, 1986; Werneck, 2011). Além do fogo, a estação seca e a composição de nutrientes do solo, gera um mosaico de fisionomias no Cerrado, variando desde campos a florestas (Oliveira-Filho e Ratter, 2002).

Quanto às ameaças, o Cerrado atualmente já perdeu mais de 46% da sua vegetação nativa (Strassburg et al., 2017), principalmente em decorrência da conversão de áreas naturais em pastagens permanentes e áreas agrícolas (Ferreira et al., 2016a; Fehlenberg et al., 2017). Essas mudanças na cobertura do solo levam a um aumento da temperatura do ar e redução da umidade (Oliveira et al., 2005; Spera et al., 2016). Outra atividade importante que modifica o clima do Cerrado são as queimadas de origem antrópica, que também acometem as áreas naturais (Roberts, 2000; Pivello, 2011). Dessa forma, as modificações antrópicas que estão causando mudanças na temperatura do ar e deixando o Cerrado mais quente e seco, podem alterar os regimes de incêndios naturais e gerar impactos negativos na biodiversidade desse bioma (Hofmann et al., 2021).

Em decorrência das ameaças e ao seus altos níveis de riqueza e endemismo de espécies, o Cerrado é considerado um hotspot global de biodiversidade (Strassburg et al., 2017). Dentre os mamíferos, existem aproximadamente 116 espécies de pequenos mamíferos pertencentes às ordens Didelphimorphia e Rodentia no Cerrado (Mendonça et al., 2018). Dentre essas, *Gracilinanus agilis* (Didelphimorphia: Didelphidae) e *Rhipidomys mastacalis* (Rodentia: Cricetidae) são frequentemente encontradas em formações florestais, assim como em áreas de cerrado denso (Emmons e Feer, 1990; Rossi et al., 2006). As duas espécies apresentam hábitos noturnos, dieta onívora, constituída frequentemente de artrópodes e partes vegetais, e são predominantemente arborícolas (Emmons e Feer, 1990; Fonseca et al., 1996; Vieira e Camargo, 2012; Camargo et al., 2013). *Gracilinanus agilis* (20-45 g os adultos) possui história de vida semélpara, com reprodução sincronizada (iniciando em julho) e machos apresentando mortalidade pós-cópula, enquanto as fêmeas sobrevivem até o desmame dos filhotes, sem ocorrência de sobreposição de gerações (Lopes e Leiner, 2015). Por outro lado, *R. mastacalis* (35-170 g os adultos) apresenta reprodução contínua ao longo do ano, porém com maior concentração de indivíduos reprodutivos na estação chuvosa (Oliveira et al., 2007), ocorrendo sobreposição de gerações.

Dentro desse contexto, essa dissertação aborda a dinâmica populacional de dois pequenos mamíferos na Estação Ecológica do Panga, uma área de preservação ambiental do bioma Cerrado, localizada na região do Triângulo Mineiro (Uberlândia, Minas Gerais). Os dados são provenientes de um monitoramento mensal (iniciado em 2010) da comunidade de pequenos mamíferos no local estudado, onde utilizei nove anos de informações para avaliar a dinâmica populacional das duas espécies mais abundantes na área de estudo: *Gracilinanus agilis* e *Rhipidomys mastacalis*. A dissertação está estruturada em dois capítulos formatados como manuscritos que serão submetidos a periódicos científicos. No primeiro capítulo, intitulado "*Feedback structure and exogenous factors affecting the population dynamics of two Neotropical small mammals*", avalio o impacto de dois incêndios nas abundâncias populacionais e utilizo a estrutura de Royama (1992) para identificar a influência de fatores endógenos e exógenos na taxa de crescimento anual das duas populações. Enquanto no segundo capítulo, intitulado "*The delayed effects of endogenous and exogenous factors on the demographic parameters of two Neotropical small mammals*", avalio a influência endógena e exógena sobre as taxas de sobrevivência e recrutamento das duas espécies, considerando diferentes defasagens de tempo.

CAPÍTULO 1

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Feedback structure and exogenous factors affecting the population dynamics of two Neotropical small mammals

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Running Title: **Small mammal population dynamics**

Resumo

Considerando as ameaças dos impactos antrópicos nos ecossistemas, torna-se fundamental compreender os reguladores das dinâmicas de populações naturais. Entretanto, até recentemente, poucos estudos usaram dados de longo prazo para avaliar os fatores que impulsionam a abundância de pequenos mamíferos nas savanas neotropicais. Usamos uma série temporal de 9 anos, baseada em capturas mensais, para entender a dinâmica populacional de dois pequenos mamíferos arbóreos do Cerrado: o marsupial semélparo *Gracilinanus agilis* e o roedor iteróparo *Rhipidomys mastacalis*, as espécies mais abundantes na Estação Ecológica do Panga (Uberlândia/MG). Testamos o impacto de dois incêndios que ocorreram em 2014 e 2017 na abundância das populações. Além disso, usamos a estrutura de Royama para identificar o papel do sistema endógeno (competição intraespecífica) e fatores exógenos (chuva anual, dias com temperaturas mínimas e máximas, NDVI, e SOI) na regulação populacional. O fogo afetou negativamente a abundância das populações. Ademais, uma estrutura de feedback de primeira ordem regulou as dinâmicas populacionais, indicando um importante papel da competição intraespecífica por recursos em ambas espécies. O sistema endógeno foi o principal regulador da dinâmica de *R. mastacalis*, enquanto a população de *G. agilis* foi governada pelo efeito vertical do NDVI mínimo e do sistema endógeno. Modelos incluindo dias com temperaturas mínimas e máximas, chuva e SOI (instantâneo e com atraso) foram pior ranqueados que os modelos endógenos, entretanto observamos que para *R. mastacalis* o modelo incluindo a estrutura endógena e o efeito vertical da temperatura mínima com um ano de atraso capturou efetivamente a dinâmica observada. Incêndios extensivos e severos tiveram um efeito duradouro e negativo nas populações estudadas, possivelmente devido à redução na capacidade de suporte ambiental. Apesar das semelhanças ecológicas das espécies estudadas (hábito, dieta), as populações foram reguladas por diferentes pressões ecológicas, e o tempo de resposta e recuperação a tais pressões foi variável, possivelmente devido às distintas histórias de vida. Enfatizamos a necessidade de considerar as histórias de vida das espécies e os atributos ambientais para entender as respostas dos pequenos mamíferos a eventos extremos, também reforçamos a importância de avaliar efeitos sinérgicos de fatores endógenos e exógenos em estudos futuros de dinâmicas populacionais.

Palavras-chave: Cerrado, fogo, competição intraespecífica, temperatura, Normalized Difference Vegetation Index, Southern Oscillation Index, *Gracilinanus agilis, Rhipidomys mastacalis*

Abstract

Considering the current threat of human-induced impacts on ecosystems, understanding the drivers of natural population dynamics is an urgent issue. However, until recently, few studies have used long-term data to assess the factors driving small mammal abundance in Neotropical savannas. We used a 9-year time series, based on monthly captures, to understand the population dynamics of two arboreal small mammals inhabiting the Brazilian Cerrado: the semelparous marsupial *Gracilinanus agilis* and the iteroparous rodent *Rhipidomys mastacalis*, the most abundant species at Panga Ecological Station (Uberlândia/MG). We tested the impact of two fires that occurred in 2014 and 2017 on the abundance of both populations. Moreover, we used Royama's framework to identify the role of the endogenous system (intraspecific competition) and exogenous factors (annual rainfall, days with minimum and maximum temperatures, annual minimum Normalized Difference Vegetation Index, and Southern Oscillation Index) in population regulation. Fire negatively affected the abundance of both populations. Moreover, a first-order feedback structure regulated population dynamics, indicating an important role of intraspecific competition for resources in both species. The endogenous system seems to be the main driver of *R. mastacalis* dynamics, while the *G. agilis* population seems to be governed by the vertical effects of annual minimum NDVI and the endogenous system. Models including number of days with minimum temperatures, maximum temperatures, rainfall, and SOI (current and lagged) were worse-ranked than endogenous models, although for *R. mastacalis* we observed that the model including the vertical effect of one-year lagged minimum temperatures with the endogenous structure captured the observed dynamics effectively. Extensive and severe fires had a lasting, negative effect on the studied populations, probably by reducing the carrying capacity of the environment. Despite ecological similarities shared by both species (diet, habit), their populations were regulated by different ecological pressures, and their response and recovery time to these pressures also varied, probably due to their distinct life-histories. Hence, we emphasize the need to consider species life-histories and environmental attributes to understand small mammals responses to extreme events, and reinforce the importance to evaluate the combined effects of endogenous and exogenous variables on future population dynamics studies.

Keywords: Brazilian Cerrado, fire, intraspecific competition, temperature, Normalized Difference Vegetation Index, Southern Oscillation Index, *Gracilinanus agilis, Rhipidomys mastacalis*

Introduction

Population changes are the result of basic demographic processes, such as survival, recruitment, immigration and emigration, which are affected by the endogenous and exogenous factors. The endogenous structure regulate species abundance through feedback mechanisms, leading to direct (first-order) and delayed (second or higher order) density-dependence (Berryman, 1999; Münster-Swendsen and Berryman, 2005), whereas exogenous factors include climate, weather and disturbances that affect populations directly or indirectly as density-independent effects. Determining the relative importance of endogenous and exogenous factors on seasonal and interannual population changes remains a central question in demographic studies (Betini et al., 2013). Moreover, considering the current threat of human impacts on ecosystems, describing the key drivers of natural population dynamics is an urgent issue, enabling to ensure population and species persistence (Stenseth et al., 2002).

Small mammals have been the subject of several population dynamics studies due to their considerable fluctuations in abundance, which could lead to irregular dynamics or multinannual periodic population cycles (Andreassen et al., 2021), and their important negative and positive impacts on economy and health through crop production and disease transmission (Dickman, 1999; Keesing et al., 2009; Lessa and Costa, 2010; Camargo et al., 2017). In this sense, in the last decades Royama´s framework (1992) has been used to understand how exogenous factors act independently or in conjunction with population density as drivers of small mammals demographic fluctuations (Ferreira et al., 2016; Mason-Romo et al., 2018). In the former, these factors act as vertical effects, by changing reproduction and survival, while in the latter, these factors may act as lateral or nonlinear perturbation effects, by altering the carrying capacity of the environment and the strength of density dependence (Royama, 1992).

Population dynamics of temperate small mammals have been extensively discussed (see review in Andreassen et al., 2021), while a far less number of studies assessed the factors driving small mammal abundance and rodent outbreaks in tropical regions (see Magnusson et al., 2010, 2020; Owen et al., 2013). In highly seasonal environments, such as tropical savannas, research indicates that seasonal and interannual small mammal fluctuations are mainly triggered by rainfall and the subsequent pulses in primary productivity (Jacksic and Lima, 2003; Ghizoni et al., 2005; Letnic and Dickman, 2006; Chidodo et al., 2019). Among small mammals, intense local rainfall usually increases the extent of breeding (Madsen and Shine, 1999) and reduces mortality rates through changes in resource availability and alterations in the strength of density-dependent competition for food and shelter (Lima et al., 2001, 2006). However, several studies suggest that large-scale climate indices (Southern Oscillation Index – SOI – and North Atlantic Oscillation – NAO) may explain population changes more accurately than local weather variables (Stenseth et al., 2003; Hallett et al., 2004), because these weather packages may capture additional environmental variables (e.g. temperature), apart from rainfall. Indeed, the role of large-scale climate indices on small mammal populations have been extensively demonstrated in several ecosystems (see Letnic and Dickman, 2006; Magnusson et al., 2010; Previtali et al., 2010).

Among tropical savannas, models of climate change predict an increase in the frequency and intensity of fires, due to drier and warmer conditions (Legge et al., 2008; Hofmann et al., 2021). Although fire is a major and frequent form of disturbance affecting community structure and population dynamics in these ecosystems (e.g. Briani et al., 2004; Griffiths and Brook, 2014; Lawes et al., 2015), not all plant formations in this environment are well adapted to fire (Hoffmann and Solbrig, 2003). For instance, forest formations tend to burn less frequently and recover more slowly (Miranda et al., 2002). Moreover, the magnitude of fire effects on small mammals vary according to the intensity and extension of this disturbance (Legge et al., 2008; Lindenmayer et al., 2013). Usually, extreme fire events cause sharp declines in population abundance of small mammals in seasonal ecosystems, through the direct effect of fire on species survival or through indirect changes in habitat structure, resource availability and productivity following disturbance (Lindenmayer et al., 2013; Griffiths and Brook, 2014). In this way, extensive fires may reduce biodiversity, instead of promoting it as expected for natural and/or controlled fires (Yates et al., 2008; Lawes et al., 2015).

The Cerrado is the largest tropical savanna, and is considered a biodiversity hotspot due to high levels of biodiversity, endemism and habitat loss (Myers et al., 2000; Klink and Machado, 2005). In fact, intense anthropogenic pressure in this biome, mainly as a result of the transformation of natural areas into monocultures and pastures has reduced its native cover to less than 50% of the original habitat (Silva et al., 2006). To date, only a few long-term studies investigated the drivers of small mammal population dynamics in the Cerrado (see Magnusson et al., 2010; Rocha et al., 2017). As expected, most studies demonstrate that rainfall and SOI are positively associated with species abundance, because these variables may indirectly predict food availability and primary productivity (Ghizoni et al., 2005; Magnusson et al., 2010; Rocha et al., 2017). However, the effects of these variables in population changes in the Cerrado seem to vary according to small mammal life-history (see Puida and Paglia, 2015). Regarding fire, short-term studies indicate that the decline in arboreal/scansorial species and the invasion of open-habitat specialists following fire events are mainly caused by changes in habitat structure (Briani et al., 2004; Mendonça et al., 2015). Moreover, these studies suggest that recovery of populations to pre-fire patterns depends on fire severity (see Mendonça et al., 2015).

Considering the impacts of land-use changes on habitat productivity and the effect of global climate disruption leading to more frequent and intense drought periods and fire events in the Cerrado (Hofmann et al., 2021), it seems urgent to understand the key drivers of small mammal population changes in this biome, especially for the scansorial and arboreal species, which are probably more vulnerable to these changes in habitat quality. The marsupial *Gracilinanus agilis* and the rodent *Rhipidomys mastacalis* share nocturnal and arboreal/scansorial habits along with a diet composed of insects and plant material, including fruits (Pinotti et al., 2011; Ribeiro et al., 2018). However, they differ in body mass and reproductive strategy. *Gracilinanus agilis* (20-45 g) presents synchronized breeding and a semelparous life-history, with males presenting post-mating die-off and females disappearing from the population after weaning their young, thus characterizing a lack of overlap in generations (Lopes and Leiner, 2015). On the other hand, *Rhipidomys mastacalis* (35-170 g) is iteroparous, with females presenting continuous reproduction throughout the year (Oliveira et al., 2007). Hence, based on Royama´s framework, we used a 9-year time series to investigate the role of endogenous and exogenous factors on the population regulation of these two species from forested habitats in the Cerrado. The following hypothesis were tested: 1) population abundance of both species are negatively affected by fire, through a shift in the point of equilibrium of the populations following fire events; 2) population dynamics of both species are regulated by population density in the previous year (first-order feedback mechanism); 3) rainfall and SOI positively affect both species dynamics, in the same year and with a one-year time lag; 4) reduced productivity and extreme temperatures (both maximum and minimum) negatively affect species dynamics, in the same year and with a one year time lag. Additionally, we tested if the exogenous factors tested operate, in the same year or with a one-year time lag, as 1) vertical perturbation effects, acting on reproduction and survival, 2) lateral perturbation effects, altering the carrying capacity of the environment, or 3) nonlinear perturbation effects, altering the strength of density dependence.

Materials and Methods

Study site

We carried out the study at Panga Ecological Station (PES, 19°10' S, 48°23' W), the largest preserved Cerrado remnant (404 ha) situated in the Triângulo Mineiro region (municipality of Uberlândia/Minas Gerais – Brazil). PES contains several vegetation physiognomies, including open and closed plant formations, such as dense and typical cerrado, grasslands, gallery forests and palm swamps (Gonçalves et al., 2021). We conducted trapping of small mammals in a closed plant formation, classified as "cerrado denso" by Gonçalves et al. (2021), and characterized by abundant shrubs and trees reaching 4-10 meters high. During the study, average annual rainfall was about 1300 mm^3, while mean minimum and maximum annual temperature were 18.65 ± 2 °C (mean ± SD) and 29.9 ± 2 °C, respectively. The region is located in the humid subtropical zone and has two well-defined seasons: a dry and cooler winter (April to September), characterized by low temperatures (17.5 ± 2 ºC/month; minimum mean ± SD) and reduced rainfall (34.70 ± 32 mm/month), and a rainy and warmer summer (October to March), characterized by higher temperatures (29.9 ± 2 ºC/month; maximum mean ± SD) and abundant rainfall (205.65 ± 76 mm/month).

Data collection

We trapped small mammals monthly, in trapping sessions lasting four consecutive nights, between September 2010 and August 2019. Initially, we set a trapping grid of 0.96 ha, composed of five parallel transects of 120 meters, spaced 20 meters apart. At each transect, we set seven capture stations, also equidistant 20 meters, totaling 70 traps. From July 2012 to the end of the study, we added one capture station to each transect following the same distancing pattern (20 meters), thus increasing the trapping grid to 1.12 ha and totaling 80 traps. At each trapping station, we placed two Sherman traps (37.5x10x12 cm; 23.5x8x9 cm, H. B. Sherman Trap Co., Tallahassee, Florida), one on the ground and one on the understory (fixed to a tree between 1.5-2 meters high). To attract small mammals, we used a mixture of banana, oatmeal, peanut butter and bacon as bait. We checked and baited the traps daily, and every captured specimen was marked with numbered ear-tags (Zootech). SISBIO/ICMBio authorized the capture and handling of the animals (License Number: 22629-1 to Natália O. Leiner), and we followed the ethical principles on animal research as regulations of National Advice of Control and Animal Experimentation (CONCEA/Brazil). Moreover, the Ethics Committee on Use of Animals of the Federal

University of Uberlândia, Brazil (permit number: 152/13 and 041/19) approved the protocol of trapping and handling of small mammals.

Climate data

We obtained local climatic data (monthly rainfall, minimum and maximum temperatures between 2009 and 2019) from the climatic station of the Instituto Nacional de Meteorologia (Uberlândia/MG), situated approximately 30 km away from the study site. From these data we obtained the cumulative annual rainfall of each year. We also calculated, for each year, the number of days with minimum temperatures below 14.15 ºC, which is 2.5 standard deviations (following Dhawan et al., 2018) below the mean minimum temperature (18.65 °C) during the entire study period (2009-2019). Finally, we also calculated for each year the number of days with maximum temperatures above 34.44 ºC, which is 2.5 standard deviations above the mean maximum temperature (29.9 °C) during the entire study period. We used the Southern Oscillation Index (SOI), an index that compares the differences in climatic conditions between two areas of the Pacific Ocean: Darwin (Australia) and Taiti (Allan et al., 1996). As a large-scale climatic index, SOI allows the identification of years with La Niña (consistently positive values) and El Niño events (consistently negative values), as well as years with no occurrence of such events (neutral years). We used as a predictor variable the average annual SOI, obtained from the website of Queensland Department of Primary Industries, Australia (https://www.longpaddock.qld.gov.au).

Productivity/Plant cover and Fire

Normalized Difference Vegetation Index (NDVI) is an index that represents the difference between energy absorbed and reflected by the vegetation, serving as an indicator of photosynthetic activity. NDVI is directly related to habitat primary productivity (Pettorelli et al., 2005) and has been used as a proxy of food availability and vegetation cover for small mammals (Andreo et al., 2009; Puida and Paglia, 2015; Chidodo et al., 2019). Moreover, this index may act as a predictor of habitat heterogeneity and complexity (Cabacinha and Castro, 2009), which in turn modifies predator-prey interactions and species survival, through its role in providing protection against predators (Andreo et al., 2009; Smith et al., 2019). In our study, we used NDVI as a proxy for food availability and as an indicator of plant cover and habitat quality. We obtained monthly NDVI values using data from the MODIS/Terra sensor (MOD13Q1), and used annual minimum NDVI as a predictor variable of population abundance.

