Universidade de Brasília

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Programa de Pós-Graduação em Ecologia

Dispersão de quatro espécies de Scarabaeoidea (Insecta: Coleoptera) em habitats preservado e agrícola no Cerrado

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Tese apresentada ao Programa de Pós-graduação em Ecologia da Universidade de Brasília como requisito parcial à obtenção do título de Doutor em Ecologia.

Orientadora: Profa. Dra. Marina Regina Frizzas (UnB)

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Tese de Doutorado

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RESUMO

Os besouros da superfamília Scarabaeoidea são cosmopolitas, consomem fontes variadas de recurso e possuem antenas lameladas. Esta superfamília é dividida em doze famílias e o presente estudo avaliou quatro espécies, inseridas nas famílias Scarabaeidae e Melolonthidae. Os besouros rola-bosta (Scarabaeidae: Scarabaeinae) utilizam várias fontes de alimento, sendo as fezes de mamíferos o recurso mais comum. Devido aos seus hábitos alimentares e forma como manipulam e nidificam no recurso, eles promovem uma série de serviços ecossistêmicos, como a ciclagem de matéria orgânica, dispersão secundária de sementes, controle de parasitas, auxiliam na aeração do solo, dentre outros. Há cerca de 7.000 espécies descritas e 726 ocorrem no Brasil, sendo que no Cerrado, eles estão distribuídos pelas várias fitofisionomias que ocorrem no bioma, desde as mais abertas formadas por gramíneas e herbáceas, até as mais densas, que são formações florestais, e este grupo possui período de atividade sincronizado à sazonalidade do bioma, pois no período chuvoso são mais ativos e abundantes. Na família Melolonthidae foram descritas cerca de 19.000 espécies, e as larvas dos besouros se alimentam de raízes de plantas, podendo ser pragas agrícolas e causar danos muito expressivos aos diferentes cultivos e impactar negativamente a economia do país. Pouco se sabe sobre os aspectos populacionais e a capacidade de dispersão dos indivíduos em Scarabaeoidea, desta forma o presente trabalho teve como objetivo verificar a capacidade de dispersão de quatro espécies desta superfamília, e a tese foi dividida em dois capítulos. O primeiro capítulo investigou, utilizando a técnica de marcação e recaptura, a capacidade de dispersão de *Oxysternon palemo*, *Coprophanaeus sptizi* e *Diabroctis mirabilis* no cerrado *sensu stricto*, além de avaliar parâmetros populacionais das três espécies ao longo de um ano. Todos os indivíduos foram capturados exclusivamente no período chuvoso, e as abundâncias, recrutamentos e taxas de sobrevivência foram mais expressivas entre os meses de novembro e janeiro nas três espécies. *Oxysternon palemo* apresentou a maior abundância, seguido de *C. spizi* e *D. mirabilis*, e os deslocamentos máximos também seguiram esta ordem. *Oxysternon palemo* foi dominante no cerrado *sensu stricto* e suas altas abundâncias e capacidade de dispersão possivelmente amenizam o efeito da fragmentação, porém o mesmo não foi observado para *D. mirabilis*, que teve as menores abundâncias e apenas um evento de dispersão registrado, de curta distância. O segundo capítulo investigou a capacidade de dispersão de *Phyllophaga capillata* em campo em plantio de soja, ao longo do período de revoada desta espécie e, a atividade de voo desta espécie em laboratório. A maior parte dos adultos foram recapturados à menor distância estabelecida no estudo, 50 m e apenas seis indivíduos machos foram recapturados à maior distância experimental, de 250 m. O experimento de atividade de voo em laboratório apontou que a maioria dos indivíduos (cerca de 70% dos machos e 53% das fêmeas) apresentaram o comportamento de deixar o solo e voar diariamente. Com capacidade de dispersão de 250 m em uma noite, é possível que estes insetos colonizem novas propriedades ou talhões de grandes plantios de soja no início do período chuvoso e se dispersem pelas plantações ao longo da revoada.

Palavras-chave: Deslocamento, marcação e recaptura, cerrado *sensu stricto*, soja, rola-bosta, coró.

ABSTRACT

Beetles of the superfamily Scarabaeoidea are cosmopolitan, consume varied sources of food, and have lamellated antennae. This superfamily is divided into twelve families and the present study evaluated four species, in the families Scarabaeidae and Melolonthidae. Dung beetles (Scarabaeidae: Scarabaeinae) use various food sources, with mammal feces being the most common resource. Due to their feeding habits and the way they manipulate and nest in the resource, they provide a number of ecosystem services, such as the cycling of organic matter, secondary seed dispersal, parasite control, and help aerate the soil, among others. There are about 7,000 described species and 726 occur in Brazil, and in the Cerrado, they are distributed among the various physiognomic forms that occur in the biome, from the more open ones formed by grasses and herbaceous plants, to the denser ones, which are forest formations, and this group has a period of activity synchronized to the seasonality of the biome, because in the rainy season they are more active and abundant. In the Melolonthidae family there are about 19,000 described species, and the larvae of the beetles feed on plant roots, so they can become agricultural pests and cause very significant damage to different crops and negatively impact the country's economy Little is known about the population aspects and the dispersal ability of individuals in Scarabaeoidea, thus the present work aimed to verify the dispersal ability of four species of this superfamily, and the thesis was divided into two chapters. The first chapter investigated, using the mark-and-recapture technique, the dispersal ability of *Oxysternon palemo*, *Coprophanaeus sptizi*, and *Diabroctis mirabilis* in cerrado *sensu stricto*, and evaluated population parameters of the three species over the course of a year. All individuals were captured exclusively in the rainy season, and the abundance, recruitment and survival rates were higher between November and January for the three species. *Oxysternon palemo* had the highest abundance, followed by *C. spizi* and *D. mirabilis*, and the maximum displacements also followed this order. *Oxysternon palemo* was dominant in cerrado *sensu stricto* and its high abundance and ability to disperse possibly mitigate the effect of fragmentation, but the same was not observed for *D. mirabilis*, which had the lowest abundance and only one displacement recorded, a short distance. The second chapter investigated the ability of *Phyllophaga capillata* to disperse in a soybean field during the swarm period and the flight activity of this species in the laboratory. Most adults were recaptured at the shortest distance established in the study, 50 m, and only six male individuals were recaptured at the greatest experimental distance, 250 m. The flight activity experiment in the laboratory showed that most individuals (about 70% of males and 53% of females) showed the behavior of leaving the ground and flying daily. With displacements of 250 m in one night, it is possible that these insects colonize new properties or plots of large soybean plantations at the beginning of the rainy season and disperse throughout the plantations during the swarm.

Keywords: Displacement, marking-and-recapture, cerrado *sensu stricto*, soybean, dung beetles, white grubs.

SUMÁRIO

INTRODUÇÃO GERAL

A superfamília Scarabaeiodea contém cerca de 35.000 espécies descritas, é um grupo cosmopolita, com habitats distintos e hábitos alimentares muito variados (Ratcliffe 2002, Ratcliffe & Paulsen 2008). A característica morfológica diagnóstica desses besouros são suas antenas lameladas (Ritcher 1958). Não há um consenso em relação à divisão das famílias, que estão em constante revisão, e para o presente estudo foi adotada a classificação de Morón (2010) que divide esta superfamília em 12 famílias, sendo elas: Cetoniidae, Geotrupidae, Glaphyridae, Glaresidae, Hybosoridae, Lucanidae, Melolonthidae, Ochodeidae, Passalidae, Pleocomidae, Scarabaeidae e Trogidae.

Família Scarabaeidae

Os besouros rola-bosta, representantes da família Scarabaeidae e subfamília Scarabaeinae, estão distribuídos em diversos tipos de ambientes, e somam cerca de 7.000 espécies (Vaz-de-Mello et al. 2011), sendo que 726 deste total ocorrem no Brasil (Vaz-de-Mello 2019). No Distrito Federal foram registradas 112 espécies distribuídas em 34 gêneros (Oliveira 2019). Esses besouros podem ser divididos em três guildas funcionais de acordo com a maneira como manipulam o recurso, sendo endocoprídeos aqueles que ficam sobre, dentro ou logo abaixo do recurso utilizado, sem transportá-lo; paracoprídeos aqueles que tiram parte do recurso, e depositam esta porção em tuneis que cavam logo abaixo da fonte, promovendo um transporte vertical; e telecoprídeos aqueles que tiram parte do recurso, e rolam a porção, em forma de esfera, para longe do recurso antes de a enterrarem, promovendo um transporte horizontal (Halffter & Matthews 1966).

Os representantes desta subfamília podem utilizar diversas fontes de alimento, como frutos em decomposição (saprófagos), carcaças de animais (necrófagos), fungos (micetófagos) e, principalmente fezes de mamíferos (coprófagos) (Halffter & Matthews 1966, Filgueiras et al. 2009). Em função de seus hábitos alimentares e por manipularem e nidificarem utilizando o recurso como substrato, este grupo realiza importantes serviços ecossistêmicos que incluem: a ciclagem de nutrientes provenientes de matéria orgânica, o controle de populações de parasitas que ovipositam sobre fezes e carcaças (Nichols et al. 2008), ajudam na aeração e fertilidade do solo, aumentar as taxas de mineralização do mesmo, e atuar na dispersão secundária de sementes (Vulinec 2002, Alves et al. 2009, Amézquita & Favila 2010, Doube 2018, Oliveira et al. 2021). Um estudo na Amazônia brasileira demonstrou que a dispersão secundária de sementes é mais eficiente em grandes paracoprídeos, pois eles removem mais fezes da fonte, consequentemente dispersando mais sementes, e as enterram em profundidades maiores as protegendo de predação e auxiliando numa melhor regeneração das florestas (Vulinec 2000). Estes serviços decrescem com o aumento de impactos antropogênicos, pois a diversidade de rola-bostas é afetada negativamente (Noriega et al. 2021).

Devido à necessidade de utilização de fezes, a diversidade de rola-bostas geralmente está relacionada com a diversidade de mamíferos (Hanski & Cambefort 1991). Os locais que abrigam a maior diversidade de Scarabaeinae são as savanas africanas em virtude do grande número de espécies de grandes mamíferos que ainda possuem. Estes besouros são apontados como um táxon foco para monitoramento da biodiversidade por possuírem procedimentos de coletas padronizados, informações taxonômicas completas, ampla distribuição geográfica, respostas variadas a mudanças no ambiente, correlação com outros grupos, como os mamíferos, e desempenharem um papel ecológico com importância econômica (Spector 2006).

Família Melolonthidae

A família Melolonthidae se encontra inserida na superfamília Scarabaeoidea, tem cerca de 19.000 espécies descritas no mundo e estão presentes em todos os continentes (Morón et al. 2014). Algumas de suas principais características são a clava antenal formada por 3 a 7 lamelas que são usualmente maiores nos machos, escapo antenal muito menor que o flagelo, corpo de forma oval com diversas colorações, tamanho variável entre 3 e 170 mm, os 3 últimos espiráculos abdominais situados na porção superior dos esternitos, dentre outras (Cherman & Morón 2014, Morón et al. 2014). Os adultos se alimentam de diversas partes vegetais, como folhas, flores, frutos, pólen, seiva, néctar, detritos vegetais e em menor grau podem ser predadores, ao passo que as larvas se alimentam de raízes, húmus e xilema (Morón et al. 2014).

As larvas de Melolonthidae, ou corós como são comumente conhecidos, auxiliam na qualidade do solo escavando galerias e promovendo a ciclagem de nutrientes associados à matéria orgânica presente no solo, mas seus hábitos alimentares rizófagos também as tornam importantes pragas agrícolas (Valmorbida et al. 2018), principalmente por que, devido ao seu comportamento de ficarem enterradas e indetectáveis, o ataque às plantas somente fica evidente uma vez que os danos já foram causados (Oliveira et al. 2007, Cherman et al. 2013). No Brasil, alguns os gêneros englobam espécies praga de muito sucesso, caso de *Phyllophaga* e *Lyogenis* em culturas de soja e *Aegopsis* no milho, e estes organismos atacam as plantas pela parte radicular, causando cada vez mais danos à medida que o desenvolvimento da larva avança para novos ínstares (Oliveira & Frizzas 2021).

Os insetos causam grandes danos à produção agrícola brasileira gerando perdas de quase 8% do total produzido e prejuízos que chegam aos US$ 15 bilhões/ano, de forma direta por ataques aos plantios ou indireta pelo gasto com aplicação de pesticidas (Oliveira et al. 2014) e provavelmente são subestimados. Em Melolonthidae as larvas podem reduzir a produção de milho e soja em cerca de 60% (Oliveira & Frizzas 2021). Dada sua importância como pragas, para algumas espécies de Melolonthidae os ciclos biológicos assim como os sítios de oviposição são conhecidos e isto contribui para o manejo das suas populações visando reduzir o dano causado as culturas (Oliveira & Frizzas 2013, Oliveira & Frizzas 2017).

Espécies de insetos pragas agrícolas sofrem pressões seletivas das plantas de que se alimentam, como sua abundância e variações espaciais e temporais no plantio (Abdallah et al. 2016). É imperativo o conhecimento da capacidade de dispersão e parâmetros populacionais destas espécies para adotarmos estratégias eficazes de controle populacional, visto que estas variáveis influenciam no estabelecimento e na infestação de novas áreas (Lessio et al. 2021). A capacidade de dispersão de espécies praga varia de espécie para espécie, desde aquelas que apresentam valores baixos, como foi observado em *Phyllophaga bruneri* Chapin, 1932, cerca de 20 m (Oliveira & Garcia 2003), até aquelas que apresentaram altos valores de dispersão como verificado em *Popillia japonica* Newman, 1838, se deslocando por até 12 km em 24 h (Lessio et al. 2021).

Espécies modelo utilizadas no estudo

Para avaliar a capacidade de dispersão de insetos em habitats preservado e agrícola foram selecionadas quatro espécies de besouros, três da família Scarabaeidae e uma da família Melolonthidae.

No habitat preservado, representado pela fitofisionomia cerrado *sensu stricto*, foram selecionadas as espécies *Oxysternon palemo* Castelnau, 1840 (Fig. 1ª); *Coprophanaeus spitzi* (Pessôa, 1934) (fig. 1B) e *Diabroctis mirabilis* (Harold, 1877) (Fig. 1C), representantes de subfamília Scarabaeinae. Estas espécies foram selecionadas por serem comuns na fitofisionomia de cerrado *sensu stricto* e por terem um tamanho adequado para a marcação individual dos insetos (> 10 mm). Todas as três espécies apresentam dimorfismo sexual, machos de *O. palemo* possuem chifres no pronoto que estão ausentes nas fêmeas, e machos de *D. mirabilis* e *C. spitzi* apresentam chifres cabeça, estando ausentes nas fêmeas, apesar de fêmeas de *C. spitzi* apresentarem carena reta na cabeça. As três espécies fazem parte da tribo Phanaeini, que apresenta distribuição restrita às Américas (Cupello & Vaz-de-Mello 2013) e as três são paracoprídeas, visto na Região Neotropical esta guilda é mais numerosa que as outras duas (Cajaiba et al. 2017). A maioria da comunidade é amostrada rapidamente utilizando fezes (Larsen et al. 2006) porém algumas espécies apresentam preferencias ou especializações distintas, caso do gênero *Coprophanaeus*, que apresenta preferência pela necrofagia, mas ainda é atraído pelas iscas de fezes (Cajaiba et l. 2017, Silva et al. 2012).

