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Dieta e potencial de dispersão de sementes por canídeos no Cerrado

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RESUMO

A ordem Carnivora apresenta diversos representantes que consomem frutos e potencialmente atuam na dispersão de sementes. Apesar disso, poucas espécies de carnívoros Neotropicais possuem a dieta estudada em detalhe, incluindo a identificação do material de origem vegetal e seu papel potencial como dispersor de sementes, principalmente em relação a aspectos qualitativos e quantitativos. Neste estudo destacamos duas espécies de canídeos (Canidae, Carnivora), o lobo-guará (*Chrysocyon brachyurus*) e o cachorro-do-mato (*Cerdocyon thous*), que apresentam dieta frugívora e potencial como dispersores de sementes. Nós quantificamos a dieta de ambos canídeos baseado em amostras focais obtidas em campo no sudeste do Brasil por 15 meses. O lobo-guará apresentou dieta generalista, baseada principalmente em roedores, aves, frutos diversos e o fruto da lobeira (*Solanum lycocarpum*). A dieta variou sazonalmente: o consumo de roedores e *S. lycocarpum* foi maior durante a estação seca, enquanto o consumo dos demais frutos foi maior na estação chuvosa. O lobo-guará selecionou positivamente algumas presas como os gêneros de roedores *Necromys* e *Clyomys*, e alguns frutos (como *Psidium grandifolium* e *S. lycocarpum*). Em relação ao papel destes canídeos na dispersão de sementes, comparamos a porcentagem e tempo de germinação de sementes que passaram pelo trato digestivo deles com sementes plantadas com polpa da fruta (controle 1) e sementes limpas (controle 2). Para o lobo-guará, 18 das 23 espécies de sementes presentes na sua dieta continuaram viáveis após a ingestão, enquanto que para o cachorro-do-mato, oito das 12 espécies continuaram viáveis após consumidas. Ambos os canídeos demonstraram ser dispersores legítimos das espécies do Cerrado, principalmente de plantas com frutos médios e grandes (>1cm), mas também de frutos menores (*Miconia* sp.). Das 14 espécies de plantas testadas, cinco germinaram mais após passarem pelo trato digestivo dos canídeos em relação aos controles, enquanto duas germinaram menos. Para as demais espécies testadas não houve diferença na porcentagem de germinação entre as espécies consumidas e o controle das sementes limpas. Por fim, a partir do cálculo do tempo de passagem no trato digestivo do cachorro-do-mato (17.8 ± 5 horas), é possível assumir que estes possuem a capacidade de depositar sementes a longas distâncias da planta-mãe. O estudo aprofundou o conhecimento sobre a dieta do lobo-guará, destacando quais os recursos essenciais para sua ocorrência em áreas naturais e nos forneceu informações sobre seletividade e sazonalidade da dieta. Por fim, nos permitiu afirmar a legitimidade dos dois canídeos como dispersores de sementes para muitas espécies e nos deu pistas de sua importância para a dinâmica e manutenção deste processo no Cerrado.

ABSTRACT

The order of carnivores has several representatives that consume fruit and could potentially act in seed dispersal. Despite this, few Neotropical carnivore species have their diet studied in detail, including identification of plant material, and their potential as seed dispersers, especially in relation to qualitative and quantitative aspects. In this study, we highlight two species of canids (Canidae, Carnivora), the Maned wolf (*Chrysocyon brachyurus*) and the Crab-eating fox (*Cerdocyon thous*), which simultaneously have a diet based largely on frugivory and great potential as seed dispersers. We quantified the diet of both canids based on fecal samples obtained in the field in southeastern Brazil for 15 months. The Maned wolf showed an omnivorous, generalista diet, based mainly on rodents, birds, various fruits and the fruit of the wolf tree (*Solanum lycocarpum*). The diet varied seasonally: The Maned wolf consumed more rodents and *S. lycocarpum* during the dry season, while the other fruits were consumed more during the rainy season. In addition, the Maned wolf positively selected some prey such as the rodent genera *Necromys* and *Clyomys*, and some fruits (such as *Psidium grandifolium* and *S. lycocarpum*). Regarding the role of these canids in seed dispersal, we compared the germination percentage and time of seeds that had passed through their digestive tract with seeds planted with fruit pulp and seeds cleaned by hand. For the Maned wolf, we identified that 18 species, out of the 23 present in its diet, to have viable seeds after ingestion. For the Crab-eating fox, from 12 species present in its diet, eight has seeds viable after being eaten. Both canids proved to be legitimate dispersers of Cerrado species, mainly of plants with medium and large fruits (>1cm), but also of species with smaller fruits (*Miconia* sp.). From the 14 plant species tested, five germinated more after passing through the digestive tract of canids compared to the controls, while two germinated less. For the other species there was no difference in the germination percentage between the seeds defecated and those in whole fruits. Finally, by calculating the gut passage time of the Crab-eating fox (17.8 ± 5 hs), it is possible to infer they can deposit seeds at long distances from the mother plant. The study made it possible to deepen our knowledge about the diet of the Maned wolf, highlighting which resources are essential for their occurrence in natural areas, providing us with information on food selectivity and how seasonality influences its diet. Finally, it allowed us to affirm their legitimacy as seed dispersers for many species and to understand their importance for the dynamics and maintenance of this process in the Cerrado.