Within the last two decades (2000-2020), three events of fire occurred at the study site (one in September 2006, and the others in October 2014 and September 2017). Prescribed, periodic fires are suppressed at the study site, but human activities may trigger severe and extensive fires (Vasconcelos et al., 2009), such as the two last fire events at PES, which burned about 50% of the Ecological station. These events associated to the continuous monitoring of small mammal populations since 2010 allowed the evaluation of fire effects on the population dynamics of *G. agilis* and *R. mastacalis*, despite the limitations posed by lack of replication of burned remnants and unburned controls, which are common in studies including unpredicted disturbances (Mendonça et al., 2015). Hence, we were able to compare pre- and post-fire population dynamics, following a before-after approach.

Data analysis

We defined years ecologically, from September through August, since in *G. agilis* juveniles are first captured between September and October and adult males increase their post-mating mortality at the same period. Moreover, by defining years this way, we were able to include the instantaneous effect of fire on the population growth rate of both species. We estimated the population size of *G. agilis* and *R. mastacalis* as the minimum number of individuals known alive (MNKA – Krebs, 1966) from 2010 to 2019. MNKA may be as robust as other estimators (Banks-Leite et al., 2014), especially in populations with low densities and recaptures as observed in the studied species. We divided the population size of each species by the size of the capture grid in each year (0.96 or 1.12 ha), thus obtaining a rough estimate of population density in each year, which was log-transformed ($\ln N_t$). To test for a possible trend in the time series, we used Kendall's rank correlation coefficient (τ – Legendre and Legendre, 2012).

We used time series diagnostic tools (Berryman, 1999) to evaluate the processes regulating the time series of *G. agilis* and *R. mastacalis*. The autocorrelation function (ACF) investigates the periodicity of time series oscillations, through the estimates of the correlation coefficient between pairs of population sizes ($\ln N_{t-1}$) separated by different time lags. On the other hand, the partial rate autocorrelation function (PRCF) detects the dimension and order of the feedback system in the time series. The PRCF is based on the partial correlation coefficients between the population growth rate ($R_t = N_{t+1}/N_t$) and log-transformed population sizes with different time lags (Berryman and Turchin, 2001). The significance of ACF and PRCF was assessed using Bartlett´s criterion (Berryman and Turchin, 2001).

After detecting the order and dimension of the population dynamic system, we used a nonlinear model derived from Ricker´s (1954) logistic equation as a starting point to model the *R-function*, in order to examine the causes of population fluctuations (Royama, 1992; Berryman, 1999). Assuming that population dynamics of each species was regulated by endogenous feedback mechanisms, we fitted a simple nonlinear logistic model (model 1), as proposed by Royama (1992) and following Ricker´s (1954) logistic equation (equation 1), to describe the role of the intraspecific competition for resources (endogenous system) on population regulation

$$\mathrm{R_t} = \mathrm{R_m} - \exp^{(a*\ln \mathrm{N_{t-1}}+\mathrm{C})} \qquad (1)$$

where R_m is a constant, indicating maximum per capita population growth rate; $\ln N_{t-1}$ is the log-transformed population density with one year time lag (indicated by PRCF – see Results below); *a* is the effect of interference of each individual as density increases and C is a constant indicating resource depletion and competition between individuals.

To analyze the effect of fire on population densities of each species, we verified differences in the *R-function* (endogenous model) before and after fire. Whenever differences were detected, we corrected these effects by calculating the difference between the average $\ln N_t$ before and after the disturbance. To remove the effect of fire on population density *G. agilis* and *R. mastacalis*, we added these differences between average $\ln N_t$ to the population density of each species after fire events. This correction leads to a new *R-function*, which should be used in the following analyses, as suggested by Rodríguez-Caro et al. (2016). This approach for evaluating fire effects yields the same results as including fire as a dummy variable into the models.

From this basic equation, including only endogenous factors, we added extra-terms to include the effect of each exogenous factor as direct (vertical) or indirect perturbations, following Royama´s framework (1992). Vertical perturbations directly affect survival and reproduction of individuals, thus causing changes in population growth rate independent of population density. This model is expressed by equation 2

$$\mathrm{R_t} = \mathrm{R_m} - \exp^{(a*\ln \mathrm{N_{t-1}}+\mathrm{C})+d*\,\mathrm{x_1}} \qquad (2)$$

where *d* is a simple linear function, which may be positive or negative, and x_1 represents the exogenous factor under evaluation.

We added extra-terms to account for additive (lateral) and non-additive (nonlinear) exogenous perturbations affecting population changes. In the lateral perturbation (equation 3), the exogenous factor (x_2) affects a limiting resource; hence, the *R-function* shifts horizontally following oscillations in the exogenous factors. In this case, perturbations influence the carrying capacity of the environment, thus shifting the point of equilibrium of the population, but not the maximum per capita rate of population growth. Finally, nonlinear perturbations (equation 4) affect the strength of intraspecific competition, by changing the shape of the *R-function*. In this case, the exogenous factor (x_3) acts on the maximum per capita growth rate of the population through the endogenous feedback mechanism of the system. Models expressing lateral (equation 3) and nonlinear (equation 4) perturbations are expressed below:

$$\mathrm{R_t} = \mathrm{R_m} - \exp^{((a * \ln \mathrm{N_{t-1}}) + (\mathrm{C} + d * \mathrm{x_2}))} \qquad (3)$$

$$\mathrm{R_t} = \mathrm{R_m} - \exp^{((a + d * \mathrm{x_3}) * \ln \mathrm{N_{t-1}} + \mathrm{C})} \qquad (4)$$

We fitted the endogenous and exogenous models using the nls library within the package “stats” in R environment (R Core Team, 2019). We modeled the effect of each exogenous factor separately. Each model had only one predictor variable modeled as one perturbation effect, which could be SOI, rainfall, minimum temperature, maximum temperature or minimum NDVI (surrogate for productivity/vegetation cover) modeled as vertical, lateral or nonlinear perturbation, thus totaling 30 different models with instantaneous or one-year lagged parameters. We compared models using Akaike's Information Criterion corrected for small samples (AICc), ΔAICc and Akaike weights (w_i), following Burnham and Anderson (2002). Moreover, we calculated the adjusted R^2 using the package “MuMIn” in R environment (R Core Team, 2019), as it indicates the coefficient of determination of each model and hence the proportion of variance explained by them. We used the endogenous model as a null model to compare the explanatory power of the exogenous variables under test. Finally, we selected models with lowest AICc (difference lower than 2 from other models) to draw inferences, and used Akaike weights to quantify the proportion of evidence supporting the model.

Results

We captured 381 *Gracilinanus agilis* (253 males and 128 females) and 109 *Rhipidomys mastacalis* (61 males and 48 females) individuals during the entire study period. Both temporal series were stationary according to Kendall's test (*G. agilis*: $\tau = -0.29$, $p = 0.29$; *R. mastacalis*: $\tau = -0.40$, $p = 0.14$). We were unable to detect the periodicity of oscillations of either populations (Supplementary Data SD1) through the autocorrelation function (ACF), probably due to small sample size ($N = 9$) as discussed by Royama (1992).

Annual population density averaged 48 (*SD*= ± 10) individuals/ha for *G. agilis* and 13 (*SD*= ± 7) individuals/ha for *R. mastacalis* during the entire study period (2010 to 2019). We observed a sudden decline in both species following the first fire event that occurred in 2014/2015 (Fig. 1A). Actually, although we failed to detect differences in the point of equilibrium (the point where population growth rate is zero) of both populations when comparing post-fire periods, population equilibrium points of both species were lower in the years after the fire events (Figs. 1C and 1E), thus supporting hypothesis 1 that predicted a negative effect of fire on species population abundances. Hence, we applied a correction to remove fire effects on population changes. This correction was performed by adding the difference between average $\ln N_t$ before and after fire to the annual population density of each species after each fire event, as presented in Figure 1B.

After applying this correction, we obtained new *R-functions*, which confirmed that population dynamics of both species are regulated by a first-order negative feedback, as indicated by PRCF results (*G. agilis*: PRCF(1)= -0.835; Bartlett´s criterion= ± 0.666; *R. mastacalis*: PRCF(1)= -0.789; Bartlett´s criterion = ± 0.666 - Supplementary Data SD2). Additionally, the corrected *R-function* of both species (Figs. 1D and 1F) indicated a linear relationship between annual population density with one-year time lag ($\ln N_{t-1}$) and population growth rate (R_t). Such results indicate an important role of the first-order feedback mechanism in population dynamics of the studied species, as predicted by hypothesis 2. In the following analyses, we utilized corrected time series and their respective *R-functions*.

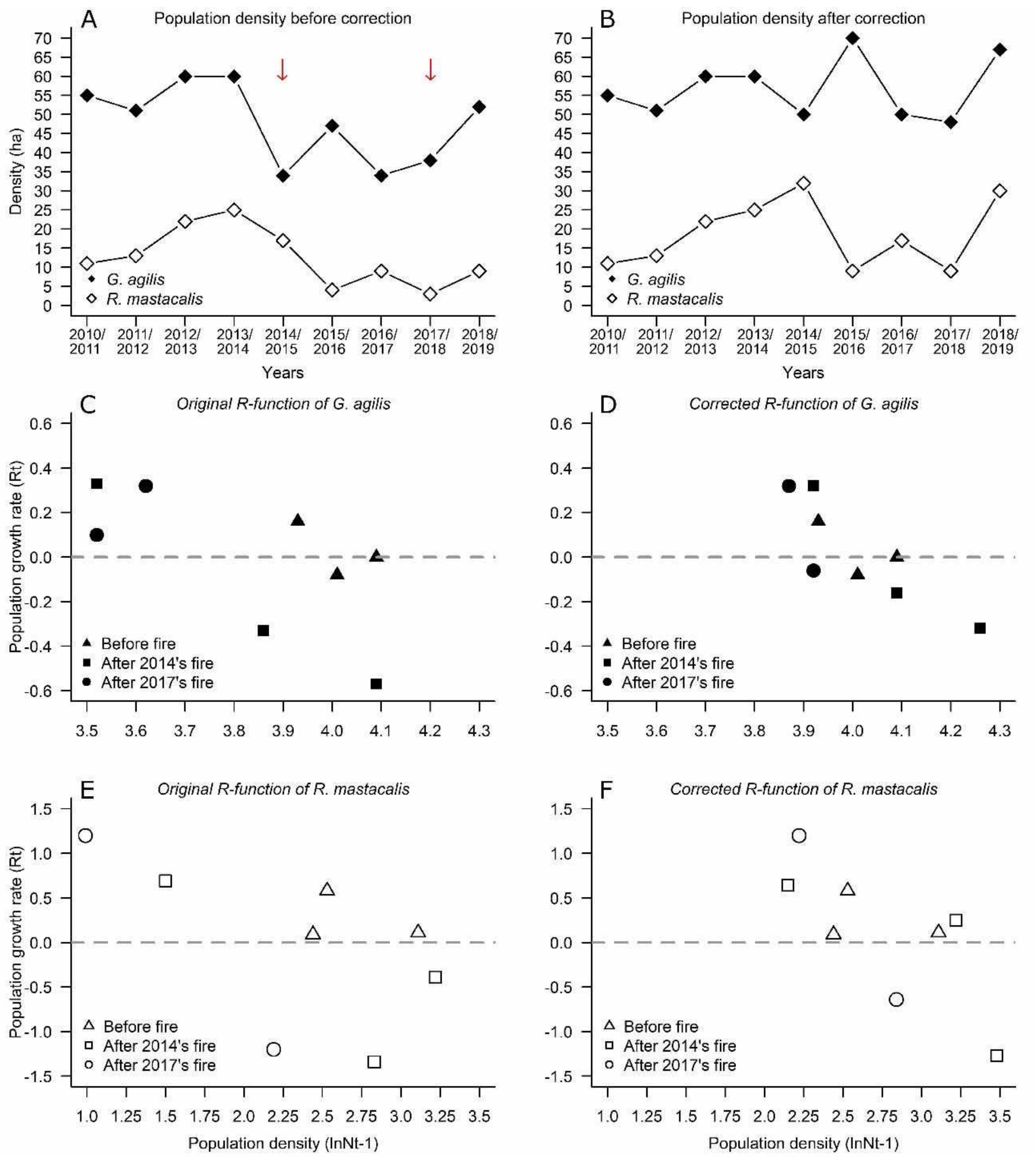

Figure 1. Annual population fluctuation of *Gracilinanus agilis* and *Rhipidomys mastacalis* before (A) and after correction for the fire effects (B); Relationship between population growth rate (R_t) and annual population density ($\ln N_{t-1}$) of *Gracilinanus agilis* before (C) and after correction (D); Relationship between population growth rate (Rt) and annual population density ($\ln N_{t-1}$) of *Rhipidomys mastacalis* before (E) and after correction (F). Red arrows in (A) indicate years with fire occurrence.

Contrary to hypothesis 3, which predicted a positive effect of rainfall and SOI on species population dynamics (in the same and in the previous year), models including SOI and rainfall were worse-ranked. On the other hand, we found mixed support for hypothesis 4, which predicted negative, direct effects of minimum NDVI and extreme temperatures on population dynamics of both species. For *G. agilis*, two models were considered equally parsimonious and selected as candidates to explain population dynamics of this species (see Fig. 2A). The first model included only the endogenous effect, while the second model included the vertical effects of minimum NDVI and the endogenous effect (first-order negative feedback) governing population growth rate of *G. agilis*. Using the endogenous model as a null model, as discussed in the methods, we point out that the model including minimum NDVI was the only model capable of improving the AICc of the endogenous model (see Table 1). Based on both selected models and as indicated by Figure 3A, population growth rate of *G. agilis* was negative if population density was higher in the previous year; however this decline in population growth rate was steeper if NDVI values were lower. Hence, the magnitude of the effect of intraspecific competition on *G. agilis* population regulation was shaped by productivity/plant cover.

Table 1. Result of the selection of the main models predicting the population growth rate (R_t) of *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2019) at Panga Ecological Station, Uberlândia, Brazil. Endogenous model used for comparison in bold.

ID	Models	Parameters estimates				AICc	ΔAICc	w_i	Adjusted R²
		a	R_m	C	*d*				
Gracilinanus agilis									
G1	NDVI vertical	1.45	0.32	-5.82	1.33	1.62	0.00	0.35	0.70
G0	**Endogenous model**	**3.69**	**0.32**	**-16.09**	**-**	**1.98**	**0.36**	**0.29**	**-**
G2	NDVI lateral	4.58	0.32	-17.21	-4.73	5.03	3.41	0.06	0.54
G3	NDVI nonlinear	5.22	0.32	-19.79	-1.17	5.13	3.51	0.06	0.54
G4	MAX vertical $_{t-1}$	4.00	0.32	-17.01	0.01	6.48	4.87	0.03	0.45
G5	RAIN vertical	3.35	0.32	-14.77	0.08	7.73	6.11	0.02	0.36
Rhipidomys mastacalis									
R0	**Endogenous model**	**1.11**	**1.20**	**-3.10**	**-**	**22.57**	**0.00**	**0.55**	**-**
R1	MIN vertical $_{t-1}$	5.37	1.20	-17.86	-0.04	25.40	2.83	0.13	0.56
R2	SOI vertical	1.76	1.20	-4.97	-0.11	26.34	3.77	0.08	0.50
R3	MIN nonlinear	0.91	1.20	-2.86	0.01	29.62	7.06	0.02	0.25
R4	RAIN vertical $_{t-1}$	1.26	1.20	-3.56	0.19	29.84	7.28	0.01	0.23
R5	MIN lateral	1.08	1.20	-3.38	0.02	29.90	7.33	0.01	0.22

ID= model identification; AICc= Akaike's Information Criterion for small samples; ΔAICc= $AICc_i$ - minimum AICc; w_i = Akaike weights; R_m= maximum population growth rate; Values of the parameters *a*, C and *d* were estimated by nonlinear regression analysis. The complete table is located in Supplementary Data SD3 and SD4.

For *R. mastacalis*, the top-ranked model explaining population growth rate of this species included only the effect of the first-order negative feedback. Moreover, using this as a null model, we observed that neither model improved the AICc of the endogenous model or presented ΔAICc ≤ 2 (Table 1). However, the second-ranked model (see Table

1; model R1), which includes the endogenous effect and the vertical effect of the number of days with extreme cold temperatures with one year time lag, was able to accurately capture the observed population dynamics of *R. mastacalis* (Fig. 2B). According to this exogenous model, the role of intraspecific competition in population regulation increases when *R. mastacalis* coped with colder temperatures in the previous year (see Table 1; Figure 3B), indicating the delayed response of this species to both endogenous and exogenous factors.

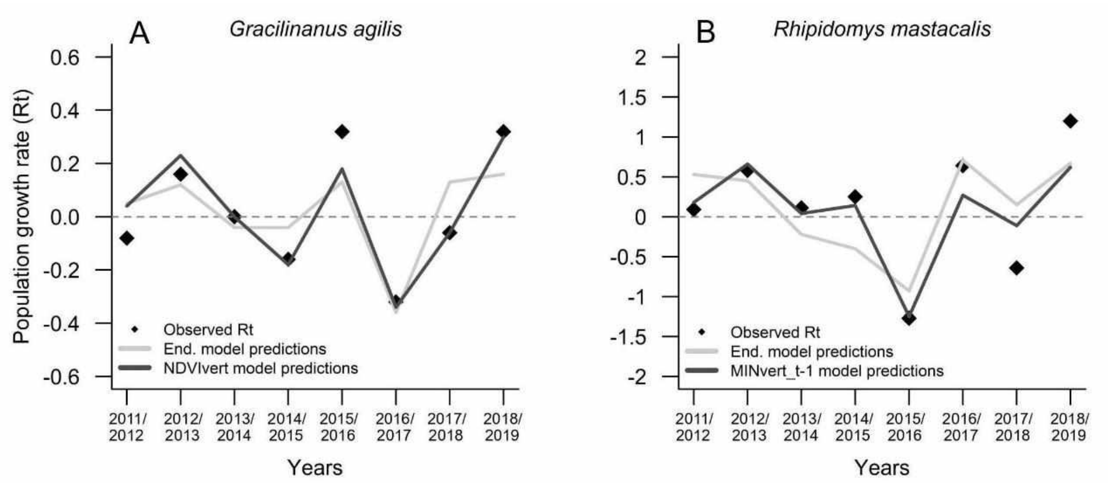

Figure 2. (A) Comparison between the observed population growth rate (R_t), the endogenous model predictions and the model with vertical NDVI effects for *Gracilinanus agilis*; (B) Comparison between the observed population growth rate (R_t), the endogenous model predictions and the model with vertical effects of the number of days with minimum temperatures below 14.15 ºC with one year lag for *Rhipidomys mastacalis*.

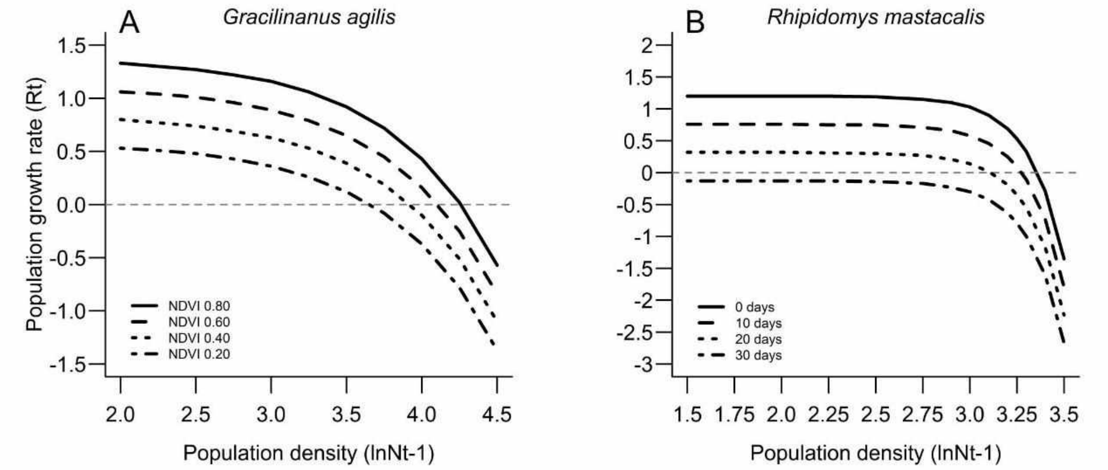

Figure 3. (A) Relationship between the logarithmic population growth rate (R_t), population density with one year lag ($\ln N_{t-1}$) and the vertical effect of NDVI, according to the model G1 for *Gracilinanus agilis*; (B) Relationship between the logarithmic population growth rate (R_t), population density with one year lag ($\ln N_{t-1}$) and number of days with minimum temperatures below 14.15 ºC with one year lag, according to the model with vertical effects (R1) for *Rhipidomys mastacalis*.

