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MIRELLA LIMA COSTA

PREFERÊNCIA E ATRATIVIDADE POR DIFERENTES DIETAS NA DETERMINAÇÃO DAS COMUNIDADES DE BESOUROS ROLA BOSTA

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de mestre(a) em Biologia Animal. Área de concentração: Biologia Animal

Orientador (a): Dra. Luciana Iannuzzi

Coorientador (a): Dr. Renato Portela Salomão

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Dedico esta dissertação aos meus pais, vocês são tudo pra mim.

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“Continue a nadar”. (Dory, Procurando Nemo, 2003)

RESUMO

A dieta de espécies e de taxocenoses envolve o reconhecimento, a escolha e a utilização dos alimentos. Os besouros rola bosta são majoritariamente coprófagos, mas em alguns ecossistemas outros hábitos alimentares são complementares ou substituem a coprofagia. A necrofagia é um desses hábitos, mas ainda estudado de forma incipiente. O objetivo deste estudo foi avaliar o efeito de diferentes tipos de carne apodrecida sobre a diversidade taxonômica de rola bosta em uma região da Amazônia Central. Testamos a atratividade e a preferência de três tipos de carne (boi, ave e peixe) pelos os besouros rola bosta, analisando a composição de espécie e a estrutura da comunidade atraída a cada tipo de carne. O experimento de atratividade consistiu em testar o potencial atrativo de cada tipo de carne de maneira isolada, enquanto o experimento de preferência tinha como objetivo avaliar a escolha do tipo de carne na presença dos três diferentes tipos. Foram coletados 3.151 indivíduos de 24 espécies de rola bosta. A abundância de indivíduos não variou entre os tipos de carne, mas os valores de diversidade foram diferentes, sendo a isca de carne bovina a mais atrativa. O experimento de preferência demonstrou abundância e diversidade menores em armadilhas não iscadas (controle) quando comparadas às iscadas. *Canthidium* sp., *Canthon triangularis*, *Deltochilum* gr. *submetallicum*, *Eurysternus atrosericus*, *Ateuchus simplex* e *Eurysternus caribaeus* foram indicadores de carne bovina, demonstrando que o tipo de carne influencia a estrutura da comunidade de rola bosta. Os dados de dispersão foram diferentes entre os tipos de carne no experimento de atratividade e o frango apresentou os maiores valores de dispersão quando comparado ao peixe. O mesmo não aconteceu no experimento de preferência. A estrutura da assembléia de rola bosta foi reunida em três grupos (cluster) em ambos os experimentos. Os dados foram agrupados em dois grupos de frango e um grupo com os três tipos de carne no experimento de atratividade. No de preferência, um grupo reuniu os dados de frango e peixe, um grupo agregou os dados de todos os tipos de carne e outro grupo uniu os dados de carne bovina e frango. Nossos resultados indicam que o tipo de carne em decomposição influencia a estrutura das assembléias de rola bosta na Amazônia, nos fazendo supor que esses besouros desenvolvem estratégias na busca por recursos alternativos quando o alimento principal é escasso. Esse estudo fornece dados importantes relacionadas aos hábitos dos rola bosta necrófagos, que servirão de base para estudos futuros relacionados à alimentação dos rola bosta.

Palavras-chave: Carcaça; Floresta Amazônica; Necrofagia; Scarabaeinae.

ABSTRACT

The diet of species and taxocenoses involves the recognition, choice and utilization of food. Dung beetles are mostly coprophagous, but in some ecosystems other feeding habits complement or replace coprophagy. Necrophagy is one of these habits, but it is still incipiently trained. The objective of this study was to evaluate the effect of different types of rotten meat on the taxonomic diversity of dung beetles in a region of Central Amazonia. We tested the attractiveness and preference of three types of meat (beef, poultry and fish) by dung beetles, analyzing the species composition and structure of the community attracted to each type of meat. The attractiveness experiment consisted of testing the attractiveness potential of each type of meat in isolation, while the preference experiment aimed to evaluate the choice of the type of meat in the presence of three different types. A total of 3,151 individuals of 24 species of dung beetles were found. The abundance of individuals did not vary between meat types, but diversity values were different, with beef bait being the most attractive. The preference experiment demonstrated lower abundance and diversity in unbaited traps (control) when compared to baited ones. Canthidium sp., Canthon triangularis, Deltochilum gr. submetallicum, Eurysternus atrosericus, Ateuchus simplex and Eurysternus caribaeus were indicators of beef, demonstrating that the type of meat influences the structure of the dung beetle community. Dispersal data were different between meat types in the attractiveness experiment, and chicken showed the highest dispersion values when compared to fish. The same did not occur in the preference experiment. The structure of the dung beetle assemblage was grouped into three groups (cluster) in both experiments. The data were grouped into two groups of chicken and one group with the three types of meat in the attractiveness experiment. Non-preferably, one group pooled data on chicken and fish, one group pooled data on all meat types, and another group pooled data on beef and chicken. Our results show that declining meat types influence the structure of dung beetle assemblages in the Amazon; however, it is necessary for these beetles to develop strategies to search for alternative resources when their main food is scarce. This study provides important data on the habits of dung beetle scavengers, which will serve as a basis for future studies on dung beetle feeding.

Keywords: Carcass; Amazon rainforest; Necrophagy; Scarabaeinae.

SUMÁRIO

1 APRESENTAÇÃO

O presente trabalho tem como objetivo avaliar o efeito da atratividade e preferência de iscas na diversidade taxonômica de escaravelhos em uma região da Amazônia Central. Hipóteses foram testadas através de análises ecológicas comparativas, a fim de entender a estruturação e preferências da comunidade de besouros rola bosta. A dissertação consta de uma introdução geral sobre os conceitos de atratividade e preferência, e como ocorre essa seleção pelo recurso. Além disso, foram abordados principais temas relacionados a besouros rola bosta, tais como: distribuição, alimentação e serviços ecossistêmicos, no qual foram obtidos por meio de levantamento bibliográfico. Adiante, apresentamos os objetivos do trabalho (geral e específicos), seguindo para o item 4, representado por um artigo único. Este trabalho apresenta formatação de dissertação em forma de artigo, no qual será submetido a revista Ecology and Evolution(https://onlinelibrary.wiley.com/journal/20457758), em que possui modelo de formatação livre. Por fim, apresentamos as considerações finais do trabalho.

Espero que esse trabalho seja de grande proveito para entender a estrutura e preferências da comunidade de besouros rola bosta, além disso, que possa servir de base para o desenvolvimento de trabalhos futuros acerca do tema.

Boa leitura!

2 INTRODUÇÃO GERAL

Os besouros rola bosta (Coleoptera, Scarabaeidae, Scarabaeinae) são comumente reconhecidos no Brasil por esse termo devido a prática de rolar bolotas de excrementos até o local de alimentação e nidificação (Peck & Forsyth, 1982). Esses besouros são amplamente distribuídos em ecossistemas tropicais, subtropicais e temperados, com notável riqueza em áreas tropicais que abrangem desde florestas úmidas até savanas (Hanski & Cambefort, 1991; Vaz-de-Mello, 2009). Estima-se que exista cerca de 6.200 espécies descritas de rola bosta (Tarasov & Génier, 2015; Tarasov & Dimitrov, 2016), sendo 1.500 espécies encontradas na América do Sul, e aproximadamente 700 no Brasil (Vaz-de-Mello, 2019).

Em virtude dos seus hábitos, os rola bosta desempenham importantes serviços ambientais (Doube, 2018; Decastro-Arrazola et al., 2020), pois ao removerem porções de fezes e degradarem matéria orgânica, contribuem para a melhoria da qualidade nutricional do solo. Por meio do escavamento de galerias subterrâneas, que podem atingir profundidades de vários metros, contribuem para a aeração do solo (Nichols et al., 2008). Ao transportar e depositar excremento dentro dos túneis, depositam material rico em nutrientes, o que favorece a atividade da microbiota e alterações físico-químicas nas camadas superiores do solo, aumentando a fertilidade (Calafiori, 1979). Além disso, auxiliam na redução da emissão de gás metano na atmosfera, que é produzido em grande quantidade pelas fezes do gado (Holland, 2013).

Além disso, estes besouros realizam dispersão secundária de sementes, sendo essa uma contribuição significativa, pois possibilitam o aumento das chances de germinação e sucesso reprodutivo das plantas, ao depositarem essas sementes em local favorável e longe da competição com a planta mãe (Andresen, 2001; Andresen & Feer, 2005; Scholtz et al., 2009). Os rola bosta também promovem o controle de moscas ao removerem fezes contendo larvas (Scholtz et al., 2009). Ademais, também realizam polinização de algumas famílias de plantas, como por exemplo, Lowiaceae e Araceae, podendo inclusive, ser polinizadores exclusivos (Meeuse & Hatch, 1960; Gibernau et al., 2004; Sakai & Inoue, 1999).