A espécie praga selecionada para o habitat agrícola foi *Phyllophaga capillata* (Blanchard, 1851) (Fig. 1D) representante da família Melolonthidae. Esta espécie foi selecionada por ser a principal praga de soja no Distrito Federal, por ser abundante no início do período chuvoso e por ter um tamanho adequado para a marcação individual (> 10mm). Esta espécie também apresenta dimorfismo sexual, onde machos possuem as lamelas antenais mais longas que as fêmeas. *Phyllophaga capillata* é uma espécie univoltina e suas larvas apresentam três instares, além de seu ciclo de desenvolvimento durar em torno de 12 meses. O período de revoada desta espécie se encontra no início do período chuvoso, entre Outubro e Dezembro, que é o período dos cultivos no Cerrado. Assim como outros Melolonthidae, *P. capillata* procura áreas com presença de plantas altas para a postura de seus ovos, visto que a presença de plantas indica raízes, que são a fonte de alimento dos imaturos (Oliveira et al. 2007, Oliveira & Frizzas 2017).

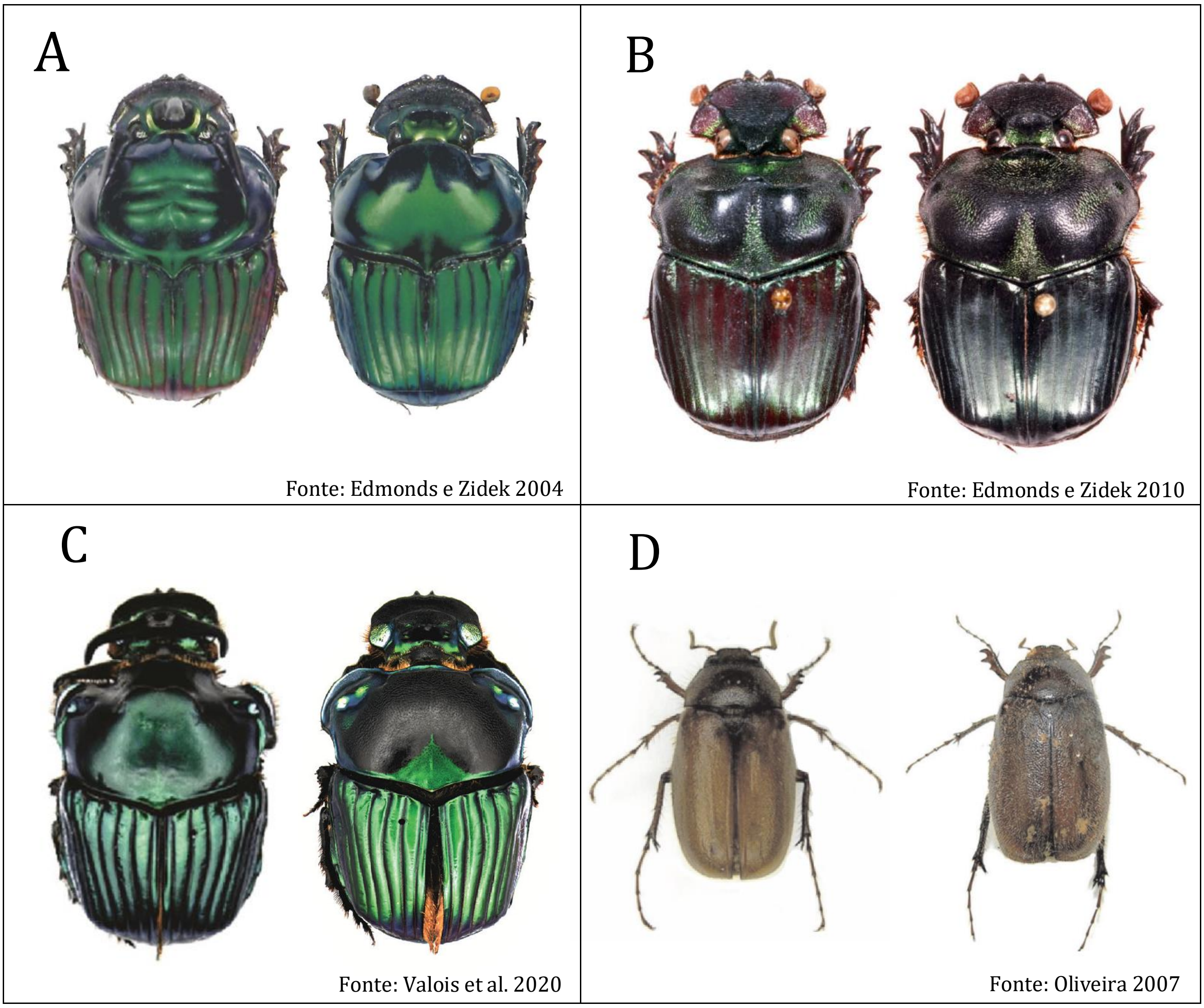

Figura 1. Espécies modelo para avaliar a dispersão de Scarabaeoidea em habitats preservado e agrícola. A) *Oxysternon palemo*; B) *Coprophanaeus spitzi*; C) *Diabroctis mirabilis*; D) *Phyllophaga capillata*. Machos de cada espécie estão à esquerda e fêmeas à direita.

Distribuição e dispersão de insetos

Organismos se dispersam por diversos motivos, geralmente ligados à procura de recursos, e realizam três tipos de deslocamento, sendo o primeiro local com ênfase no forrageamento de recursos, como alimento ou parceiros reprodutivos; o segundo voltado a explorar além de seu habitat, pela procura de recursos como tocas ou ninhos que eventualmente serão seu novo habitat, mais comum em aves mamíferos; e o terceiro a migração, que é a dispersão para fora do habitat que ocorre entre regiões. Inicialmente não é interrompido quando recursos como alimento ou tocas são encontrados, é permanente em organismos com baixa longevidade e pode ser repetido em espécies que vivem por anos (Dingle & Drake 2007).

A dispersão em insetos, pincipalmente em pragas, é essencial à sobrevivência pois afeta o fluxo gênico, a capacidade de colonizar novos plantios e a transmissão de caracteres benéficos como a resistência à inseticidas, e o controle destes organismos é problemático devido à infestações ocorrerem via dispersão de outras áreas (Kim & Sappington 2013). Desta forma o conhecimento da capacidade de dispersão destes organismos se torna imperativo para adotar estratégias de manejo eficazes.

A distribuição geográfica das espécies está diretamente relacionada às limitações na capacidade de dispersão dos organismos (Hortal et al. 2012) pois observa-se que insetos ápteros possuem menor capacidade de dispersão, possivelmente resultando em uma distribuição mais restrita que aqueles que voam.

O voo é uma das formas mais comuns para a dispersão encontrada nos insetos e do ponto de vista metabólico, é a atividade que mais demanda energia destes estes organismos (Verdú et al. 2006). A razão entre o comprimento e a largura das asas membranosas não apresenta diferenças em diversas tribos de Scarabaeinae (Bai et al. 2012). Além de adaptações na asa membranosa, os élitros entre diferentes famílias de Coleoptera podem ser diferenciados e adaptados ao voo, caso de alguns gêneros que possuem fissuras nas laterais dos élitros e permitem um voo com as asas membranosas abertas, mas os élitros completamente fechados, que neutralizam o efeito de turbulência e baixa aerodinâmica de voo, de maneira contrária ao que ocorre nas espécies de besouros que voam com os élitros abertos (Frantsevich et al. 2015).

Diferentes gêneros apresentam períodos de atividade assincrônicos, e um trabalho com rola-bostas na Guiana Francesa constatou que o gênero *Oxysternon* apresenta atividade de voo durante o dia, ao passo que o gênero *Coprophanaeus* voou em horários crepusculares, além de vários outros gêneros apresentarem voos noturnos, matinais e bimodais, voando em diferentes períodos do dia (Feer & Pincebourde 2005). O voo é uma atividade que gera calor (Verdú et al. 2006) e foi constatado que espécies florestais diurnas tendem a ter menor tamanho corporal que espécies noturnas e crepusculares, além das colorações variarem de vibrantes para escuras dependendo do período de atividade (Feer & Pincebourde 2005). Essas diferenças na coloração e no tamanho podem estar ligadas à termorregulação.

O tamanho corporal varia de espécie para espécie, e também entre indivíduos da mesma espécie. Provavelmente espécies de maior tamanho corporal dispersam melhor que espécies pequenas, visto que em habitats antropizados a abundâcia de insetos pequenos é superior (Nichols et al. 2007, Tonelli et al. 2018) pois provavelmente dispersam para áreas de melhor qualidade. Além disso, foi observado que espécies de tamanhos distintos apresentam diferentes comportamentos em relação ao voo, onde as pequenas esperam por um estímulo olfatório com as lamelas antenais abertas enquanto estão em repouso, e após a percepção do odor, voam em direção ao recurso à menos de 1 m de altitude, ao passo que as de grande tamanho corporal apresentam voo de cruzeiro, pois voam e forrageiam ativamente à procura de recurso ao invés de repousarem sobre a vegetação, normamente entre 1 e 2 m de altura (Peck & Forsyth 1982). Em Scarabaeinae, um estudo na Guiana Francesa constatou que besouros coprófagos são geralmente menores que os necrófagos, e não apresentam diferenças de tamanho entre as guildas funcionais (Feer & Pincebourde 2005).

A diminuição da similaridade entre comunidades em diferentes áreas pode ser explicada por dois fatores: características do nicho da espécie, como tolerâncias ambientais, capacidade de colonização, sobrevivência, reprodução; e o outro fator é a capacidade de dispersão, pois organismos com baixa capacidade que apresentam distribuição agregada, independentemente das características ambientais mostram que aquelas populações são estruturadas espacialmente (Kobayashi & Sota 2016). Logo podemos concluir que a distribuição dos organismos está diretamente relacionada à variáveis ambientais, que filtram as espécies presentem naquele ambiente, e da capacidade de dispersão dos indivíduos.

As variáveis ambientais também podem influenciar na distribuição das espécies (Lobo & González-Chang 2022). Fatores como a temperatura e períodos do ano podem influenciar na atividade dos organismos, pois altas temperaturas coincidem com maior dispersão dos insetos e diferentes períodos do ano resultam em picos de atividade distintos entre machos e fêmeas (Mansfield et al. 2016). O tipo de cobertura vegetal é um fator importante na distribuição das espécies no habitat (Barretto et al. 2019). Fatores como a vegetação rasteira e a topografia encontradas em diferentes locais de coleta podem ser responsáveis por uma modificação na proporção e abundância das espécies de Scarabaeinae e outros insetos encontradas nestes sítios (Peck & Forsyth 1982, Winterbourn et al. 2007). Em outras famílias de Coleoptera, como Tenebrionidae, e em áreas desérticas dos Emirados Árabes Unidos, foi observado que uma maior abundância e riqueza de espécies ocorre, durante o período mais quente do ano, geralmente em áreas com presença de vegetação arbustiva (Bartholomew & Moghrabi 2018). Em Carabidae foi observado, em uma paisagem agrícola, que diferentes tratamentos relacionados ao manejo das plantações resultaram em respostas distintas da comunidade, onde áreas de vegetação mais homogênea apresentaram maior densidade de besouros, ao passo que áreas de maior diversidade funcional de plantas abrigaram uma maior riqueza (Rouabah et al. 2015). Desta forma, percebe-se que a estrutura vegetal (seja pelo tipo de formação, como a arbustiva, seja pelo microclima ou pela heterogeneidade) influenciam a distribuição, riqueza e abundância das espécies de besouros.

Em uma paisagem de floresta tropical alagada por hidroelétrica, observou-se que as ilhas mais isoladas e de menor área suportaram uma menor diversidade de rola-bostas, e em ilhas pequenas a abundância de besouros diminutos foi superior à de grandes besouros, o que demonstra diferentes capacidades de dispersão (Storck-Tonon et al. 2020). Dependendo da capacidade de dispersão algumas espécies podem até ocupar áreas antropizadas caso haja recursos suficientes, caso de certos rola-bostas e as fezes de mamíferos domésticos (Simões-Clivatti & Hernández 2022). Há relatos de espécies de Melolonthidae que apresentam maior dispersão em ambientes fragmentados, visando a procura de habitats de melhor qualidade (Camacho et al. 2021), ao passo que espécies com menor capacidade de dispersão estão sujeitas à maiores chances de extinção local em habitats antropizados (Fattorini 2020).

Um estudo na Nova Zelândia avaliou a dispersão em Plecoptera, Trichoptera e Ephemeroptera, e observaram que mais fêmeas foram capturadas, demonstrando um viés sexual claro naquelas populações, e algumas dispersaram para amadurecer após sua emergência, procurando novos habitats, ao passo que outras procuravam sítios de oviposição. Os autores também perceberam que diferentes espécies utilizaram a paisagem de forma distinta, demonstrando preferência por áreas específicas dentro da paisagem (Winterbourn et al. 2007). Um estudo australiano com Ephemeroptera verificou se populações colonizavam novas áreas dispersando pela água, como ninfas ou pelo voo como adultos, e com marcadores genéticos constataram que diferentes riachos tendem a ser colonizados por adultos, visto que as populações apresentaram composição genética similar entre riachos próximos, de diferentes bacias (Schmidt et al. 1995).

No Japão um estudo com insetos micetófagos avaliou se as comunidades florestais eram estruturadas pela capacidade de dispersão, através da composição genética dos insetos. Foi constatado que a dispersão teve influência negligenciável na estrutura da comunidade, que provavelmente foi estruturada por fatores ambientais não avaliados (Kobayashi & Sota 2016). Estes insetos utilizam recursos distribuídos de forma aleatória (fungos decompositores de madeira e madeira em decomposição) e possivelmente têm boa capacidade de dispersão para forragear. Aqui pode-se fazer um paralelo com rola-bostas, que também utilizam recursos distribuídos aleatoriamente, e que são efêmeros (fezes e carcaças), apontando para a hipótese de que devem ser bons dispersores.

Escala populacional

Nas regiões tropicais os rola-bosta são mais ativos no período chuvoso (Halffter & Mathews 1966) e no Cerrado este aumento na atividade dos insetos resulta em maiores abundâncias encontradas durante as chuvas deste período (Milhomem et al. 2003, Frizzas et al. 2020). O período chuvoso no Distrito Federal (Outubro-Março) também é o período de maior atividade para *Phyllophaga capillata*, pois é neste intervalo que ocorre a revoada nesta espécie (Oliveira et al. 2007), e este período é caracterizada pela forte atividade dos adultos, que deixam o solo em grande número de maneira sincrônica e procuram parceiros para reproduzir. Dois fatores importantes para a emergência dos adultos de rola-bosta são disponibilidade de recursos e precipitação (Halffter & Edmonds 1982), e como os adultos estão em diapausa no período de seca (Oliveira & Frizzas 2013, Martínez et al. 2022), observa-se que os insetos parecem acompanhar a sazonalidade no Cerrado. Apesar de todos os serviços prestados pelos rola-bosta, na região Neotropical pouco se conhece de aspectos de dinâmica populacional, habitat e capacidade de dispersão (Barretto et al. 2019), e apesar da simplicidade aparente de “NMIE” (natalidade, mortalidade, imigração e emigração), a dinâmica populacional não é tão simples quanto aparenta quando são adicionadas interações, ecologia química e história de vida dos organismos (Price & Hunter 1995).