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INTRODUÇÃO

A frugivoria (i.e., o consumo de frutos por animais) e a dispersão de sementes são processos ecológicos fundamentais para a manutenção das populações de plantas e animais, levando em conta a evolução das características e diversidade dos agentes envolvidos (Van Der Pjil, 1982; Jordano et al., 2007; Galetti et al., 2013). Ambos os processos são afetados por características tanto dos frutos, quanto dos frugívoros dispersores (Howe & Smallwood, 1982; Jordano, 2007). Assim, os agentes dispersores contribuem para a legitimidade e efetividade de dispersão de sementes e o recrutamento e reprodução da planta de maneiras diferentes (Nevo et al., 2023). Este processo é influenciado tanto por aspectos quantitativos, como o número de sementes dispersas, quanto qualitativos, como a probabilidade de recrutamento de cada semente dispersa (Schupp et al., 2010; González-Castro et al., 2015; Nevo et al., 2023). O número de sementes dispersas (aspecto quantitativo) dependerá do número de visitas feitas pelo frugívoro à planta mãe e pelo número de sementes consumidas e transportadas por visita. Por outro lado, os aspectos qualitativos são influenciados pelo tratamento dado as sementes pelo frugívoro (taxa de destruição das sementes, escarificação, limpeza das sementes) e o micrositio de deposição, por exemplo (Schupp et al., 2010).

Dessa forma, a ecologia, comportamento e fisiologia dos frugívoros são fatores a serem levados em conta. Nesse sentido, a ordem Carnivora apresenta características particulares distintas de outros grupos amplamente estudados (Cruz et al., 2021; Draper et al., 2022), como aves e mamíferos herbívoros, apresentando comumente maiores áreas de vida (Coelho et al., 2008; Graham & Stenhouse, 2014; Draper et al., 2022), tempos distintos de passagem no trato digestivo, geralmente maior do que o de aves e menor quanto comparado com mamíferos herbívoros de porte semelhante (Varela & Bucher, 2006; Escribano-Avila et al., 2014; Draper et al., 2021), bem como a capacidade de depositar sementes intactas após passagem pelo trato digestivo (Draper et al., 2022) e diferenças no uso de habitat e local de deposição das sementes. Além disso, tais particularidades podem influenciar os fatores quantitativos, como o número de sementes ingeridas e qualitativos, como a distância de dispersão da planta-mãe e os microsítios de deposição (Traveset & Verdú, 2002; Jordano et al., 2007; Schupp et al., 2010; Delciellos et al., 2017).

No Brasil, canídeos como o lobo-guará (*Chrysocyon brachyurus*) e o cachorro-do-mato (*Cerdocyon thous*), são carnívoros que apresentam amplo potencial de estudos relacionados a frugivoria e dispersão de sementes. Essas espécies apresentam uma dieta composta em grande parte por frutos, capacidade de defecar sementes intactas e possuem grande plasticidade ecológica, explorando desde habitats naturais até áreas com algum grau de antropização (Bueno & Motta-Junior, 2004; Souza et al., 2021; Reis et al., 2023; Draper et al., 2022). O lobo-guará é o maior canídeo da América do Sul, com uma massa corpórea variando de 20 a 30 kg e entre 95 e 120cm de comprimento (Dietz, 1985; Nowak, 1999). Apresenta ampla distribuição geográfica, ocorrendo no Peru, Bolívia, Paraguai, Argentina, Brasil e Uruguai (Nowak, 1999). Sua ocorrência é amplamente relacionada com áreas de savanas, campinas e gramíneas, apresenta uma ampla área de vida (20 a 115 km²) e hábitos generalistas, como a maioria dos canídeos, alimentando-se de frutos, sementes, invertebrados, vertebrados e ovos (Bueno et al., 2002; Jácomo et al., 2009; Paula et al., 2013; Motta-Junior et al., 2014; Reis et al., 2023). Apresenta hábitos solitários, com formação de casais somente durante o período reprodutivo e maior atividade em horários crepusculares ou noturnos (Jácomo et al., 2009). Atualmente é uma espécie classificada como quase ameaçada pela IUCN (2024) e como vulnerável no contexto do Brasil (ICMBio, 2024), tendo como principais ameaças a perda de habitat, a introdução de espécies invasoras (competição e introdução de doenças) e atropelamentos (Paula et al., 2013).