Quanto ao hábito alimentar, os besouros rola bosta são considerados detritívoros, utilizando fezes, frutas e carcaças animais como alimento (Filgueiras et al., 2019; Mayer et al., 2019; Gimenez et al., 2021). Atualmente, os besouros rola bosta apresentam diversos hábitos alimentares, sendo a coprofagia e a necrofagia os mais comuns, principalmente nas espécies de florestas tropicais e bem característico na América do Sul (Halffter; Halffter, 2009; Hanski; Cambefort, 1991). Além desses, a frugivoria tem sido bem documentada na região Neotropical (Halffter; Halffter, 2009) e as musáceas representam um recurso altamente atrativo para esses besouros (Gill, 1991; Pereira & Halffter, 1961; Silva et al., 2012). A micetofagia, embora mais rara, também é observada entre os rola bosta, especialmente em florestas tropicais úmidas na América do Sul, com os fungos basidiomicetos da família Polyporaceae sendo os principais alvos (Hanski & Cambefort, 1991; Anduaga, 2000; Anduaga & Halffter, 1991; Navarrete-Heredia & Miranda, 1997). A predação é outro hábito relatado para alguns rola bosta, mesmo que de forma incipiente, e as principais presas utilizadas por eles são milípides e formigas (Larsen et al., 2009; Silva et al., 2012; Forti et al., 2012).

A maioria das espécies de besouros rola bosta é considerada generalista quanto a dieta, enquanto apenas uma minoria dentro das comunidades depende exclusivamente de um único tipo de alimento (Medina et al., 2014; Tonelli et al., 2021; Salomão et al., 2014; Gimenez et al., 2021; Frank et al., 2018). A extensão da plasticidade alimentar e a disponibilidade de recursos figuram entre os fatores ecológicos primordiais que influenciam a coexistência de espécies em ecossistemas de grande diversidade, como as florestas tropicais e subtropicais (Brown, 1984; Gaston et al., 1997). Espécies e comunidades com ampla plasticidade alimentar proporcionam um suprimento mais diversificado de energia para os processos biológicos fundamentais, como eventos reprodutivos, o que, portanto, influencia positivamente a dinâmica populacional e a coexistência de espécies (Krebs & Davies 1981; Paine et al., 1981). Dessa forma, essa amplitude pode favorecer a distribuição espacial de espécies generalistas e limitar a conquista de novos habitats por espécies especialistas (Sexton et al., 2017). Estudos sobre as preferências tróficas dos rola bosta tem sido bastante explorados, para explicar padrões ecológicos, como por exemplo, diversidade de espécies, competição entre espécies e distribuição espacial de comunidades (Errouissi et al., 2004; Larsen et al., 2006; Larsen et al., 2008; Franco et al., 2018; Giménez Gómez et al., 2018; Ebert et al*.,* 2019).

Originalmente, esses besouros se alimentavam de material vegetal em decomposição (Halffter; Halffter, 2009), mas com o surgimento de grandes animais na era Cenozóica (Paleoceno), a exemplo os mamíferos herbívoros (Wings et al., 2003), passaram a utilizar excrementos desses animais. Esse tipo de recurso era abundante na era Cenozóica, além de ser rico em proteínas, momento em que passaram de uma dieta baseada na saprofagia para a coprofagia, utilizando as fezes de vertebrados como fonte alimentar principal (Halffter; Halffter, 2009; Halffter; Matthews, 1966; Scholtz et al., 2009; Davis et al., 2002). Mudanças ambientais ocorridas ao longo do tempo resultaram na alta mortalidade, e consequente extinção de muitos mamíferos herbívoros durante a transição do período Pleistoceno para o Holoceno (Buchman et al.; Scherer & Rosa, 2003; Galetti, 2004). A morte dos mamíferos resultou em grande disponibilidade de carcaças, levando os besouros rola bosta a se alimentarem também de carne em decomposição e adquirindo o hábito necrófago na sua alimentação (Gill, 1991).

Apesar da diversidade alimentar dos besouros rola bosta ao longo da sua evolução, alguns fatores influenciam na mudança dos hábitos alimentares, os levando a explorar recursos alternativos. Mudanças ambientais que geram um estresse significativo dos ambientes, como o hídrico e alta exposição solar, alteram as características do recurso o tornando menos atrativo. Em locais nessa condição, é comum se encontrar espécies com dietas especializadas em um tipo de recurso e o desenvolvimento de comportamentos específicos (Holter et al., 2009; Ocampo; Philips, 2005). Tal especialização pode se dar, por exemplo, por um tipo específico de fezes. Dentro de uma comunidade é possível se encontrar espécies especializadas na busca por fezes de vertebrados herbívoros, ou carnívoros, mas a maioria é mais atraída e prefere fezes de mamíferos onívoros (Filgueiras et al., 2009; Martín-Piera; Lobo, 1996).

A seleção do recurso pelos besouros rola bosta depende de diversos fatores, entre eles a natureza e a disponibilidade do recurso no ambiente (Galetti et al., 2018). Em regiões da África, onde a megafauna de mamíferos é preservada em termos de diversidade e abundância, os rola bosta tendem a ser principalmente coprófagos. Isso ocorre porque essas áreas possuem uma oferta abundante de matéria orgânica proveniente das fezes dos grandes mamíferos (Cambefort & Walter, 1991; Ebert et al., 2019). Por outro lado, em regiões onde a megafauna é escassa ou não está mais presente, como nos Neotrópicos, os rola bosta tendem a diversificar seus hábitos alimentares, com um aumento na ocorrência de espécies necrófagas (Keast, 1969; Giménez Gómez et al., 2018; Ebert et al., 2019). Isso sugere que a ausência ou redução da megafauna pode alterar significativamente a disponibilidade e a natureza dos recursos alimentares disponíveis para os rola bosta, levando a mudanças em sua ecologia e comportamento alimentar (Galetti, 2018).

Entre as diferentes formas de alimentação, a necrofagia é vista como uma dieta suplementar ou alternativa (Amézquita & Favila, 2011; Scholtz et al., 2009). Segundo a história evolutiva da diversificação de hábitos alimentares dos besouros rola bosta, considera-se a necrofagia como uma condição que derivou da dieta coprófaga (Hanski & Cambefort, 1991; Scholtz et al., 2009). Esse fato provavelmente está relacionado com as transformações das florestas tropicais, vinculadas às mudanças climáticas e a extinção de grandes vertebrados, entre os períodos do Plioceno e Pleistoceno (Por volta de 2-5 milhões de anos atrás) (Halffter & Matthews, 1966; Hanski & Cambefort, 1991).

As carcaças em decomposição, chamada de carniça, é um recurso altamente nutritivo devido à presença abundante de microrganismos e a sua textura pastosa as torna atrativa para uma grande diversidade de animais, como por exemplo, os rola bosta (Dawson et al., 2022; Favila, 1993; Selva et al., 2005). Esses besouros são especialmente atraídos por carniças variadas, desde vertebrados terrestres e peixes até artrópodes (Halffter & Matthews, 1966; Gimenez Gómez et al., 2021). A maioria dos rola bosta que utilizam esse recurso é generalista, mas algumas espécies demonstram uma preferência ou especificidade por certos tipos de carniças (Stavert et al., 2014; Stone et al., 2021; Correa et al., 2023). Os estudos geralmente tem utilizado carne (baço bovino) como um recurso para investigar a diversidade de besouros rola bosta em ecossistemas tropicais (Costa et al., 2013; Iannuzzi et al., 2016; Salomão & Iannuzzi, 2017). No entanto, a carniça é frequentemente utilizada como atrativo adicional para investigar a dinâmica ecológica dos rola bosta, geralmente ofertados com outros tipos de iscas, como por exemplo, fezes (Mora-Aguilar et al., 2023).

A carniça possui uma limitada disponibilidade temporal e espacial, além da alta competição por esse recurso por outros animais (Selva et al., 2005), tendo assim sua disponibilidade reduzida para os rola bosta (Barton et al., 2013). Os besouros rola bosta possuem a capacidade de localizar esses recursos pelos voláteis liberados por eles, utilizando como pistas olfativas (Dormont et al., 2010; Stavert et al., 2014). Dessa forma, conseguem detectar as carniças por um período prolongado, pois elas permanecem atrativas por cerca de um mês (Mayer & Vasconcelos, 2013), o que pode indicar um potencial de aproveitamento maior. Entretanto, só é possível determinar a preferência dos besouros rola bosta por um tipo específico de carniça quando há disponibilidade de diferentes tipos em um local (Stavert et al., 2014; Correa et al., 2023).

Quando se trata da alimentação dos besouros rola bosta, a atração pelo recurso pode envolver uma variedade de interações, desde o reconhecimento até a sua utilização (Tonelli et al., 2021; Larsen et al., 2006; Salomão et al., 2017. A preferência alimentar, ou seja, a escolha alimentar, refere-se à eleição de uma categoria/tipo particular de alimento diante as alternativas disponíveis (Stavert et al., 2014; Salomão et al., 2017; Salomão et al., 2023; Ebert, 2019). Portanto, para se testar a atratividade é necessário que os recursos sejam oferecidos de forma isolada, enquanto na preferência, os recursos devem ser ofertados simultaneamente. Dessa forma, a escala espacial específica de cada um dos testes pode ser distinguida (Salomão et al., 2023).