A compreensão da dinâmica de populações é de extrema importância para facilitar a formular estratégias viáveis de conservação dos organismos, e é mais fácil de ser observada em indivíduos adultos, porém em espécies longevas a identificação de parâmetros populacionais como a estimativa de tamanho populacional, sobrevivência e recrutamento fica mais complexa (VanderWerf & Young 2016). Levando em consideração que dinâmica de populações é mais facilmente observada em adultos, e que em diversas espécies de besouros os imaturos estão abaixo do solo, provavelmente as estimativas populacionais nestes grupos são subestimadas. Por outro lado estes organismos não são tão longevos quanto vertebrados, logo a mensuração desses parâmetros deve ser menos complexa.

Pequenos mamíferos adotam a estratégia de aumentar seu potencial reprodutivo (ou seja, o recrutamento de novos indivíduos) para manterem suas populações, ao invés de focarem na sobrevivência e longevidade dos adultos, porém foi constatado que em condições de alimento em abundância, a taxa de reprodução não é significativamente alterada, mas a sobrevivência dos indivíduos dispara, resultando em uma infestação (Korpimaki et al. 2004). Algo similar ocorre em insetos praga, que sincronizam seu desenvolvimento com variáveis climáticas favoráveis que acabam coincidindo com plantios, gerando uma situação de abundância de recursos, e subsequente infestação (Oliveira & Frizzas 2017).

Estudos na escala de populações oferecem a possibilidade de determinar a estrutura populacional, que engloba parâmetros como a densidade populacional, interação entre indivíduos e variáveis ambientais, variabilidade genética, sucesso reprodutivo, fluxo gênico, estratégias adaptativas ao meio, além dos padrões de distribuição e dispersão dos organismos (Martins 1987, Caldato et al. 1999). Nesta escala, os estudos em Scarabaeinae ocorrem em menor número quando comparados aos trabalhos na escala de comunidade, e trabalhos que visam avaliar a longevidade das espécies são ainda mais escassos, porém há relatos que o desenvolvimento dos imaturos (da oviposição à emergência do adulto) leve até um mês e meio, e o tempo de vida médio dos adultos varie entre um mês e meio até três anos, com o relato do tempo de vida do adulto para uma espécie de *Dichotomius* ultrapassando cinco anos de vida (Cultid-Medina & Martínez-Quintero 2019). Possivelmente o longo tempo de vida de algumas espécies está associado ao comportamento de diapausa, que potencializa a sobrevivência de indivíduos nos períodos desfavoráveis como o inverno rigoroso, forte seca ou falta de recursos (Nayar & Evans 2019) ocorrendo em Scarabaeinae (Edwards 1986, Edwards 1988, Bang et al. 2004), Melolonthidae (Nayar & Evans 2019) e também em outras famílias de Coleoptera, como Chrysomelidae (Lehmann et al. 2012).

O bioma Cerrado e a fragmentação de habitat

O Cerrado é o segundo maior bioma brasileiro, com cerca de 2 milhões de km^2, sendo superado apenas pela Amazônia (Klink & Machado 2005, Prevedello & Carvalho 2006). É um bioma que possui rica biodiversidade, ainda parcialmente descrita, e desempenha um papel de capital importância para a manutenção de diferentes serviços ecossistêmicos e oferta de água doce no Brasil (Overbeck et al. 2015). É um bioma formado por diversas fitofisionomias, desde as mais abertas, como os campos compostos por gramíneas e herbáceas, até as mais fechadas, compostas por matas e árvores de grande porte (Ribeiro 2011). Estas diferentes fitofisionomias suportam uma comunidade de rola-bosta distinta pois é possível encontrar espécies como *Oxysternon palemo* e *Coprophanaeus sptzi* em áreas de cerrado *sensu stricto* (Cunha & Frizzas 2020, Gigliotti et al. 2022), ao passo que gêneros como *Dichotomius* e *Eurysternus* são mais comuns em fitofisionomias mais fechadas como matas (Corrêa et al. 2019, Silva et al. 2020).

Apesar de sua relevância, o bioma vem sofrendo uma severa perda e fragmentação de áreas nativas. O Cerrado perdeu cerca de 143 mil km^2 entre 2002 e 2018 e o norte do bioma é considerado um ponto crítico de desmatamento (Rosan et al. 2022), gerando diversos fragmentos, que são remanescentes de vegetação nativa circundados por uma matriz antropizada diferente da original; o tamanho e o grau de isolamento destes fragmentos podem influenciar na permanência de certas espécies, e áreas de plantio se mostraram mais danosas e resultaram em mais fragmentos do que áreas de pastagens (Carvalho et al. 2009). No Distrito Federal, antes da construção de Brasília o tamanho médio dos fragmentos no Cerrado era de aproximadamente 5,8 mil km^2 em 1953 e foram reduzidos para um tamanho médio de 4,3 km^2 em 2013, ao passo que a matriz urbana se desenvolveu e hoje o DF se divide em 43,81% em áreas nativas de Cerrado, 44,38% em áreas agrícolas e 10,14% em áreas urbanas (Jacob et al. 2021).

Um estudo italiano com várias famílias em Coleoptera verificou que os Scarabaeoidea coprófagos (Scarabaeidae) foram os besouros mais suscetíveis à extinção por perda de habitat, onde 25% de perda de habitat resultaria na extinção de 9% das espécies, e em cenários mais drásticos 50% de perda de habitat resultaria na extinção de 21% das espécies de rola-bosta daquela área, ao passo que os Scarabaeoidea fitófagos (grupo onde Melolonthidae se encontra) apresentaram maior resistência à este impacto potencialmente pela sua boa dispersão, perdendo apenas 11% das espécies em 50% de redução de habitat.

No entanto, tamanho dos fragmentos se mostrou consistentemente importante para ambos, coprófagos e fitófagos (Fattorini 2020).

O uso da terra também pode influenciar de forma negativa nas comunidades de rola-bosta, caso da pecuária, que é uma das principais razões para a fragmentação de habitat devido à conversão de áreas nativas em pastos. Foi constatado que áreas designadas à pecuária alteraram a comunidade de Scarabaeinae e afetaram negativamente os serviços ecossistêmicos que o grupo realiza (Arias-Álvarez et al. 2022), além de reduzir a riqueza e a abundância em Cetoniidae (Correa et al. 2021).

Desta forma, ambientes fragmentados como o Cerrado podem afetar negativamente a comunidade de rola-bostas e conhecer como estas espécies utilizam o habitat e o quanto conseguem dispersar é de extrema importância para o manejo do grupo. Como os rola-bosta são organismos sensíveis à impactos antrópicos (Nichols et al. 2007) e tendo em vista a condição de alerta em que o Cerrado se encontra, o monitoramento do grupo e sua capacidade de dispersão em unidades de conservação pode ser uma ferramenta útil para inferir se estes organismos seriam capazes de dispersar entre fragmentos de áreas mais afetadas, com a possibilidade de manter populações viáveis e capazes de prover seus serviços ecossistêmicos. Tem-se ainda o outro lado de se conhecer a dispersão, caso de espécies pragas, que causam grandes danos anuais aos diferentes cultivos brasileiros. No Distrito Federal cerca de 60% das áreas cultivadas cultivam soja durante o período chuvoso (IBGE 2022; CONAB 2022) e as propriedade ficam muito próximas umas das outras, pelo pequeno tamanho do DF. Compreender o quanto estas espécies dispersam é um passo essencial para adotarmos estratégias de controle populacional e prevenção às infestações em outras áreas.

Portanto, esta tese tem como objetivo avaliar a capacidade de dispersão de quatro espécies de Scarabaeoidea em habitats preservado e agrícola. Para atingir esse objetivo esta tese foi estruturada em dois capítulos. O primeiro, focado na conservação, foi dedicado a avaliar a dispersão e os parâmetros populacionais de três espécies de rola-bosta (Scarabaeidae: Scarabaeinae) em uma área nativa de Cerrado, visando entender a capacidade de estabelecimento destas espécies no bioma pensando no seu atual cenário, composto por vários fragmentos, e auxiliar no manejo desse grupo em parques e unidades de conservação. Já o segundo capítulo, focado no manejo de pragas, é dedicado a estudar a dispersão de uma espécie praga de Melolonthidae em uma área de plantio de soja, durante o período de revoada da espécie para auxiliar no manejo do inseto em talhões ou propriedades próximas às áreas infestadas.

Capítulo 1: "Dispersão, estrutura e tamanho populacional de três espécies de Scarabaeinae em cerrado *sensu stricto* no Distrito Federal, Brasil" com o objetivo de avaliar parâmetros populacionais de três espécies de rola-bosta (*Oxysternon palemo*, *Coprophanaues spitzi* e *Diabroctis mirabilis*), sua capacidade de dispersão ao longo de um ano e o tamanho dos indivíduos de forma intraespecífica, em uma área de cerrado *sensu stricto* do Parque Nacional de Brasília.

Capítulo 2: "Padrões de dispersão e atividade de voo de *Phyllophaga capillata* (Blanchard) (Coleoptera: Melolonthidae) em plantio de soja no Brasil Central" com o objetivo de comparar a capacidade de dispersão de machos e fêmeas de *P. capillata* ao longo do período de revoada desta espécie, verificando se ocorrem diferenças nesta distância no início, meio e fim do período reprodutivo, além de observar a atividade de voo dos adultos.

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Capítulo 1

Dispersal, structure and population size of three species of Scarabaeinae in cerrado *sensu stricto* in Distrito Federal, Brazil

Manuscrito submetido para Landscape Ecology e formatado nas normas da revista

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ABSTRACT

Context Knowledge of the dispersal capacity, population structure and size, and the pattern of spatial distribution of species, seems to be essential for the design of conservation strategies. For Scarabaeinae few studies have evaluated the ability of individuals to disperse within different landscapes.

Objectives Here, we evaluate the dispersal capacity and estimate population parameters of three species of dung beetles (*Oxysternon palemo*, *Coprophanaeus spitzi*, and *Diabroctis mirabilis*) in cerrado *sensu stricto*.

Methods Three species were selected for the study conducted in an important Conservation Unit of the Brazil. The method used was Capture-mark-recapture. Adult capture were conducted monthly for 12 months using pitfall traps baited with human feces that remained in the field for three alternate days of the week.

Results We found 2,297 individuals, all captured exclusively in the rainy season, of which 1,639 were *O. palemo*, 354 *C. spitzi* and 304 *D. mirabilis*. There was a significant difference in the abundance of the species, where *O. palemo* was dominant. November and December were the months of highest abundance, and the period between November and January was the most important in recruitment and survival rate.

Conclusions We identify species that can disperse long distances and have high abundance, being important from the point of view of conservation because these species may be able to perform ecosystem services in different environments. On the other hand, species with more local habits, are dependent on management policies and conservation, since habitat fragmentation may represent a threat to the survival of the species.

Keywords Dung beetles, Jolly-Seber, Displacement, Population parameters, Fragmentation

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Introduction

Beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae) are commonly called dung beetles due to the habit of some species to form spheres of feces and roll them. These organisms use carcasses, fungi, decaying fruits, and mainly mammal feces as food resources (Halffter and Mathews 1966). They perform important ecosystem services such as feces removal, secondary seed dispersal, parasite suppression, and nutrient cycling (Nichols et al. 2008). In Brazil, around 784 species of Scarabaeinae have been reported, many of which occur in the Cerrado biome (Vaz-de-Mello 2023), which, despite constantly suffering from anthropogenic action, harbors a unique and specific community of dung beetles (Oliveira et al. 2021).

Knowledge of the spatial distribution of species is an important factor, whether for pest species, aiming at population control, or in native species, aiming at management and conservation. Spatial distribution, in turn, is influenced by several biotic and abiotic factors, such as seasonality and ability of individuals to disperse, which are determinants for Artrhopoda activity (Halffter and Mathews 1966; Milhomem et al. 2003; Durães et al. 2005; Silva et al. 2010; Martello et al. 2016; Filho et al. 2021; Mavasa et al. 2022), resulting in changes in the displacement of these organisms in different seasons of the year.

Knowledge of the dispersal capacity, population structure and size, and consequently the pattern of spatial distribution of species, seems to be essential for the design of conservation strategies for different species of organisms. For Scarabaeinae some studies have sought to understand the dispersal capacity of individuals within different landscapes, seeking to understand which types of land uses are more or less attractive to these species (Arellano et al. 2008; Cultid-Medina et al. 2015; Barretto et al. 2019). With data on habitat preference, dispersal ability, population structure and size, and activity period throughout the year, conservation strategies can be adopted. For most dung beetles, a group that features several bioindicator species, little information is available regarding dispersal ability. Some species have a large dispersal capacity, for example *Digitonthophagus gazella* who could disperse over 800 km in a year (Barbero and López-Guerrero 1992) and others show a lesser dispersal ability like *Heteronychus arator*, dispersing 0.7 m a day (Mansfield et al. 2016).

The Capture-mark-recapture (CMR) method has been one of the most widely used to track the dispersal of individual organisms within different landscapes (Arellano et al. 2008; Martínez-Quintero et al. 2013; Cultid-Medina et al. 2015; Barretto et al. 2019). This method allows estimating some population parameters, such as population size, recruitment and survival rate (Arellano et al. 2008; Cultid-Medina et al. 2015; Barretto et al. 2019), as well as enabling specific monitoring for each individual. Depending on the length of the study or the longevity of the target species, permanent marking methods, which do not affect the survival of individuals, are indicated (Cultid-Medina and Martínez-Quintero 2019). These markings last for years, resist abiotic factors, and can be applied to species with different habits, such as those that burrow. The marking of identifying numerals on the pronotum of target insects using a grinding tool has been indicated for studies with dung beetles because it is a permanent and non-invasive marking, but with the disadvantage that it is only applicable for medium and large individuals (Martínez-Quintero et al. 2013).

Changes in a given population occur primarily through births, deaths, and the dispersal of individuals, such as emigration and immigration (Price and Hunter 1995). These changes in turn interfere directly in the population density of species. Population density can be used as a tool in the conservation of species, and can be analyzed by how a given population responds to environmental change on a local or regional scale (Nichols et al. 2013).

Body size in insects shows inter- and intraspecific variations, and this characteristic is affected by factors such as temperature (Kingsolver and Huey 2008) and the quality and quantity of food sources available to individuals (Moczek and Nijhout 2003). Larger body size rollers usually remove a more expressive amount of resource than smaller beetles (Gregory et al. 2015; Carvalho et al. 2018), and in general large excavators (paracoprids) require a greater amount of resource than large rollers (telecoprids) (Sullivan et al. 2016). Body size may be linked to the ability to cope with anthropogenic impacts, such as habitat fragmentation, which in turn has a bearing on the ability of individuals to disperse and, consequently, the spatial distribution of species. Scarabaeinae of larger body size tend to be less abundant in fragmented and anthropized environments (Nichols et al. 2007; Tonelli et al. 2018), and these larger individuals generally have longer flights in search of food resources while smaller species seem to have a more restricted dispersal (Peck and Forsyth 1982).