Por sua vez, o cachorro-do-mato é um animal de menor porte, pesando entre 4 e 10 kg e com tamanho por volta de 60 a 70 cm (Nowak, 1999). Sua distribuição se dá entre Argentina, Bolívia, Brasil, Colômbia, Equador, Guiana Francesa, Guiana, Panamá, Suriname, Uruguai e Venezuela, abrangendo tanto América Central, quanto do Sul (Nowak, 1999). Assim como o lobo guará, apresentam hábitos generalistas e uma ampla plasticidade ecológica, o que possibilita com que explore diversos ambientes, desde savanas, pradarias, campos, florestas tropicais, áreas semi-áridas e ambientes antropizados (Jácomo et al., 2009; Cazetta & Galetti, 2013; Souza et al., 2021). Sua área de vida varia entre 0,5 e 12,8 km² (Juarez & Marinho-Filho, 2002; Faria-Corrêa et al., 2009) e sua dieta consiste em invertebrados, vertebrados e frutos (Bueno & Motta-Junior, 2004; Jácomo et al., 2004; Bianchi et al., 2014). Podem apresentar hábitos solitários, formar casais permanentes ou bandos familiares, tendo os períodos crepusculares e noturnos os de maior atividade (Juarez & Marinho-Filho, 2002; Gatti et al., 2006; Faria-Corrêa et al., 2009). Não é considerado como ameaçado, conseguindo se adaptar bem a ambientes antropizados como pastagens, plantações e, inclusive, aproveitando recursos em cidades.

Os estudos já realizados com estes canídeos focaram principalmente na descrição da sua dieta e com maior enfoque sobre o conteúdo ingerido de origem animal (Dietz, 1985; Aragona & Setz, 2001; Juarez & Marinho-Filho, 2002; Bueno et al., 2002; Bueno & Motta-

Junior, 2004; Gatti et al., 2004; Rocha et al., 2004; Jácomo et al., 2004; Rodrigues et al., 2007; Rocha et al., 2008; Bianchi et al., 2014; Dutra-Vieira et al., 2024), sendo muitas vezes os conteúdos de origem vegetal caracterizados com menor especificidade taxonômica ou como "conjunto de frutos". Em relação à dispersão de sementes, a contribuição de ambos os canídeos é bem documentada e reconhecida. Contudo, os estudos tendem a apresentar resultados para uma ou poucas espécies por vez, sendo raros os casos em que abrangem mais de cinco espécies de sementes dispersas em uma mesma localidade (Lombardi & Motta-Junior, 1993; Motta-Junior et al., 1994; Varela & Bucher, 2006; Raíces & Bergallo, 2010; Cazetta & Galetti, 2013; Reis et al., 2023). Além disso, grande parte dos estudos compara as sementes ingeridas pelos canídeos apenas com o tratamento de sementes limpas, deixando de comparar com a porcentagem e velocidade de germinação de sementes ainda com polpa e, por consequência, avaliando apenas aspectos relacionados à escarificação da semente e não a remoção da polpa pelos canídeos (Samuels & Levey, 2005). Em geral, são ignorados aspectos relacionados à remoção de componentes inibidores de germinação presentes na polpa ou de alteração das regulações osmóticas, assim como o papel do frugívoro para cada caso, ou seja, influenciar na germinação como agente de escarificação da semente, como removedor da polpa ou influenciando ambos os aspectos simultaneamente. Dessa forma, um fenômeno de ocorrência natural comum, a deposição das sementes ainda com o fruto após cair da planta-mãe, é geralmente ignorado por grande parte dos estudos relacionados à germinação de sementes (Samuels & Levey, 2005).