Para investigar como os besouros utilizam os recursos de acordo com sua disponibilidade ou especialização em um alimento específico, geralmente têm se utilizado armadilhas iscadas em estudos de campo, que testam a atratividade dos recursos para os besouros rola bosta (Bourg et al., 2016; Salomão et al., 2017; Correa et al., 2023). A nível de comunidade, se pode utilizar dados de diversidade de espécies associadas a cada tipo de recurso (Alvarado et al., 2021; Salomão et al., 2023;) – indicando como as comunidades locais respondem com respeito à atratividade a determinados alimentos. A nível de espécie, índices de preferência, como INDVAL, CLAM ou o índice de Levins servem como aproximações para verificar a preferência de cada espécie por um determinado tipo de alimento (Correa et al., 2020; Correa et al., 2023). De maneira prática, pesquisas sobre dieta em rola bostas consistem em ofertas de recursos alimentares próximos um do outro, utilizando uma distância de 2 m a 30 m entre cada tipo de isca (Filgueiras et al., 2009; Noriega, 2012; Correa et al., 2016; Ferreira e cols. 2020; Salomão et al., 2023). Ditos experimentos podem ser realizados em campo ou em laboratório (Stone et al., 2021; Stavert et al., 2014; Tshikae et al., 2008), sendo que os de campo podem sugerir com maior fidelidade o que de fato é atrativo e preferível pelos besouros, devido a fatores ambientais que influenciam na localização, quantidade, disponibilidade e qualidade do recurso, que vai interferir diretamente na seleção pelos besouros (Bourg et al., 2016).

Diante dos cenários atuais de mudanças ambientais, é possível que o hábito alimentar dos besouros rola bosta estejam sendo afetados. Estudos que avaliem a preferência e atratividade alimentar desses organismos são importantes, pois essas respostas podem fornecer informações sobre a estrutura das comunidades dos besouros e ajudar na elucidação do funcionamento dos ecossistemas (Halffter & Halffter, 2009; Scholtz, 2009).

3 OBJETIVOS

3.1.1 Geral

Avaliar o efeito da atratividade e preferência de iscas na diversidade taxonômica de escaravelhos em uma região da Amazônia Central

3.1.2 Específicos

1. Testar o efeito de três tipos de carniça (fígado de frango, baço bovino e carne de peixe) na composição de espécies e na estrutura da comunidade de escaravelhos;
2. Verificar se as espécies de besouros rola bosta apresentam preferência por um dos tipos de carniça.

HIPÓTESE

Há diferença entre os tipos de carniça na atratividade e preferência da comunidade de rola bosta.

PREDIÇÃO

Há diferença entre os tipos de carniça na atratividade e preferência da comunidade de rola bosta.

4 CONSIDERAÇÕES FINAIS

Os resultados encontrados neste estudo nos permitiram concluir que a comunidade de besouros rola bosta apresenta atratividade por um tipo de carne em decomposição, mas não tem preferência por um tipo específico.

Consideramos que ao fornecermos informações sobre a preferência e atratividade de diferentes tipos de recursos pelos besouros, foi possível contribuir para que estudos futuros referentes às respostas funcionais dos besouros frente a diferentes distúrbios ambientais.

Ainda, esse trabalho servirá como modelo padronizado a ser utilizado em futuras pesquisas utilizando carne em decomposição, uma vez que se percebeu que o uso de um tipo de isca é suficiente para atrair os besouros rola bosta necrófagos, não necessitando utilizar-se de outros tipos de isca.

Por fim, acreditamos que estudos futuros devam ser realizados na tentativa de se entender quais fatores influenciam a atratividade desses besouros. Sugerimos a realização de experimentos de olfatometria, em que possa descrever quais compostos voláteis são emitidos por cada tipo de recurso

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ANEXO - THE MOST ATTRACTIVE IS NOT ALWAYS THE PREFERRED: LESSONS FROM NECROPHAGOUS DUNG BEETLE ASSEMBLAGES IN A REGION OF THE CENTRAL AMAZON

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4.1 Abstract

Resource attractiveness and preference is determinant to assess how biodiversity is structured in different ecosystems. Necrophagy is the alternative or complementary dietary habit of dung beetles, but few studies has focused on evaluating different carrion types attract different species. The goal of this study was to assess the effect of carrion type on attractiveness and preference of dung beetle taxonomic diversity in a region of Central Amazon. Pitfall traps baited with bovine spleen, chicken liver, and fish (freshwater sardine) were installed. Bait attractiveness was estimated by sampling designs that allowed exclusively one food type in the field, while bait preference comprised a sampling design with more than one food type offered simultaneously in a restricted space. We collected 3,151 individuals from 24 dung beetle species. Bovine spleen was the most attractive bait in both food preference and food attractiveness experiments. Bovine spleen was the only carrion type in which indicator species were recorded.. Our results indicate that the dung beetle species and assemblages perceive and are attracted differently to each carrion type. This study provides important data related to the habits of necrophagous dung beetles, serving as a basis for future studies related to dung beetle diet.

Keywords: Carcass; Amazon rainforest; Scarabaeinae.

4.2 Introduction

Animals face many choices in their lifetimes, including which foods to eat. The choice of food is a complex process that comprises food recognition and use, as well as the trade-offs between the energy invested and gained by using such resources (Schallhart et al., 2012; Latty and Trueblood, 2022). In addition, food choice reflects how individuals perceive and select food resources in their habitats (Agetsuma, 1996; Bourg et al., 2016; Salomão et al., 2022). It is expected that animals have evolved mechanisms that enable them to choose resources that maximize their fitness (Schallhart et al., 2012; Bailes et al., 2018; Latty and Trueblood, 2022). For example, when presented with a set of options, honeybee colonies will choose the most concentrated sugar syrup (up to a threshold concentration; Bailes et al., 2018). Depending on the availability of food resources in time and space in the environments, animals may recognize and use them differently (Lemke, 1984; Alm et al., 2002). The assessment of how species are attracted to- and prefer different food types may also aid in the understanding of the spatial coexistence of species (Salomão et al., 2023).

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are a taxonomically and functionally diverse insect group that primarily consume vertebrate feces, with most adult beetles burying portions of the fresh dung of mammals into the soil for nesting and feeding their offspring (Halffter & Edmonds, 1982; Hanski & Cambefort, 1991; Scholtz et al., 2009). However, in some regions, such as the Ethiopian, Australian, and especially in the Neotropics, dung beetle species show a greater diversity of feeding habits (Halffter & Halffter, 2009). Among the dung beetle diets, necrophagy may be a complementary or alternative diet that is broadly observed in these beetles (Amézquita & Favila, 2011; Scholtz et al., 2009). According to dung beetle evolutionary history, necrophagy is a derived condition from coprophagy (Hanski and Cambefort, 1991; Scholtz et al., 2009). It is likely that this happened because of the tropical forests evolutionarily linked to climate changes and species extinction of large vertebrates between the Pliocene and Pleistocene (5–2 Mya) (Halffter & Matthews, 1966; Hanski and Cambefort, 1991).

Decomposing carcasses (e.g., carrion) are nutritiously rich in microorganisms and bear a doughy texture, which favors their use by a wide array of animals (Dawson et al., 2022; Favila, 1993; Selva et al., 2005). Dung beetles are attracted to fresh and decomposing tissues from dead animals (Halffter & Matthews, 1966; Gimenez Gómez et al., 2021). Although most carrion-feeders among dung beetles are carrion generalists (Correa et al., 2023), there are some species that exhibit a degree of specificity/preference to carrion resources (Stavert et al., 2014; Stone et al. 2021; Correa et al., 2023). Empirical studies often use bovine spleen as a type of carrion to survey dung beetle assemblages in tropical ecosystems (Costa et al., 2013; Iannuzzi et al. 2016; Salomão & Iannuzzi, 2017). Regarding coprophagy, many studies has analyzed the role of dung types in attractiveness of dung beetle species (e.g. Filgueiras et al., 2009; Bogoni et al., 2014). However, most studies use carrion as a complementary attractant to assess dung beetle ecological dynamics (Mora-Aguilar et al., 2023). To assess the importance of carrion in necrophagous dung beetle ecological patterns, it is determinant to understand the potential role of carrion types in species distribution, attractiveness and food choice.

Due to the limited spatio-temporal availability of carrion, allied with high competition for this food resource (Selva et al., 2005), its availability may be reduced for dung beetles (Barton et al., 2013). The high competition for carrion may result in a scenario in which species may need to rapidly detect and choose to use or not this decaying food. Dung beetles detect volatile compounds that are released by food resources (e.g. feces, fruits and carrion), using them as olfactory cues to locate resources (Dormont et al., 2010; Stavert et al., 2014). This fact is critical for carrion search, given that it remains attractive for necrophagous beetles for longer periods (c.a., 1 month; see Mayer & Vasconcelos, 2013). Moreover, carrion is widely used by vertebrates (Lira et al., 2020), which may consume the whole carcass rapidly in natural conditions (*personal observation*). In this sense, the attractiveness of each carrion, in the first moment, may be an important indicator of the potential for use by dung beetles. However, only under circumstances where there is availability of different carrion we can detected if dung beetles prefer any specific carrion (Stavert et al., 2014; Correa et al., 2023). Therefore, by assessing the attractiveness and preference for carrion within a dung beetle assemblage, it is possible to better understand the mechanisms of coexistence and distribution of necrophagous organisms in space, and how assemblages are structured depending on the available carrion type.