Generally in tropical regions, Scarabaeinae are active when rainfall is present (Halffter and Mathews 1966). Several studies have shown that in the Cerrado the abundance of dung beetles is higher in the rainy period of the year (Milhomem et al. 2003; Durães et al. 2005; Silva et al. 2010; Martello et al. 2016; Frizzas et al. 2020) being the activity of these organisms strongly marked by seasonality, consequently affecting the dispersal of Scarabaeinae species throughout the year.

The Cerrado, Brazil's second largest biome, is a tropical savanna that presents diverse types of habitats, with herbaceous, grassy, shrub formations and the forests (Goodland 1971; Ribeiro 2011). Due to the complexity and high biodiversity of this biome and because this ecosystem is highly threatened by anthropic actions, it is imperative that government agencies adopt management and conservation measures. In this context, Scarabaeinae can be important tools as bioindicators to assist in decision making and in the formulation of management and conservation protocols for this ecosystem, because they are abundant on a local and global scale, have a relatively uniform collection methodology and the ability to be representatively sampled in a few days of collection (Nichols and Gardner 2011). Studies of sensitive organism groups in threatened habitats are important to assess how populations and communities are responding to these disturbances. Knowing the population parameters of dung beetles in the Cerrado, and knowing how well individuals are able to disperse can help management and conservation strategies for this habitat and also for this important group of organisms.

The objective of this study was to evaluate the dispersal ability and estimate population parameters (population size, recruitment and survival rate) for three species of dung beetles in an area of cerrado *sensu stricto* in the Brasília National Park/DF (Brazil).

Materials and methods

Study area

The study was conducted in the Brasília National Park (PNB), an important Conservation Unit of the Federal District. The PNB has an area of 42,355.54 ha, and is located in the northwestern portion of the Federal District (Fig. 1). The main soil types are Latosols, Cambisol and Hydromorphic soils. According to Köppen's climate classification, the climate is of the Aw type: tropical savanna, and the average monthly temperatures range from 18° C in the coldest months to 22° C in the hottest months. The average annual rainfall is close to 1,600 mm, and is concentrated during the rainy season in the Federal District, between October and March. The National Park is home to several types of Cerrado physiognomic forms, such as gallery forest, cerrado *sensu stricto*, and variations of grassland formations.

Five areas were selected in the Brasília National Park (Fig. 1), all located in the cerrado *sensu stricto*, which is the most common and widely found Cerrado physiognomy in the park. This physiognomy is characterized by being more open with sparse trees and an open canopy of 3 to 8 meters high, with the presence of grasses and herbaceous plants (Oliveira-Filho and Ratter 2002).

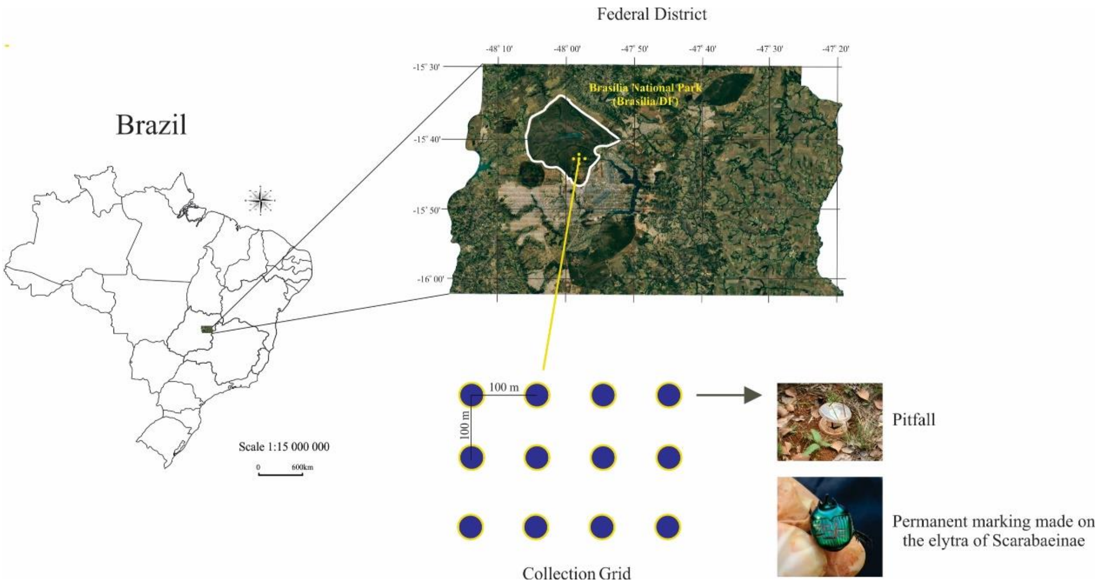

Figura 2. Location of the study areas showing the five grids and the pitfall used to collect and mark the specimens of *Coprophanaeus spitzi*, *Oxysternon palemo* and *Diabroctis mirabilis* in the Brasilia National Park (PNB) between October/2020 and March/2021

Capture-mark-recapture of adult Scarabaeinae

Initially, three previous collections were conducted in the PNB in February 2020 to verify which were the most abundant species of dung beetles and with size greater than 10 mm. The collections were made with three pitfall traps baited with human feces in each of the selected areas, totaling 12 pitfalls that remained in the field for 96 h. The individuals collected were taken to the laboratory, morpho specified and identified. The three most abundant species (*Oxysternon palemo*; *Coprophanaeus spitzi* and *Diabroctis mirabilis*) were selected for the study.

Adult capture periods of the three selected Scarabaeinae species were conducted monthly for 12 months (August 2020 to July 2021), using modified pitfall-type traps baited with human feces that remained in the field for three alternate days of the week. On one week of each month, on Mondays, Wednesdays, and Fridays the pitfalls were set up in the field. On Tuesdays, Thursdays, and Saturdays the pitfalls were monitored and individuals of all three species were counted, marked, and released at the capture site, and the pitfalls were removed from the field. On these days the previously marked and recaptured individuals were recorded. The days when pitfalls were removed were necessary to allow the marked animals to disperse freely across the landscape (Peck and Forsyth 1982; Barretto et al. 2019).

Each pitfall consisted of a 1-liter plastic pot, buried with the opening above ground level. A smaller container containing about 20 g of human feces was placed over the opening of the larger pot, secured by a wire. Holes were drilled in the side of the pots to prevent them from overflowing in the rainy season. As it was necessary to collect live specimens, the pitfall did not have the mixture of water and detergent to kill the insects (Cultid-Medina et al. 2012). Instead, soil (200 g) was added from the same site where the pitfall was installed, allowing the beetles to bury themselves, decreasing the chance of escaping the trap by flight. After the collecting pot was buried, a lid was placed with openings that allowed the beetles to enter but did not allow the specimens to leave.

The captures were made in five areas of cerrado *sensu stricto*, and in these areas on each collection date, 12 pitfalls were installed, 100 m apart from each other (Silva and Hernández 2015), arranged in a 3x4 grid (Fig. 1), totaling 60 pitfalls/collection date.

The adults of the three captured species were marked with Arabic numerals in sequence, from number 1 to the umpteenth captured. Each species had its own number sequence. The markings were made on the elytra with the aid of a grinder (Dremel 8220) according to previous work done with Scarabaeinae (Martínez-Quintero et al. 2013; Cultid-Medina et al. 2015; Barretto et al. 2019). The advantage of this type of marking is that it does not interfere in the behavior and dispersal of the individuals, besides being permanent.

Variables analyzed

The following variables were evaluated for each captured individual: body size, sex and period of the year (dry and rainy), as well as population parameters in the three species. The marking of individuals, as well as the measurements of size and sex, were measured *in loco* on the same days that the traps were removed from the field.

The body size of the beetles was measured using a digital pachymeter (Mtx 150 mm), and the length (mm) from the clypeus to the pygidium was recorded. A posteriori the individuals were ranked by size, continuously, from smallest to largest within species. The sex of individuals was verified by sexual dimorphism in the three species, with males of *O. palemo* and *D. mirabilis* having horns, which are absent in females, and in *C. spitzi* females have a carina on the underside of a concavity on the pronotum, while males have the carina on the top (Edmonds & Zidek 2004, Edmonds & Zidek 2010, Valois et al. 2020).

Population parameters of the three species were checked at the end of the study, and data such as population size, recruitment rate, and survival rate of the populations of the three species were estimated.

The variation in abundance of the species was compared in the rainy season. A thermo-hygrometer (Minipa Mt-242a) and a pluviometer were used to record the temperature and precipitation at each capture site throughout the study period. As the collections spanned 12 months, the period of the year in which the individuals were collected was also evaluated, being the rainy period considered from October to March, and the dry period considered from April to September in the Federal District.

Data analysis

All data analyses were performed with R Program (R Core Team 2019). The data obtained did not meet normality assumptions relating to the residues and the homogeneity of the variance (Shapiro-Wilk $p < 0.0001$). Therefore, nonparametric analyses were used to verify the differences in abundance and size among beetle species.

The beetle species abundance was compared by Kruskal–Wallis analysis (Hollander and Wolfe 1973; Conover 1980), and the means were separated by a post hoc analysis using Nemenyi post hoc comparison with a Tukey correction using the 'kwAllPairsNemenyiTest' function in the R package 'PMCMRplus' (Pohlert 2014).

The Wilcoxon-Mann Whitney U-test (Conover 1980) was used for size comparison between the sexes for each beetle species, also using the package 'PMCMRplus' (Pohlert 2014). For each species, we determined the proportion of burrowing beetles recaptured during the study.

We used the Jolly-Seber method (Jolly 1965; Seber 1965) and estimated, for each collection date, three population parameters: population size (Nt), new beetles (Bi: from recruitment and immigration), and survival rate (Φ) (Southwood and Henderson 2000). For open populations, the survival rate is calculated assuming that migration and mortality of individuals are equal (Jolly 1965; Seber 1965). The R package FSA (Ogle 2017) was used to calculate the population parameters.

To quantify the dispersal of individuals, the program Google Earth Pro was used, measuring the distance of the recapture points in a straight line. The distance was separated into two components, monthly distance (m) and total distance (t). The monthly distance represents the distance an individual disperses from month to month, and the total distance represents the sum of an individual's monthly distances over the twelve months.

Results

We captured 2,297 individuals of the target species throughout the study, of which 1,639 (71.3%) were *O. palemo*, 354 (15.4%) were *C. spitzi* and 304 (13.2%) were *D. mirabilis* (Table 1), and all other specimens were discarded. There were 183 recapture records for the three species, and the most recaptured species was *O. palemo*, with 156 recaptures, followed by *C. spitzi*, with 19 recaptures and *D. mirabilis* with 8 recaptures. All captures and recaptures of the three species occurred exclusively in the rainy season (between October 2020 and March 2021).

Population parameters

We observed a significant difference in abundance among the three species studied (Kruskal-Wallis chi-squared = 12.956, df = 2, p-value = 0.004733), with *O. palemo* showing the highest abundance (Table 1; Fig. 2). There was no significant difference in abundance between *C. spitzi* and *D. mirabilis* (Table 1). The abundance peaks occurred in November for *C. spitzi* (126 individuals) and *D. mirabilis* (209 individuals) and December for *O. palemo* (707 individuals) (Fig. 2).

With respect to population parameter estimates, the largest population size for *O. palemo* occurred in December, with 14,036 individuals, and November showed the highest survival and recruitment rates for this species. In *C. spitzi* the largest population size (7,021 individuals) and survival rate occurred in January, while the highest recruitment occurred in November. In *D. mirabilis*, the largest population size (1,296 individuals) occurred in December, as well as the highest recruitment and survival rate (Table 2).

The size of adult dung beetles did not differ between males and females for *C. spitzi* (Wilcoxon-Mann Whitney U-test = 0.23594, df = 1, p-value = 0.6272); but there was a significant difference in the size of males and females in *D. mirabilis* (Wilcoxon-Mann Whitney U-test = 11.344, df = 1, p-value = 0.0007) and in *O. palemo* (Wilcoxon-Mann Whitney U-test = 80.501, df = 1, p-value < 2.2e-16), where females showed larger body size than males. The sex ratio in all three species was close to 1:1, with *O. palemo* and *C. spitzi* showing about 55% males and *D. mirabilis* showing about 53% females (Table 1).

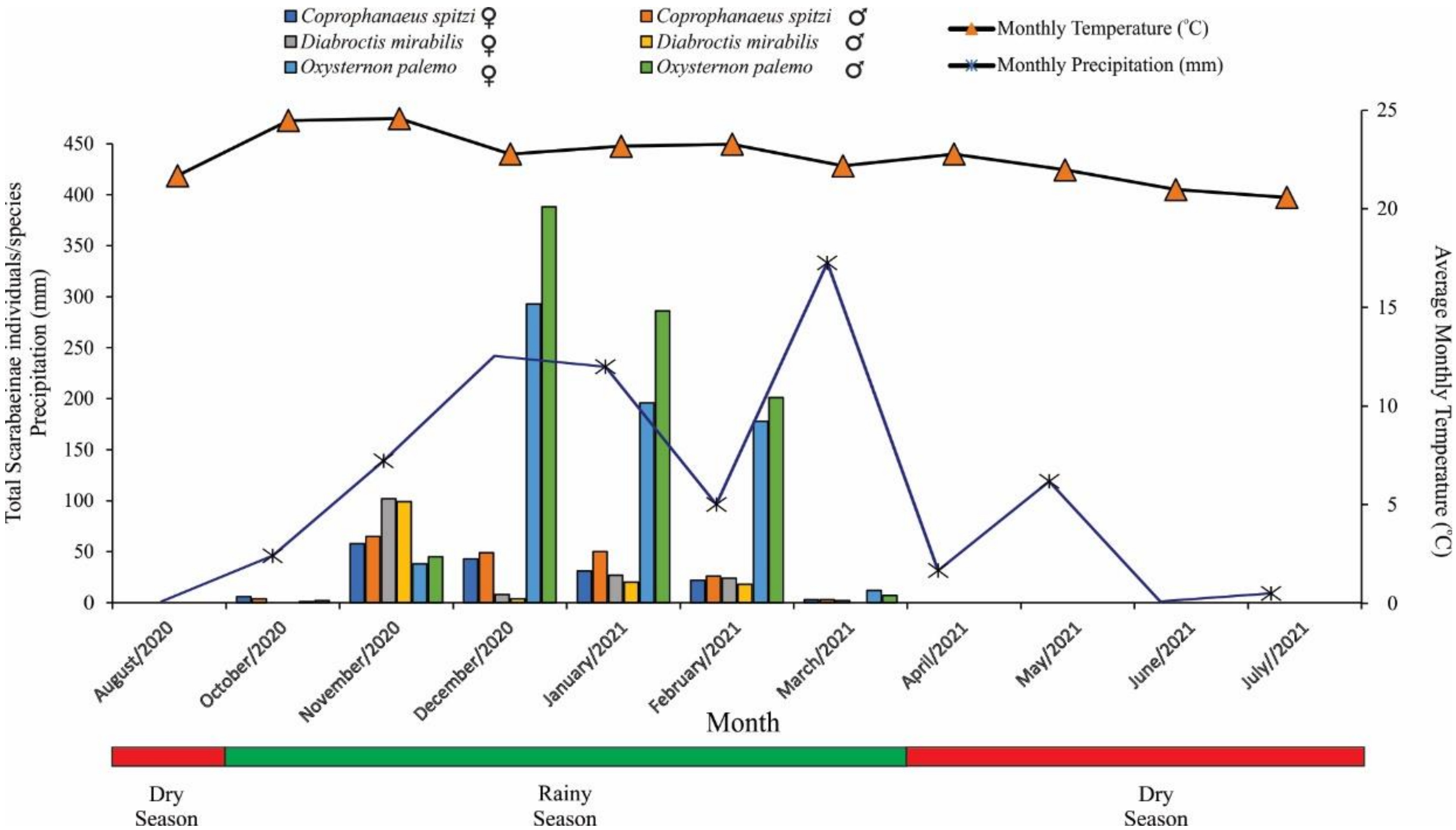

Fig. 2 Total number of males and females of *Coprophanaeus spitzi*, *Oxysternon palemo* and *Diabroctis mirabilis* collected using pitfall and climate variables [precipitation (mm) and mean monthly temperature (oC)] in Brasilia National Park (PNB) between October/2020 and March/2021.