Discussion

Our results indicate that population dynamics of *Gracilinanus agilis* and *Rhipidomys mastacalis* are governed by a combination of endogenous and exogenous factors, which interact leading to rapid oscillations. As expected, both species were regulated by a first-order negative feedback and were negatively influenced by intense fire events, which reduced their population equilibrium points; thus supporting hypothesis 1 and 2. Contrary to hypothesis 3, we failed to find any effect of local rainfall or large-scale climatic indexes on population dynamics of both species. Finally, we find mixed support for the role of productivity/plant cover (NDVI) and extreme temperatures on fluctuations of the studied species, as predicted by hypothesis 4. In *G. agilis*, productivity/plant cover (NDVI) operated as a vertical perturbation effect, regulating the marsupial population, although this variable was not selected in *R. mastacalis* models. On the other hand, the observed *R. mastacalis* population dynamics were effectively captured by a model with lagged, vertical effects of the number of days with extreme minimum temperatures, although density-dependence was the major force determining this rodent local fluctuations.

Population growth rates of both species were strongly determined by population density in the previous year, indicating the occurrence of a first-order negative feedback regulating *G. agilis* and *R. mastacalis* populations. Indeed, several studies reported the importance of first-order feedback as an endogenous mechanism governing the population dynamics of small mammal populations in tropical and temperate environments (Lima et al., 2001; Lima et al., 2006; Kajin et al., 2008; Ferreira et al., 2015). The main causes involved in the first-order feedback are 1) intraspecific competition for resources (e.g. food, space or mating partners), leading to territoriality and aggressiveness between individuals, 2) action of generalist predators and intraguild competitors and 3) emergence of diseases (Berryman, 1999; Lima et al., 2006). However, the role of each of these factors may depend on species life-history, their social and trophic interactions in the environment (Fowler, 1981; Herrando-Pérez et al., 2012).

Intraspecific competition seems to be the main regulator of the *G. agilis* population, since individuals may compete for food, space and mating partners due to a semelparous life-history and a promiscuous/polygynous mating system (Lopes and Leiner, 2015; Shibuya et al., 2018). A seasonal and synchronized breeding period in *G. agilis* (Lopes and Leiner, 2015) leads to competition between males for access to reproductive females, which may be intensified by a male-biased sex ratio in this species (Andreazzi et al., 2011), and evidenced by signs of aggression in males during the breeding season (Lopes and Leiner, 2015). Individuals may also compete for food and space, since population density reaches a peak during the dry season (Lopes and Leiner, 2015), which coincides with the period of food scarcity in the Cerrado. In fact, the extremely low overlap between female home ranges indicates that females may defend and maintain territories (Shibuya et al., 2018) in order to get exclusive access to food and/or to safe and restricted shelters for their offspring (Ostfeld, 1990; Wolff, 1993), thus increasing their reproductive success. In *R. mastacalis*, intraspecific competition is less intense than in *G. agilis* (check C values in the endogenous models in Table 1), although it certainly plays a role in this rodent population dynamics. Competition may be less intense due to the continuous reproduction throughout the year in this species (Oliveira et al., 2007) and a diet composed mainly of plant material (60% of the diet - Ribeiro et al., 2018). However, *R. mastacalis* individuals may face stronger competition during the period of fruit scarcity (e.g. dry season), as suggested by observed decrease in the number of reproductive females and reduced body condition of *R. macrurus* individuals in this period (Burghausen, 2020). Hence, we suggest that the intraspecific competition in *R. mastacalis* occurs mainly for access to fruits during the dry season.

Because both studied species feed on insects and plant material, including fruits, and present a scansorial habit (Pinotti et al., 2011; Ribeiro et al., 2018), they may engage in interference competition. Previous studies have already discussed interference competition between dominant and subordinate small mammal species with similar ecological traits (Dickman, 1991; see Moura et al., 2009); however further studies are needed to test if and how the density of each species affects the population dynamics of the other. In addition, generalist predation and parasitism could also modulate the effect of density on both populations (Berryman, 1999). At the study site, four species of Strigidae owls (Marçal-Júnior et al., 2009) and several mammalian carnivores (Bruna et al., 2010; Luma A. Lopes, unpublished results) may act as generalist predators, although their abundance was not estimated by these studies. The medium-sized omnivorous marsupial *Didelphis albiventris* may also feed on the studied species, but their abundance was low at the study grid (personal observation). In fact, although no carcasses were found during this study, we recorded small mammal traps damaged by domestic dogs, which may prey on small and medium-sized mammals (Galetti and Sazima, 2006) and are frequently observed in our study grid. Finally, parasites may play a role in host population regulation, through their effects in host health (Strona et al., 2015; Zangrandi et al., 2019), although future studies are needed in this direction at the study site.

As in other tropical savannas, fire is a recurrent natural disturbance in the Cerrado (Miranda et al., 2002), acting both directly and indirectly in the dynamics of populations and communities (Briani et al., 2004; Griffiths and Brook, 2014). The reduced population densities of *G. agilis* and *R. mastacalis* following the fire events in our study site seem to be explained by the indirect effects of fire, as a previous study indicated that the 2014/2015 fire event at the study site did not exert direct effects on the survival of *G. agilis* (Rossi, 2018). Moreover, we failed to find a collapse of either populations following fires. In this way, our results support the idea that the direct effects of fire on small mammal mortality in the Cerrado are negligible when compared to the indirect effects of fire on population dynamics, caused by reduced availability and quality of food resources (Recher et al., 2009), loss of shelter and increased probability of predation (Banks et al., 2011), and changes in habitat structure (Vieira and Briani, 2013; Mendonça et al., 2015). Indeed, the shift in the equilibrium point of populations of both species after fires strongly suggests that fire negatively affects the population dynamics of both species indirectly, through a reduction in the carrying capacity of the environment. The equilibrium point represents the point where population ceases to grow (population growth rate is zero - Royama, 1992), and in both species this equilibrium was reached at lower densities after fires than before.

Several studies have evaluated the impact of fire on small mammals in tropical savannas, indicating that this disturbance influences these animals in complex ways (Banks et al., 2011; Griffiths and Brook, 2014). Previous studies have already suggested that fire has stronger negative effects on populations of arboreal-scansorial species from forested plant formations than on small mammals typical of open savanna physiognomies (Vieira and Briani, 2013; Mendonça et al., 2015). Our results support this, as predicted by their habitats and the frugivore-insectivore diet. In the Cerrado, fire reduces woody cover, thus altering habitat complexity and decreasing the density and richness of tree species (Miranda et al., 2002; Legge et al., 2008), which are crucial attributes for the survival of arboreal small mammals (Legge et al., 2008). Hence, we believe that fire impact may have driven intraspecific competition for resources in both populations, or even interference competition, since both have similar functional attributes. Moreover, we observed an increase in the abundance of terrestrial, open-habitat specialists after the fire events (*Cerradomys subflavus*, *Necromys lasiurus* and *Calomys tener*), probably as a result of the reduced woody cover that may favor the invasion of small mammal species that are specialists of open Cerrado areas (Briani et al., 2004; Vieira and Briani, 2013) and the relaxed competition with the dominant species at the study site (*G. agilis* and *R. mastacalis*).

In most small mammals, populations suffer a reduction and recovery fire response, which could take 4 to 6 months in fire-adapted small mammal species (e.g. terrestrial, open-habitat specialists - Vieira and Briani, 2013) or less than a year for scansorial small mammals in North America (Tiejte et al., 2008). In our study, neither species was able to return to their pre-fire abundances, demonstrating a slow recovery (at least more than a year), probably due to fire severity and arboreal small mammal sensitivity to fire events. Indeed, a previous study with *G. agilis* and *R. macrurus* in a woodland habitat found similar results, although in this case both species declined to very low numbers, indicating population crashes (Mendonça et al., 2015). This suggests that the negative effects of fire are more severe in woodland than “cerrado denso” habitats, although the population crashes observed in woodland habitats could also be explained by the increased chances of extinction of the small, isolated populations found at that site (Mendonça et al., 2015). Although in our study site both populations declined due to indirect effects of fire, the response and recovery time varied between species. *Gracilinanus agilis* presented an abrupt, immediate response to fire, while *Rhipidomys mastacalis* showed a delayed response, occurring in the following year. Moreover, the population growth rate of *G. agilis* returned to positive values more rapidly than in *R. mastacalis*. Three factors may interact to explain these differences. First, the contrasting life-histories of the species (semelparous marsupial x iteroparous rodent) may determine the velocity of their response to disturbance. Indeed, Sæther et al. (2013) point out that the response to environmental disturbances tends to be rapid in semelparous species, since changes in abundance are caused by demographic variation in the life cycle, while in iteroparous species the response tends to be delayed, as observed in *R. mastacalis*. Second, the higher degree of arboreality and the stronger reliance on fruits of *Rhipidomys* sp. when compared to *G. agilis* (Pinotti et al., 2011; Ribeiro et al., 2018) may increase the time of recovery of the former species after a disturbance event that affects carrying capacity and woody cover. Third, and finally, *R. mastacalis* may take a longer recovery time due to their smaller population size, which leads to oscillations around lower population values and a higher chance of population crash.

Besides fire and population density in the previous year, our results indicate that minimum NDVI may operate as a vertical perturbation effect on *G. agi*lis population dynamics. We believe that the observed effect of NDVI is not via productivity, since we failed to detect lateral or nonlinear perturbation effects of this variable on *G. agilis* population dynamics. Rather, NDVI values could act as a proxy of vegetation structure/plant cover, as this variable may indicate more structurally complex and less disturbed environments (Cabacinha and Castro, 2009). Usually, arboreal small mammals select habitats with dense understory obstruction and vegetation cover (Leiner et al., 2010; Camargo et al., 2018), as increased vegetation connectivity may lead to optimized habitat exploitation (Wells et al., 2004). Moreover, dense vegetation cover may reduce perceived predation risks and provide safe routes for marsupials to escape from predators (Stokes et al., 2004; Nersesian et al., 2012; Lindenmayer et al., 2013). Although microhabitat features (understory obstruction, litter depth, canopy cover, fallen logs) were not measured in our study, lower minimum NDVI values were observed in the months following fire events, which are known to reduce woody cover and form canopy gaps in the Cerrado (Miranda et al., 2002). It is possible that reduced structural habitat complexity, indicated by low minimum NDVI, causes a decline in *G. agilis* population density; however, this result should be viewed and interpreted with caution as this model was equally parsimonious as the null model (endogenous system). Indeed, previous studies found no effects of productivity (via NDVI) on survival and recruitment of *G. agilis* in the Cerrado, suggesting that the extreme life-history of this species are responsible for their fluctuations in demographic parameters (Puida and Paglia, 2015). Actually, in our long-term study, we suggest that the effect of NDVI on population growth rate is modulated by the endogenous feedback system; hence, population of *G. agilis* suffer a steeper decline in abundance when population density in the previous year was higher and individuals have to deal with reduced habitat complexity (lower minimum NDVI values) (see Figure 3A).

Like productivity, temperature is assumed to be a key driver of population dynamics in tropical environments (Deitloff et al., 2010; Magnusson et al., 2010). In the Brazilian Atlantic forest, extreme temperatures (maximum and minimum) act on population growth rate of several marsupial species (Ferreira et al., 2016) and the rodent *Rhipidomys itoan* (Simas, 2017). In our study, intraspecific competition seems to be the main regulator of *R. mastacalis* population, as no exogenous variable was able to improve the endogenous model based on the criteria used. However, we suggest that the model with the negative vertical effect of the number of very cold days in the previous year (ΔAICc 2.83) cannot be completely discarded, based on its strong predictive power to capture the observed dynamics (see Figure 2B). Such a model acts in conjunction with population density and indicates an amplification of intraspecific competition when individuals face extreme minimum temperatures for longer periods in the previous year (see parameter C values of models R0 and R1 in Table 1), causing a decrease in growth rate (Figure 3B). Extreme air temperatures may affect small mammal's life-history parameters directly, through an increase in mortality, or indirectly by reducing survival and limiting reproduction of individuals (Deitloff et al., 2010). At low temperatures, small mammals lose heat quickly, demanding an increase in metabolic rate to maintain body temperature (Ribeiro and Bicudo, 2007). We suggest that *R. mastacalis* faces a shift in their energy balance during periods with extreme low temperatures, and that this shift influences their population dynamics. Indeed, we found a direct effect of low temperatures on *R. mastacalis* survival, as we captured nearly dead individuals of this species during very cold days, and some of these individuals were found dead at the release point, on the day after their first capture. However, the negative impact of low temperatures on *R. mastacalis* density was only verified in the following year, suggesting that direct mortality is not the major determinant of temperature-driven population dynamics. To cope with the costs of thermoregulation, rodents may limit their daily activity patterns (Williams et al., 2014) and reduce investment in reproduction (Sassi et al., 2017). Both strategies enable changes in population dynamics, although the former could increase intraspecific competition for resources, as observed in the selected model for the *R. mastacalis* population. In this way, future studies should test the role of extreme temperatures on survival, reproduction and behavior of *R. mastacalis* individuals at the study site, to disentangle the role of temperature on their population dynamics.

Contrary to our hypothesis, we found no evidence that rainfall and SOI influence the dynamics of the studied populations. Both variables are related to primary productivity, modifying the quality and quantity of available food (Lima et al., 2006; Chidodo et al., 2019). Indeed, several studies in tropical and subtropical zones report that the population dynamics of small mammals are indirectly influenced by rainfall (Lima et al., 2006; Andreo et al., 2009; Mason-Romo et al., 2018) and SOI (Jaksic and Lima, 2003; Murúa et al., 2003, Previtali et al. 2010), mainly through the changes generated in the carrying capacity of the environment and food availability. However, the effects of these variables may vary between species and among habitats. For example, in the Brazilian

Atlantic Forest, populations of marsupials and rodents that use the same habitat and resources respond differently to the action of rainfall and SOI (Kajin et al., 2008; Ferreira et al., 2016; Simas, 2017). On the other hand, Owen (2013) found no relationship between SOI and small mammal richness and diversity in the Cerrado. Although there is generally a correlation between rainfall and SOI (see Stenseth et al., 2003), we found no relationship between the two at the studied site. The use of the annual mean SOI may have masked the relationship between these variables, which on a smaller scale could be detected. Although we failed to detect any correlation between climatic variables, we observed that both were indirectly associated with fire events at the study site. Fire events occurred following the drier years (lowest rainfall values in the time series), and the SOI gradually decreased over the years preceding the fire event. Thus, we suggest that climatic variables may predict years susceptible to fire occurrence in the study area. Actually, Magnusson et al. (2010, 2020) found a complex relationship between rainfall, SOI and fires in the population dynamics of *Necromys lasiurus* in a Cerrado enclave in Amazonia.

This is the first study demonstrating how the interaction between endogenous and exogenous factors regulate population dynamics of arboreal/scansorial small mammals in the Cerrado using a long-term time series. Our results emphasize the importance of intraspecific competition for resources in shaping small mammal population dynamics. However, in our study, the magnitude of competition and its effect on population oscillations varied according to disturbances and fluctuations in climate and habitat quality, pointing to the need to evaluate the combined, synergistic effects of endogenous and exogenous variables on population dynamics of small mammals. Severe and extensive fires were a major form of disturbance, affecting small mammals at the population and community level through a shift in carrying capacity that favored the invasion of terrestrial, open habitat specialists in detriment of arboreal/scansorial species that perform important ecosystem services (seed dispersal, biological control - Lessa and Costa, 2010; Camargo et al., 2017). Despite the ecological similarities shared by the studied species, their populations were regulated by different ecological pressures, indicating a lack of consensus on the main factors determining small mammal population fluctuations in tropical savannas and the need for more long-term studies in this biodiversity hotspot. Furthermore, species response and recovery time to these pressures also varied, probably due to the distinct life histories (semelparous marsupial x iteroparous rodent) that may account for a rapid versus delayed response in *G. agilis* and *R. mastacalis* populations, respectively. Hence, we conclude that species life histories and environmental characteristics determine the response of small mammals to extreme events and reinforce the importance of considering such attributes in population dynamics studies.

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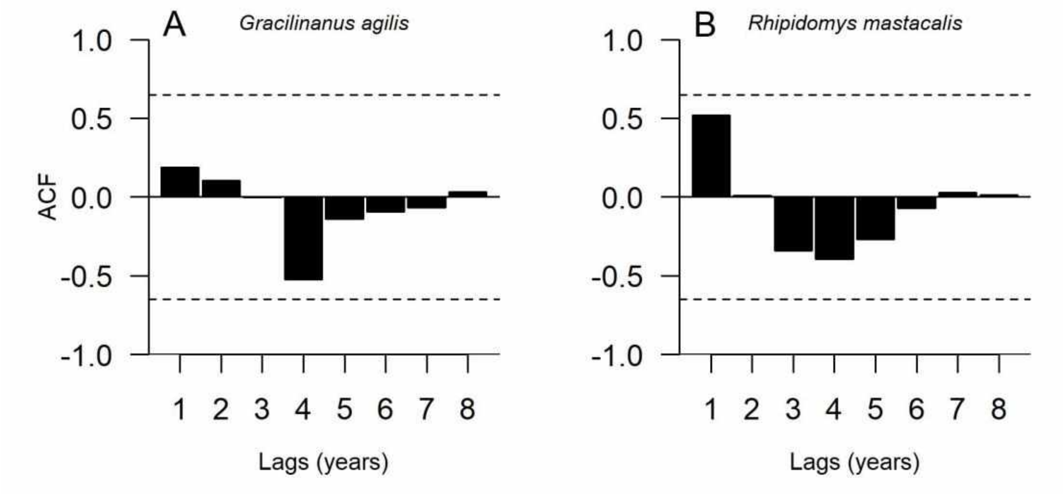
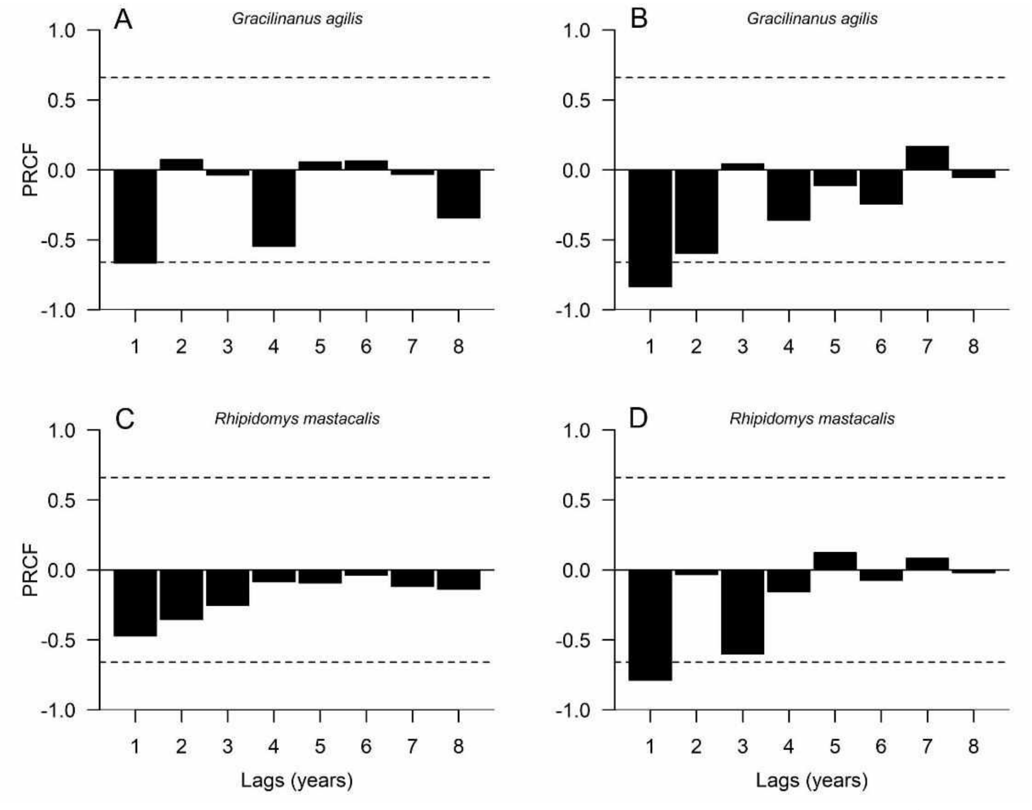
Supporting Information



Supplementary Data 1. Autocorrelation function (ACF) for *Gracilinanus agilis* (A) and *Rhipidomys mastacalis* (B) from 2010 to 2019, in Cerrado in Panga Ecological Station (PES), Uberlândia, Brazil. Dotted lines indicate the level of significance, according to Bartlet's criterion (Berryman and Turchin, 2001).