The goal of this study was to assess the effect of bait attractiveness and preference on dung beetle taxonomic diversity in a region of Central Amazon. More specifically, we tested the effect of three carrion types (chicken liver, bovine spleen, and freshwater sardine – hereafter 'fish') on dung beetle diversity numbers, abundance, and assemblage structure (i.e. the distribution of species and its abundance). We also tested whether species presented a preference towards one of the carrion types. Bait attractiveness was estimated by sampling designs that allowed exclusively one food type in the field, while bait preference comprised a sampling design with more than one food type offered simultaneously in a restricted space (Salomão et al., 2023, see Material and Methods). Based on previous data (Stavert et al., 2014; Iannuzzi et al., 2016;), we expect that a higher diversity and abundance of dung beetles will be attracted to- and prefer bovine spleen when compared to chicken liver and fish.

4.3 Material and Methods

4.3.1 Study site

We carried out this study in Adolpho Duckes' Forest Reserve (2°57' S, 59°55' W, ca. 90 m a. s. l.), located in Manaus, Amazonas state, Brazil. This reserve is directed by Instituto Nacional de Pesquisas da Amazônia and contains approximately 10,000 ha of conserved area, mostly composed by *terra firme* forest, with minimal disturbance levels (Brito, 2010). Vegetation physiognomy is composed mostly by ombrophilous dense forest and floodable forests (*igapós*). The climate of the region is classified as tropical, hot and humid (Af) according to Köppen's classification and has a mean annual temperature of 26 ºC, ranging between 19 and 39 ºC throughout the year (Climate Data, 2022). The region has a mean annual rainfall ranging between 1,900 and 2,300 mm, with two marked seasons – a rainy season between December and May (mean monthly rainfall: 277.76 mm) and a dry season between June and November (mean monthly rainfall: 78.93 mm) (Ferreira et al., 2012; Climate Data, 2022).

Surrounding the studied reserve there are two large blocks of land-cover types: (1) an urban landscape, comprising Manaus, one of the largest cities in the Amazon region; and (2) a conserved forest continuum. The experiment was performed in conserved forests at least 3 km distant from the direct urban influence of the city of Manaus and other human establishments (e.g. villages). As this reserve has never been deforested due to urban expansion or any Western practices, such as cattle ranching, mineral extraction or selective logging, this study site serves as a good model to assess ecological patterns of native ecosystems.

4.3.2 Food attractiveness and food preference experiments

Dung beetles were sampled in July 2022, comprising the dry season of the region (Baccaro, 2008). The dry season of this Amazonian region is marked by a high activity of dung beetles (Ratclife, 2013), allowing adequate representativeness of their assemblages. Samplings were performed for two experiments: (1) food attractiveness, which tests the attractive potential of different carrion types separately; and (2) food preference, which tests the preference when carrion types are offered together. These experiments were adapted from previous studies encompassing bait attractiveness and preference of dung beetles (Filgueiras et al., 2009; Bogoni et al., 2014; Salomão et al., 2017, 2023).

The experiment of attractiveness aimed to test the potential of each carrion type to attract dung beetle species. This setup minimized potential bias from the attractive effects that might have been caused by the availability of other neighboring food types. The experiment of preference investigated which types of carrion dung beetles prefer when multiple options are available. For each experiment, pitfall traps were installed in the field to capture dung beetles that were attracted or preferred one of the carrion types. These pitfall traps were baited with different carrion types (bovine spleen, chicken liver, and fish), which had been allowed to decompose in sealed containers for 48 hours prior to the experiment. The carrion types selected have been effective in previous ecological studies of dung beetles in Neotropical region (Mora-Aguilar et al., 2023).

Each pitfall trap consisted of a 1,000 mL cylindrical plastic container (13 cm high and 15 cm diameter), buried at soil surface. Above pitfall trap, ca. 25 g of carrion was deposited in a metal recipient. Inside pitfall trap, a 200 mL water, salt (ca. 5 g), and detergent (ca. 5 mL) solution were used in order to preserve captured dung beetles and prevent their escape. A plastic lid was secured over the trap to prevent the entry of rainwater and debris. After a 48-h period, dung beetles that had fallen into the traps were collected and stored in plastic vials containing 70% ethanol.

The attractiveness experiment comprised 15 sets of pitfall traps for each carrion type, arranged in linear transects. Each set consisted of two pitfall traps, each baited with one type of the carrion and spaced 5 m apart. In the setup, pitfall sets containing the same carrion type were installed sequentially, while sets with different carrion types were spaced at least 150 m apart to minimize interference (Fig. S1A). In total, the experiment involved 45 replicates, consisting of 15 for each of the three bait type, with sampling effort encompassed 90 pitfall traps (15 replicates x 2 pitfall traps x 3 treatments). The carrion preference experiment comprised 15 sets of pitfall traps, each offering all three carrion types simultaneously. Additionally, control pitfall traps (without bait) were used in this approach. Each set comprised of eight pitfall traps (two for each carrion type and two the control traps), installed 2 m apart from one another (see Fig. S1B). In both experiments, the sets were spaced at least 150 m apart to ensure independence between samples (Larsen & Forsyth, 2005; Silva & Hernández, 2015). Overall, the experiment included 60 replicates, 15 for each carrion type and 15 for the control (15 replicates x 2 pitfall traps x 4 treatments [3 bait types and a control] = 120 pitfall traps).

The collected material was identified to species level by using literature (Génier, 2009; Vaz-de-Mello et al., 2011; González-Alvarado & Vaz-de-Melo, 2021) and by comparisons with deposited specimens in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (Manaus, Amazonas, Brazil). The specimens were subsequently deposited in the Entomological Collection of Universidade Federal de Pernambuco (CEUFPE, Recife, Pernambuco, Brazil).

4.3.3 Data analyses

To estimate the completeness of dung beetle diversity in each experiment, we performed Sample Coverage estimation in iNEXT online software (Hsieh et al., 2016). This estimation considers the species richness, relative abundance, and the rare species in the samples. We performed Sample Coverage for each bait type in each experiment (food attractiveness and food preference).

We estimated taxonomic diversity of dung beetles collected in each bait type and in each experiment by calculating the Hill numbers (Jost, 2006). Diversity numbers were estimated in the orders q = 0 (q0, species richness, which does not account species abundance), q = 1 (q1, exponential of Shannon entropy, which is sensitive to species abundance and is a proxy of the number of abundant species in a sample), q

= 2 (q2, inverse of Simpson, which gives higher weight to species abundance than q1 and indicate the number of dominant species) (Hill, 1973; Jost, 2006). The estimation of diversity numbers was performed in iNEXT online software (Chao et al., 2016; Hsieh et al., 2016).

To assess the effect of carrion type in each experiment (food preference and food attractiveness) on dung beetles' diversity numbers and abundance, we performed Generalized Linear Models (GLMs). For species richness (q0) data, we used Poisson error distribution. Due to the overdispersion in abundance data (Residual deviance/Residual d. f. > 2), we used negative binomial error distribution. For the number of abundant (q1) and dominant species (q2), we used Gaussian distribution. We tested homocedasticity of the GLMs by using Fligner-Killeen test (Fligner & Killeen, 1976). We checked data distribution visually by using q-q plots, and we used Cook's distance to test the presence of outliers (Cooks' Distance > 1.0). Data were analyzed in R software version 4.1.2 (R Development Core Team, 2022).

For a finer assessment of dung beetle species attractiveness towards carrion types, we used Indicator Value (IndVal). This analysis combines specificity degree, estimated through relative abundances, and fidelity degree, estimated by the degree of incidence – both specificity and fidelity degree were assessed relative to the carrion types (Dufrene & Legendre, 1997; Mcgeoch et al., 2002). For a broader comprehension and clearer biological meaning of carrion specificity among dung beetle species, we used data from both experiments together. We perfomed IndVal in labdsv package (De Cáceres & Legendre, 2009) in R software (R Development Core Team, 2022).

To test whether carrion types affected the dung beetle assemblage structure (i.e. species composition considering its abundances) in each experiment, we performed Permutational Analysis of Variances (PERMANOVA). Moreover, we performed Permutational Analysis of Dispersion (PERMDISP) to statistically compare the multivariate dispersion of dung beetle assemblage structure in each carrion type. For PERMANOVA, we used 9,999 randomizations, while for PERMDISP we performed 999 random events (Anderson, 2006). We used post-hoc Tukeys' test to compare dispersion (PERMDISP) observed of assemblage structure data recorded in each carrion type. Both PERMANOVA and PERMDISP were ran in vegan package (Oksanen et al., 2020), in R software (R Development Core Team, 2022). To test how carrion types in the different experiments grouped dung beetle data according to assemblage structure, we performed the Similarity Profiles (SIMPROF) test. We performed SIMPROF in Primer software version 6.0 (Clake & Gorley, 2006). For a visual interpretation of SIMPROF patterns, we performed a heatmap for data from both experiments. We performed heatmap in ggplot2 package (Wickham et al., 2016). For PERMANOVA, PERMDISP, and SIMPROF, we used similarity matrices obtained from Bray-Curtis' similarity index.