Table 1. Total number of individuals collected and recaptured, maximum number of recaptures, and maximum distance traveled by individuals of *Coprophanaeus spitzi*, *Oxysternon palemo* and *Diabroctis mirabilis* collected by pitfall in the Brasília National Park (PNB) between October/2020 and March/2021.

Specie	TI[1]			TRI			MNR		MDT		ASI	
	Female	Male	Total	Female	Male	Total	Female	Male	Female	Male	Female	Male
Oxysternon palemo	714	925	1639a[2]	54	102	156 (9.52)	2	4	1700 (545,7)	1730(546,9)	16.5a[3]	15.9b
Coprophanaeus spitzi	160	194	354b	6	13	19 (5.37)	1	1	1475(798,3)	1000(484,2)	22.1a	22.4a
Diabroctis mirabilis	163	141	304b	5	3	8 (2.63)	1	1	150(30)	0(0)	21.2a	20.3b

[1] TI - Total of individuals collected per species; TRI - Total of recaptured individuals; MNR - Maximum number of recaptures; MDT - Maximum and average (parentheses) distance traveled, ASI - Average size of individuals (mm). [2] - Number in parentheses represents the percentage of individuals of each species recaptured in relation to the total collected. 2 – Numbers followed by the same letter within column are not significantly different according to the Nemenyi test post hoc comparison with a Tukey correction ($p = 0.05$); 3 - Averages followed by the same letter within the row do not differ when according to the Wilcoxon-Mann–Whitney U test ($p < 0.05$).

Table 2. Estimated population size (Nt), changes in the probability of survival (Φ) and the number of beetles gained by the population (Bi) on each of the sampling dates for the *Coprophanaeus spitzi*, *Oxysternon palemo* and *Diabroctis mirabilis* collected by pitfall in the Brasília National Park (PNB) between October/2020 and March/2021.

	Oxysternon palemo			*Coprophanaeus spitzi*			*Diabroctis mirabilis*		
Date	Nt	Φ	Bi	Nt	Φ	Bi	Nt	Φ	Bi
20/10/20	NA	1.000	NA	NA[1]	1.000	NA	NA	0.174	NA
22/10/20	3.0	5.000	285.0	36.0	2.000	124.0	512	0.113	41.3
24/10/20	300.0	0.429	9.9	196.0	2.294	2592.4	99	0.000	1.0
10/11/20	138.4	4.118	834.0	3042.0	0.639	4655.9	1	0.000	6.0
12/11/20	1404.0	0.231	2381.7	6600.8	1.566	-3988.8	6	1.000	30.0
14/11/20	2705.7	1.502	3341.4	6350.0	0.139	-116.3	36	0.545	16.4
27/12/20	7405.8	1.845	369.6	769.5	0.646	284.1	36	3.273	1178.2
29/12/20	14036.0	0.272	1551.4	781.0	1.420	4605.3	1296	0.113	-82.0
31/12/20	5364.9	0.643	-1102.8	5714.2	0.219	-860.4	64	0.067	19.7
12/01/21	2346.6	1.090	1062.2	392.0	1.710	1714.8	24	0.000	16.0
14/01/21	3619.3	0.134	1253.1	2385.0	2.597	826.7	16	0.000	2.0
16/01/21	1736.8	0.554	92.2	7021.3	0.072	334.0	2	0.000	1.0
09/02/21	1054.5	0.512	-93.6	839.5	0.234	79.4	1	NA	NA
11/02/21	446.1	0.046	15.3	276.0	0.200	25.8	NA	NA	NA
13/02/21	36.0	NaN	NaN	81.0	0.059	1.2	(-)	(-)	(-)
09/03/21	9.0	NA	NA	6.0	0.167	1.0	(-)	(-)	(-)
11/03/21	NA	NA	NA	2.0	NA	NA	(-)	(-)	(-)
13/03/21	(-)[2]	(-)	(-)	NA	NA	NA	(-)	(-)	(-)

[1] NA - not estimated because there were no recaptures on the first and last collection dates; [2] (-) no individuals collected on these dates.

Dispersal ability

Oxysternon palemo was the only species that showed more than one recapture of the same individual throughout the study. Males dispersed an average of 546.97 m per month, and 641.67 m over the entire study, and females averaged 545.77 m per month and 562.81 m over the total duration of this study. Eleven individuals of *O. palemo* were recaptured twice (7 males and 4 females) and one male individual was recaptured four times (Table 1).

The species *C. spitizi* and *D. mirabilis* did not show multiple recaptures of the same individual, so the mean monthly and total dispersal distances are the same. *Coprophananeus spitizi* presented males that dispersed an average of 484.23 m and females for 798.33 m, and *D. mirabilis* presented average displacement of females in 30 m and the males were recaptured in the same traps of the first capture, showing no displacement (Table 1).

Regarding the total monthly distance (sum of all distances traveled by the recaptured individuals) traveled by the species, of the five individuals of *O. palemo* that disperse the most, four were males, and all flew a distance greater than 1,500 m, being 1,730 m in 24h the longest distance traveled, by a small male. In *C. spitzi* of the five most mobile individuals, 3 were females and two males that showed flight distances ranging from 940 m to 1,475 m, with one large female flying the most in this species. *Diabroctis mirabilis* showed the lowest recapture rate, and of the eight individuals recaptured only one dispersed between different traps, a large female that traveled 150 m (Table 1).

The three species used the available space differently (with the caveat of the number of individuals, as the larger the n, the larger the area of displacement is likely to be). *Diabroctis mirabilis* made only one dispersal event in grid 3, *C. spitzi* dispersed through all five grids, but made most of its dispersals in grid 1, and *O. palemo* made extensive use of all available space in the present study, with most dispersal events in grid 2 (Table 3; Fig 3).

Table 3. Dispersal direction and number of dispersal events between all five capture grids, for *Oxysternon palemo*, *Coprophaaneus spitzi* and *Diabroctis mirabilis*. Recaptures on the same pitfall traps were not shown.

	Dispersal events		
Dispersal direction between grids	*Oxysteron palemo*	*Coprophanaeus spitizi*	*Diabroctis mirabilis*
1-1	4	4	-
1-2	7	1	-
1-3	5	1	-
1-4	1	1	-
1-5	3	1	-
2-1	11	3	-
2-2	14	1	-
2-3	2	-	-
2-4	7	1	-
2-5	1	1	-
3-1	1	-	-
3-2	11	-	-
3-3	11	-	1
3-4	2	-	-
3-5	5	-	-
4-1	4	-	-
4-2	7	-	-
4-3	3	-	-
4-4	8	1	-
4-5	4	-	-
5-1	3	1	-
5-2	7	-	-
5-3	1	1	-
5-4	-	-	-
5-5	11	-	-

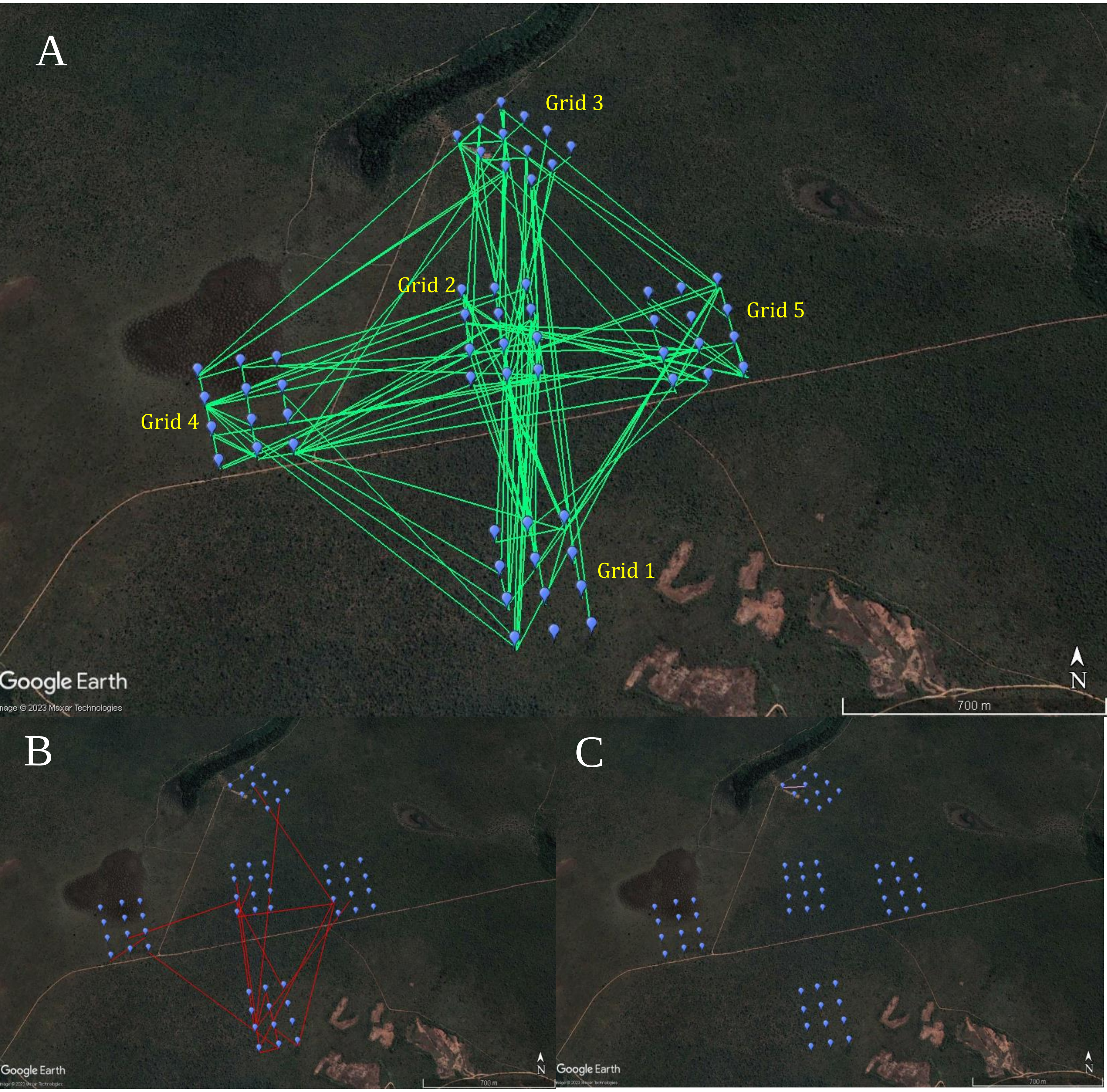

Fig. 3 Dispersal (linear distance) of Scarabaeinae individuals during capture-mark-recapture studies in Brasilia National Park (PNB) between October/2020 and March/2021. A) *Oxysternon palemo*, B) *Coprophanaeus spitzi*, and C) *Diabroctis mirabilis*.

Discussion

Our study represents an effort to understand the dispersal ability and seasonal variation in the population structure of three large species of paracoprids that are commonly found and collected in the Cerrado biome, considered one of the 25 priority hotspots for the conservation of global biodiversity and appointed as the most diverse tropical savanna in the world. However, despite its relevance, it has suffered a severe loss and fragmentation of native areas in recent years due to anthropogenic actions, being the expansion of agriculture and cattle raising the factor that has caused the greatest impacts (Dias 2008).

The three species studied are part of the tribe Phanaeini, which is endemic to the Americas and has at least 150 described species distributed in 12 genera (Hamel-Leigue et al. 2009; Arcanjo et al. 2013; Cupello and Vaz-de-Mello 2013). These species were also three of the most abundant in a study in the same phytophysiognomy in the PNB (Gigliotti 2022). *Oxysternon palemo* was the most abundant species in the present study being considered a dominant species in the dung beetle community in cerrado *sensu stricto* (Rocha 2016; Cunha and Frizzas 2020). Belonging to a genus that is strongly concentrated in South America (Vaz-de-Mello 1999), very common in Cerrado vegetation formations (Edmonds and Zídek 2004), it withstands extreme environmental variations and can be found in degraded and urbanized areas in the Federal District (Nunes et al. 2012). *Coprophanaeus spitzi* was the second most collected species, and the genus *Coprophanaeus* is also mostly distributed throughout South America, presenting nocturnal activity period and preferentially necrophagous feeding habits (Edmonds 1972), even though this genus still gets attracted to dung baits (Cajaiba et l. 2017, Silva et al. 2012), so it can be classified as a generalist depending on the study (Silva & Di Mare 2012). Probably if rotten meat was also used as bait, more *C. sptizi* would have been captured and recaptured. This genus has about 38 described species, and among these, *C spitzi* is commonly found in the Cerrado biome (Edmonds and Zidek 2010; Cunha and Frizzas 2020). *Diabroctis mirabilis* was the least abundant species in the present study, and this genus contains representatives with large body size and coloration ranging from green to metallic yellow, and *D. mirabilis* is commonly found in the south-central region of the country, in states of the Midwest and Southeaster Brazil (Valois et al. 2020). All three species have been previously collected in the Federal District, and also in Brasília National Park (Rocha 2016; Cunha and Frizzas 2020).

We obtained relatively high recapture rates for the species *O. palemo* and *C. spitzi* (9.5% and 5.3% respectively – Table 1), which are similar to those recorded in two studies in Mexico with *Deltochilum mexicanum* and *D. satanas* (14%) (Barretto et al. 2019) and *Canthon cyanellus cyanellus* (5%) (Arellano et al. 2008). The low recapture in *D. mirabilis* (2.6% - Table 1) resembled the recapture rates (2.25%) recorded in Colombia with seven Scarabaeinae species (Escobar and Ulloa 2000).

High recapture rates (18%) were recorded in Colombia for *Dichotomius cf. alyattes* and *O. conspicillatum*. However these species did not show seasonality which increases the chance of recapture (Cultid-Medina et al. 2015). The species in the present study presented markedly seasonal characteristics being collected only in the rainy season, with higher abundances, recruitment and survival rates in the months of November and December, which represent the first half of the rainy season in the Federal District. These results confirm previous studies showing that Scarabaeinae follow the seasonality in rainfall distribution that is marked in the Cerrado (Milhomem et al. 2003; Oliveira et al. 2011; Cunha and Frizzas 2020; Frizzas et al. 2020).