O trabalho contemplou o estudo da dieta do lobo-guará e a dispersão de sementes pelo lobo-guará e cachorro do mato na Estação Ecológica e Estação Experimental de Itirapina, região central do Estado de São Paulo, Brasil. A Estação Ecológica (22°00'S; 47°45'O) e a Estação Experimental (22°15'S; 48°00'O) de Itirapina são duas Unidades de Conservação de remanescentes de Cerrado no Estado de São Paulo, localizando-se no município de Itirapina. As duas áreas em conjunto abrangem um território de cerca de 5.500 ha, sendo um dos maiores remanescentes de Cerrado do estado. O clima da região é caracterizado como subtropical de inverno seco (Cwa), de acordo com a classificação de Koppen, a altitude da região é de aproximadamente 770 m acima do nível do mar, precipitação média anual de 1.320 mm e a temperatura média anual de 22,2 °C (Bueno et al., 2002; São Paulo, 2006). Por ter um clima com variações sazonais características, o período de chuvas concentra-se entre a primavera e verão (de outubro a março) e a seca no outono e inverno (entre abril e setembro), variações que influenciam diretamente aspectos fenológicos no domínio do Cerrado (Kuhlmann & Ribeiro, 2016). As áreas abrigam uma grande diversidade de fitofisionomias de Cerrado, contemplando desde gradientes caracterizados por gramíneas e campinas, áreas abertas e mais fechadas de Cerrado (como campo sujo, Cerradão e Cerrado *Sensu stricto*), até florestas relacionadas a corpos d'água, como matas ciliares e matas de galeria (São Paulo, 2006). Ambas as Unidades de Conservação apresentam grande biodiversidade, com mais de 300 espécies de plantas (Tannus & Assis, 2004) e representantes emblemáticos da fauna do Cerrado, como aproximadamente 30% das espécies de aves que ocorrem no Estado de São Paulo (Motta-Junior et al., 2008), além de mamíferos como o lobo-guará, o cachorro do mato, jaritataca (*Conepatus semistriatus*) e outros (São Paulo, 2006).

Dessa forma, neste trabalho avaliei os papeis do lobo-guará e do cachorro-do-mato na dispersão de sementes, abrangendo tanto o aspecto quantitativo, quanto parte dos fatores qualitativos que estão envolvidos (até o estágio da germinação). Em relação à dieta do lobo-guará, quantifiquei os itens consumidos em relação à frequência de ocorrência e biomassa ingerida, de forma a entender a contribuição de cada item. Busquei identificar em nível de espécie os itens vegetais consumidos e investiguei a influência da sazonalidade na dieta, avaliando diferenças entre período seco e chuvoso no conteúdo alimentar da espécie.

Somado a isso pude, a partir de índices, testar a seletividade do lobo-guará em relação aos frutos e pequenos mamíferos consumidos. Por fim, foi possível avaliar o tempo de passagem de sementes de sete espécies distintas no trato digestivo do cachorro-do-mato.

Dividi este trabalho em dois capítulos, que estão escritos em formato de artigos científicos, para facilitar sua submissão para futura publicação. Desta forma, a base de dados é comum para os capítulos, bem como informações pertinentes a serem reforçadas sobre a ecologia das espécies alvo, contudo, o enfoque e o tema abordado em cada capítulo é distinto. O primeiro capítulo acrescenta dados ao conhecimento da dieta do lobo-guará e do cachorro do mato, principalmente em relação à seleção de presas e aos itens de origem vegetal consumidos. O segundo capítulo trata do papel destes dois canídeos na dispersão de diferentes espécies de frutos do Cerrado brasileiro, extrapolando o foco para além do consumo da lobeira (*Solanum lycocarpum*), apontada por vários estudos como a principal fonte alimentar do lobo guará.

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1. CHAPTER I: A WOLF THAT EATS FRUITS? FRUIT AND SMALL MAMMAL SELECTION IN THE DIET OF THE LARGEST CANID OF THE BRAZILIAN CERRADO