4.4 Results

A total of 3,151 individuals were collected, 3,145 in baited traps and six in control traps, belonging to 13 genera and 24 species (Table 1).Three species were highly abundant *Deltochilum* gr. *submetalicum*, *Deltochilum* gr. *aspericolle* and *Canthon triangularis* comprising together ca. 60% of the individuals collected. Fourteen species comprised less than 1% of the total assemblage abundance (Table 1). Two species were singleton – *Oxysternon* aff. *osculatti* and *Oxysternon durantoni*. Regarding data distribution among carrion types in both experiments, 1,560 individuals identified in 22 species were collected in pitfall traps baited with bovine spleen; 837 individuals identified in 19 species were collected in fish-baited pitfall traps; 748 individuals from 18 species were collected in chicken-baited pitfall traps. Sample coverage ranged between 98% and 100% (see Table 1), indicating that we had an appropriate effort to represent the dung beetle assemblages in our study.

For the experiment of food attractiveness, a total of 1,562 individuals from 22 species were recorded. Pitfall traps baited with bovine spleen captured most individuals (n = 856) and species (s = 19), followed by fish-baited traps (n = 430, s = 18), being chicken-liver baited pitfall traps those that captured the least abundance and species richness of dung beetles (n = 276, s = 16). There was no statistical difference in dung beetle abundance recorded among the three carrion types ($X^2_{2,42} = 3.46$, $P = 0.52$). Species richness (q0) ($X^2_{2,42} = 18.08$, $P < 0.01$), number of abundant species (q1) ($X^2_{2,42} = 56.59$, $P < 0.01$) and number of dominant species (q2) ($X^2_{2,42} = 55.17$, $P < 0.01$ see Fig. 1) were higher in bovine-spleen baited traps compared to the other carrion types. For the food preference experiment, 1,583 individuals from 21 species were collected. Bovine-spleen baited traps recorded a total of 704 individuals from 18 species, chicken-liver baited traps recorded 472 individuals from 14 species, while fish-baited pitfall traps recorded a total of 407 individuals from 17 species. For the control traps, six individuals of five species were collected. They are *Canthidium* sp. (n = 1), *Deltochilum* gr. *aspericolle* (n = 1), *Coprophanaeus jasius* (n = 1), *Ateuchus globulus* (n = 2) and *Deltochilum* gr. *submetallicum* (n = 1). There was a significantly lower abundance (X2 3,56 = 7.50, P < 0.01), species richness ($X^2_{3,56}$ = 4.48, P < 0.01), number of abundant ($X^2_{3,56}$ = 0.70, P < 0.01) and dominant species ($X^2_{3,56}$ = 0.71, P < 0.01) in control traps compared to carrion baited traps (Fig. 2).

Regarding species distribution, *Ateuchus simplex* (n = 5), *Onthophagus* aff. *osculatti* (n = 1), *Scybalocanthon pygidialis* (n = 4), and *Oxysternon durantoni* (n =1) were collected exclusively in bovine-spleen baited traps, and *Hansreia coriacea* (n = 5) was exclusively recorded in chicken liver and fish-baited traps (Table 1). Six species were classified as indicators of bovine-spleen baits: *Canthidium* sp. (IndVal = 0.52, P < 0.01), *Canthon triangularis* (IndVal = 0.64, P < 0.01), *D.* gr. *submetalicum* (IndVal = 0.51, P < 0.01), *Eurysternus atrossericus* (IndVal = 0.38, P < 0.01), *A. simplex* (IndVal = 0.13, P = 0.03), and *Eurysternus caribaeus* (IndVal = 0.63, P < 0.01) (Table 1). No species were classified as indicator of the other carrion types. According to PERMANOVA, carrion types structured different dung beetle assemblages, both in food attractiveness (F = 6.64; P < 0.01) and food preference experiments (F = 3.82, P < 0.01). Data dispersion was distinct among carrion types in food attractiveness experiment (PERMDISP: F= 6.43, P < 0.01), with chicken-liver pitfall traps presenting a higher data dispersion when compared to fish-baited pitfall traps (Fig. 3). There was no difference in data dispersion of carrion types in food preference experiment (PERMDISP: F = 0.65, P = 0.52). Dung beetle assemblage structure was segregated in three groups, in both food attractiveness and food preference experiments (SIMPROF: P < 0.05, Fig. 4). In food attractiveness experiment, two groups clustered data obtained from chicken liver, and a third group clustered data obtained from the three carrion types (Fig. 4A). In food preference experiment, one of the three clusters grouped data obtained from chicken liver and fish-baited traps, a second group clustered data from all carrion types, and a third group clustered data from bovine spleen and chicken-liver baited traps (Fig. 4B).

4.5 Discussion

Dung beetles have an extensive range of feeding habitats, from highly specific dietary preferences to more generalist approaches – as the species of the genus

Bradypodidium Vaz-de-Mello, 2008 that apparently feeds exclusively in sloths' dung – to species that feed from a wide variety of food types – as some *Dichotomius* Hope, 1838 and *Deltochilum* Eschscholtz, 1822 species (Vaz-de-Mello, 2008; Hallfter & Halffter, 2009; Costa et al., 2013; Salomão et al., 2014, 2017). While natural history has presented surprising diet patterns of dung beetles (Scholtz et al., 2009; Halffter & Halffter, 2009), there is a lack of standardization among studies that focus on assessing the recognition of different food types by these insects. Regarding necrophagy on dung beetles, some species are clearly recognized as necrophagous, such as some *Coprophanaeus* Olsoufieff, 1924 species (Edmonds & Gillet, 2010). Nonetheless, there are few studies focusing on the assessment of the effect of different carrion types in food attractivity and preference of dung beetles (e.g. Stavert et al., 2014; Stone et al., 2021; Correa et al., 2023). The current study deepens the comprehension regarding necrophagous diet of Amazonian dung beetles. Carrion types attracted species differently, with bovine spleen capturing a higher diversity than chicken liver and fish meat. Moreover, bovine spleen was the only carrion type in which species showed a high fidelity, confirming our hypothesis. Carrion is usually used only as a complementary bait type in ecological studies of dung beetle assemblages (Ebert et al., 2019; Mora-Aguilar et al., 2023; Salomão et al., 2023). The results presented herein allowed us to expand the knowledge of food recognition among necrophagous dung beetles in Amazonian forests.

Bovine spleen attracted a higher dung beetle diversity than the other carrion types and was the only carrion in which indicator species were recorded. Higher diversities of dung beetles in a treatment (e.g. spatio-temporal and trophic resource) are often related to its broader usage by the species (Liberal et al., 2011; Salomão et al., 2017; 2022; Correa et al., 2021). The high diversity observed in bovine spleen could suggest that this carrion type could allow the co-utilization of this food type by of a higher number of species when compared to the other carrions. There is a fierce competition for food among dung beetles (Hanski & Cambefort, 1991; Scholtz et al., 2009). As the quality of the resources can affect the fitness of the individuals (Favila, 2001), dung beetle could prefer high-quality resources (but see Frank et al., 2017) carrion quality could be affecting the diversity patterns observed herein. For example, the necrophagous dung beetle *Canthon cyanellus* LeConte can breed on different qualities of carrion, although low-quality food led to a reduced parental fitness (Favila, 2001).

Besides food quality, higher amounts of food tend to attract a higher diversity of dung beetles (Finn & Giller, 2000). Although is unlikely that bovine carrion represents a common food resource in Amazonian forests, such carrion could be a proxy of native mammal carrion, as jaguars, tapirs, and sloths. On average, tropical forests harbor small and medium-sized mammals, and proportionally, they are larger than most birds and fish. Since olfactory cues are the main mechanisms to perceive food resource in dung beetles, the preference for specific food types depend on the volatile compounds produced by the food resource – which may be related to nutritional quality of such resources (Hanski & Cambefort, 1991; Holter & Scholtz, 2007; Bogoni & Hernandez, 2014). Dimethyl trisulfate is a notable volatile compound produced by bovine carrion (Stavert et al., 2014). One hypothesis is that mammalian carrion shares volatile bouquets that could attract dung beetles similarly. By detailing the similarities and differences presented in carrion types of different vertebrates, it is possible to draw clearer conclusions regarding the effect of bovine carrion volatiles on dung beetle diversity. Likewise, disentangling the importance of quantity and quality of carrion types could deepen the findings of the current study.

Curiously, in food attraction experiment chicken-liver baited traps presented a higher dispersion of their data when compared to the other carrion types. Such trend was reinforced with the SIMPROF clusters, where dung beetle assemblage was segregated in three clusters, two of them comprised exclusively chicken-liver data, and one of the comprised the three carrion types. Although ecological data are commonly asymmetrically distributed (Greenacre, 2016), dung beetles attracted to bovine spleen and fish meat showed a more homogenous dispersion of their assemblage structure. The multivariate approach used herein served as a proxy of Beta diversity (Anderson et al., 2006), and suggested that chicken liver recorded more unstable (heterogeneous) dung beetle assemblages. For instance, studies on saproxylic beetles in Central Amazonia and canopy beetles in Australia within tropical forests have both found that resource heterogeneity within tropical tree canopies plays a crucial role in maintaining beta diversity (Alencar et al., 2021; Wardhaugh et al.,2012). A previous study with *Dichotomius* beetles from Atlantic forest suggested that food recognition mediated by olfactory cues could diverge depending on individual traits, as sex and age (Salomão et al., 2021). We hypothesize that bovine spleen and fish provide trustworthy and stable olfactory cues for dung beetles, while the attractiveness of chicken liver may be more context-dependent, thus leading to more heterogeneous dung beetle assemblages.