The periodicity of rainfall in the Cerrado is fundamental in the life cycle of insects in this biome and the peak abundance of most adult insects occurs at the beginning of the rainy season (Silva et al. 2011). Studies suggest that the life cycle of dung beetles, especially nesting and emergence of new individuals, is modulated by temperature, precipitation, and resource availability (Halftter and Edmonds 1982; Huerta et al. 2010). Our results suggest that in tropical savannas the activity of most dung beetles is practically restricted to the rainy season and that in the Cerrado, during the dry season, these beetles probably enter a state of inactivity below ground as already reported in other studies (Halftter and Matthews 1966; Bang et al. 2008). In the case of dung beetles, this relationship with the seasonality characteristic of savannas is evident elsewhere, such as in the savannas of the Ivory Coast, where two rainy seasons occur and the beetle community also shows two peaks in abundance (Cambefort 1991).

We observed a gradient in the ability of the three species to explore the landscape, with *O. palemo* able to explore the entire area, *C. spitzi* using practically only one half of the experimental area, *and D. mirabilis* not moving (Fig. 3). *Oxysternon palemo* showed the longest dispersal distances (up to 1,700 m), suggesting a good ability to colonize other areas, being able to leave impacted sites, such as small fragments, more easily than the other two species, confirming its status as a dominant species in the Cerrado dung beetle community (Rocha 2016; Cunha and Frizzas 2020). *Diabroctis mirabilis* in turn only dispersed for about 150 meters and showed the lowest abundance and recruitment, suggesting it is a local species with a low capacity for colonization of new areas. No individual traveled the maximum distance possible in the experiment (about 1,840 m between the farthest pitfalls). One male of *O. palemo* traveled 1,730 m, confirming that males generally have greater distance traveled than females (Arellano et al. 2008). A congeneric species (*O. conspicillatun*) was able to disperse for long distances during the day (1,700 m) (Cultid-Medina et al. 2015) suggesting that this genus has wide dispersal capabilities.

It has been documented that the dispersal of species and the permanence of their populations is, in part, determined by the spatial arrangement of the elements that make up the landscape, i.e., the types of vegetation cover and degree of isolation of habitat patches, along with the life history of the species. Based on our results, the species *O. palemo* and *C. sptizi* seem to have more chances of establishing and dispersing in the Cerrado, considering both the large distances traveled by some individuals and the estimated population size, with the caveat that our study area was a homogeneous and continuous cerrado *sensu stricto*, so individuals might show a different dispersal ability in a highly degraded landscape. Considering that the Cerrado is formed by a mosaic of fragments of different vegetational physiognomic forms (forest, savanna, and grasslands) and anthropized areas (agriculture, pasture, and urban areas), these two species may be able to disperse more easily between these fragments. These species have already been collected in other studies conducted in the Cerrado both in urban and agricultural areas (Nunes et al. 2012; Frizzas et al. 2020; Oliveira et al. 2021). On the other hand *D. mirabilis* is a species that deserves attention because it showed a little dispersal distance, performed only by females and a much smaller estimated population size, facts that may indicate a greater difficulty in establishing itself in fragmented areas, besides being a large species of dung beetle, which usually require relatively extensive areas for their survival (Cultid-Medina et al. 2015).

Scarabaeinae form a heterogeneous group of organisms with respect to diversity and the ability of different species to exploit the landscape (Cunha and Frizzas 2020). Although studies have shown that ecosystem services can be provided similarly in natural and anthropized environments, the dung beetle community found in native areas is unique and specific (Oliveira et al. 2021). Our results showed that, based on only three species of dung beetles, we were able to identify through dispersal ability and population structure, species that can disperse long distances and have high abundance as *O. palemo*, being important from the point of view of conservation because, due to the current fragmentation of the Cerrado, these species may be able to perform ecosystem services in different environments. On the other hand, species like *D. mirabilis*, with more local habits, are dependent on management policies and conservation of the Cerrado areas, since habitat fragmentation may represent a threat to the survival of the species, which would have difficulties in moving in search of other areas to establish itself. Finally, conservation actions for the Cerrado biome and Scarabaeinae are imperative, since many representatives of this group of organisms are on the red list of threatened species by the International Union for Conservation of Nature (IUCN 2022).

Author Contributions All authors contributed to the conception, design and writing of this manuscript. Field work and data collection were performed by MVCR. Data analysis were performed by CMO and MRF. The first draft of this manuscript was written by MVCR and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Competing interests *The authors have no relevant financial or non-financial interests to disclose.*

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Capítulo 2

Dispersal patterns and daily activity of *Phyllophaga capillata* (Blanchard) (Coleoptera: Melolonthidae) in soybeans in central Brazil

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Abstract Mark-release-recapture studies have been used to evaluate the dispersal ability of different insect species. In the field, we evaluated the dispersal ability of the soil pest species *Phyllophaga capillata* (Blanchard) (Coleoptera: Melolonthidae) in soybean (*Glycine max* L.) crop, and the flight activity of this species under controlled conditions. Field studies were conducted on a soybean seed production farm in Planaltina/DF, Brazil. On four dates, adults of *P. capillata* were collected, sexed, marked and released in a soybean plot (~230 ha). Twelve light traps were set in three concentric circles, with four traps each, at distances of 50, 150 and 250 m from the point of adult release. Under controlled conditions, groups of adults (males and females) were separated into pots containing soil, and the flight ability of the specimens was evaluated daily for 72 h. The average recapture rate of adults was 1.93% for the four collection dates. The highest recapture rate was observed at a distance of 50 m, at the beginning and middle of the swarming period, and at 250 m at the end of the swarm. Males, in general, were more active than females and reached the greatest distance of displacement (250 m). Most specimens (69.5% of males and 52.9% of females) were prone to leave the ground on the three consecutive days of the study. These results provide insights for understanding the dispersal patterns of this pest species in agricultural landscapes.

Keywords soil pest, dispersal, mark-release-recapture, flight activity, *Glycine max* L.

Introduction

Dispersal is part of the life history of organisms and influences populations ecologically and genetically, shaping the distribution patterns of individuals, usually involving trade-offs between moving and staying in the same location, and is influenced by factors such as habitat variability and the probability of survival to the dispersal event (Harrison 1980; Roff 1984; Johnson and Gaines 1990; Zera and Denno 1997; Nasu and Tokuda 2021). Free-living species' survival is related to their ecological needs and dispersal ability. For example, Coleoptera species with greater dispersal ability have a lower chance of becoming extinct than less mobile species (Fattorini 2020).

The use of mark-release-recapture techniques in insect dispersal studies, while presenting temporal and spatial constraints, can aid in understanding the dispersal patterns of individuals of a species (Fontanillas et al. 2004). Several studies have used mark-release-recapture to understand insect dispersal patterns using different collection techniques, such as pitfall, light trapping, pheromones, and sentinel hosts (Robbins et al. 2008; Moore et al. 2017; Camargos et al. 2018; Barreto et al. 2019); and different marking techniques, such as the use of paints, radioactive isotopes, radio transmitters and elytra scarification (Ranius and Hedin 2001; Arellano et al. 2008; Schallhart et al. 2009; Viljanen 2009; Moore et al. 2017).

The genus *Phyllophaga* (Coleoptera, Melolonthidae) is represented by approximately 865 species in the new world (Evans and Smith 2009), with 31 species currently described in Brazil (Morón 2001; 2004). Among these species, *Phyllophaga capillata* (Blanchard) has been considered, since the 1990s, an important soil pest in soybeans (*Glycine max* L.), one of the main Brazilian agricultural commodities, and is able to reduce crop productivity in the Cerrado region by more than 58% (Oliveira et al. 2007; Oliveira and Frizzas 2021). In addition to *P. capillata,* two other species are pests in southern Brazil, *P. triticophaga* (Morón and Salvadori) and *P. cuyabana* (Moser) (Oliveira and Garcia 2003; Cherman and Morón 2014).

Adults of both sexes of *P. capillata* are capable of flight, and for this species there is synchrony between the onset of rains in September/October and the swarming period, which occurs in October/November each year after the first rains. During the short swarming period, adults fulfill two main activities, copulation and dispersal (Oliveira and Frizzas 2019). Studies have shown an asynchrony in the emergence of adults from the ground in relation to sexes (Oliveira and Frizzas 2019), with males being more abundant at the beginning and females being more abundant at the end of the swarm. However, there is a balance between the sexes in the middle of the swarming period (Oliveira and Frizzas 2019; 2020). This temporal asynchrony suggests that there may be a difference in dispersal distance between the sexes in the pre- and postcopulation periods.

Although it is known that populations of *P. capillata* larvae show spatial stability, dispersing very little (Oliveira et al. 2006), the dispersal capacity and flight activity of adults of this species are not known. Knowing the ability of *P. capillata* to disperse is important to understand how the insect colonizes new areas of soybeans. Determining whether displacement occurs over short distances (colonization between fields within farms) or over long distances (colonization between farms) can help in the design of strategies for the management of this pest at the regional level, allowing the delimitation of areas vulnerable to attack by the pest according to the distance to infestation foci of *P. capillata*.

The objectives of this study were to field evaluate the ability of *P. capillata* adults to disperse in soybean crops during the swarming period by means of mark-release-recapture techniques and to verify whether there is a difference in the dispersal ability between sexes. In addition, the flight activity of adults under controlled conditions was also evaluated.

Materials and Methods

Study area

The study was conducted on a farm (Fazenda Sementes Três Pinheiros) with an area of 1,438 ha located in Planaltina/DF, Brazil, destined mainly for soybean seed production. The farm was selected for the study because of the history of damage caused by *P. capillata* larvae in soybean crops. The experiment to evaluate the dispersal capacity of *P. capillata* was conducted in a soybean field (15°36'50.1"S, 47°29'44.3"W, 1126 m a.s.l) of approximately 230 ha.

Insect collection and marking

In this study, the insects were marked using ink markings (nail polish) on the elytra of the specimens. To determine whether the marking used would be able to remain integral, due to the adults' habit of burrowing during the daytime period, 20 initial specimens of *P. capillata* were captured in October 2019 using a light trap (model INTRAL - Oliveira and Frizzas 2019) equipped with a black light (F15T12 Black Light 350) (Havells Sylvania Brazil Ltda, SãoPaulo/SP, Brazil) and powered by an automotive battery 12 V-60 Ah (Cral Batteries Ltd., Bauru/SP, Brazil). These adults, 10 males and 10 females, were painted with different shades of colors and kept in pots with moist soil in the laboratory for 15 days. There was no negative effect on the survival of individuals compared to unpainted specimens, and the colors used remained intact during this period.

For the mark-release-recapture studies, four collections of *P. capillata* adults were conducted at 7-10 day intervals in October and November 2019, representing the beginning, middle, and end of the swarming period. These months were chosen because they represent the species' swarming period (Oliveira and Frizzas 2019). Collections of *P. capillata* adults were made in soybean fields near the experimental area, in the same farm, using six light traps (see description above). The traps remained turned on between 18:00 and 6:00 hours, and in each trap, a plastic pot (40 cm diameter and 50 cm height) filled to approximately ¾ of its volume with soil from the collection site was attached. The captured individuals were transported to the entomology laboratory of Embrapa Cerrados (Planaltina/DF, Brazil). The soil contained in the plastic pots was sieved, and *P. capillata* specimens were separated from the other insects and sexed based on sexual dimorphism (antennal lamella length - see Oliveira and Frizzas 2019).

The number of males and females was counted on each of the four collection dates, and specimens were marked with ink on the right elytra and kept in plastic pots (50 L) with moistened soil until the time of release.

Release and recapture of insects

Before the release of the insects, 12 light traps were installed in the center of the experimental area under the same conditions described above. The traps were arranged in 3 concentric circles with 4 traps equidistant from each other around the perimeter of each circle, and the central point of the circle was the area for releasing the insects (Fig. 1). The first four traps were set at 50 m from the release point, the subsequent four traps at 150 m, and the last at 250 m, covering an area of approximately 19.6 ha (Fig. 1). Due to a lack of information about *P. capillata*, the distances were established according to the maximum displacement capacity (137 m) already reported for the congener species *P. bruneri* Chapin (Wolfenbarger et al. 1976). Rounding that number up, we took this distance as the midpoint and added 100 m for the longest distance (250 m) and reduced 100 m for the shortest distance (50 m).

The release of *P. capillata* adults occurred at 17:00 h, with the same adults captured earlier that day. A trench (0.64 m^2 by 30 cm deep) was dug in the center of the experimental plot, and the specimens were placed in this trench and covered with soil from the site. Approximately 15 h after the release of the adults, the release point was inspected, and the number of males and females that did not leave the site was counted. The insects collected in the light traps were transported to the laboratory. Following the procedure described above, the adults of *P. capillata* were sorted, and the total number of individuals and the number of marked specimens (males and females) that were recaptured were counted. Adults were captured and released in 4 events.

The meteorological data (temperature, humidity and precipitation) were obtained throughout the study from the Biophysics Laboratory of Embrapa Cerrados.

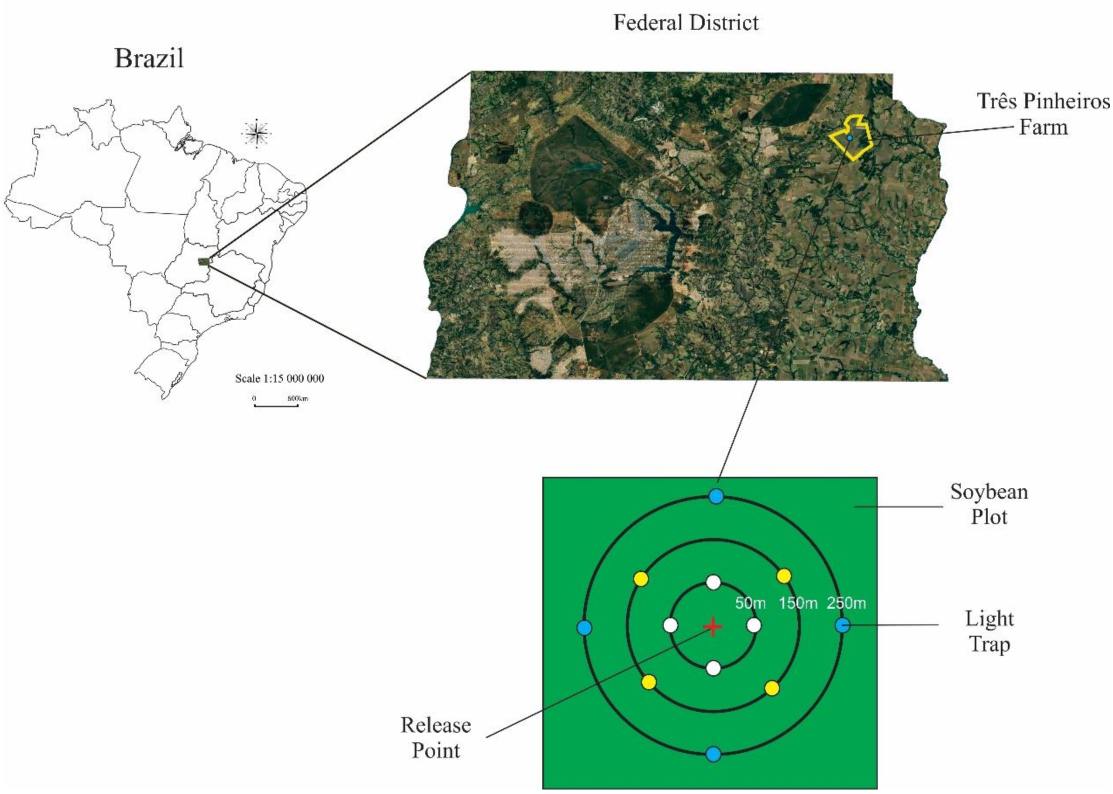

Fig. 1 Geographic location and distribution scheme of the 12 light traps used in studies of the dispersal capacity of *Phyllophaga capillata* adults in a soybean crop in the Federal District (Fazenda Sementes Três Pinheiros, Planaltina/DF, Brazil) in October and November 2019. Colored circles represent the arrangement of light traps and their distances from the point of adult release. White circle: 50 m from the release point, yellow = 150 m from the release point, and blue = 250 m

Daily activity of *P. capillata*

The daily activity of *P. capillata* was evaluated in a climate-controlled chamber (26.3 ± 1.5 °C, 60.2 ± 6.3% RH and 12 h photophase) at Embrapa Cerrados. In November 2019, adults of *P. capillata* were captured with a light trap and separated into males and females following the sex ratio present in the field at the time of collection. A total of 100 males and 40 females were used.