Supplementary Data 2. Partial rate correlation function (PRCF) for *Gracilinanus agilis* before (A) and after correction for the fire effects (B) and *Rhipidomys mastacalis* before (C) and after correction (D) from 2010 to 2019, in Cerrado in Panga Ecological Station (PES), Uberlândia, Brazil. Dotted lines indicate the level of significance, according to Bartlet's criterion (Berryman and Turchin, 2001).

Supplementary Data 3. Model selection predicting the population growth rate (R_t) of *Gracilinanus agilis* (2010-2019) in the Panga Ecological Station, Uberlândia, Brazil. Endogenous model used for comparison in bold.

ID	Models	Parameters estimates				AICc	ΔAICc	w_i	Adjusted R²
		a	R_m	C	*d*				
G1	NDVI vertical	1.45	0.32	-5.82	1.33	1.62	0.00	0.35	0.70
G0	**Endogenous model**	**3.69**	**0.32**	**-16.09**	**-**	**1.98**	**0.36**	**0.29**	**-**
G2	NDVI lateral	4.58	0.32	-17.21	-4.73	5.03	3.41	0.06	0.54
G3	NDVI nonlinear	5.22	0.32	-19.79	-1.17	5.13	3.51	0.06	0.54
G4	MAX vertical $_{t-1}$	4.00	0.32	-17.01	0.01	6.48	4.87	0.03	0.45
G5	RAIN vertical	3.35	0.32	-14.77	0.08	7.73	6.11	0.02	0.36
G6	MIN vertical	3.07	0.32	-13.17	0.01	7.78	6.16	0.02	0.36
G7	MIN vertical $_{t-1}$	5.44	0.32	-23.93	-0.01	7.95	6.34	0.01	0.34
G8	MIN lateral $_{t-1}$	2.91	0.32	-13.75	0.05	8.17	6.56	0.01	0.32
G9	MAX lateral $_{t-1}$	6.13	0.32	-25.64	-0.03	8.31	6.69	0.01	0.31
G10	NDVI lateral $_{t-1}$	3.08	0.32	-16.24	4.77	8.32	6.71	0.01	0.31
G11	MIN nonlinear $_{t-1}$	2.68	0.32	-12.81	0.01	8.37	6.75	0.01	0.31
G12	MAX nonlinear $_{t-1}$	6.19	0.32	-25.89	-0.01	8.41	6.79	0.01	0.30
G13	NDVI nonlinear $_{t-1}$	2.46	0.32	-13.72	1.17	8.45	6.83	0.01	0.30
G14	SOI vertical $_{t-1}$	4.46	0.32	-19.29	-0.01	8.58	6.96	0.01	0.29
G15	SOI nonlinear $_{t-1}$	5.13	0.32	-21.97	0.01	8.84	7.23	0.01	0.27
G16	SOI lateral $_{t-1}$	5.07	0.32	-21.75	0.03	8.84	7.23	0.01	0.27
G17	MIN lateral	4.74	0.32	-20.05	-0.02	9.37	7.76	0.01	0.22
G18	MIN nonlinear	4.85	0.32	-20.48	-0.01	9.42	7.80	0.01	0.21
G19	MAX vertical	3.00	0.32	-13.09	0.01	9.76	8.14	0.01	0.18
G20	SOI vertical	3.45	0.32	-15.06	-0.01	9.84	8.23	0.01	0.17
G21	RAIN lateral	3.35	0.32	-14.78	-0.15	10.24	8.62	0.00	0.13
G22	RAIN nonlinear	3.36	0.32	-14.81	-0.04	10.33	8.71	0.00	0.12
G23	NDVI vertical $_{t-1}$	5.47	0.32	-23.95	-0.26	10.81	9.20	0.00	0.06
G24	MAX lateral	3.48	0.32	-15.10	-0.02	10.89	9.28	0.00	0.05
G25	MAX nonlinear	3.52	0.32	-15.26	0.00	10.93	9.31	0.00	0.05
G26	SOI lateral	3.48	0.32	-15.20	0.02	11.06	9.44	0.00	0.03
G27	SOI nonlinear	3.49	0.32	-15.28	0.00	11.11	9.49	0.00	0.03
G28	RAIN nonlinear $_{t-1}$	4.05	0.32	-17.55	-0.01	11.16	9.54	0.00	0.02
G29	RAIN lateral $_{t-1}$	4.00	0.32	-17.38	-0.05	11.19	9.57	0.00	0.02
G30	RAIN vertical $_{t-1}$	3.57	0.32	-15.63	-0.01	11.22	9.61	0.00	0.01

ID= model identification; AICc= Akaike's Information Criteria for small samples; ΔAICc= $AICc_i$ - minimum AICc; w_i = Akaike weights; R_m= maximum population growth rate; Values of the parameters *a*, C and *d* were estimated by nonlinear regression analysis.

Supplementary Data 4. Model selection predicting the population growth rate (R_t) of *Rhipidomys mastacalis* (2010-2019) in the Panga Ecological Station, Uberlândia, Brazil. Endogenous model used for comparison in bold.

ID	Models	Parameters estimates				AICc	ΔAICc	w_i	Adjusted R²
		a	R_m	C	*d*				

R0	**Endogenous model**	**1.11**	**1.20**	**-3.10**	**-**	**22.57**	**0.00**	**0.55**	**-**
R1	MIN vertical $_{t-1}$	5.37	1.20	-17.86	-0.04	25.40	2.83	0.13	0.56
R2	SOI vertical	1.76	1.20	-4.97	-0.11	26.34	3.77	0.08	0.50
R3	MIN nonlinear	0.91	1.20	-2.86	0.01	29.62	7.06	0.02	0.25
R4	RAIN vertical $_{t-1}$	1.26	1.20	-3.56	0.19	29.84	7.28	0.01	0.23
R5	MIN lateral	1.08	1.20	-3.38	0.02	29.90	7.33	0.01	0.22
R6	SOI lateral	1.55	1.20	-4.29	0.05	30.23	7.66	0.01	0.19
R7	NDVI vertical	0.45	1.20	-0.39	2.50	30.43	7.86	0.01	0.17
R8	RAIN lateral $_{t-1}$	1.19	1.20	-3.33	0.14	30.64	8.07	0.01	0.15
R9	MAX nonlinear $_{t-1}$	0.92	1.20	-2.76	0.01	30.69	8.12	0.01	0.14
R10	SOI nonlinear	1.50	1.20	-4.13	0.01	30.76	8.19	0.01	0.13
R11	RAIN nonlinear $_{t-1}$	1.18	1.20	-3.29	0.04	30.82	8.25	0.01	0.13
R12	NDVI lateral	1.07	1.20	-2.04	-1.81	31.01	8.44	0.01	0.11
R13	MAX lateral $_{t-1}$	1.05	1.20	-3.11	0.02	31.03	8.47	0.01	0.10
R14	MIN lateral $_{t-1}$	1.39	1.20	-4.23	0.02	31.09	8.52	0.01	0.10
R15	NDVI nonlinear $_{t-1}$	1.34	1.20	-2.98	-0.51	31.16	8.59	0.01	0.09
R16	SOI nonlinear $_{t-1}$	0.89	1.20	-2.48	-0.01	31.23	8.66	0.01	0.08
R17	MIN vertical	1.42	1.20	-4.25	-0.02	31.25	8.68	0.01	0.08
R18	NDVI nonlinear	1.35	1.20	-3.04	-0.50	31.33	8.76	0.01	0.07
R19	MAX nonlinear	0.80	1.20	-2.37	0.00	31.38	8.81	0.01	0.06
R20	SOI lateral $_{t-1}$	0.95	1.20	-2.65	-0.02	31.50	8.93	0.01	0.05
R21	NDVI lateral $_{t-1}$	1.11	1.20	-2.49	-1.14	31.50	8.93	0.01	0.05
R22	MAX lateral	0.87	1.20	-2.56	0.01	31.50	8.93	0.01	0.05
R23	MIN nonlinear $_{t-1}$	1.23	1.20	-3.63	0.00	31.56	8.99	0.01	0.04
R24	RAIN nonlinear	1.03	1.20	-2.88	0.02	31.63	9.06	0.01	0.03
R25	RAIN lateral	1.06	1.20	-2.97	0.04	31.76	9.20	0.01	0.02
R26	MAX vertical $_{t-1}$	1.16	1.20	-3.30	-0.01	31.78	9.22	0.01	0.01
R27	RAIN vertical	1.14	1.20	-3.20	0.04	31.83	9.26	0.01	0.01
R28	MAX vertical	1.09	1.20	-3.09	-0.01	31.88	9.31	0.01	0.00
R29	SOI vertical $_{t-1}$	1.13	1.20	-3.15	0.00	31.90	9.33	0.01	0.00
R30	NDVI vertical $_{t-1}$	1.72	1.20	-3.80	-0.59	31.93	9.36	0.01	0.00

ID= model identification; AICc= Akaike's Information Criteria for small samples; ΔAICc= AICc$_i$ - minimum AICc; w_i = Akaike weights; R$_m$= maximum population growth rate; Values of the parameters a, C and d were estimated by nonlinear regression analysis.

CAPÍTULO 2

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The delayed effects of endogenous and exogenous factors on the demographic parameters of two Neotropical small mammals

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Resumo

Devido aos crescentes impactos antrópicos nos ecossistemas, entender os efeitos de fatores endógenos e exógenos na sobrevivência e recrutamento das espécies é essencial para avaliar o mecanismo responsável pela persistência das populações no ambiente. Usamos uma série temporal de 9 anos, baseada em capturas mensais, para testar os efeitos atrasados de fatores endógenos (densidade) e exógenos (chuva, qualidade do habitat, fogo e dias muito frios) sobre a sobrevivência e recrutamento de dois pequenos mamíferos arborícolas do Cerrado: o marsupial semélparo *Gracilinanus agilis* e o roedor iteróparo *Rhipidomys mastacalis*. Nossos resultados indicam que fatores endógenos e exógenos foram importantes na regulação das populações. Como em outros pequenos mamíferos neotropicais, encontramos efeitos dependentes da densidade no recrutamento de ambas espécies, provavelmente relacionados à competição intraespecífica, além da história de vida semélpara em *G. agilis*. Realmente, as diferenças na história de vida impactaram a importância dos fatores exógenos nas dinâmicas populacionais e o tempo de recuperação e resposta aos incêndios. A semelparidade em *G. agilis* foi a principal reguladora das taxas demográficas, enquanto a chuva teve um papel relativamente menor. Em contrapartida, a diminuição na qualidade do habitat (através da menor cobertura vegetal após incêndios) atrasou (1 ano depois) os efeitos positivos na sobrevivência e negativos no recrutamento de *R. mastacalis*. Finalmente, nossos resultados sugerem que mudanças ambientais devido aos impactos antrópicos, como o aumento da frequência e intensidade dos incêndios e as alterações climáticas, podem ter efeitos severos na dinâmica e persistência das populações de pequenos mamíferos no Cerrado.

Palavras-chave: Cerrado, *Gracilinanus agilis*, recrutamento, *Rhipidomys mastacalis*, sobrevivência

Abstract

Understanding the effects of exogenous and endogenous factors on species survival and recruitment rates is crucial to investigate the chances of species persistence, due to increased anthropic pressures on natural ecosystems. We used a 9-year time series, based on monthly captures, to test the delayed effects of endogenous (density) and exogenous (rainfall, habitat cover/heterogeneity, fire, very cold days) factors on the survival and recruitment rates of two arboreal small mammals inhabiting the Brazilian Cerrado: the semelparous marsupial *Gracilinanus agilis* and the iteroparous rodent *Rhipidomys mastacalis*. As in most neotropical small mammals, we found density-dependent effects on recruitment of both species, which are probably related to intraspecific competition, in addition to the semelparous life-history in *G. agilis*. Actually, this difference in their life-history impacted the importance of exogenous factors on population dynamics of each species and the recovery and response time to disturbances. *Gracilinanus agilis* vital rates were mainly determined by their semelparous life-history, while rainfall had a minor role on demography. On the other hand, a decrease in habitat quality (via lower vegetation cover following fire events) had delayed (1 year after) positive and negative effects on survival and recruitment of *R. mastacalis*, respectively. Our results indicated that endogenous and exogenous factors are important in population regulation of both species. Finally, our results suggest that environmental changes brought by human-activities, such as increased frequency and intensity of fires and global climate disruption, may have severe effects on the dynamics and persistence of small mammals populations in the Cerrado.

Keywords: Brazilian Cerrado, *Gracilinanus agilis*, recruitment, *Rhipidomys mastacalis*, survival

Introduction

One of the main goals of ecology is to understand how the population dynamics change in time, by understanding the mechanism that influence the population growth rate (Sibly and Hone 2002). Recruitment, which represents the individuals who enter the population, through births or immigration, and survival are the main determinants of population growth rate (Stearns 1992; Korpimäki et al. 2004). The independent or simultaneous action of endogenous and exogenous factors is the main cause of variation in the survival and recruitment of individuals in a population (Lundberg et al. 2000; Hixon 2002; Coulson et al. 2005). Endogenous factors affect the population growth rate through a density-dependent mechanism, usually through negative feedback affecting the survival and reproduction of individuals (Berryman 1999; Sibly et al. 2005). In contrast, exogenous factors are density-independent and act on populations either directly, through climatic disturbances (e.g. fires, floods), or indirectly, through variation in environmental and climatic conditions (Berryman 1999; Wang et al. 2013). Due to the constant increases in greenhouse gas emissions and the conversion of natural environments into pastures and croplands, ecosystems are experiencing disruption in climatic patterns leading to extreme weather events and an increase in the frequency and intensity of disturbances (Ramanathan et al. 2001; Foley et al. 2005). Hence, it is urgent to identify and understand how endogenous and exogenous factors influence the demographic parameters of natural populations (Stenseth et al. 2002).

Small mammals provide an excellent model of study for understanding the regulation of demographic parameters, once this group exhibits fluctuations in abundance that lead to irregular population cycles or multiannual dynamics (Korpimäki et al. 2004; Lambin et al. 2006; Andreassen et al. 2021). In addition, they play an important role in the ecosystems where they occur, generating both positive and negative impacts on ecosystems and economy (Brewer and Rejmánek 1999; Dickman 1999; Azevedo et al. 2006; Lessa and Costa 2010; Camargo et al. 2017). Although the role of endogenous and exogenous factors in the population regulation of small mammals is extensively studied in the North Hemisphere (see review in Andreassen et al. 2021), less studies have been conducted in tropical environments. In general, in temperate zones ecosystems, small mammals exhibit regular cyclic fluctuations in response to climate seasonality and direct density dependence (Stenseth et al. 2003; Singleton et al. 2005; Andreassen et al. 2021). There is a higher abundance of individuals in summer, as a result of increased reproduction, while in winter decrease in survival and recruitment of individuals is observed due to negative effects of direct or delayed density dependence leading to population abundance decline (Stenseth et al. 2003; Korpela et al. 2014; Kleiven et al. 2018).

In the Southern Hemisphere, while marsupials present a fluctuation pattern related to seasonality and food availability (Tyndale-Biscoe 2005; Martins et al. 2006; Lopes and Leiner 2015), rodents generally show irregular and non-cyclical fluctuations, resulting from stochastic variation in environmental and climatic factors (Rocha et al. 2017; Andreassen et al. 2021). Hence, most long-term studies in the tropics suggest that marsupial population dynamics are mainly determined by density dependence (direct or delayed), while exogenous factors, such as local climate, play a relatively less important role in the demography of these populations (Ferreira et al. 2015, 2016b, 2020; Brigatti et al. 2016). In contrast, rodent outbreaks are suggested to be triggered by the indirect effects of rainfall on the availability of food resources and shelter in tropical ecosystems (Bergallo and Magnusson 1999; Gallardo e Mercado 1999; Bovendorp et al. 2020). However, few long-term studies have attempted to address the combined role of endogenous and exogenous factors on the demographic parameters of small mammals in tropical savannas.

The Cerrado is the largest tropical savanna, extending 25% of the Brazilian territory and to some regions in eastern Bolivia and northwestern Paraguay (Oliveira-Filho and Ratter 2002). A markedly seasonal climate and the occurrence of fires contributes to the predominance of shrub and tree species, generating a mosaic of physiognomies, varying from grassland to forest areas (Walter and Breckle 1986; Oliveira-Filho and Ratter 2002). This global biodiversity hotspot has so far lost 46% of its native vegetation cover, mainly because of the conversion of natural environments into pastures and croplands (Ferreira et al. 2016a; Fehlenberg et al. 2017; Strassburg et al. 2017). Moreover, global climate change has been currently increasing the frequency and intensity of drought and fire events, also affecting plant and animal species of this Biome (Hofmann et al. 2021). At least 116 species of small mammals (Didelphimorphia and Rodentia) have been reported in the Cerrado (Mendonça et al. 2018). Among them, *Gracilinanus agilis* (Didelphimorphia: Didelphidae) and *Rhipidomys mastacalis* (Rodentia: Cricetidae) are commonly found in typical forest formations, as well as in areas of “cerrado denso” (Emmons and Feer 1990; Rossi et al. 2006). Both species are nocturnal and predominantly arboreal, eating mainly insects and plant material (Emmons and Feer 1990; Pinotti et al. 2011; Camargo et al. 2013; Ribeiro et al. 2018). *Gracilinanus agilis* (20-45 g) have a semelparous life-history, presenting a synchronized breeding season (starting in July) and male post-mating die-off, while females disappear from the population after weaning their young (Lopes and Leiner 2015), leading to a lack of generation overlap. On the other hand, *Rhipidomys mastacalis* (35-170 g) is iteroparous, with females presenting continuous reproduction throughout the year (Oliveira et al. 2007).

As a result of human pressure on ecosystems, it becomes urgent to understand the processes that influence the dynamics of natural populations (Stenseth et al. 2002), especially in a biodiversity hotspot such as the Cerrado. Based on this, our study mainly focused on the investigation of which factors influence survival and recruitment rates of two Neotropical sympatric small mammals with distinct life-histories: the semelparous marsupial *Gracilinanus agilis* and the iteroparous rodent *Rhipidomys mastacalis*. We used a 9-year capture-mark-recapture data set in a Cerrado remnant in Central Brazil to test the following hypothesis: 1) population density exerts negative effects on the future survival and recruitment of both populations, as higher densities have delayed negative effects on demographic parameters of small mammals (Lima et al. 2006; Reed and Slade 2008; Ferreira et al. 2016b), including the annual population growth rate of these studied species (Rossi and Leiner unpublished results); 2) rainfall and habitat cover/heterogeneity exert positive effects on the future survival and recruitment of these species, since rainfall generates higher primary productivity and consequently an increase in the availability of food resources (Bergallo and Magnusson 1999; Gallardo e Mercado 1999; Bovendorp et al. 2020), while habitat cover/heterogeneity protects small mammals from predators (Stokes et al. 2004; Andreo et al. 2009; Nersesian et al. 2012; Lindenmayer et al. 2013); and 3) fires and very cold days negatively influence the future survival and recruitment of *G. agilis* and *R. mastacalis*, since they can negatively influence survival and reproduction of small mammals (Deitlof et al. 2010; Griffiths and Brook 2015; Mendonça et al. 2015; Ferreira et al. 2016b). We assumed differences between sexes in both species, due to physiological and behavioral differences in males and females of small mammals (Gittleman and Thompson 1988; Speakman 2008). In addition, due to a semelparous life-history in *G. agilis* (Lopes and Leiner 2015), we expected variation in survival and recruitment rates, once post-mating male die-off and maternal care could generate contrasting responses between males and females.