When comparing the results found between food attractiveness and food preference, we observed two interesting patterns: diversity was markedly different between food types in food attractiveness – with bovine spleen recording higher diversity than the other food types – but not in food preference experiment (1). Moreover, according to SIMPROF, in food attractiveness experiments chicken liver recorded different assemblages from those recorded in bovine spleen and fish-baited traps, and such difference was not clearly observed in food preference experiments (2). Different aspects may be considered in the differences observed between experiments, as the energy demanded by dung beetles for foraging activities and its consequent rewards, the confounding factor that could be acting on dung beetle perception of food types, and the selectiveness whenever different food types are simultaneously offered. Carrion and dung are randomly distributed in the ecosystems, and finding and removing food resources is energetically costly for dung beetles (Heinrich & Bartholomew, 1979; Cambefort & Hanski, 1991; Krell et al., 2003; Scholtz et al., 2009). Although food choice can be strict in some scenarios (e.g. Salomão et al., 2017; 2023), confounding factors may also affect the selection of food types by dung beetles. For example, dung beetles may find misleading odor cues that lead them to interact and pollinize *Orchidanta* Brown flowers in Malaysia, although not using them as a food resource (Sakai & Inoue, 1999). One hypothesis is that, under the condition of specific food types that are available and spaced from other food types (i.e. food attraction experiment), the energetical investment to find them will lead to a more marked food choice when compared to scenarios where different food types are simultaneously offered (i.e. food choice experiment). This would lead to clear differences in dung beetle diversity and assemblage structure between food types in food attraction experiments. Thus, when different food types of a similar kind of resource (carrion) are close, olfactory cues could lead to a random selection of food, masking the differences between them and leading to similar dung beetle assemblages among carrion types. In addition, considering that necrophagy is relatively recent in Scarabaeinae beetles, speciation processes to use the different carrion types by such beetles are still in progress (Gillet & Toussaint, 2020). Thus, this could lead to a potential lack of carrion speciation among the most dung beetle species, resulting in an absence of carrion preference at assemblage level.

In synthesis, this study highlighted the pivotal role of different carrion types in the segregation of dung beetle assemblages in Amazonian forests. Like studies that demonstrated the importance of different dung types for the assemblage structuration in other tropical rainforests (Filgueiras et al., 2009; Bogoni et al., 2014), here we demonstrate that dung beetle species can present preferences toward specific carrion types – although such preferences can depend on the spatial scale of food availability, and it was not find at assemblage level. Our study presented broad and still superficial patterns, which may be deepen by future finer assessment of the mechanisms that drives carrion choice by dung beetle species. Volatile dispersion, arena observations, physiological and electroantennogram experiments can be future study fields that aid in deepening the knowledge of carrion perception and use by dung beetles.

4.6 References

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4.7 Figure captions

Figure 1. Abundance and taxonomic diversity (Hill numbers) of dung beetle collected through pitfalls baited with bovine spleen, chicken liver, and fish in Adolpho Ducke Forest Reserve, Amazonas, Brazil. Preference experiment.

Figure 2. Abundance and taxonomic diversity (Hill numbers) of dung beetle collected through pitfalls baited with bovine spleen, chicken liver, and fish in Adolpho Ducke Forest Reserve, Amazonas, Brazil. Attractiveness experiment.

Figure 3. Tukey's post hoc test comparing dispersion patterns of samples between bait types for the food attractiveness experiment. Traps baited with chicken liver showed greater data dispersion.

Figure 4. Dendrograms of dung beetles grouped into specific bait types, using the Bray-Curtis similarity index. The presence of dashed lines highlights significant differences between bait types, as analyzed with SIMPROF. The heatmap illustrates the distribution of dung beetle species based on abundance data recorded in the study resources. Food attractiveness (A), Food preference (B).

Figure 1.

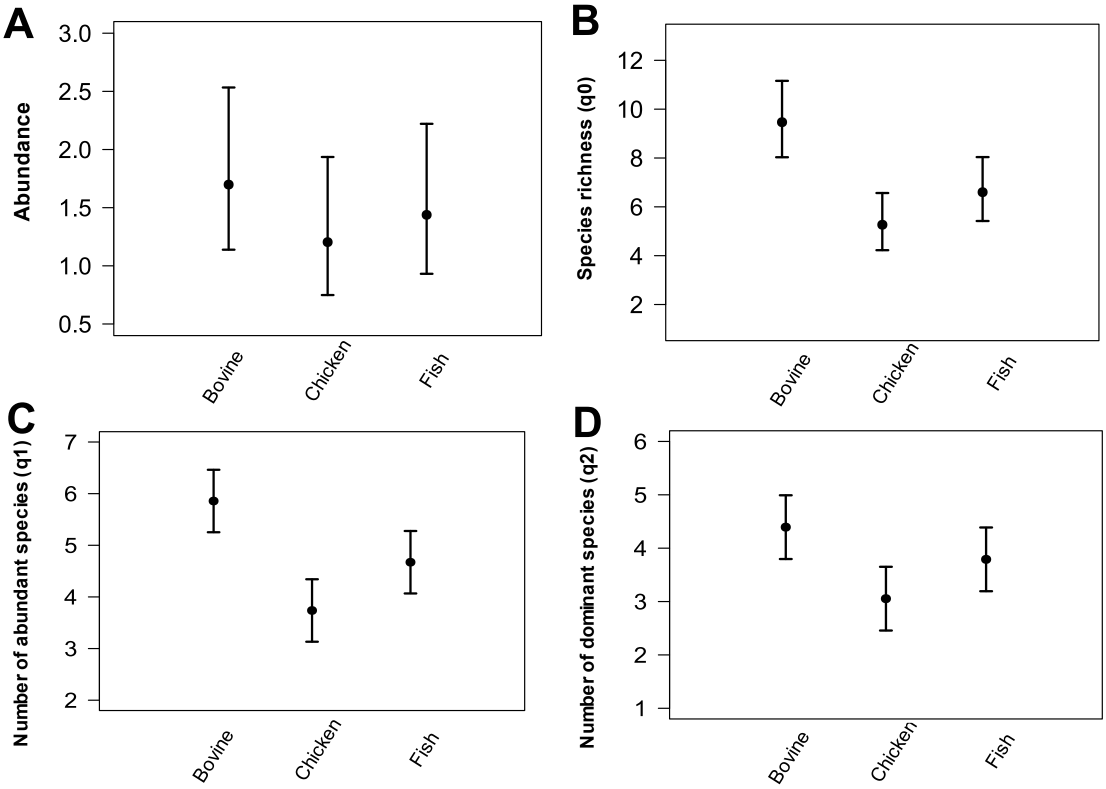

A
Abundance
3.0
2.5
2.0
1.5
1.0
0.5
Bovine
Chicken
Fish
B
Species richness (q0)
12
10
8
6
4
2
Bovine
Chicken
Fish
C
Number of abundant species (q1)
7
6
5
4
3
2
Bovine
Chicken
Fish
D
Number of dominant species (q2)
6
5
4
3
2
1
Bovine
Chicken
Fish

Figure 2.