The adults were separated by sex and placed in groups of 10 individuals in plastic pots (9 cm diameter and 7 cm high) filled with soil collected from the experimental area. Each pot was separately placed inside a cage (40 x 40 x 70 cm wide, length and height) made of voil fabric containing a layer of soil (3 cm) on the bottom. The pots were placed on a support so that they were at a height of approximately 30 cm from the bottom of the cage. The adults were observed for three days, and each day that the specimen was found outside the vase, it was marked with paint (nail polish) on the elytra, one color for each day. After the paint had dried, the adults were placed back in the pots. To check if there was re-entry of adults in the pots, we compared the number of adults outside the pots with the number of exit holes on the soil surface of the pots. At the end of the three days, the colors on the elytra of the adults allowed us to recognize how many times and on which specific days each adult had left the soil.

Data analysis

All analyses were performed using R version 4.0.3 (R Core Team 2020). The variable percentage of *P. capillata* specimens recaptured in the light traps did not meet the assumptions of normality for residue and homogeneity of variance (Shapiro–Wilk test and Bartlett test, $p < 0.01$).

On each release date, the number of *P. capillata* adults recovered in each of the light traps was converted into a percentage of the total number of adults released on that date. The data of the average percentage of *P. capillata* adults recovered at each of the distances (50, 150, and 250 m) within each release date were subjected to a nonparametric Kruskal–Wallis analysis (Conover 1980), and the means were separated by a post hoc analysis using Dunn's tests with Bonferroni correction using the PMCMR (Pohlert 2014) and dunn.test (Dinno 2017) packages. Comparison between the percentage recapture of males and females within each release date was performed using the Wilcoxon-Mann–Whitney U test (Conover 1980) using the PMCMR package (Pohlert 2014).

In the daily activity experiment, the number of insects that left the soil were transformed into percentages.

Results

Capacity of *P. capillata* dispersal

Over all four dates, 4,022 adults of *P. capillata* (1,985 males and 2,037 females) were collected, marked and released, with 820 specimens (550 males and 270 females) on the first date, 1,119 (202 males and 917 females) on the second date, 1,675 (887 males and 788 females) on the third date and 408 (346 males and 62 females) on the last date. Of the released specimens, 919 individuals did not leave the release site, of which 34 specimens (4.14%) did not fly on the first date, 455 (40.66%) on the second, 374 (22.32%) on the third and 56 (13.72%) on the last.

A total of 60 marked adults were recovered (40 males and 20 females), which corresponded to an effective recapture percentage of 1.93% of the released insects (percentage relative only to the total number of insects that effectively left the release point). Regarding release dates, the percentage of recapture was 10 (1.27%), 13 (1.98%), 34 (2.61%) and 3 (0.85%) specimens for the first, second, third and fourth release dates, respectively.

The highest number of recaptures occurred at the 50 m distance (n = 44, 28 males and 16 females). The intermediate point (150 m) recaptured 10 specimens (6 males and 4 females), and the 250 m distance recaptured 6 individuals (all males). It was observed that on the first collection date, there was no significant difference between collection distances (p = 0.1638; Kruskal–Wallis test). On the second date, a significantly higher number (p = 0.0153; Kruskal–Wallis test) of specimens were recaptured at 50 m compared to 150 and 250 m (50 m x 150 m: p = 0.0073 and 50 m x 250 m: p = 0.0231; Dunn test). On the third collection date, we observed significantly greater recapture (p = 0.0335; Kruskal–Wallis test) at 50 m relative to the 250 m distance (50 m x 250 m: p = 0.0107; Dunn test), with no difference between 50 m and 150 m and between 150 m and 250 m. On the last collection date, the 250 m distance recaptured significantly (p = 0.0256; Kruskal–Wallis test) more specimens than the 50 and 150 m distances (50 m x 250 m: p = 0.0190 and 150 m x 250 m: p = 0.0190; Dunn test) (Fig. 2).

Regarding sexes, it was observed that on the second and fourth collection dates, the number of males recaptured was significantly higher than the number of females (second collection date: p = 0.0027; Wilcoxon-Mann–Whitney U test; fourth collection date: p = 0.0069; Wilcoxon-Mann–Whitney U test) (Fig. 3).

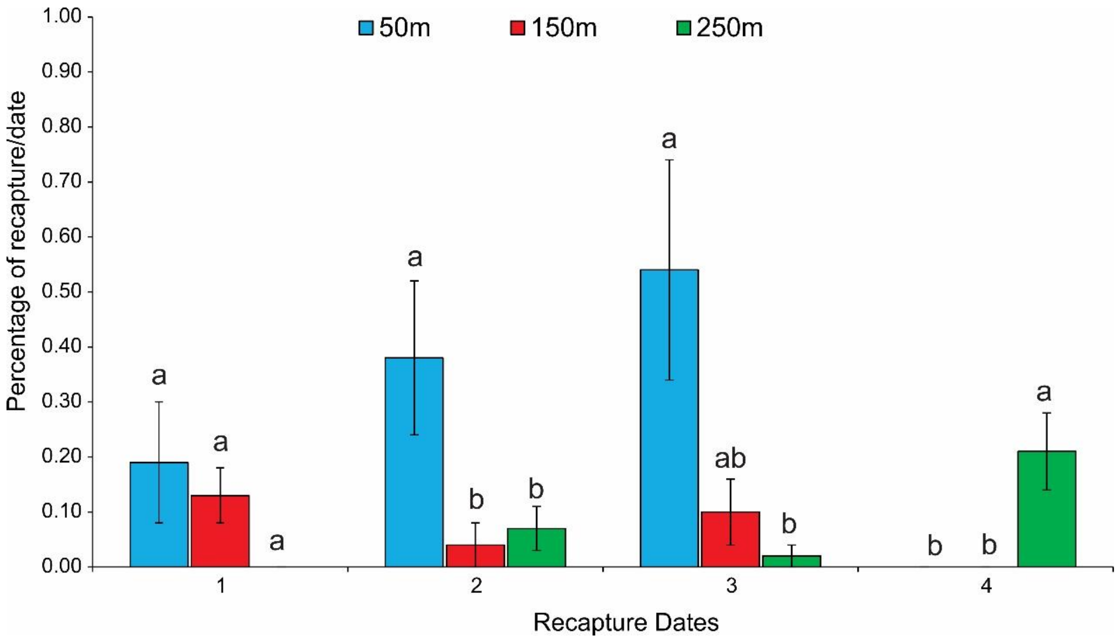

Fig. 2 Mean percentage (±SE) of adults recaptured at different release distances (50, 150 and 250 m) on four collection dates in studies of the dispersal capacity of *Phyllophaga capillata* adults in soybean crop in the Federal District (Fazenda Sementes Três Pinheiros, Planaltina/DF, Brazil) in October and November 2019. Bars followed by the same letter within each recapture date do not differ when subjected to the Kruskal–Wallis test ($p < 0.05$)

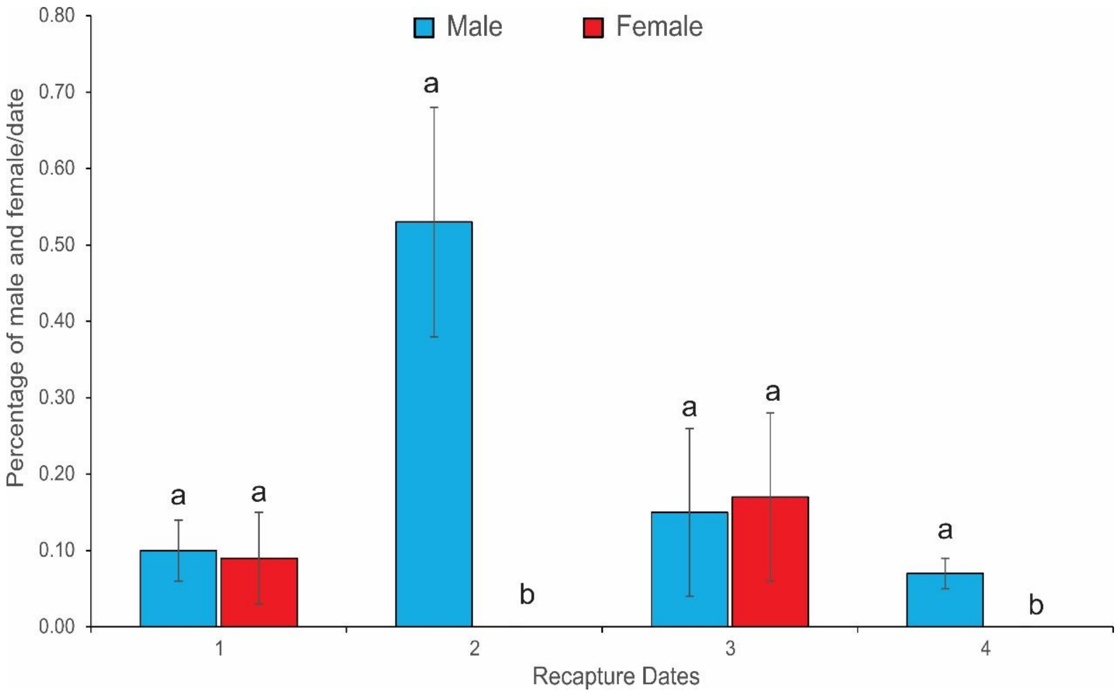

Fig. 3 Mean percentage (±SE) of males and females recaptured on the four collection dates in studies of adult dispersal capacity of *Phyllophaga capillata* in soybean crop in the Federal District (Fazenda Sementes Três Pinheiros, Planaltina/DF, Brazil) in October and November 2019. Bars followed by the same letter within each recapture date do not differ when subjected to the Wilcoxon-Mann–Whitney U test ($p < 0.05$)

Daily activity

Adults of *P. capillata*, both males and females, showed similar patterns with respect to daily activity (Fig. 4). Although, for both sexes, we observed individuals who did not leave the ground any day, individuals who left the ground only one day, and those that left the soil two days (in a row or alternating), the majority of specimens (69.5% of males and 52.9% of females) were prone to leave the ground on all three consecutive days of the study.

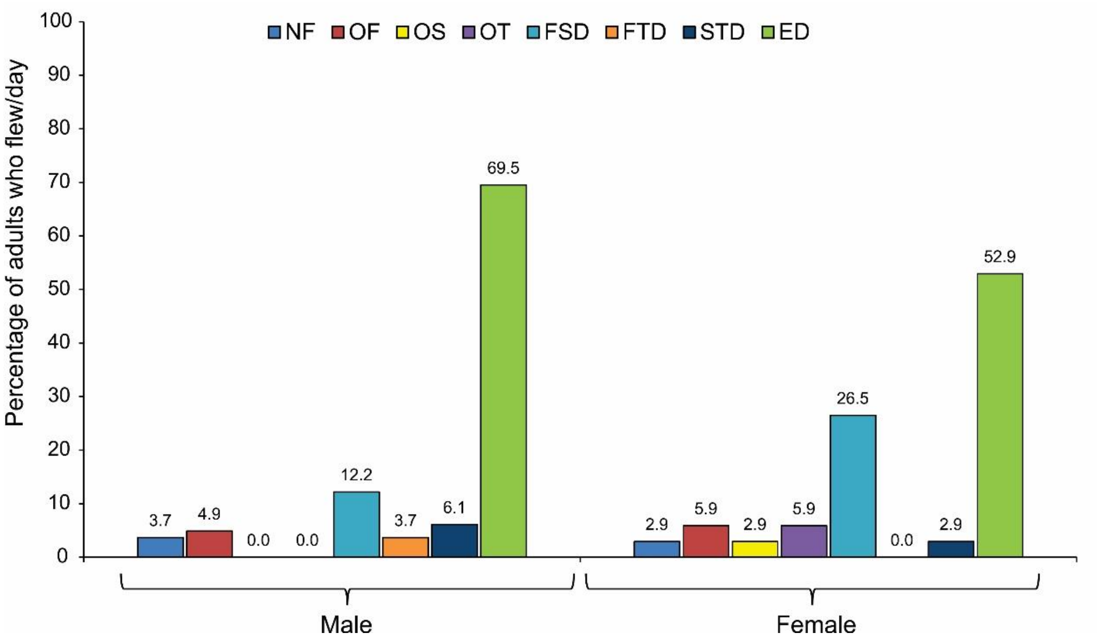

Fig. 4 Percentage of daily activity of *Phyllophaga capillata* adults evaluated during 72 h under controlled conditions (26.3 ± 1.5 °C, 60.2 ± 6.3% RH and 12 h photophase) at Embrapa Cerrados (Planaltina/DF, Brazil) in November 2019. Number of days that adults showed flight activity: NF - no flight; OF - flew only on the first day; OS - flew only on the second day; OT - flew only on the third day; FSD - flew on the first and second day; FTD - flew on the first and third day, STD - flew on the second and third day; and ED- flew every day (on all three days)

Discussion

Phyllophaga capillata is recognized for producing swarms with high population densities in a relatively short time of the year (~30 days), making it possible to collect from 3 to 7 thousand specimens in a single collection night with light traps (Oliveira 2019; Oliveira and Frizzas 2019). Modifications in the areas attacked by larvae between plots within the same property or between nearby properties over consecutive harvests are common for this pest, suggesting that the dispersal ability of adults is the determining factor for infestation patterns of the pest over time. This is the first study to evaluate the ability of *P. capillata* to displace in the field. Our main findings show that the species has a low recapture rate, with the largest number of adults recaptured at 50 m; however, we found that the species disperses at least 250 m, that the distance of displacement increases over the swarming period, and that males appear to have a greater ability to disperse. We also observed that adults of this species showed a greater predisposition to leave the soil on consecutive days. The caveat for lower recapture in greater distances might be the effect of previous light traps being more atractive than farther ones, capturing insects before they got to the ones farther back.