Materials and Methods

Study site

Small mammal populations were sampled during nine years of long-term monitoring in the Panga Ecological Station (PES, 19°10'S, 48°23'W), a Cerrado remnant (404 ha) situated in the municipality of Uberlândia (Minas Gerais, Brazil). PES contains several vegetation physiognomies, including open and closed plant formations, and our study was carried out in an area classified as "cerrado denso" (Gonçalves et al. 2021). During the study, average annual rainfall was about 1300 mm^3, while mean minimum and maximum annual temperature were 19.0 ± 2°C (mean ± SD) and 29.2 ± 2°C, respectively. The region has two well-defined seasons: a “dry winter” (April to September), characterized by low temperatures (17.5 ± 2°C/month) and reduced rainfall (34.70 ± 32 mm/month), and a “wet summer” (October to March), characterized by higher temperatures (29.9 ± 2°C/month) and abundant rainfall (205.65 ± 76 mm/month).

Data collection

We trapped small mammals generally at monthly intervals, in trapping sessions lasting four consecutive nights, between August 2010 and March 2020. From the beginning of the study until June 2012, we established a grid within 0.96 ha, composed of five parallel transects 120 m long, spaced 20 m from each other. Each transect had seven capture stations, equidistant 20 m from each other, where we placed two Sherman traps (37.5x10x12 cm; 23.5x8x9 cm, H. B. Sherman Trap Co., Tallahassee, Florida), one on the ground and the other on the understory (fixed to a tree between 1.5-2 meters high). From July 2012 to the end of the study, we included an additional capture station on each of the five transects, increasing the capture grid area to 1.12 ha. We baited the traps with a mixture of banana, peanut butter, oatmeal and bacon and checked them daily.

During the handling process of the captured animals, we identified the sex and species and marked them with numbered ear tags. After data collection the animals were released at their respective capture stations. SISBIO/ICMBio authorized the capture and handling of the animals (License Number: 22629-1 to Natália O. Leiner), and we followed the ethical principles on animal research as regulations of National Advice of Control and Animal Experimentation (CONCEA/Brazil). Moreover, the Ethics Committee on Use of Animals of the Federal University of Uberlândia, Brazil (permit number: 152/13 and 041/19) approved the protocol of trapping and handling of small mammals.

Explanatory variables

We estimated population size of *G. agilis* and *R. mastacalis* using the Minimum Number Known Alive (MNKA – Krebs 1966). MNKA may be as robust as other statistical estimators (Banks-Leite et al. 2014), especially in populations with low captures. Density was calculated by dividing the population size by the size of the capture grid (0.96 or 1.12) at 3, 6, 9 and 12 months before the sampling occasions. Then, we built models to check for density-dependent effects in survival and recruitment using density at these four distinct time lags as covariates. We obtained daily rainfall and minimum temperature data from 2009 to 2020 from the climatic station of the Instituto Nacional de Meteorologia (Uberlândia/MG), situated approximately 30 km away from the study site. To test for the effects of rainfall on survival and recrutiment, we calculated the cumulative rainfall in each period (3, 6, 9, and 12 months before the sampling occasion) to use as covariates in the data analysis. We also calculated, for each period, the number of days with minimum temperatures below 14.00 ºC (hereafter, very cold days), which is 2.5 standard deviations (following Dhawan et al. 2018) below the mean minimum temperature (19.00 °C) during the entire study period (2009-2020). Then, we built models including rainfall or very cold days as a covariate, each model following one of the time lags used with density-dependent effects (3, 6, 9, and 12 months before the sampling occasion).

As a metric for assessing vegetation cover and habitat heterogeneity, we used the Normalized Difference Vegetation Index (NDVI), an index derived from remote sensing that represents the difference between energy absorbed and reflected by the vegetation. NDVI may act as a predictor of habitat heterogeneity and complexity in the Cerrado (Cabacinha and Castro 2009) and has been used as a proxy of food availability and vegetation cover for small mammals (Andreo et al. 2009; Puida and Paglia 2015; Chidodo et al. 2019). In our study, we obtained monthly NDVI values using data from the MODIS/Terra sensor (MOD13Q1), and used the minimum NDVI in each period (3, 6, 9, and 12 months before the sampling occasion), in order to reflect the lowest habitat quality faced by populations of *G. agilis* and *R. mastacalis*.

Once fire is an important disturbance causing changes in population dynamics of small mammals inhabiting tropical savannas (Briani et al. 2004; Griffiths and Brook 2015; Mendonça et al. 2015), we also checked the effects of fire on the demographic parameters of both studied species. Three events of fire occurred at PES between 2000 and 2020 (one in September 2006, and the others in October 2014 and September 2017). Even though PES does not include a prescribed fire program in its management plan, anthropogenic activities in the surroundings may lead to extensive fires (Vasconcelos et al. 2009). The two most recent fires burned approximately 50% of the Ecological station, and continuous population monitoring of *G. agilis* and *R. mastacalis* since 2010 has allowed the evaluation of fire effects on the demographic parameters of these species. Despite the limitation of the lack of replication of burned areas and unburned controls, which are common in studies predicting fire impacts (see Griffiths and Brook 2015; Mendonça et al. 2015), here we used the before-after approach to verify the impact of fires on the demography of *G. agilis* and *R. mastacalis*. We characterized time since fire (ts.fire) as a continuous covariate. Hence, we calculated the time (in months) after a fire occurred and assigned as zero the months in which there was one (following Pardon et al. 2003). Finally, we modeled the before-after fire covariate as a categorical variable, indicating the periods before the fires occurred (before), after the 2014 fire (after.2014), and after the 2017 fire (after.2017).

Models and analysis

We estimated recapture (*p*), apparent survival (φ) and recruitment (1-γ) rates through the capture history of individuals using the program MARK v9.0 (White and Burnham 1999). We calculated the recapture (*p*) in order to find the best parameterization to use in the apparent survival (φ) and recruitment (1-γ) models, since such models need the indication of this parameter. Recapture is defined as the probability that an animal tagged on one occasion (t), remains in the study area, and is recaptured on a later occasion (t+1) (Cooch and White 2007). We used Cormack-Jolly-Seber models (CJS - Lebreton et al. 1992) in estimates of apparent survival (hereafter, survival), the probability that an individual is alive at time t+1, given that it was alive at t (Williams et al. 2001). To estimate recruitment rates, we used Pradel models (Pradel 1996), which use capture history in reverse time to estimate the *Seniority* parameter (γ), the probability that an individual that was alive in the population on one occasion (t+1) is a survivor of a previous sampling occasion (t). From this parameter, it is possible to calculate the recruitment rate (1- γ), the probability that an individual present at time t+1 was not present at a previous time (t), in other words, is a new recruit to the population (from birth or immigration).

Since there were few months without sampling occasions and a variation in the intervals between capture sessions, we divided the interval in days between the start of each sampling session by 28 (the most common interval). In this way, we standardize the interval between sampling occasions to obtain comparable monthly rates without the need for additional calculations. For *G. agilis* we removed individuals with only one capture during the study period (transients), since the presence of such individuals may generate biases in estimates of demographic parameters (Pradel et al. 1997; Lloyd et al. 2009). In addition, we performed the analyses separately for males and females of this species, due to the occurrence of male post-mating die-off (Lopes and Leiner 2015) and the sex-ratio biased towards males (Andreazzi et al. 2011), which could generate a bias in the estimates of the population demographic parameters (see Puida 2013). In contrast, we maintained the transient individuals in the *R. mastacalis* analyses, since the low captures of individuals could generate over-parameterization in the models created. Finally, we pooled males and females to perform the analyses of this species, including sex as a categorical covariate in the CJS and Pradel models.

Due to the amount of parameters and models included, we performed the modeling through a step-by-step procedure (Lebreton et al. 1992). First, we identified the most parsimonious model for the recapture parameter (*p*) in the CJS and Pradel models. In *G. agilis* we created 16 models for each sex, considering season (dry or wet), time (in years) and no time variation (constant) as categorical variables, while for *R. mastacalis* we considered the same variables, but included sex as a covariate and also tested the additive effect of sex with season and time, totaling 64 models created (Supplementary Data SD1 and SD2). After finding the parsimonious *p* for each analysis, we included this parameterization to check the influence of endogenous and exogenous factors on the survival and recruitment rates of *G. agilis* and *R. mastacalis*. We included as covariates in this models: population density, rainfall, very cold days, and habitat cover/heterogeneity (measured by minimum NDVI) considering four time intervals (3, 6, 9, and 12 months before the sampling occasion), in addition to fire (ts.fire and before-after), thus totaling 18 models for each sex of *G. agilis*. For *R. mastacalis*, we also checked the additive effect of sex on each of the endogenous and exogenous covariates, totaling 36 candidate models (Supplementary Data SD5 and SD6).

To assess if the data were overdispersed, we tested the quality of fit from adherence tests (goodness of fit - GOF) in MARK program, using 1000 simulations from the global CJS models for each species (*G. agilis* Females and Males: φ(season+time) *p*(season+time); *R. mastacalis*: φ(sex+season+time) *p*(sex+season+time)). In case of an unsatisfactory fit due to overdispersion, an adjustment of the variance inflation factor ($\hat{c}$) according to the value found in the GOF test was needed (Cooch and White 2007). We compared and selected models using the lowest Akaike's Information Criterion corrected for small samples (AICc - Burnham and Anderson 2002), and we also quantified the proportion of evidence supporting each model (Akaike weights - w_i). Models with ΔAICc ≤ 2 were considered equally plausible (Richards 2005). Finally, to interpret the estimates obtained with the model selection, we created figures in the R environment (R Core Team 2019) using the package "ggplot2".

Results

From August/2010 to March/2020 we conducted 104 sampling occasions, in which we captured 231 individuals of *Gracilinanus agilis* (80 females and 151 males) and 122 individuals of *Rhipidomys mastacalis* (55 females and 67 males). Goodness-of-fit tests on global CJS models for each species revealed no evidence for lack of fit or overdispersion (*G. agilis* Females: $\hat{c}$ = 0.92; *G. agilis* Males: $\hat{c}$ = 1.00; *R. mastacalis*: $\hat{c}$ = 0.94), thus we used $\hat{c}$ = 1 for all the models.

Recapture rates

Both survival (CJS) and recruitment (Pradel) models indicated that the probability of recapture of females and males of *G. agilis* varied with season and time (in years) (Supplementary Data SD1 and SD2). According to these models, in both sexes recapture was highest in the dry season of each year, varying between years (Supplementary Data SD3). For *R. mastacalis*, the survival models did not indicate a consensus on the variables that influence recapture in this species (Supplementary Data SD1), so we choose to select the most parsimonious model with a reduced number of parameters (*p*(sex+season)). Recruitment models, on the other hand, consensually indicated these same covariates as influencing the recapture rates of this rodent (Supplementary Data SD2). In this way, there were more recaptures in the dry season and females were more recaptured than males (Supplementary Data SD4).

Survival rates

We found no effect of population density, fire, and very cold days on survival of neither studied species. *Gracilinanus agilis* female survival was influenced by cumulative rainfall nine months before the sampling occasions (Table 1). This model suggests a positive effect of rainfall on female survival (0.85 ± 0.04) of *G. agilis* (Figure 1A), due to low Akaike weight (w_i=0.25). In contrast, rainfall with a nine-month delay (AICc= 908.13; w_i= 0.63) exerted a positive effect on *G. agilis* male survival (0.74 ± 0.15), where higher rainfall in the previous nine months caused an increase in the survival of these individuals (Figure 1B). A second model involving habitat quality three months before was selected to explain *G. agilis* males survival (ΔAICc ≤ 2 - Table 1), however, the 95% confidence interval for the β parameter of this model included 0, indicating low or no effect of habitat quality on survival of these individuals (Supplementary Data SD7 for β estimates of the selected models).

For *R. mastacalis*, we found strong evidence for the influence of habitat quality one year before the sampling occasions on survival of this species, represented by two plausible models (Table 1). The top-ranked model (AICc= 527.72; w_i= 0.43) indicated a positive effect of habitat quality, varying by sex, on the survival of females (0.59 ± 0.15) and males (0.69 ± 0.14) of *R. mastacalis*, so that individuals increased survival rates when they faced greater habitat quality one year before (Figure 1C). The second plausible model (AICc= 529.20; w_i= 0.21), indicated a positive effect of the same variable, but no differences in survival rates between the sexes (0.65 ± 0.14; Figure 1D).

Table 1. Result of the selection of the main models predicting the survival rates (Φ) of *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2020) at Panga Ecological Station, Uberlândia, Brazil. Selected models in bold.

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Gracilinanus agilis – Females					
Φ(rain.9) *p*(season+time)	**777.85**	**0.00**	**0.25**	**14**	**1.00**
Φ(rain.6) *p*(season+time)	780.05	2.19	0.08	14	0.33
Φ(ndvi.3) *p*(season+time)	780.54	2.69	0.06	14	0.26
Φ(cold.9) *p*(season+time)	780.55	2.70	0.06	14	0.26
Φ(dens.6) *p*(season+time)	780.91	3.06	0.05	14	0.22
Gracilinanus agilis – Males					
Φ(rain.9) *p*(season+time)	**908.13**	**0.00**	**0.63**	**14**	**1.00**
Φ(ndvi.3) *p*(season+time)	**910.12**	**1.99**	**0.23**	**14**	**0.37**
Φ(rain.6) *p*(season+time)	911.30	3.17	0.13	14	0.20
Φ(cold.6) *p*(season+time)	923.88	15.75	0.00	14	0.00
Φ(cold.9) *p*(season+time)	934.28	26.15	0.00	14	0.00
Rhipidomys mastacalis					
Φ(sex+ndvi.12) *p*(sex+season)	**527.72**	**0.00**	**0.43**	**6**	**1.00**
Φ(ndvi.12) *p*(sex+season)	**529.20**	**1.47**	**0.21**	**5**	**0.48**
Φ(sex+ndvi.3) *p*(sex+season)	530.57	2.85	0.10	6	0.24
Φ(ndvi.3) *p*(sex+season)	531.37	3.65	0.07	5	0.16
Φ(sex+ndvi.6) *p*(sex+season)	532.93	5.21	0.03	6	0.07

AICc= Akaike's Information Criterion for small samples; ΔAICc= AICc_i - minimum AICc; w_i = Akaike weights; K= number of model parameters. Complete table is located in Supplementary Data SD5.

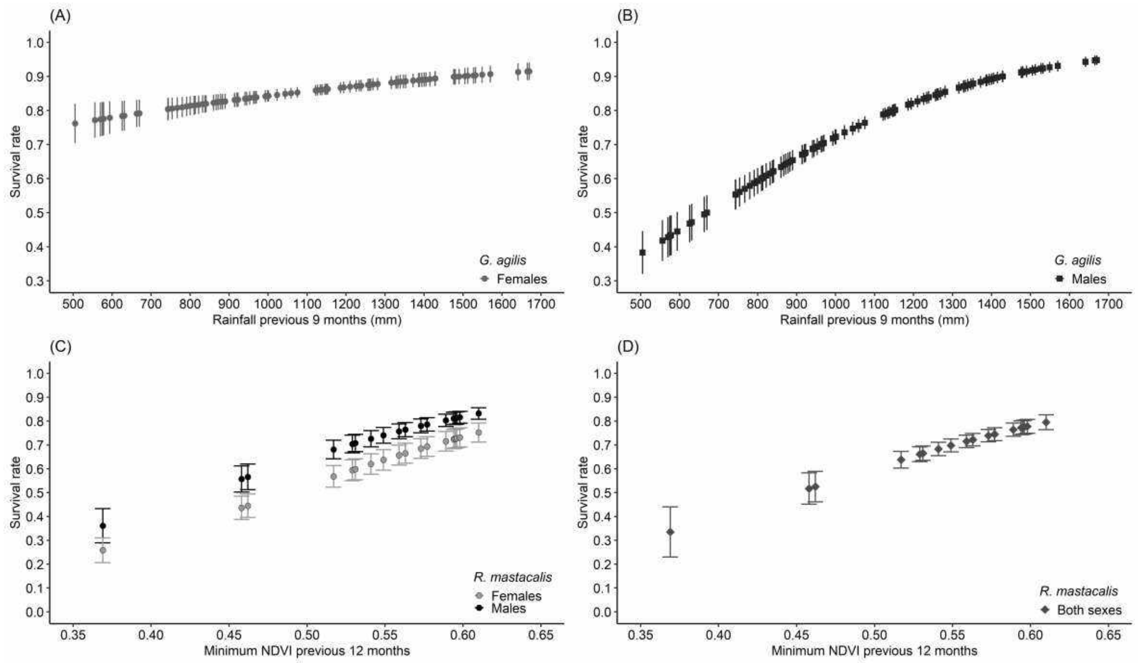

Figure 1. Model-averaged estimates (± SE) of survival rates of *Gracilinanus agilis* and *Rhipidomys mastacali*s (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Panels relate positive effects of rainfall on survival of *Gracilinanus agilis* females (A) and males (B). Positive effects of minimum NDVI on survival rates of *Rhipidomys mastacalis* with effect of sex (C) and no sex differences (D).

Recruitment rates

We found no evidence of the exogenous effects of fire and very cold days on the recruitment rates of *G. agilis* and *R. mastacalis*. A single model including cumulative rainfall was selected to explain recruitment rates of *G. agilis* females (AICc= 761.42; w_i= 0.91 - Table 2), indicating a positive exogenous effect of rainfall in the previous three months on the recruitment of these individuals (0.18 ± 0.13; Figure 2A). In contrast, two models were considered equally plausible to explain the recruitment rates of *G. agilis* males (Table 2). The top-ranked model (AICc= 954.31; w_i= 0.51) indicated a negative endogenous effect of density in the previous three months, such that higher population densities negatively influenced *G. agilis* male recruitment rates (0.28 ± 0.12; Figure 2B). The second ranked model (AICc= 954.70; w_i= 0.42) indicated a positive exogenous effect of rainfall in the previous three months on male recruitment rates, as occurred in females. Hence, higher rainfall increased the recruitment rate of *G. agilis* males (0.25 ± 0.13; Figure 2A).

For *R. mastacalis*, we selected two equally plausible models capable of explaining the recruitment rates of this rodent, one including endogenous and the other exogenous effects (Table 2). The top-ranked model (AICc= 526.05; w_i= 0.21) indicated an additive effect of sex and habitat quality one year before (exogenous effect), in a way that recruitment was higher in lowest quality habitats, and females (0.41 ± 0.13) were more recruited than males (0.30 ± 0.12; Figure 2C). The second ranked model (AICc= 526.55; w_i= 0.17) indicated an additive effect of sex and density three months before (endogenous effect). In this model, recruitment rates were negatively affected by increased densities (with a three months time lag) and females (0.41 ± 0.09) were more recruited than males (0.30 ± 0.08; Figure 2D).

Table 2. Result of the selection of the main models predicting the recruitment rates (1 - γ) of *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2020) at Panga Ecological Station, Uberlândia, Brazil. Selected models in bold.

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Gracilinanus agilis – Females					
1-γ(rain.3) *p*(season+time)	**761.42**	**0.00**	**0.91**	**14**	**1.00**
1-γ(dens.3) *p*(season+time)	767.12	5.70	0.05	14	0.06
1-γ(rain.6) *p*(season+time)	767.94	6.53	0.03	14	0.04
1-γ(cold.3) *p*(season+time)	772.64	11.22	0.00	14	0.00
1-γ(dens.6) *p*(season+time)	783.62	22.20	0.00	14	0.00
Gracilinanus agilis – Males					
1-γ(dens.3) *p*(season+time)	**954.31**	**0.00**	**0.51**	**14**	**1.00**
1-γ(rain.3) *p*(season+time)	**954.70**	**0.39**	**0.42**	**14**	**0.82**
1-γ(cold.3) *p*(season+time)	958.28	3.97	0.07	14	0.14
1-γ(rain.6) *p*(season+time)	971.88	17.57	0.00	14	0.00
1-γ(dens.6) *p*(season+time)	974.02	19.71	0.00	14	0.00
Rhipidomys mastacalis					
1-γ(sex+ndvi.12) *p*(sex+season)	**526.05**	**0.00**	**0.21**	**6**	**1.00**
1-γ(sex+dens.3) *p*(sex+season)	**526.55**	**0.50**	**0.17**	**6**	**0.78**
1-γ(ndvi.12) *p*(sex+season)	528.14	2.09	0.08	5	0.35
1-γ(sex+ndvi.3) *p*(sex+season)	528.36	2.31	0.07	6	0.31
1-γ(sex+ndvi.9) *p*(sex+season)	528.40	2.36	0.07	6	0.31

AICc= Akaike's Information Criterion for small samples; ΔAICc= $AICc_i$ - minimum AICc; w_i = Akaike weights; K= number of model parameters. Complete table is located in Supplementary Data SD6.