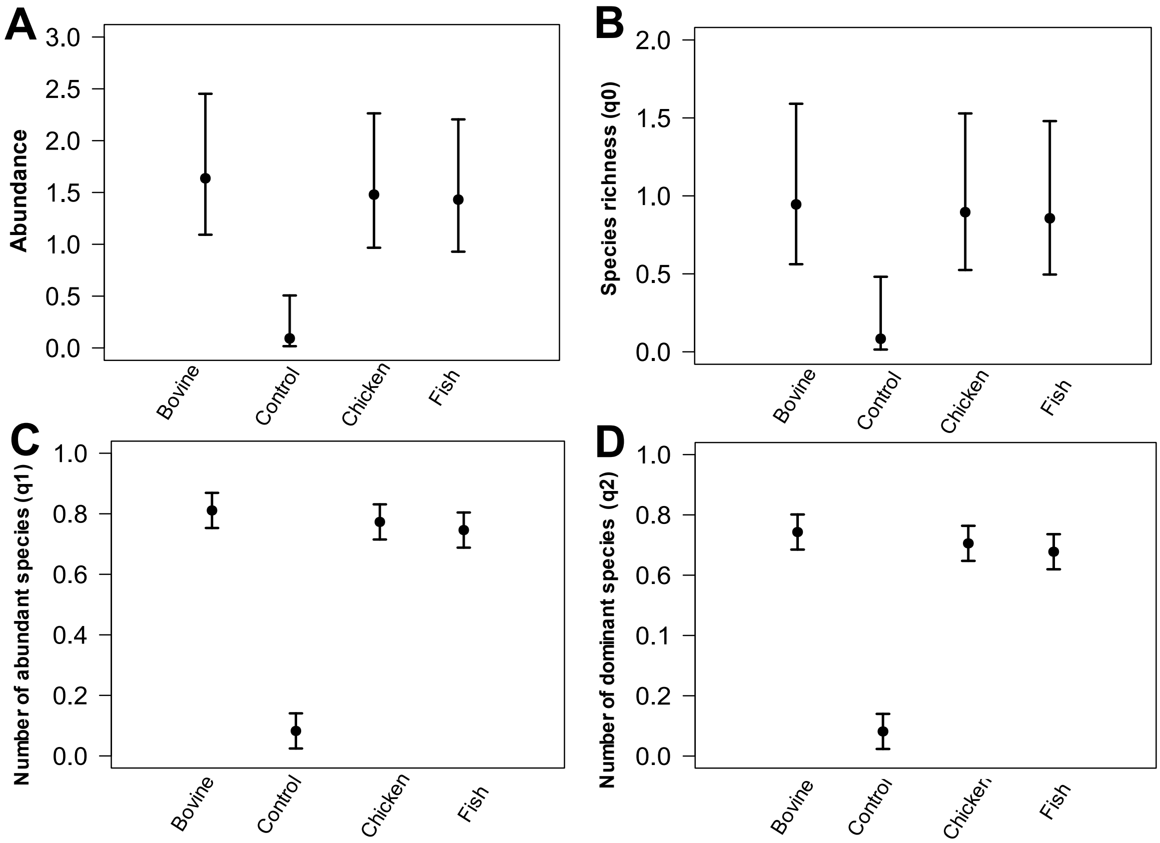


Figure 3.

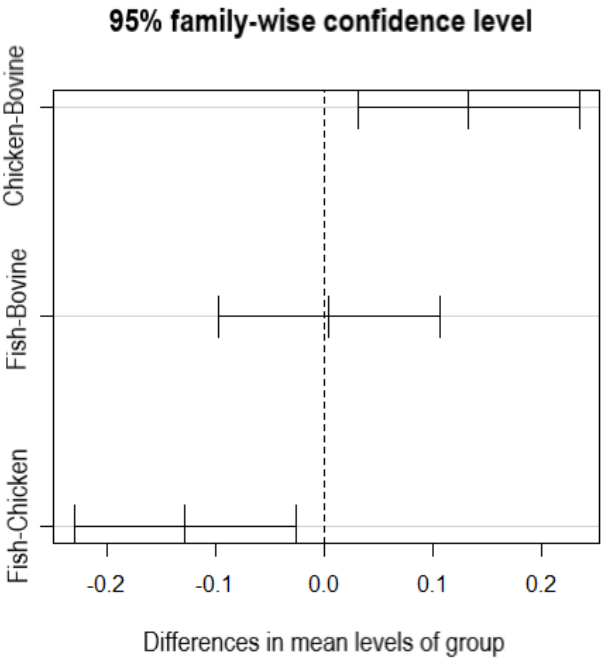


Figure 4.

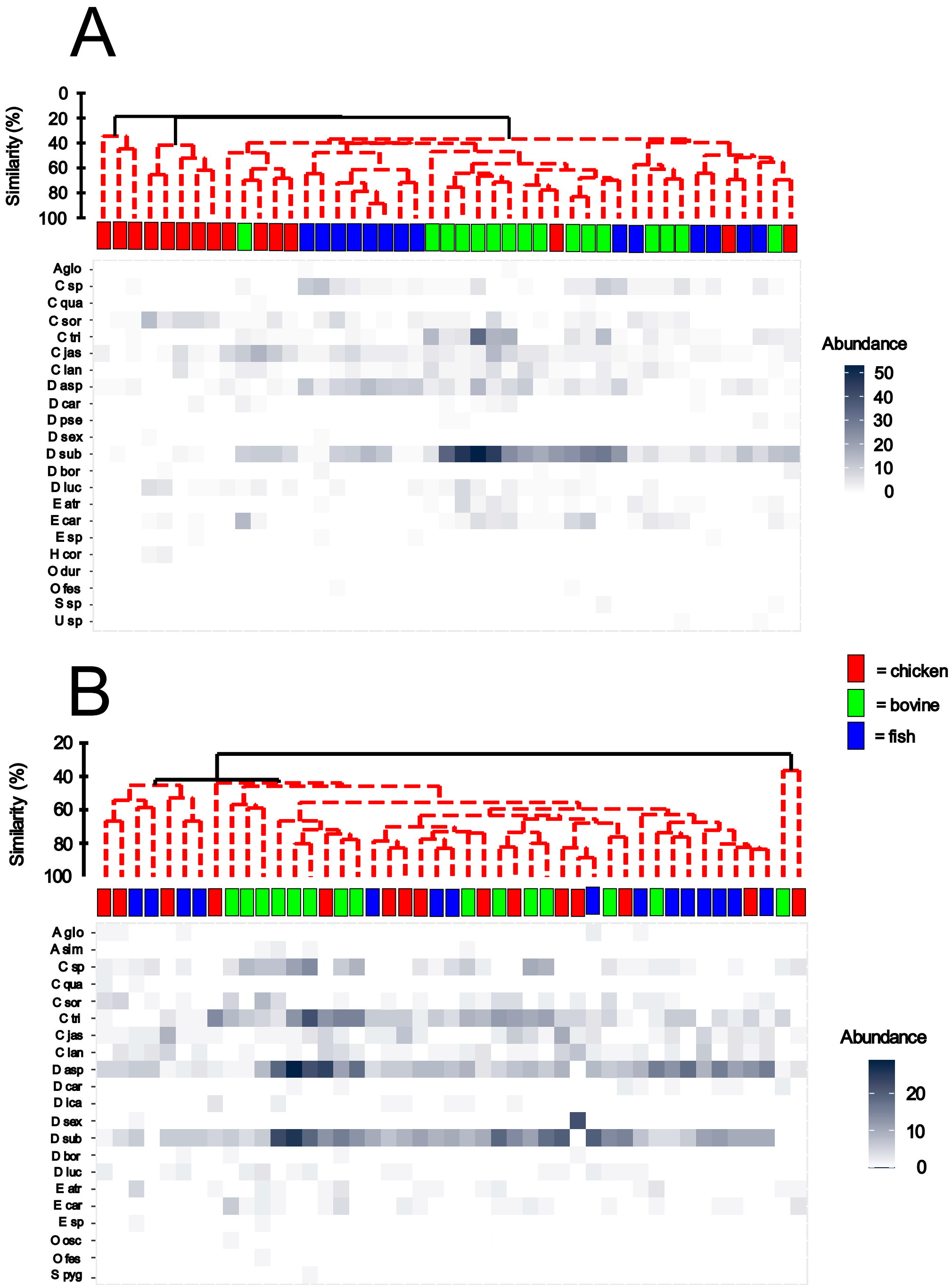

A
Similarity (%)
0
20
40
60
80
100
Aglo
C sp
C qua
C sor
C tri
C jas
C lan
D asp
D car
D pse
D sex
D sub
D bor
D luc
E atr
E car
E sp
H cor
O dur
O fes
S sp
U sp
Abundance
50
40
30
20
10
0
B
= chicken
= bovine
= fish
Similarity (%)
20
40
60
80
100
A glo
A sim
C sp
C qua
C sor
C tri
C jas
C lan
D asp
D car
D ica
D sex
D sub
D bor
D luc
E atr
E car
E sp
O osc
O fes
S pyg
Abundance
20
10
0

Table1. Abundance, species richness and resource preference (Indicator Value - IndVal) of dung beetle species collected through pitfalls baited with bovine spleen, chicken liver, and fish. Data obtained from food preference and attractiveness experiments, in the Adolpho Ducke Forest Reserve, Amazonas, Brazil. A- Food attractiveness experiment and P- food preference experiment.