In general, the recapture rates for Coleoptera in mark-release-recapture studies are not very high (Ranius and Hedin 2001; Arellano et al. 2008; Mansfield et al. 2016). The capture rates for *P. capillata* found in the present work ranged from 0.85% to 2.61%. In a study conducted in the United States, adult males of *P. anxia* (LeConte) were recaptured in traps containing the species' sex pheromone at rates ranging from 11% to 28% over the three years of the experiment (Robbins et al. 2008). It is possible that the differences in recapture rates may be related to the distances and type of trap used. For *P. anxia*, traps were positioned 20 m from the release point with 15 m between them, and we used longer distances (50, 150, and 250 m), which may have reduced the potential for insect recapture. Trap density (number of traps/area) decreases greatly with increasing distance (Lacey et al. 1995). In fact, higher recapture rates of *P. capillata* were observed where trap density was higher (at 50 m). Studies have also shown that pheromone traps are more efficient than light traps. The species *P. brevidens* (Bates) and *P. lenis* (Horn), for example, were attracted approximately 3.3 times more by sex pheromone traps than by light traps, and using both attractants in the same trap attracted approximately 17.5 times more adults than light alone (Zaragoza-Ortega et al. 2017). If *P. capillata* responds similarly to other congeneric species, the use of sex pheromones could help increase recapture rates for this species, once these pheromones are described and available for use in the field.

Another factor that may have influenced the recaptures was the phases of the moon, since usually the fuller it is, the less are the chances of capturing insects (Souza et al. 2015, Keszthelyi et al. 2019). The four recapture periods occurred on 1/11/19, 8/11/19, 14/11/19, and 29/11/19, and the full moon for that month occurred on 12/11/19. The second and third recapture periods may have been affected by the brightness, and in these the insects were recaptured at all three distances. Possibly a higher number of recaptures could have been achieved, even at 250 m, if collections had occurred on another date. In the first and fourth recapture periods, the phase was the beginning of the crescent moon, which probably generated little interference in the captures. This strengthens the hypothesis that at the end of the swarm, the individuals are dispersing to other areas, since they were only recaptured at 250 m, the longest experimental distance.

We observed that throughout the swarming period, the adults of *P. capillata* tended to increase the distance of displacement. In fact, in the first two collection dates, corresponding to the first half of the swarming period, the displacement was predominant up to 50 m (Fig. 2), suggesting that in this phase, the adults concentrate their activities in finding mating partners and show a tendency to disperse less. In the second half of the swarming period, recaptures at 150 m were similar to 50 m (third collection date), and 250 m became the predominant distance at the end of the swarm (fourth collection date) (Fig. 2), indicating that specimens may be more likely to disperse after copulation events.

Overall, males were more recaptured (66.7%) than females (33.3%), only this sex reached the greatest distance of displacement (250 m), and only males were collected on the second and fourth collection dates. These data suggest a greater ability of *P. capillata* males to disperse. Interestingly, on the second release date, although approximately 82% of females were released, only males were recaptured, confirming that males were more active on this date, perhaps in search of mating partners. Studies of *P. crinita* (Burmeister) have shown greater activity of males than females, which are less attracted to light traps and fly short distances to oviposit (Teetes et al. 1976; Stone 1986). We observed that females of *P. capillata*, however, are able to fly at least 150 m, a distance much greater than that reached by females of a congener, *P. cuyabana*, which in Brazil reached 20 m (Oliveira and Garcia 2003). In another study, *P. bruneri* was able to disperse for approximately 137 m (Wolfenbarger et al. 1976). The data obtained suggest that adults *of P. capillata* were able to disperse greater distances than other species of the genus *Phyllophaga* already studied (Wolfenbarger et al. 1976; Oliveira and Garcia 2003).

Studies have shown a pattern in the sex ratio of *P. capillata* throughout the reproductive period, with a predominance of males at the beginning and females at the end of the swarm and equal rates of males and females in the middle of the swarming period (Oliveira and Frizzas 2019). Here, we did not find this pattern in the insects collected to conduct the mark-release-recapture study on the four collection dates, with more males on the first and fourth collection dates, more females on the second date, and balance between the sexes on the third collection date. This result may have occurred because the present study was carried out in an atypical, drier year. The first rains in September and October of each year are the trigger for the resumption of adult insect activity in the Cerrado (Silva et al. 2011; Oliveira and Frizzas 2008; 2013; 2019). In the studies by Oliveira and Frizzas (2019), also in the Federal District, there was a rainfall of 201 mm, while in the present study, rainfall rates reached less than 50 mm in the same period. This factor may have affected the swarming pattern and consequently the sex ratio of *P. capillata*.

Regarding daily activity, we observed that most specimens of *P. capillata* (> 69% of males and > 52% of females) showed activity on consecutive nights. In contrast, adults of *P. cuyabana* showed activity on alternate nights, with this behavior being more marked for males (Oliveira and Garcia 2003). The results of the studies of daily activity under controlled conditions were confirmed in the field, since on the four collection dates, the percentage of adults that abandoned the release point ranged from 59.3% to 95.8%; on the dates when more males were released (first and fourth release), the percentages of insects that left the soil ranged from 86.3 to 95.8%; and on the dates with a predominance of females, this percentage ranged from 59.3% to 77.7%. These results, along with the recapture data, reinforce the hypothesis that males have a greater tendency to fly than females. We suggest that males disperse more during the entire swarming period in search of a mating partner and that females during some moments of the swarming, especially after copulation, may dedicate themselves more to oviposition, being less captured or becoming less attracted to the light trap.

During summer plantings in the Federal District, approximately 60% of the cultivated area is occupied with soybean crops, and the Federal District is responsible for the fourth highest productivity of the crop in Brazil (IBGE 2022; CONAB 2022). This wide crop coverage has as a consequence the spatial proximity between crops in the various soybean producing properties. Our results showed that adults of *P. capillata* showed good dispersal capacity (at least 250 m), with most adults flying on consecutive days. In addition, *P. capillata* presents a synchrony between the resumption of adult activity and the onset of rainfall in the Cerrado, a time when soybean planting occurs, allowing larvae of this species to find host plant availability (Oliveira and Frizzas 2019). This set of factors may explain, at least in part, the colonization of new plots or new properties by *P. capillata*, since adults can disperse for distances ranging from 50 to 250 m in just one night, facilitated by the proximity between the various soybean growing areas at the beginning of the rainy season. Several factors, however, influence the choice of new soybean areas during the swarming process by *P. capillata* adults. For example, *P. capillata* adults prefer to colonize areas with the presence of taller plants, which serve as points for sexual pheromone release by the female (Oliveira and Frizzas 2019; 2020). Thus, future studies that determine the main factors that influence the choice of adults for new areas for colonization, coupled with the knowledge of the dispersal capacity of this species, may allow design of preventive management strategies for *P. capillata* in Central Brazil.

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Author Contributions All authors contributed to the conception, design and writing of this manuscript. Field work, specimen preparation and data collection were performed by MVCR and CMO. Data analysis was performed by CMO.

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Data Availability Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Financial Interests The authors have no financial or proprietary interests in any material discussed in this article.

Conflict of interest The authors declare no conflict of interest.

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CONSIDERAÇÕES FINAIS

Conhecer a capacidade de dispersão dos organismos é de extrema importância tanto na área de conservação quanto no manejo de pragas, já que em um caso podemos focar esforços de conservação nas espécies que possuem baixa capacidade de dispersão, e no outro, focar no controle populacional das espécies que apresentam ampla capacidade de dispersão. Aliado ao conhecimento da capacidade de dispersão, estimativas de tamanho populacional também podem ser utilizadas tanto na conservação quanto no controle, indicando quais populações estão em declínio e necessitando de rápida intervenção, quanto nas populações que estão em forte ascensão e devem ser reduzidas antes que atinjam uma explosão populacional e se tornem um problema. Estes temas são relevantes tanto em áreas naturais, que vem cada vez mais sendo degradadas, reduzidas, isoladas e circundadas por matrizes urbanas; quanto em áreas agrícolas, que todos os anos perdem toneladas de commodities e bilhões de dólares devido à danos causados por insetos praga nas plantações.

Em Scarabaeinae foi observado que as espécies se dispersaram de formas distintas pelo cerrado *sensu stricto. Oxysternon palemo* e *Coprophanaeus spitzi* apresentaram múltiplos eventos de dispersão, com deslocamentos máximos de 1.730 m e 1.475 m respectivamente, e *Diabroctis mirabilis* apresentou apenas um evento de dispersão, de 150 m. Tanto *O. palemo* quanto *C. spitzi* se dispersaram por todos os grids de captura, mas *D. mirabilis* demonstrou uma baixa capacidade de utilizar a área como um todo. Vale destacar que todos os cinco grids foram instalados na fitofisionomia de cerrado *sensu stricto* que era representada por uma área de Cerrado homogênea e contínua, não havendo fragmentos ou outros tipos de fitofisionomias entre os grids. Os resultados encontrados neste estudo sugerem que *O. palemo* e *C. spitzi* podem ser mais resistentes à impactos antropogênicos pelo fato de essas espécies demonstrarem boa capacidade de dispersão, facilitando o deslocamento entre fragmentos. Já o oposto ocorre em *D. mirabilis*, que provavelmente será mais impactada que as outras duas espécies, pois a maioria das recapturas ocorreu na mesma armadilha onde foram capturados e o único evento de dispersão ocorreu a uma distância muito menor que a média das outras duas espécies.

Os parâmetros populacionais das três espécies foram distintos. *Oxysternon palemo* apresentou a maior abundância com 1.639 indivíduos capturados, seguido por *C. spizi* com 354 capturas e *D. mirabilis* com 304. As maiores abundâncias ocorreram em dezembro para *O. palemo* e novembro para *C. spitzi* e *D. mirabilis*. Novembro foi o mês de maior Sobrevivência (Φ) e Taxa de Recrutamento (Bi) para *O. palemo*. *Coprophanaeus sptizi* apresentou maior Sobrevivência em janeiro e Recrutamento em novembro. A maior Sobrevivência e Recrutamento em *D. mirabilis* ocorreram em dezembro. As estimativas populacionais entre as espécies variaram significativamente, onde *O. palemo* apresentou 14.036 indivíduos em dezembro, *C. spitzi* 7.021 indivíduos em janeiro e *D. mirabilis* 1.296 em dezembro. Estes dados corroboram que rola-bostas são organismos que acompanham a sazonalidade marcante no bioma Cerrado, visto que os parâmetros populacionais destas espécies foram maiores na primeira metade do período chuvoso (Outubro-Dezembro), e que nenhum indivíduo foi coletado no período de seca (Abril-Setembro).

Quando observamos os dados percebe-se que a alta capacidade de dispersão (que provavelmente está subestimada, pelo fato de a distância ser medida em linha reta, não levando em consideração o caminho feito pelo indivíduo) apresentada por *O. palemo* e *C. sptizi*, aliados aos parâmetros populacionais encontrados nessas espécies indicam que elas possuem boa capacidade de se dispersar para novos fragmentos e estabelecer populações nessas áreas, principalmente durante o período chuvoso. *Diabroctis mirabilis* tem uma maior possibilidade de sofrer extinção local pela perda e fragmentação de habitat, visto que sua capacidade de dispersão e estimativa de tamanho populacional foram muito menores que as encontradas nas outras duas espécies.

No segundo capítulo da tese, para *Phyllophaga capillata* foi observada uma maior taxa de recapturas na menor distância avaliada (50 m) recapturando 44 indivíduos, seguida pela distância intermediária (150 m) com 10 recapturas e por fim, a maior distância (250 m) com 6 recapturas, apenas de indivíduos machos. Também foi observado que as recapturas nas maiores distâncias aumentaram de acordo com o avanço do período de revoada de *P. capillata*, onde no início as maiores recapturas foram aos 50m, no meio da revoada as recapturas ocorreram tanto em 50 m quanto em 150 m, e no final da revoada só foram recapturados machos à 250 m. Machos apresentaram maior capacidade de dispersão que as fêmeas, porém ambos os sexos aparentam se deslocar por distâncias maiores que outras espécies congêneres.

No mês de novembro a fase de lua cheia ocorreu no dia 12/11, e este fenômeno pode ter influenciado nos dois eventos intermediários de recaptura (segundo e terceiro), que ocorreram nos dias 8/11 e 14/11. Nestes dias específicos ocorreram recapturas nas três distâncias avaliadas, e possivelmente a luminosidade da lua pode ter afetado na eficácia das armadilhas permitindo uma menor recaptura dos insetos . O primeiro período de recaptura, dia 01/11/19, apresentou o início da lua crescente, visto que a lua nova ocorreu em 28/10/19 e possivelmente as recapturas foram pouco afetadas. O quarto e último evento de recaptura ocorreu dia 29/11/19, na fase de lua nova, logo a interferência lunar foi minimizada. Isto aponta para a hipótese de que os indivíduos estavam dispersando para novas áreas ao final do período de revoada, já que nesta data os insetos só foram recapturados na maior distância do experimento, 250 m. Novembro de 2019 foi um período atípico, pois em anos anteriores foram registrados mais de 200 mm de chuva, porém menos de 50 mm foram registrados durante o presente trabalho, logo acredita-se que os maiores efeitos nas taxas de recaptura sejam devido ao regime das chuvas do período, e as fases da lua tiveram menor interferência.

Phyllophaga capillata apresentou predisposição para deixar o solo todos os dias, diferentemente de outras espécies congêneres que deixam o solo em dias alternados. Cerca de 70% dos machos e 53% das fêmeas saíram do solo diariamente no experimento controlado em laboratório, e estes dados corroboram o que foi observado em campo, pois um maior número de fêmeas permaneceu no solo, no mesmo local em que foram liberados, quando comparados aos machos. O comportamento de machos deixarem o solo com mais frequência, e dispersarem por distâncias maiores pode estar relacionado à procura de parceiros reprodutivos, visto que as fêmeas costumam procurar plantas mais altas, liberar o feromônio de atração e esperar que machos se aproximem.

O presente trabalho foi o primeiro a abordar a capacidade de dispersão destas quatro espécies no Cerrado. *Oxysternon palemo* e *C. spitzi* demonstraram maior capacidade de dispersão comparado com *P. capillata*, porém esta espécie é praga e é altamente adaptada ao cultivo da soja e ao clima do Cerrado, e sua capacidade de dispersão e propensão à deixar o solo diariamente, que são maiores que em outras

Phyllophaga, são suficientes para afetar áreas vizinhas e causar danos econômicos nos sucessivos eventos de revoada à cada ano. *Diabroctis mirabilis* apresentou baixa capacidade de dispersão em uma Unidade de Conservação bem preservada, com cerrado *sensu stricto* contínuo, nos levando a conclusão que esta espécie merece atenção especial pois ela pode não resistir à impactos antropogênicos e sofrer extinção local.

Futuramente estudos que acompanhem as populações devem ser mais longos tendo em vista a longevidade de alguns rola-bosta, a imprevisibilidade de anos atípicos na questão climática e para uma coleta mais completa de dados. Uma metodologia que possibilite marcar besouros de pequeno tamanho corporal iria contribuir para o acompanhamento de outras espécies, resultando em um monitoramento mais robusto das populações, e da comunidade como um todo. As metodologias que utilizam armadilhas luminosas precisam ser estabelecidas em períodos em que não haja lua cheia, visto que a luminosidade da lua pode afetar a eficácia das armadilhas. Um outro ponto metodológico que merece atenção é a forma de disposição das armadilhas, visto que as luminosas posicionadas mais próximas do ponto de liberação podem interferir na atratividade das que estão mais distantes.