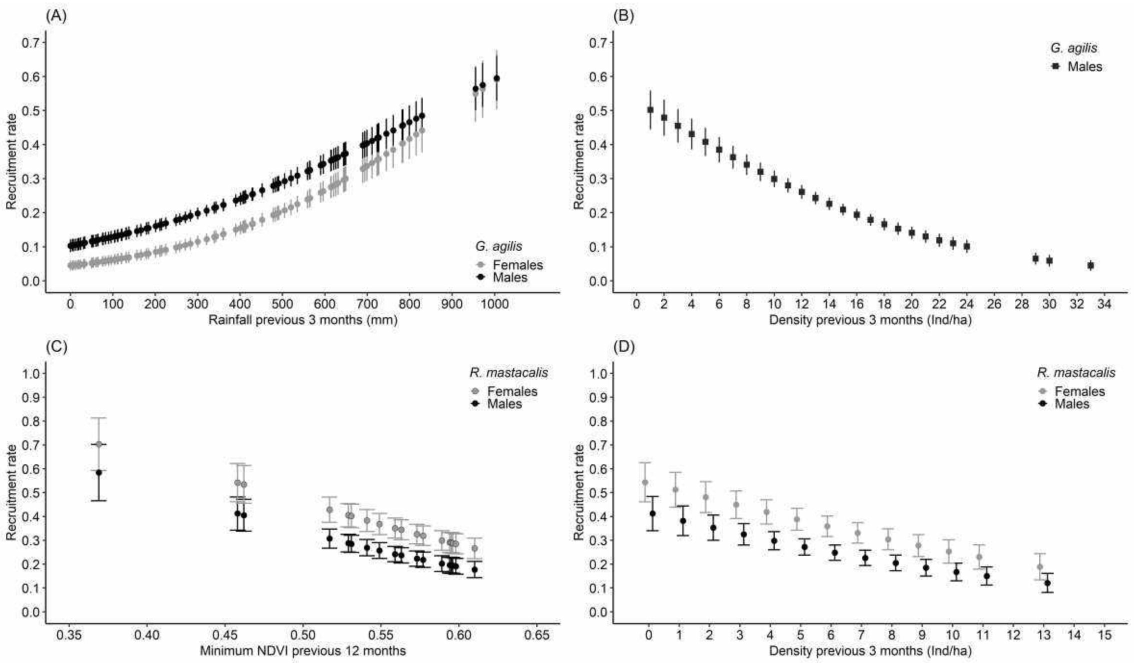

Figure 2. Model-averaged estimates (± SE) of recruitment rates of *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Positive effects of rainfall on recruitment of males and females (A) and negative effects of density in only males of *Gracilinanus agilis* (B). Negative effects of minimum NDVI (C) and density (D) on recruitment of *Rhipidomys mastacalis*.

Discussion

Our results indicated that survival and recruitment rates of *Gracilinanus agilis* and *Rhipidomys mastacalis* varied between the sexes and were affected by endogenous and exogenous factors. Based on our assumption, females of *G. agilis* showed higher survival, while males were more recruited. In contrast, for *R. mastacalis*, males showed higher survival, while females were more recruited. We found no influence of population density on the survival of the populations studied, however, recruitment rates of *G. agilis* males and *R. mastacalis* males and females were negatively affected by population density, thus partially corroborating our hypothesis 1. We found mixed support for the effect of rainfall and habitat cover/heterogeneity on the survival and recruitment rates of the studied species, as predicted by hypothesis 2. In *G. agilis*, rainfall had a positive effect on male and female survival and recruitment, however there were no effects of habitat cover/heterogeneity on this species. In contrast, habitat cover/heterogeneity positively affected the survival of *R. mastacalis*, but exerted a negative effect on the recruitment of this rodent. Finally, contrary to hypothesis 3, we were unable to detect effects of fires and very cold days on any demographic parameters of the populations.

Density dependence (endogenous effect) can be identified as a negative relationship that affects at least one demographic parameter of the population growth rate (Fowler et al. 2006). In previous analyses with the same studied system, we found strong evidence for a density-dependent effect on the annual growth rate of *G. agilis* and *R. mastacalis* populations (Rossi and Leiner unpublished results). In the present study, we found that the density-dependent effect negativelly affects the population growth rate of each species through a decline in the recruitment of *G. agilis* males and both sexes of *R. mastacalis*. However, in *G. agilis* we believe that the negative effect of density on male recruitment is an artefact of their semelparous life-history and the delayed capture of juveniles (Lopes and Leiner 2015). In this species, the highest recruitment rates take place in March/April, just three months after the population reaches lowest density values (December), due to increased male mortality following breeding (Lopes and Leiner 2015). At the same time, the lowest recruitment rates occurred three months after a peak in population density, which takes place during the breeding season (May-July) (see Fig. 2B). Because *G. agilis* presents male-biased sex ratio (Lopes and Leiner 2015), there was a stronger effect of density on male than female recruitment (see Table 2). Moreover, the lack of density effects on recruitment of *G. agilis* females may be a result of the higher survival in this sex (Fig. 1A), in addition to their reduced vagility and adoption of territoriality (Shibuya et al. 2018), which reduces the chances of establishment of new recruits. For *R. mastacalis*, we believe that the effect of density on recruitment may occur mostly through the effects of intraspecific competition, resulting in a limitation of food resources on a lower time scale (Turchin and Batzli 2001). A low availability of resources per capita can decrease reproductive success of females (Koskela et al. 1999; Webb et al. 2005), leading to reduced offspring production and consequently lower recruitment (Lima et al. 2001; Reed and Slade 2008). Actually, a previous study with *Rhipidomys macrurus* in the Cerrado found that higher densities of this rodent cause a reduction in individual body condition (males and females) and a lower proportion of reproductive females in the dry season (Burghausen 2020). Future studies should investigate the role of intraspecific competition on *R. mastacalis* reproductive success.

Demographic rates of *G. agilis* were mainly affected by rainfall. Both males and females of this species presented higher survival nine months after periods of increased rainfall, which probably reflect the positive impact of rainfall on primary productivity and food availability (Bergallo and Magnusson 1999). Increased food availability leads to higher survival of both sexes, thus attaining increased body condition (Meserve et al.

2001; Previtali et al. 2010) and allowing females to sustain the elevated costs of lactation (Speakman 2008). Independent of rainfall, *G. agilis* females had a higher survival than males, due to their semelparous reproductive strategy (Lopes and Leiner 2015). In this species, females disappear from the population after weaning their young, while males present post-mating die-off (Lopes and Leiner 2015). Hence, we found that male survival does not increase linearly according to rainfall (Fig. 1B). Further research should investigate if this non-linear relationship between rainfall and male survival occurs 1) due to semelparity, as males present programmed mortality independent of the variation in accumulated rainfall in previous months or 2) due to the existence of an optimal threshold of the exogenous effect, as has been documented for other small mammals in China and Mongolia (Zhang et al. 2003; Chen et al. 2015).

In addition to affecting survival rates, rainfall affected the recruitment rates of *G. agilis* with a three month delay. As other Neotropical marsupials (Mares and Ernest 1995; Gentile et al. 2000), *G. agilis* juveniles are recruited during the rainy season (Puida and Paglia 2015), which corresponds to the period of increased food availability, thus providing higher investment in reproduction and elevated chances of survival among individuals (Lopes and Leiner 2015; Puida and Paglia 2015). Actually, previous studies demonstrated that reduced food availability in tropical forests may increase juvenile mortality in populations of *Caluromys philander* and *Philander opossum* (Julien-Laferriere and Atramentowicz 1990), while increased rainfall contribute to survival of offspring in the rodent *Octodon degus*, via number and size of young produced (Meserve et al. 1984; Previtali et al. 2010). Finally, changes in food availability promoted by rainfall, including the amount of arthropods and fruits (Bergallo and Magnusson 1999) which are the main items in the diet of *G. agilis* (Camargo et al. 2013; Ribeiro et al. 2018), may attract immigrants to the capture grid. Males were more recruited than females, probably because they move through larger areas and have a greater capture rate, leading to a male-biased sex ratio in the studied population (Lopes and Leiner 2015).

Although we failed to find any effects of rainfall on *R. mastacalis* demographic parameters, the survival and recruitment rates of this species were influenced by habitat cover/heterogeneity (measured by NDVI), which is usually linked to rainfall patterns in most ecosystems (Gurgel and Ferreira 2003; Barbosa and Kumar 2016). Individuals of *R. mastacalis* presented reduced survival when habitat cover/heterogeneity was lower in the previous year, suggesting that reduced habitat quality may impact rodent survival through decreased availability of foraging areas and shelters, and increased exposure to predators

(Bilenca and Kravetz 1998; Bowne et al. 1999; Andreo et al. 2009). One of the selected models indicates higher male survival, while the other indicates similar survival between males and females. Since the analysis does not permit us to separate mortality from emigration (Lebreton et al. 1992), we are unable to distinguish if the reduced survival of females comes from mortality or from their behavior in breeding seasons, where they could emigrate to more favorable habitats. Indeed, in the rodent *Akodon azarae*, breeding females occupy habitats with higher plant cover than non-breeding females (Bilenca and Kravetz 1998); however, in the Cerrado, females of *Rhipidomys macrurus* present reduced body condition at peak population densities (Burghausen 2020), which could also lead to elevated mortality. We were unable to test the combined effect of density and habitat cover/heterogeneity on population demographic parameters, but suggest that future studies should follow this direction.

Habitat cover/heterogeneity also affected the recruitment rates of *R. mastacalis*, however, instead of a positive relationship as expected, we found a negative effect of habitat quality on *R. mastacalis* recruitment rates. We suggest that this result reflects the recovery of this species following fire events. In the Cerrado, vegetation suffers with reduced woody cover and formation of canopy gaps in the months following fires (Miranda et al. 2002), as detected by the minimum NDVI values used in our analysis (0.369 and 0.458), which corresponded to post-fire months. After a few months of burning, Cerrado vegetation often exhibits regrowth (Souza et al. 2017), which in turn, increases the availability of arthropods and seeds (Vasconcelos et al. 2009; Diniz et al. 2011), frequent items in the diet of *R. mastacalis* (Sousa et al. 2004; Pinotti et al. 2011). Thus, we assume that these fire-induced changes may increase recruitment of immigrants from unburned refuges, explaining the one-year lagged negative effect of habitat cover (lower NDVI) on the recruitment rates of *R. mastacalis* individuals. Basically, there are two ways to recover after a population disturbance: through survival and recolonization by reproduction; or through immigrants from adjacent refuge areas (Hein and Jacob 2015). Both mechanisms are not exclusive, and for example, they have been found to act together in the recovery of *Mus domesticus* populations after rodenticide application (Brown et al. 2002). In this way, we believe that the recovery of *R. mastacalis* is a result of the combined action of survival and immigration. Therefore, we reinforce the importance of refuge areas to population recovery after intense disturbances as already suggested by previous studies, since these refuge sites contribute to survival of individuals and subsequent recolonization (Milstead et al. 2007; Zhang et al. 2007; Banks et al. 2011).

Although the models with fire were not selected, we believe that there may be an effect of this variable on the population dynamics of *G. agilis* and *R. mastacalis*, as suggested by Rossi and Leiner (unpublished results). The two fire events negatively affected the population density of both species, through a reduction in the carrying capacity of the environment (Rossi and Leiner unpublished results), corroborating previous findings that fire indirectly affect the dynamics of small mammals populations in tropical areas (see Vieira 1999; Pardon et al. 2003; Banks et al. 2011; Griffiths and Brook 2015). Indeed, the impact of low habitat quality (NDVI - habitat cover) on survival and recruitment rates of *R. mastacalis* supports this suggestion, once NDVI reached minimum values following fire events. On the other hand, although we failed to find any effect of habitat cover on demographic parameters of *G. agilis*, a previous study observed vertical effects of minimum NDVI (proxy for habitat cover/heterogeneity) on annual growth rate of *G. agilis*, indicating that this variable could directly affect survival and/or reproduction of individuals. Here, one of our selected models for *G. agilis* survival indicated minimal NDVI effects, however the large confidence intervals suggest that this variable is not important or has few effects (see Troyer et al. 2014; Ferreira et al. 2020).

Contrary to our hypotheses, we also failed to find evidence for the effects of very cold days on survival or recruitment of either species. Extreme temperatures may reduce survival and affect reproductive success of small mammals, through changes in foraging patterns (Deitlof et al. 2010; Williams et al. 2014; Sassi et al. 2017). In the Brazilian Atlantic forest, extreme temperatures (minimum and maximum) affect the growth rates of marsupial species (Ferreira et al. 2016b) and the rodent *Rhipidomys itoan* (Simas 2017). Moreover, in a previous study, Rossi and Leiner (unpublished results) found that the interaction between minimum temperature and population density exerted a negative impact on *R. mastacalis* annual population growth rate, but no effects on *G. agilis* population dynamics. Future studies should assess if these variables have effects on other demographic parameters not analyzed here, such as fecundity, and check for the interaction between endogenous-exogenous factors on population vital rates.

As observed in previous studies with small mammals in tropical areas, density was a main factor regulating population dynamics of *G. agilis* and *R. mastacalis*, through increased intraspecific competition (Lima et al. 2001; Ferreira et al. 2015, 2016b; Brigatti et al. 2016). Indeed, we found density-dependent effects on both species recruitment, supporting previous studies that suggest a stronger impact of density on recruitment/fecundity than on survival rates of small mammals (Oli and Dobson 2003; Gaillard et al. 2005; Morrison and Hik 2007; Reed and Slade 2008). However, in spite of similarities in ecological attributes (diet, habit), differences in species life-history seem to account for the role of exogenous and endogenous factors on their demographic rates. Survival and recruitment rates of *G. agilis* were mainly determined by this species' semelparous life-history (Lopes and Leiner 2015) and lack of overlapping generations, with a minor role of rainfall on their dynamics, as already demonstrated by Puida and Paglia (2015). Actually, previous studies also found weaker effects of rainfall on marsupial population dynamics (Ferreira et al. 2015, 2016b). In contrast, *R. mastacalis* showed response time to exogenous factors of approximately one year (Table 1 and 2), corroborating that populations with overlapping generations tend to exhibit delayed responses to perturbations and exogenous factors, due to the different impacts of these variables on different age classes (Sæther et al. 2013). Furthermore, the irregular and non-cyclical fluctuations of *R. mastacalis* was more dependent on variation in environmental and climatic factors, as observed in other rodents in Neotropical environments (Rocha et al. 2017; Andreassen et al. 2021).

In addition to the species' life-histories, their abundance also seems to have affected the timing and mechanism of recovery following disturbances. A decline in habitat quality due to fire events impacted *Rhipidomys mastacalis* survival and recruitment, and the lower abundance of this species possibly made it difficult to recover, as density did not return to previous values observed before the disturbance in habitat quality (Rossi and Leiner unpublished results). The severity of population decline is an important attribute in post-disturbance recovery time (Gårdmark et al. 2003; Shilova and Tchabovsky 2009). Our study emphasizes that the exogenous factors acting on the regulation of small mammal populations (fire, rainfall, habitat cover/heterogeneity) are influenced by anthropic changes that are turning the Cerrado warmer and drier and increasing the frequency and intensity of fires (Oliveira et al. 2005; Spera et al. 2016; Hofmann et al. 2021). Thus, we suggest that these environmental changes may have severe effects on the dynamics and persistence of populations in natural environments, which could modify community composition and ecosystem functions.

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Supporting Information

Supplementary Data 1. Model selection for capture (p) and survival (Φ) probability of *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Select models in bold, and the tested variables were sex, season, time (in years), and no time variation (.). AICc= Akaike's Information Criterion for small samples; ΔAICc= AICc$_i$ - minimum AICc; w_i = Akaike weight; K= number of model parameters.

Gracilinanus agilis – Females

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Φ(season) p(season+time)	**774.33**	**0.00**	**0.83**	**14**	**1.00**
Φ(season) p(season)	778.51	4.18	0.10	4	0.12
Φ(.) p(season+time)	779.65	5.32	0.06	13	0.07
Φ(season) p(time)	784.16	9.84	0.01	13	0.01
Φ(season) p(.)	785.01	10.69	0.00	3	0.00
Φ(.) p(season)	785.19	10.86	0.00	3	0.00
Φ(season+time) p(season+time)	789.94	15.61	0.00	24	0.00
Φ(season+time) p(season)	792.76	18.43	0.00	14	0.00
Φ(.) p(time)	794.06	19.73	0.00	12	0.00
Φ(time) p(season+time)	795.08	20.75	0.00	23	0.00
Φ(.) p(.)	795.75	21.42	0.00	2	0.00
Φ(season+time) p(.)	798.66	24.33	0.00	13	0.00
Φ(season+time) p(time)	798.78	24.45	0.00	23	0.00
Φ(time) p(season)	800.65	26.33	0.00	13	0.00
Φ(time) p(time)	809.88	35.55	0.00	22	0.00
Φ(time) p(.)	811.48	37.15	0.00	12	0.00

Gracilinanus agilis – Males

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Φ(season) p(season+time)	**929.20**	**0.00**	**0.75**	**14**	**1.00**
Φ(season) p(season)	931.66	2.47	0.22	4	0.29
Φ(season+time) p(season)	936.66	7.46	0.02	14	0.02
Φ(season+time) p(season+time)	938.06	8.86	0.01	24	0.01
Φ(season) p(.)	939.45	10.25	0.00	3	0.01
Φ(season) p(time)	940.78	11.59	0.00	13	0.00
Φ(season+time) p(.)	943.27	14.07	0.00	13	0.00
Φ(season+time) p(time)	946.49	17.29	0.00	23	0.00
Φ(.) p(season+time)	957.12	27.92	0.00	13	0.00
Φ(.) p(season)	959.37	30.17	0.00	3	0.00
Φ(time) p(season+time)	972.96	43.76	0.00	23	0.00

Φ(time) *p*(season)	973.89	44.69	0.00	13	0.00
Φ(.) *p*(.)	977.31	48.12	0.00	2	0.00
Φ(.) *p*(time)	979.81	50.61	0.00	12	0.00
Φ(time) *p*(.)	992.02	62.82	0.00	12	0.00
Φ(time) *p*(time)	995.01	65.81	0.00	22	0.00

Rhipidomys mastacalis

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Φ(time) *p*(sex+season)	**533.17**	**0.00**	**0.09**	**14**	**1.00**
Φ(season+time) *p*(season+time)	**533.36**	**0.19**	**0.09**	**24**	**0.91**
Φ(season+time) *p*(sex+season)	**533.46**	**0.29**	**0.08**	**15**	**0.87**
Φ(time) *p*(season+time)	**533.77**	**0.60**	**0.07**	**23**	**0.74**
Φ(sex+time) *p*(sex+season)	**534.37**	**1.20**	**0.05**	**15**	**0.55**
Φ(.) *p*(season+time)	**534.44**	**1.26**	**0.05**	**13**	**0.53**
Φ(sex+season+time) *p*(sex+season)	**534.73**	**1.56**	**0.04**	**16**	**0.46**
Φ(season+time) *p*(sex+season+time)	**534.82**	**1.65**	**0.04**	**25**	**0.44**
Φ(season) *p*(season+time)	**535.14**	**1.97**	**0.04**	**14**	**0.37**
Φ(season+time) *p*(time)	535.19	2.02	0.03	23	0.36
Φ(time) *p*(sex+season+time)	535.20	2.03	0.03	24	0.36
Φ(sex) *p*(season+time)	535.42	2.25	0.03	14	0.32
Φ(.) *p*(sex+season+time)	535.65	2.48	0.03	14	0.29
Φ(sex) *p*(sex+season+time)	535.67	2.50	0.03	15	0.29
Φ(sex+season+time) *p*(season+time)	535.84	2.67	0.02	25	0.26
Φ(sex+season) *p*(season+time)	536.18	3.01	0.02	15	0.22
Φ(sex+time) *p*(season+time)	536.23	3.06	0.02	24	0.22
Φ(season) *p*(sex+season+time)	536.28	3.11	0.02	15	0.21
Φ(sex+season) *p*(sex+season+time)	536.44	3.27	0.02	16	0.20
Φ(season+time) *p*(sex+time)	536.85	3.68	0.01	24	0.16
Φ(sex+season+time) *p*(sex+season+time)	537.25	4.08	0.01	26	0.13
Φ(sex+season) *p*(sex+season)	537.34	4.17	0.01	6	0.12
Φ(time) *p*(season)	537.38	4.20	0.01	13	0.12
Φ(season+time) *p*(sex)	537.45	4.28	0.01	14	0.12
Φ(season) *p*(time)	537.53	4.35	0.01	13	0.11
Φ(sex+time) *p*(sex+season+time)	537.57	4.40	0.01	25	0.11
Φ(sex+season+time) *p*(time)	537.65	4.48	0.01	24	0.11
Φ(season+time) *p*(season)	537.83	4.66	0.01	14	0.10
Φ(sex) *p*(sex+season)	537.99	4.82	0.01	5	0.09
Φ(season) *p*(sex+season)	538.22	5.05	0.01	5	0.08
Φ(sex+season) *p*(time)	538.55	5.38	0.01	14	0.07
Φ(sex+season+time) *p*(sex)	538.73	5.56	0.01	15	0.06
Φ(.) *p*(sex+season)	538.90	5.73	0.01	4	0.06
Φ(season) *p*(sex+time)	538.97	5.80	0.01	14	0.06
Φ(.) *p*(time)	539.02	5.85	0.01	12	0.05