Abstract

The Maned wolf (*Chrysocyon brachyurus*) is the largest canid of South America. In spite some studies describe its diet, most have a low taxonomic resolution of the food items. Several studies also do not compare diet composition and food availability, precluding a detailed evaluation of diet preferences and seasonality patterns. We investigated Maned wolf prey selection and seasonality in small mammal and fruit use based on sampling dung, fruit and prey availability in savannas (Cerrado) from southeastern Brazil. We compared the frequency of occurrence and biomass of consumed items with fruit availability based on local plant phenology plots and data about small mammal abundance. The diet of Maned wolf showed a higher proportion of plant (61.4%) than animal (38.6%) items in frequency. The most common items in its diet were small rodents, birds, and fruits of several species, in special *Solanum lycocarpum*. In terms of biomass consumed, armadillos (Dasypodidae) represented a major contribution to the diet. Fruits were consumed all year round, and in dry season fruits from *S. lycocarpum* as well as rodents were specially targeted. At least nine fruit species were reported for the first time in the diet of Maned wolf. Maned wolf most often consumed medium or large fruits (> 1 cm) of orange, yellow or green colors, showing a positive selection for fruits like *Psidium grandifolium* and *Campomanesia adamantium*, as did for rodents *Necromys lasiurus* and *Clyomys laticeps*. We highlight the contribution of *S. lycocarpum* fruit for Maned wolf all over the year, in special during dry season, when other resources are less common. Maned-wolf is likely to contribute to seed dispersal of several plant species and to potentially influence the population dynamics of some of the most common (*N. lasiurus*) and (*C. laticeps*) rodents in this savanna.

Key-Words

Carnivores, Fruit selection, Maned wolf, Prey selection, Rodents, Savanna

1.1. INTRODUCTION

Mammalian carnivores stand out for their potential role as regulators of the abundance of other species, given the diversity of their diets and feeding strategies (Dobson 2014; Cruz et al. 2021; Draper et al. 2022). These species range from representatives with a hyper-carnivorous diet (>70% animal origin, e.g. grey wolf – *Canis lupus*), to meso-carnivorous (31-70% animal origin, e.g. – *Vulpes vulpes*) or hypo-carnivorous (>70% plants and invertebrates, e.g. binturong – *Arctictis binturong*) (Van Valkenburgh, 2007). Among the carnivores that exploit food resources other than meat, the Canidae family is the most notable, with most living species considered omnivorous (MacDonald and Sillero-Zubiri 2004; Fleming et al. 2017). Indeed, studies about the diet of different canids show they may consume vertebrates, invertebrates, fungi, roots, fruit, carcasses and even human waste (MacDonald and Sillero-Zubiri 2004; Fleming et al. 2017; Cruz et al. 2021).

Diet is an important component in understanding the ecology of a species, as well as being a complex factor that considers behavior, foraging characteristics, resource availability and environmental influences, such as seasonality (Birnie-Gauvin et al. 2017; King and Marshall 2022; Vettorazzi et al. 2022). Theory of optimal foraging suggests that predators will give preference to prey with the greatest cost-benefit in terms of energy return in relation to the time spent obtaining that resource, with the time taken being related to factors of the prey and the predator, such as defense mechanisms, body size, escape capacity, but also to characteristics related to the availability of the resource (prey abundance). (MacArthur and Pianka, 1966; King and Marshall 2022; Vettorazzi et al. 2022). In this way, optimal foraging allows us to understand how prey is selected, or which resources are preferred over others. Likewise, the dynamics of resource abundance and availability will influence selectivity, meaning that in cases of scarcity of the optimal resource, it is expected that non-preferred resources will be consumed to a greater extent (Vettorazzi et al. 2022). An important factor in the availability and abundance of prey is seasonality (Vettorazzi et al. 2022), which can interfere with factors such as the fruiting and flowering period (Zimmerman et al. 2007; Pereira et al. 2024), reproductive seasons and the population dynamics of animals and plants (Shimadzu et al. 2013, Nordberg and Schwarzkopf 2019, Bates-Mundell et al 2024). In this way, understanding the variations in the diet of animals considering resource availability/selectivity and seasonal differences in them enable us to understanding better predator-prey interactions and the feeding ecology of species.

In addition, niche is an important concept to consider when trying to understand the diet of organisms. Since the niche is understood as a series of environmental conditions required by a species, and the functions which are associated with this species in nature (Polechová and Storch 2019; Sherry 2023), studying the niche of the species, including niche dimension and niche partitioning, provides insight about habitat use, ecological functions, competition and predation, diet selectivity, as well as generalist or opportunistic aspects of the diet (Polechová and Storch 2019; Torretta et al. 2021).