	Carrion types							
	Bovine spleen		**Chicken liver**		**Fish**			
Taxa	**A**	**P**	**A**	**P**	**A**	**P**	**IndVal**	**Total**
Ateuchini								
Ateuchus globulus (Boucomont, 1928)	1	0	0	2	1	4	Generalist	8
Ateuchus simplex (Le Peletier & Serville, 1828)	0	5	0	0	0	0	Specialist	5
Eutrichillum sp.	0	1	1	0	3	1	Generalist	6
Deltochilini								
Canthon quadriguttatus (Olivier, 1789)	1	0	1	2	0	1	Generalist	5
Canthon sordidus Harold, 1868	31	31	51	17	22	7	Generalist	159
Canthon triangularis (Drury, 1770)	130	141	8	77	13	40	Specialist	409
Deltochilum gr. *aspericolle* Bates, 1870	54	160	17	106	111	136	Generalist	584

Deltochilum carinatum (Westwood, 1837)	10	4	3	2	1	4	Generalist	24
Deltochilum icarus (Olivier, 1789)	2	3	1	6	2	1	Generalist	15
Deltochilum gr. *sextuberculatum* Bates, 1870	0	0	1	0	1	1	Generalist	3
Deltochilum gr. *submetallicum* (Castelnau, 1840)	347	187	76	147	132	127	Specialist	1,016
Scybalocanthon pygidialis (Schmidt, 1922)	3	1	0	0	0	0	Generalist	4
Hansreia coriacea (Schmidt, 1922)	0	0	5	0	0	0	Generalist	5
Dichotomini								
Dichotomius lucasi Harold, 1869	24	10	23	8	5	5	Generalist	75
Dichotomius boreus (Olivier, 1789)	2	2	4	0	2	1	Generalist	11
Oniticellini								
Eurysternus atrossericus Génier, 2009	27	12	0	5	7	7	Specialist	58
Eurysternus caribaeus (Herbst, 1789)	71	20	8	8	2	2	Specialist	111
Onthophagini								
Onthophagus aff. *osculatii* Guérin-Méneville, 1855	0	1	0	0	0	0	Generalist	1

Phanaeini								
Coprophanaeus jasius (Olivier, 1789)	66	16	62	52	45	26	Generalist	267
Coprophanaeus lancifer (Linnaeus, 1767)	44	12	14	28	20	27	Generalist	145
Oxysternon festivum (Linnaeus, 1758)	1	1	0	0	1	0	Generalist	3
Oxysternon durantoni Arnaud, 1984	1	0	0	0	0	0	Generalist	1
Genera *incertae sedis* in Scarabaeinae								
Canthidium sp.	41	97	1	12	61	17	Specialist	229
Uroxys sp.	1	0	0	0	1	0	Generalist	2
Number of individuals (Abundance)	856	704	276	472	430	407		3,145
Number of species (Species richness)	19	18	16	14	18	17		102
Sampling coverage (%)	99.55%	99.41%	98.27¨%	100%	99.13%	99.02%		

4.8 Supplementary Material.

Figure S1. Scheme of food attractiveness. Each set of traps was distant 150 m from each other.

Figure S2. Scheme of food preference experiments. Each set of traps was distant 150 m from each other.

Figure S1.

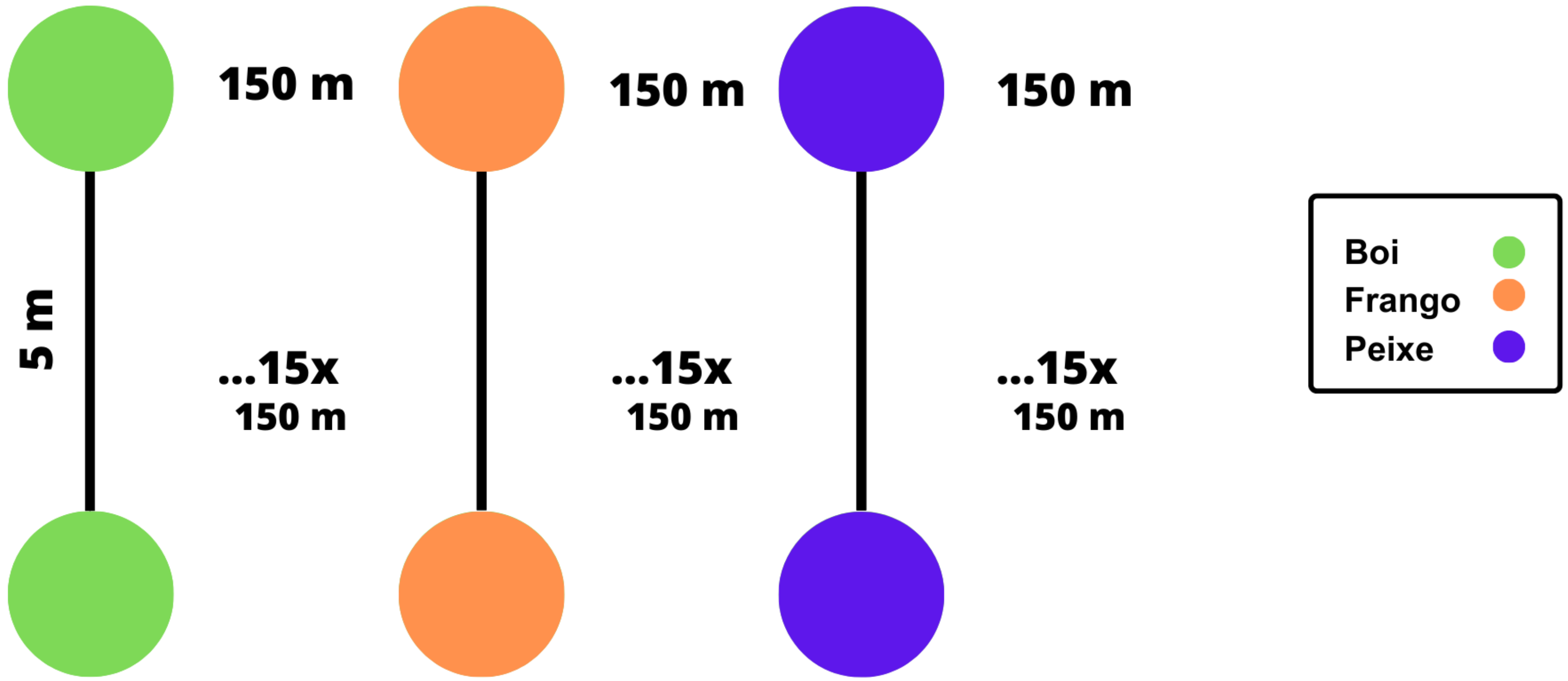
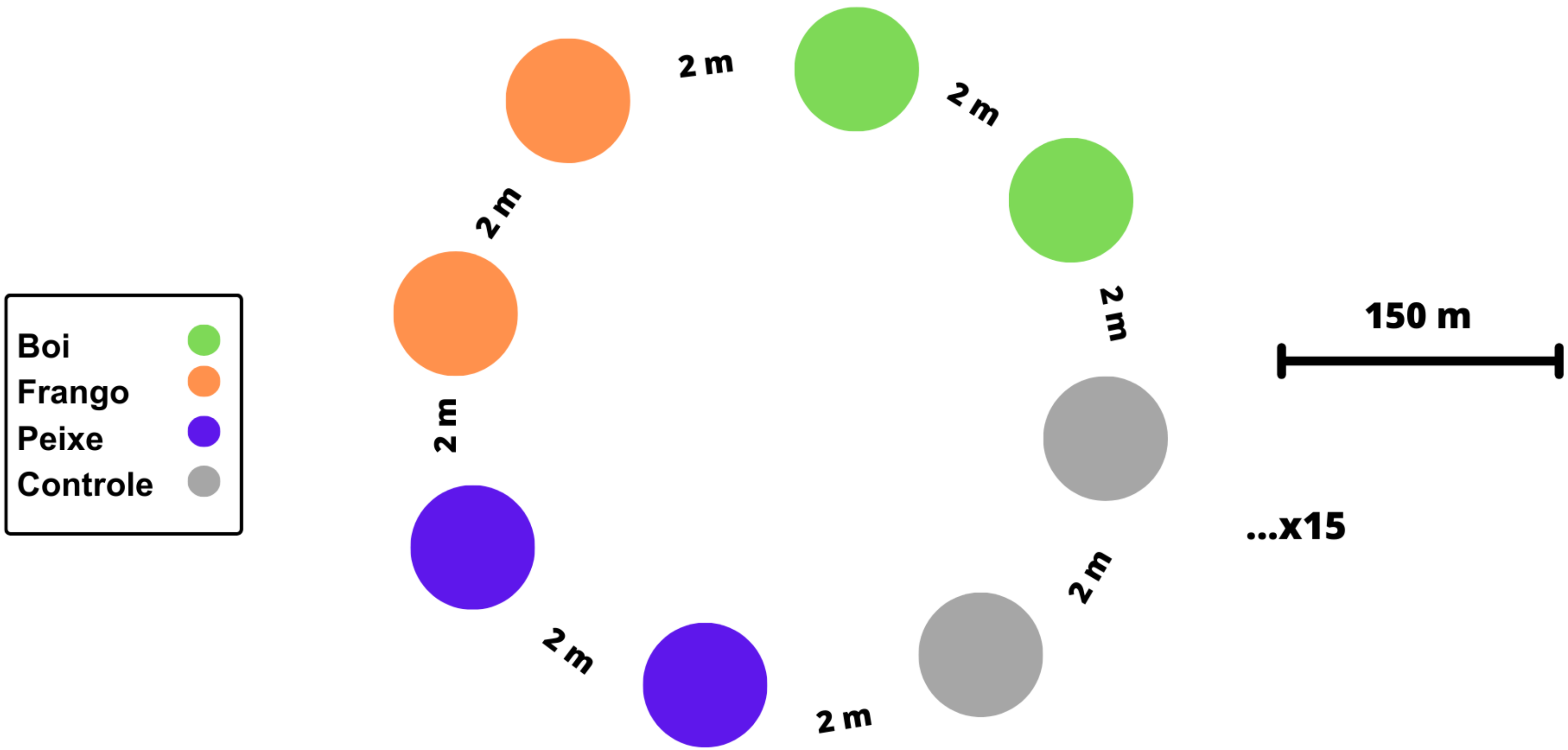


Figure S2.



4.9 Acknowledgement

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