Φ(time) *p*(time)	539.18	6.01	0.00	22	0.05
Φ(sex+season+time) *p*(sex+time)	539.27	6.10	0.00	25	0.05
Φ(sex+season) *p*(sex+time)	539.28	6.11	0.00	15	0.05
Φ(sex+time) *p*(season)	539.55	6.38	0.00	14	0.04
Φ(sex) *p*(time)	539.94	6.77	0.00	13	0.03
Φ(sex+season+time) *p*(season)	540.04	6.87	0.00	15	0.03
Φ(time) *p*(sex)	540.34	7.17	0.00	13	0.03
Φ(.) *p*(sex+time)	540.57	7.40	0.00	13	0.02
Φ(sex) *p*(sex+time)	540.78	7.60	0.00	14	0.02
Φ(time) *p*(sex+time)	540.84	7.66	0.00	23	0.02
Φ(sex+time) *p*(sex)	541.48	8.31	0.00	14	0.02
Φ(sex+time) *p*(time)	541.61	8.44	0.00	23	0.01
Φ(season+time) *p*(.)	541.83	8.66	0.00	13	0.01
Φ(sex+season) *p*(sex)	541.96	8.79	0.00	5	0.01
Φ(season) *p*(season)	542.10	8.92	0.00	4	0.01
Φ(.) *p*(season)	542.69	9.51	0.00	3	0.01
Φ(season) *p*(sex)	542.72	9.54	0.00	4	0.01
Φ(sex+time) *p*(sex+time)	543.15	9.98	0.00	24	0.01
Φ(sex+season) *p*(season)	543.27	10.10	0.00	5	0.01
Φ(sex) *p*(season)	543.82	10.65	0.00	4	0.00
Φ(sex+season+time) *p*(.)	544.00	10.83	0.00	14	0.00
Φ(time) *p*(.)	544.65	11.47	0.00	12	0.00
Φ(season) *p*(.)	546.51	13.34	0.00	3	0.00
Φ(sex) *p*(sex)	546.57	13.40	0.00	4	0.00
Φ(sex+time) *p*(.)	546.75	13.57	0.00	13	0.00
Φ(.) *p*(sex)	547.37	14.20	0.00	3	0.00
Φ(sex+season) *p*(.)	547.70	14.53	0.00	4	0.00
Φ(.) *p*(.)	551.34	18.17	0.00	2	0.00
Φ(sex) *p*(.)	552.46	19.29	0.00	3	0.00

Supplementary Data 2. Model selection for capture (*p*) and recrutiment (1-γ) probability of *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Select models in bold, and the tested variables were sex, season, time (in years), and no time variation (.). AICc= Akaike's Information Criterion for small samples; ΔAICc= AICc$_i$ - minimum AICc; w_i = Akaike weight; K= number of model parameters.

Gracilinanus agilis – Females

Model	AICc	ΔAICc	w_i	K	Model Likelihood
1-γ(.) *p*(season+time)	**792.81**	**0.00**	**0.58**	**13**	**1.00**
1-γ(season) *p*(season+time)	**794.52**	**1.71**	**0.25**	**14**	**0.43**
1-γ(time) *p*(season+time)	798.44	5.63	0.03	23	0.06
1-γ(.) *p*(season)	798.53	5.72	0.03	3	0.06
1-γ(.) *p*(time)	798.72	5.91	0.03	12	0.05

1-γ(season) *p*(season)	799.46	6.65	0.02	4	0.04
1-γ(season) *p*(time)	799.59	6.78	0.02	13	0.03
1-γ(season+time) *p*(season+time)	800.43	7.62	0.01	24	0.02
1-γ(.) *p*(.)	801.29	8.48	0.01	2	0.01
1-γ(season) *p*(.)	801.40	8.59	0.01	3	0.01
1-γ(time) *p*(time)	804.11	11.30	0.00	22	0.00
1-γ(time) *p*(season)	804.18	11.37	0.00	13	0.00
1-γ(season+time) *p*(time)	805.29	12.48	0.00	23	0.00
1-γ(season+time) *p*(season)	805.48	12.67	0.00	14	0.00
1-γ(time) *p*(.)	806.27	13.46	0.00	12	0.00
1-γ(season+time) *p*(.)	806.79	13.98	0.00	13	0.00

Gracilinanus agilis – Males

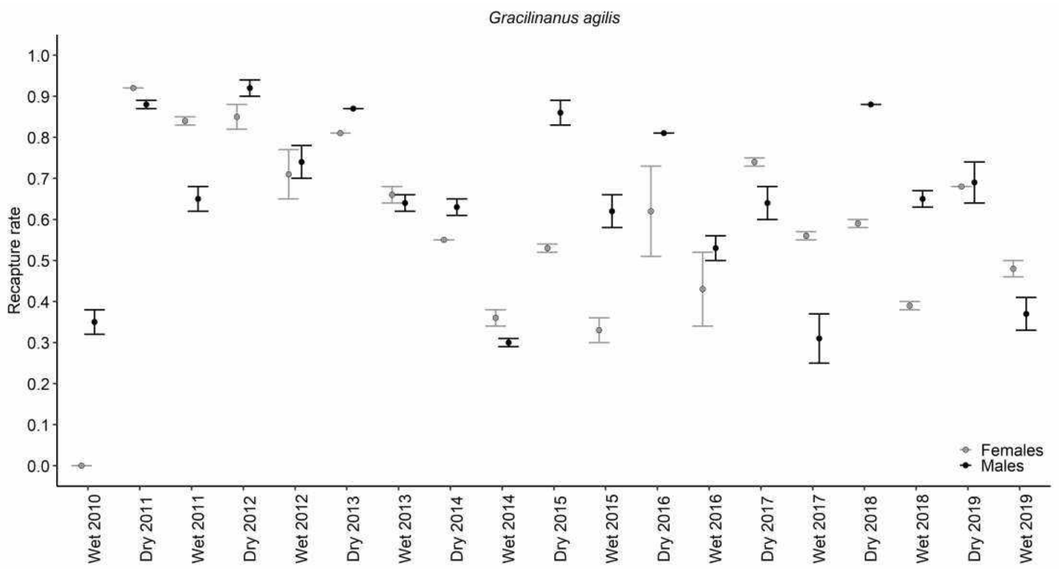
Model	AICc	ΔAICc	w_i	K	Model Likelihood
1-γ(season) *p*(season+time)	**988.30**	**0.00**	**0.56**	**14**	**1.00**
1-γ(.) *p*(season+time)	**989.75**	**1.45**	**0.27**	**13**	**0.48**
1-γ(season) *p*(season)	992.99	4.69	0.05	4	0.10
1-γ(season+time) *p*(season+time)	993.08	4.78	0.05	24	0.09
1-γ(time) *p*(season+time)	993.67	5.37	0.04	23	0.07
1-γ(.) *p*(season)	995.59	7.28	0.01	3	0.03
1-γ(season+time) *p*(season)	997.74	9.44	0.01	14	0.01
1-γ(time) *p*(season)	999.23	10.92	0.00	13	0.00
1-γ(season) *p*(.)	1000.36	12.06	0.00	3	0.00
1-γ(season) *p*(time)	1002.48	14.18	0.00	13	0.00
1-γ(season+time) *p*(.)	1004.69	16.39	0.00	13	0.00
1-γ(.) *p*(.)	1005.81	17.51	0.00	2	0.00
1-γ(.) *p*(time)	1007.03	18.72	0.00	12	0.00
1-γ(season+time) *p*(time)	1007.27	18.97	0.00	23	0.00
1-γ(time) *p*(.)	1008.49	20.19	0.00	12	0.00
1-γ(time) *p*(time)	1010.95	22.64	0.00	22	0.00

Rhipidomys mastacalis

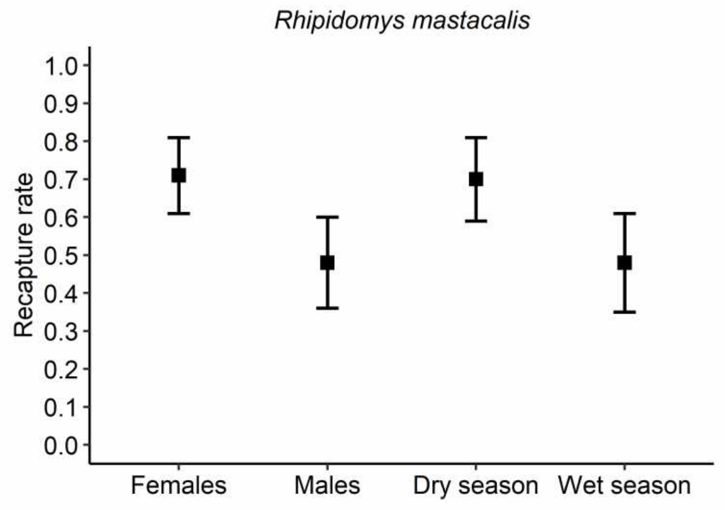
Model	AICc	ΔAICc	w_i	K	Model Likelihood
1-γ(sex+time) *p*(sex+season)	**528.65**	**0.00**	**0.22**	**15**	**1.00**
1-γ(time) *p*(sex+season)	**528.71**	**0.06**	**0.21**	**14**	**0.97**
1-γ(season+time) *p*(sex+season)	**529.21**	**0.55**	**0.17**	**15**	**0.76**
1-γ(sex+season+time) *p*(sex+season)	**529.43**	**0.78**	**0.15**	**16**	**0.68**
1-γ(time) *p*(season)	532.77	4.11	0.03	13	0.13
1-γ(sex) *p*(sex+season)	532.88	4.23	0.03	5	0.12
1-γ(season+time) *p*(sex)	533.26	4.60	0.02	14	0.10
1-γ(season+time) *p*(season)	533.41	4.76	0.02	14	0.09

1-γ(sex+season+time) *p*(sex)	533.56	4.91	0.02	15	0.09
1-γ(sex+season) *p*(sex+season)	533.63	4.97	0.02	6	0.08
1-γ(sex+time) *p*(season)	534.15	5.49	0.01	14	0.06
1-γ(.) *p*(sex+season)	534.35	5.70	0.01	4	0.06
1-γ(season) *p*(sex+season)	534.96	6.31	0.01	5	0.04
1-γ(sex+season+time) *p*(season)	534.96	6.31	0.01	15	0.04
1-γ(sex) *p*(sex+season+time)	535.28	6.62	0.01	15	0.04
1-γ(.) *p*(season+time)	535.67	7.02	0.01	13	0.03
1-γ(sex+time) *p*(sex)	535.68	7.03	0.01	14	0.03
1-γ(time) *p*(sex)	535.83	7.18	0.01	13	0.03
1-γ(sex) *p*(season+time)	535.98	7.33	0.01	14	0.03
1-γ(.) *p*(sex+season+time)	536.19	7.53	0.01	14	0.02
1-γ(sex+season) *p*(sex+season+time)	536.63	7.97	0.00	16	0.02
1-γ(season) *p*(season+time)	536.93	8.28	0.00	14	0.02
1-γ(sex+season) *p*(season+time)	537.36	8.71	0.00	15	0.01
1-γ(season) *p*(sex+season+time)	537.42	8.76	0.00	15	0.01
1-γ(season+time) *p*(.)	537.48	8.82	0.00	13	0.01
1-γ(season+time) *p*(season+time)	537.76	9.10	0.00	24	0.01
1-γ(.) *p*(season)	538.12	9.47	0.00	3	0.01
1-γ(season+time) *p*(sex+season+time)	538.30	9.65	0.00	25	0.01
1-γ(time) *p*(season+time)	538.61	9.96	0.00	23	0.01
1-γ(season) *p*(season)	538.81	10.15	0.00	4	0.01
1-γ(sex) *p*(season)	538.88	10.22	0.00	4	0.01
1-γ(time) *p*(sex+season+time)	539.02	10.37	0.00	24	0.01
1-γ(season+time) *p*(time)	539.05	10.40	0.00	23	0.01
1-γ(sex+season+time) *p*(.)	539.06	10.41	0.00	14	0.01
1-γ(sex+season) *p*(season)	539.67	11.01	0.00	5	0.00
1-γ(sex+season+time) *p*(season+time)	539.87	11.22	0.00	25	0.00
1-γ(sex+season+time) *p*(sex+season+time)	539.91	11.26	0.00	26	0.00
1-γ(time) *p*(.)	540.03	11.38	0.00	12	0.00
1-γ(season) *p*(time)	540.24	11.58	0.00	13	0.00
1-γ(season+time) *p*(sex+time)	540.28	11.63	0.00	24	0.00
1-γ(sex+time) *p*(sex+season+time)	540.42	11.76	0.00	25	0.00
1-γ(sex+season) *p*(sex+time)	540.60	11.94	0.00	15	0.00
1-γ(sex+time) *p*(season+time)	540.60	11.95	0.00	24	0.00
1-γ(sex+season) *p*(time)	540.73	12.08	0.00	14	0.00
1-γ(.) *p*(time)	541.02	12.37	0.00	12	0.00
1-γ(sex+season+time) *p*(time)	541.16	12.50	0.00	24	0.00
1-γ(season) *p*(sex+time)	541.18	12.52	0.00	14	0.00
1-γ(sex) *p*(sex+time)	541.23	12.57	0.00	14	0.00
1-γ(sex+season) *p*(sex)	541.27	12.61	0.00	5	0.00
1-γ(sex+time) *p*(.)	541.33	12.67	0.00	13	0.00
1-γ(sex) *p*(time)	541.36	12.70	0.00	13	0.00
1-γ(sex+season+time) *p*(sex+time)	541.89	13.23	0.00	25	0.00

1-γ(.) *p*(season+time)	541.99	13.34	0.00	13	0.00
1-γ(season) *p*(sex)	542.43	13.77	0.00	4	0.00
1-γ(time) *p*(time)	543.32	14.66	0.00	22	0.00
1-γ(sex) *p*(sex)	544.39	15.73	0.00	4	0.00
1-γ(time) *p*(sex+time)	544.43	15.78	0.00	23	0.00
1-γ(sex+time) *p*(time)	545.22	16.56	0.00	23	0.00
1-γ(sex+time) *p*(sex+time)	545.73	17.07	0.00	24	0.00
1-γ(.) *p*(sex)	545.91	17.26	0.00	3	0.00
1-γ(season) *p*(.)	546.27	17.62	0.00	3	0.00
1-γ(sex+season) *p*(.)	547.22	18.57	0.00	4	0.00
1-γ(.) *p*(.)	549.94	21.28	0.00	2	0.00
1-γ(sex) *p*(.)	550.67	22.02	0.00	3	0.00



Supplementary Data 3. Effects of sex, season and time (in years) on recapture rates of *Gracilinanus agilis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Estimates were average of the top-ranked models (± SE).



Supplementary Data 4. Effects of sex and season on recapture rates of *Rhipidomys mastacalis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Estimates were average of the top-ranked models (± SE).

Supplementary Data 5. Model selection evaluating the effects of endogenous and exogenous factors on survival rates (Φ) of *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Select models in bold, and the tested variables were: sex; density three, six, nine and twelve months before the sampling occasions (dens.3, dens.6, dens.9, dens.12, respectively); cumulative rainfall three, six, nine and twelve months before (rain.3, rain.6, rain.9, rain.12); minimum NDVI three, six, nine and twelve months before (ndvi.3, ndvi.6, ndvi.9, ndvi.12); number of very cold days three, six, nine and twelve months before (cold.3, cold.6, cold.9, cold.12); and fire (time since fire – ts.fire; before-after fire events – ct.fire). AICc= Akaike's

Information Criterion for small samples; ΔAICc= AICc$_i$ - minimum AICc; w_i = Akaike weight; K= number of model parameters.

Gracilinanus agilis – Females

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Φ(rain.9) *p*(season+time)	**777.85**	**0.00**	**0.25**	**14**	**1.00**
Φ(rain.6) *p*(season+time)	780.05	2.19	0.08	14	0.33
Φ(ndvi.3) *p*(season+time)	780.54	2.69	0.06	14	0.26
Φ(cold.9) *p*(season+time)	780.55	2.70	0.06	14	0.26
Φ(dens.6) *p*(season+time)	780.91	3.06	0.05	14	0.22
Φ(rain.3) *p*(season+time)	781.12	3.26	0.05	14	0.20
Φ(ndvi.6) *p*(season+time)	781.34	3.48	0.04	14	0.18
Φ(ct.fire) *p*(season+time)	781.50	3.65	0.04	14	0.16
Φ(ts.fire) *p*(season+time)	781.51	3.66	0.04	14	0.16
Φ(rain.12) *p*(season+time)	781.69	3.84	0.04	14	0.15
Φ(cold.6) *p*(season+time)	781.74	3.89	0.04	14	0.14
Φ(cold.12) *p*(season+time)	781.76	3.91	0.04	14	0.14
Φ(cold.3) *p*(season+time)	781.78	3.93	0.03	14	0.14
Φ(dens.12) *p*(season+time)	781.82	3.97	0.03	14	0.14
Φ(ndvi.12) *p*(season+time)	781.83	3.98	0.03	14	0.14
Φ(ndvi.9) *p*(season+time)	781.83	3.98	0.03	14	0.14
Φ(dens.3) *p*(season+time)	781.83	3.98	0.03	14	0.14
Φ(dens.9) *p*(season+time)	781.83	3.98	0.03	14	0.14

Gracilinanus agilis – Males

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Φ(rain.9) *p*(season+time)	**908.13**	**0.00**	**0.63**	**14**	**1.00**
Φ(ndvi.3) *p*(season+time)	**910.12**	**1.99**	**0.23**	**14**	**0.37**
Φ(rain.6) *p*(season+time)	911.30	3.17	0.13	14	0.20
Φ(cold.6) *p*(season+time)	923.88	15.75	0.00	14	0.00
Φ(cold.9) *p*(season+time)	934.28	26.15	0.00	14	0.00
Φ(ndvi.6) *p*(season+time)	947.39	39.26	0.00	14	0.00
Φ(rain.3) *p*(season+time)	952.85	44.72	0.00	14	0.00
Φ(cold.3) *p*(season+time)	955.11	46.98	0.00	14	0.00
Φ(dens.6) *p*(season+time)	956.14	48.00	0.00	14	0.00
Φ(dens.12) *p*(season+time)	957.60	49.47	0.00	14	0.00
Φ(dens.9) *p*(season+time)	958.33	50.20	0.00	14	0.00
Φ(ts.fire) *p*(season+time)	958.50	50.37	0.00	14	0.00
Φ(rain.12) *p*(season+time)	958.66	50.52	0.00	14	0.00
Φ(cold.12) *p*(season+time)	958.67	50.54	0.00	14	0.00
Φ(ct.fire) *p*(season+time)	958.82	50.69	0.00	14	0.00
Φ(ndvi.9) *p*(season+time)	958.92	50.79	0.00	14	0.00
Φ(dens.3) *p*(season+time)	959.11	50.98	0.00	14	0.00

Φ(ndvi.12) *p*(season+time)	959.21	51.08	0.00	14	0.00

Rhipidomys mastacalis

Model	AICc	ΔAICc	w_i	K	Model Likelihood
Φ(sex+ndvi.12) *p*(sex+season)	**527.72**	**0.00**	**0.43**	**6**	**1.00**
Φ(ndvi.12) *p*(sex+season)	**529.20**	**1.47**	**0.21**	**5**	**0.48**
Φ(sex+ndvi.3) *p*(sex+season)	530.57	2.85	0.10	6	0.24
Φ(ndvi.3) *p*(sex+season)	531.37	3.65	0.07	5	0.16
Φ(sex+ndvi.6) *p*(sex+season)	532.93	5.21	0.03	6	0.07
Φ(sex+ndvi.9) *p*(sex+season)	533.04	5.31	0.03	6	0.07
Φ(ndvi.9) *p*(sex+season)	533.97	6.25	0.02	5	0.04
Φ(ndvi.6) *p*(sex+season)	534.05	6.32	0.02	5	0.04
Φ(cold.9) *p*(sex+season)	534.97	7.24	0.01	5	0.03
Φ(sex+cold.9) *p*(sex+season)	535.19	7.47	0.01	6	0.02
Φ(sex+rain.9) *p*(sex+season)	535.25	7.52	0.01	6	0.02
Φ(sex+cold.6) *p*(sex+season)	535.28	7.56	0.01	6	0.02
Φ(cold.6) *p*(sex+season)	535.41	7.68	0.01	5	0.02
Φ(rain.9) *p*(sex+season)	535.95	8.23	0.01	5	0.02
Φ(cold.12) *p*(sex+season)	536.61	8.88	0.01	5	0.01
Φ(sex+cold.12) *p*(sex+season)	536.96	9.23	0.00	6	0.01
Φ(sex+rain.12) *p*(sex+season)	537.51	9.79	0.00	6	0.01
Φ(rain.12) *p*(sex+season)	538.15	10.43	0.00	5	0.01
Φ(sex+dens.9) *p*(sex+season)	538.26	10.54	0.00	6	0.01
Φ(sex+rain.6) *p*(sex+season)	538.38	10.66	0.00	6	0.00
Φ(sex+dens.12) *p*(sex+season)	538.55	10.83	0.00	6	0.00
Φ(sex+dens.6) *p*(sex+season)	538.73	11.01	0.00	6	0.00
Φ(sex+cold.3) *p*(sex+season)	538.75	11.03	0.00	6	0.00
Φ(sex+ts.fire) *p*(sex+season)	538.88	11.16	0.00	6	0.00
Φ(rain.6) *p*(sex+season)	539.19	11.46	0.00	5	0.00
Φ(cold.3) *p*(sex+season)	539.37	11.65	0.00	5	0.00
Φ(dens.9) *p*(sex+season)	539.41	11.69	0.00	5	0.00
Φ(sex+rain.3) *p*(sex+season)	539.44	11.72	0.00	6	0.00
Φ(dens.12) *p*(sex+season)	539.61	11.89	0.00	5	0.00
Φ(dens.6) *p*(sex+season)	539.91	12.18	0.00	5	0.00
Φ(sex+dens.3) *p*(sex+season)	539.92	12.19	0.00	6	0.00
Φ(sex+ct.fire) *p*(sex+season)	540.06	12.33	0.00	6	0.00
Φ(ts.fire) *p*(sex+season)	540.24	12.52	0.00	5	0.00
Φ(rain.3) *p*(sex+season)	540.32	12.60	0.00	5	0.00
Φ(ct.fire) *p*(sex+season)	540.86	13.13	0.00	5	0.00
Φ(dens.3) *p*(sex+season)	540.91	13.18	0.00	5	0.00

Supplementary Data 6. Model selection evaluating the effects of endogenous and exogenous factors on recruitment rates (1-γ) of *Gracilinanus agilis* and *Rhipidomys* *mastacalis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. Select models in bold, and the tested variables were: sex; density three, six, nine and twelve months before the sampling occasions (dens.3, dens.6, dens.9, dens.12, respectively); cumulative rainfall three, six, nine and twelve months before (rain.3, rain.6, rain.9, rain.12); minimum NDVI three, six, nine and twelve months before (ndvi.3, ndvi.6, ndvi.9, ndvi.12); number of very cold days three, six, nine and twelve months before (cold.3, cold.6, cold.9, cold.12); and fire (time since fire – ts.fire; before-after fire events – ct.fire). AICc= Akaike's Information Criterion for small samples; ΔAICc= $AICc_i$ - minimum AICc; w_i = Akaike weight; K= number of model parameters.

Gracilinanus agilis – Females

Model	AICc	ΔAICc	w_i	K	Model Likelihood
1-γ(rain.3) *p*(season+time)	**761.42**	**0.00**	**0.91**	**14**	**1.00**
1-γ(dens.3) *p*(season+time)	767.12	5.70	0.05	14	0.06
1-γ(rain.6) *p*(season+time)	767.94	6.53	0.03	14	0.04
1-γ(cold.3) *p*(season+time)	772.64	11.22	0.00	14	0.00
1-γ(dens.6) *p*(season+time)	783.62	22.20	0.00	14	0.00
1-γ(cold.6) *p*(season+time)	784.73	23.31	0.00	14	0.00
1-γ(dens.12) *p*(season+time)	788.92	27.50	0.00	14	0.00
1-γ(rain.9) *p*(season+time)	789.29	27.87	0.00	14	0.00
1-γ(ndvi.3) *p*(season+time)	789.82	28.40	0.00	14	0.00
1-γ(dens.9) *p*(season+time)	791.50	30.08	0.00	14	0.00
1-γ(ct.fire) *p*(season+time)	792.81	31.39	0.00	14	0.00
1-γ(rain.12) *p*(season+time)	793.23	31.81	0.00	14	0.00
1-γ(cold.9) *p*(season+time)	793.69	32.27	0.00	14	0.00
1-γ(ndvi.6) *p*(season+time)	793.83	32.41	0.00	14	0.00
1-γ(ndvi.9) *p*(season+time)	794.07	32.65	0.00	14	0.00
1-γ(ts.fire) *p*(season+time)	794.22	32.80	0.00	14	0.00
1-γ(cold.12) *p*(season+time)	794.29	32.87	0.00	14	0.00
1-γ(ndvi.12) *p*(season+time)	794.93	33.51	0.00	14	0.00

Gracilinanus agilis – Males

Model	AICc	ΔAICc	w_i	K	Model Likelihood
1-γ(dens.3) *p*(season+time)	**954.31**	**0.00**	**0.51**	**14**	**1.00**
1-γ(rain.3) *p*(season+time)	**954.70**	**0.39**	**0.42**	**14**	**0.82**
1-γ(cold.3) *p*(season+time)	958.28	3.97	0.07	14	0.14
1-γ(rain.6) *p*(season+time)	971.88	17.57	0.00	14	0.00
1-γ(dens.6) *p*(season+time)	974.02	19.71	0.00	14	0.00
1-γ(cold.6) *p*(season+time)	979.23	24.92	0.00	14	0.00
1-γ(dens.12) *p*(season+time)	982.00	27.69	0.00	14	0.00
1-γ(ndvi.9) *p*(season+time)	983.81	29.50	0.00	14	0.00
1-γ(dens.9) *p*(season+time)	984.47	30.16	0.00	14	0.00
1-γ(ndvi.6) *p*(season+time)	984.94	30.63	0.00	14	0.00
1-γ(rain.12) *p*(season+time)	988.84	34.52	0.00	14	0.00

1-γ(cold.9) *p*(season+time)	989.41	35.09	0.00	14	0.00
1-γ(ndvi.3) *p*(season+time)	989.73	35.41	0.00	14	0.00
1-γ(ts.fire) *p*(season+time)	990.84	36.53	0.00	14	0.00
1-γ(rain.9) *p*(season+time)	990.89	36.58	0.00	14	0.00
1-γ(ndvi.12) *p*(season+time)	991.38	37.07	0.00	14	0.00
1-γ(cold.12) *p*(season+time)	991.45	37.13	0.00	14	0.00
1-γ(ct.fire) *p*(season+time)	991.77	37.46	0.00	14	0.00

Rhipidomys mastacalis

Model	AICc	ΔAICc	w_i	K	Model Likelihood
1-γ(sex+ndvi.12) *p*(sex+season)	**526.05**	**0.00**	**0.21**	**6**	**1.00**
1-γ(sex+dens.3) *p*(sex+season)	**526.55**	**0.50**	**0.17**	**6**	**0.78**
1-γ(ndvi.12) *p*(sex+season)	528.14	2.09	0.08	5	0.35
1-γ(sex+ndvi.3) *p*(sex+season)	528.36	2.31	0.07	6	0.31
1-γ(sex+ndvi.9) *p*(sex+season)	528.40	2.36	0.07	6	0.31
1-γ(dens.3) *p*(sex+season)	528.70	2.66	0.06	5	0.26
1-γ(sex+ndvi.6) *p*(sex+season)	529.28	3.23	0.04	6	0.20
1-γ(ndvi.9) *p*(sex+season)	529.98	3.93	0.03	5	0.14
1-γ(ndvi.3) *p*(sex+season)	530.17	4.12	0.03	5	0.13
1-γ(sex+dens.6) *p*(sex+season)	530.21	4.17	0.03	6	0.12
1-γ(sex+dens.9) *p*(sex+season)	530.29	4.24	0.03	6	0.12
1-γ(sex+cold.6) *p*(sex+season)	530.30	4.25	0.03	6	0.12
1-γ(sex+dens.12) *p*(sex+season)	530.36	4.32	0.02	6	0.12
1-γ(ndvi.6) *p*(sex+season)	530.66	4.61	0.02	5	0.10
1-γ(cold.6) *p*(sex+season)	531.10	5.05	0.02	5	0.08
1-γ(sex+cold.9) *p*(sex+season)	531.79	5.74	0.01	6	0.06
1-γ(dens.12) *p*(sex+season)	531.96	5.91	0.01	5	0.05
1-γ(dens.9) *p*(sex+season)	532.06	6.01	0.01	5	0.05
1-γ(cold.9) *p*(sex+season)	532.13	6.09	0.01	5	0.05
1-γ(dens.6) *p*(sex+season)	532.14	6.10	0.01	5	0.05
1-γ(sex+cold.12) *p*(sex+season)	532.24	6.19	0.01	6	0.05
1-γ(cold.12) *p*(sex+season)	532.39	6.34	0.01	5	0.04
1-γ(sex+cold.3) *p*(sex+season)	533.02	6.98	0.01	6	0.03
1-γ(sex+rain.9) *p*(sex+season)	533.29	7.24	0.01	6	0.03
1-γ(sex+rain.6) *p*(sex+season)	534.32	8.27	0.00	6	0.02
1-γ(cold.3) *p*(sex+season)	534.40	8.36	0.00	5	0.02
1-γ(rain.9) *p*(sex+season)	534.50	8.46	0.00	5	0.01
1-γ(sex+ts.fire) *p*(sex+season)	534.53	8.49	0.00	6	0.01
1-γ(sex+rain.12) *p*(sex+season)	534.75	8.71	0.00	6	0.01
1-γ(sex+ct.fire) *p*(sex+season)	534.87	8.82	0.00	6	0.01
1-γ(sex+rain.3) *p*(sex+season)	534.96	8.91	0.00	6	0.01
1-γ(rain.6) *p*(sex+season)	535.77	9.72	0.00	5	0.01
1-γ(ct.fire) *p*(sex+season)	536.20	10.15	0.00	5	0.01

1-γ(ts.fire) p(sex+season)	536.24	10.20	0.00	5	0.01
1-γ(rain.12) p(sex+season)	536.27	10.23	0.00	5	0.01
1-γ(rain.3) p(sex+season)	536.43	10.38	0.00	5	0.01

Supplementary Data 7. Top-ranked models of survival (Φ) and recruitment (1-γ) rates for *Gracilinanus agilis* and *Rhipidomys mastacalis* (2010-2020) at the Panga Ecological Station in Uberlândia, Brazil. ΔAICc= AICc$_i$ - minimum AICc; w_i= Akaike weight; β1= intercept; β2= sex; β3= endogenous or exogenous variable selected; and SE= standard errors.

Estimates of β parameters (± SE) of the selected models for survival rates

Species	**Model**	**ΔAIC_c**	**w_i**	**β1**	**SE**	**β2**	**SE**	**β3**	**SE**
Gracilinanus agilis - Females	Φ(rainfall.m9)	0.000	0.249	0.639	0.569	-	-	0.001	0.000
Gracilinanus agilis - Males	Φ(rainfall.m9)	0.000	0.635	-1.940	0.478	-	-	0.003	0.000
	Φ(ndvi.m3)	1.991	0.235	-5.402	1.027	-	-	-0.100	737.4
Rhipidomys mastacalis	Φ(sex+ndvi.m12)	0.000	0.428	-4.380	0.705	0.487	0.245	0.100	0.000
	Φ(ndvi.m12)	1.473	0.205	-3.807	1.380	-	-	0.100	0.000

Estimates of β parameters (± SE) of the selected models for recruitment rates

Species	**Model**	**ΔAIC_c**	**w_i**	**β1**	**SE**	**β2**	**SE**	**β3**	**SE**
Gracilinanus agilis - Females	1-γ (rainfall.m3)	0.000	0.909	3.066	0.322	-	-	0.003	0.000
Gracilinanus agilis - Males	1-γ (dens.m3)	0.000	0.510	0.105	0.241	-	-	-0.095	0.016
	1-γ (rainfall.m3)	0.390	0.420	2.160	0.196	-	-	0.002	0.000
Rhipidomys mastacalis	1-γ (sex+ndvi.m12)	0.000	0.214	-3.730	1.442	0.523	0.256	-0.100	0.000
	1-γ (sex+dens.m3)	0.500	0.167	-0.173	0.329	0.528	0.256	-0.125	0.044

CONCLUSÕES GERAIS

O fogo é uma perturbação que acomete diversos ecossistemas terrestres, principalmente as savanas tropicais (Bond e van Wilgen, 1996; Moreira, 2000). Esse distúrbio é parte do histórico evolutivo do Cerrado e geralmente ocorre naturalmente entre três a cinco anos (Miranda et al., 2002). Para lidar com esse distúrbio natural, a flora possui adaptações morfológicas e fisiológicas (Bond e van Wilgen, 1996), enquanto a fauna parece ser resiliente, já que estudos relatando extinções locais são raros (Frizzo et al., 2011). O fogo pode afetar negativamente a abundância das populações de duas maneiras: 1) por meio de efeitos diretos, causando mortalidade dos indivíduos; ou 2) por meio de efeitos indiretos, alterando a disponibilidade de recursos, reduzindo a aptidão individual ou aumentando o risco de predação (Converse et al., 2006; Banks et al., 2011; Lindenmayer et al., 2013). No presente estudo, não encontrei evidências de efeitos diretos dos incêndios nas populações de *Gracilinanus agilis* e *Rhipidomys mastacalis*, uma vez que não houve efeitos desse distúrbio na sobrevivência de nenhuma das espécies, em consonância com o verificado anteriormente para *G. agilis* no mesmo sistema de estudo (Rossi, 2018). Entretanto, os incêndios impactaram negativamente a abundância das populações, por meio do efeito indireto na redução da capacidade de suporte ambiental, uma vez que as populações não retornaram aos padrões pré-fogo. Dessa forma, esse resultado está de acordo com outros trabalhos que relatam que os impactos do fogo em pequenos mamíferos de ambiente tropicais tendem a ser indiretos (Pardon et al. 2003; Banks et al. 2011; Griffiths and Brook 2015; Vieira 1999).

A densidade populacional (fator endógeno) desempenhou um importante papel na regulação das populações estudadas, uma vez tal variável impactou as taxas de crescimento anual de *G. agilis* e *R. mastacalis*, bem como o recrutamento de machos de *G. agilis* e ambos os sexos de *R. mastacalis*. Esse resultado está de acordo com outros estudos que relatam que a densidade exibe maiores impactos nas taxas de recrutamento/fecundidade do que na sobrevivência dos indivíduos (Oli and Dobson 2003; Gaillard et al. 2005; Morrison and Hik 2007; Reed and Slade 2008). Os principais impactos negativos da densidade em pequenos mamíferos advém dos efeitos da competição intraespecífica, que pode afetar a condição corporal dos indivíduos e reduzir o sucesso reprodutivo (Berryman et al., 1999; Koskela et al., 1999; Webb et al., 2005; Lima et al., 2006).

Quanto aos fatores ambientais e climáticos (exógenos), em escala anual a população de *G. agilis* foi regulada positivamente pela qualidade do habitat (medida via NDVI), enquanto a chuva exerceu efeitos positivos na sobrevivência e recrutamento desta espécie. Além de responder a eventos de incêndio, o NDVI é uma métrica que também é afetada por variáveis climáticas (Gurgel e Ferreira, 2003; Barbosa e Kumar, 2016), logo, a chuva pode ser o principal fator exógeno atuando na regulação dessa espécie, como já observado para outros marsupiais neotropicais (Ferreira et al., 2015, 2016b). Em contrapartida, *R. mastacalis* foi regulado pelos efeitos verticais dos dias muito frios um ano antes, que em pequenos mamíferos podem causar redução nos padrões de atividade e mudanças no sucesso reprodutivo (Ribeiro e Bicudo, 2007; Deitloff et al., 2010). Além disso, a população de *R. mastacalis* também foi impactada pela qualidade do habitat um ano antes, o que pode influenciar o risco de predação, como já observado em outros pequenos mamíferos (Andreo et al., 2009; Balazote Oliver et al., 2017).

Apesar de traços ecológicos semelhantes (hábito arbóreo e dieta onívora), *G. agilis* e *R. mastacalis* exibiram respostas contrastantes aos fatores analisados, possivelmente em decorrência de suas distintas histórias de vida (marsupial semélparo vs. roedor iteróparo). *Gracilinanus agilis* possui uma história de vida semélpara, onde machos apresentam mortalidade pós-cópula, enquanto fêmeas desaparecem da população após desempenharem os cuidados com a prole (Lopes e Leiner, 2015). Dessa forma, fêmeas apresentam maior sobrevivência que machos, enquanto machos são mais recrutados, pois possuem maiores áreas de movimento e razão sexual desviada para esse sexo (Lopes e Leiner, 2015). Esse resultado indica que *G. agilis* é regulado principalmente por sua característica de história de vida, como sugerido por Puida e Paglia (2015). Além disso, a chuva desempenhou um papel relativamente menor na regulação populacional dessa espécie, como verificado para outros marsupiais em florestas tropicais (Ferreira et al. 2015, 2016). Em contrapartida, *R. mastacalis* exibiu flutuações irregulares e não cíclicas, em decorrência principalmente das variações ambientais e impactos de distúrbios (dois incêndios), como geralmente observado em roedores de ambientes tropicais (Rocha et al., 2017; Andreassen et al., 2021). Ademais, essa espécie apresentou tempo de resposta aos fatores exógenos de aproximadamente um ano (dias muito frios e qualidade do habitat), corroborando que populações com sobreposição de gerações tendem a exibir respostas tardias às perturbações e fatores exógenos, em decorrência dos diferentes impactos dessas variáveis nas distintas classes etárias (Sæther et al., 2013).

Diante disso, este trabalho demonstrou que fatores endógenos e exógenos foram importantes na regulação populacional de *Gracilinanus agilis* e *Rhipidomys mastacalis* no Cerrado. As variáveis que impactaram a dinâmica das populações estudadas (incêndios, dias frios, chuva, qualidade do habitat) estão sob constante modificação em decorrência das mudanças antropogênicas que estão deixando o Cerrado mais quente e seco, além de alterar a frequência e intensidade de eventos climáticos extremos (Hofmann et al., 2021). Dessa forma, a intensificação dos impactos antrópicos no clima e na redução de áreas naturais do Cerrado podem alterar a persistência de populações naturais, modificando a estrutura das comunidades e impactando as funções ecossistêmicas. Por fim, estudos futuros devem considerar a história de vida das espécies e o papel de fatores endógenos e exógenos na dinâmica populacional de pequenos mamíferos, e quando possível, analisar os efeitos sinérgicos dessas variáveis, uma vez que os resultados encontrados aqui podem ser um padrão para outras espécies do Cerrado.

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