In the context of the diet of the world's canid species, fruits are a fundamental part of their food resources (Cruz et al. 2021; Draper et al. 2022). Canids often consume medium and large fruits (>1cm), with strong aromas and with variable colors mostly ranging from brown/orange to green (Kuhlmann and Ribeiro 2016; Valenta and Nevo 2020; Fedriani et al. 2024). Canids are also often considered important seed dispersers (Draper et al. 2022; Reis et al. 2023). Like other canids elsewhere, the neotropical genus of canids (*Speothos*, *Cerdocyon*, *Lycalopex*, *Chrysocyon* and *Atelocynus*) can exploit a wide range of food resources, including vertebrates (birds, amphibians, reptiles, mammals, fish), invertebrates (arthropods, mollusks, worms) and plants (leaves, seeds, fruit and roots) (Bueno et al. 2002; Juarez and Marinho-Filho 2002; Cruz et al. 2021). However, most of these informations tends to be anecdotic, diffuse, obtained under different approaches and often targeting specific diet items (e.g. animal prey), and with little taxonomic resolution of consumed items, like those of plant origin (Cruz et al. 2021). As a result, few inferences can be done about the effect of these canids on ecosystem functions, such as top-down control of prey (Fleming et al. 2017), their role in seed dispersal, or even which foods are essential for them to overcome periods of scarcity, like severe dry seasons or post-fire events (Leis and Baldwin 2021) that are likely to increase with climate change. A detailed evaluation of canid's diet may allow us to predict which fruits may be potentially attractive, consumed and have seeds dispersed by them based on fruit traits such as morphology and color (Ronce and Clobert. 2012). A more complete picture of canids diet may also help us to restore degraded lands into more friendly landscapes to wild canids and other species that feed on similar resources (Howe 2016).

Some of these Neotropical frugivorous canids occur in the Cerrado. The Cerrado domain in Central Brazil is covered by a species-rich tropical savanna, a global biodiversity hotspot (Myers et al. 2000). The Cerrado is characterized by having well-defined seasons, with a dry fall and winter (April to September), while spring and summer concentrate the rains (October to March) (Gottsberger and Silberbauer-Gottsberger 2006). About 60%-70% of woody plants species in this savanna rely on animals for seed dispersal (Kuhlmann and Ribeiro 2016), and many plants from Cerrado produce fruit during the rainy season, while fruit availability declines sharply in the dry season (Kuhlmann and Ribeiro 2016). Seasonality can also influence the population dynamics of animal species, like mammals (Rocha et al. 2017; Arnold 2020; Teng et al. 2022), birds (Almeida et al. 2023) and fishes (Santiago et al. 2022), as well as affecting prey selection of carnivores (Motta-Junior et al. 1996; Bueno and Motta-Junior 2006). The Cerrado is home to four of the six canid species that occur in Brazil: *Speothos venaticus*, *Cerdocyon thous*, *Lycalopex vetulus* and *Chrysocyon brachyurus* (Juarez and Marinho-Filho 2002; ICMBio 2020). The Maned wolf (*C. brachyurus*) can be considered one of the most emblematic of the canids that occur in this savannah, given that it is the largest canid in South America, its status as vulnerable and the fact that its diet is still not detailed at a specific level, especially in relation to the fruits it consumes (ICMBio 2024).

The Maned wolf is a large animal (body mass ca. 20-33 kg), which occurs in grasslands and savannas of Peru, Bolivia, Paraguay, Argentina, Brazil and Uruguay (Nowak 1999). It has a large home range (20-115 km^2) and a generalist omnivorous diet, including fruit, seeds, invertebrates, vertebrates and eggs (Bueno et al. 2002; Jácomo et al. 2009; Paula et al. 2013; Motta-Junior et al., 2014). It is a solitary species, forming pairs only during the breeding season and it is most active during the night or twilight period (Jácomo et al. 2009). It is currently considered a globally Near Threatened species (NT - IUCN, 2024), and Vulnerable by the national assessment (VU - ICMBio, 2024), facing threats like conversion of natural areas to croplands, hunting, road-kill mortality and diseases from domestic (dogs, cats) and invasive species (wild boars) (Paula et al. 2013; Lemos et al. 2023).

Thus, this study seeks to test the influence of seasonality on the maned wolf's diet, to test the selectivity of small mammals and fruits in the maned wolf's diet in the Cerrado and to deepen our knowledge of this animal's diet, especially in relation to frugivory. Therefore, this study aims to test the influence of seasonality on the Maned wolf’s diet, to test the selectivity of small mammals and fruits in the Maned wolf’s diet, and to deepen the knowledge of this important canid that occurs in the Cerrado, especially in relation to frugivory. We provide a highly detailed taxonomic resolution study about the fruits in their diet and quantified the importance of foods from plant and animal origin across seasons. We also investigated the potential selection of fruit and small mammal in the diet based on availability and use.

1.2.MATERIALS AND METHODS

We assessed the diet of Maned wolves between December 2022 and January 2024 (14 months), at two nearby study sites, the Itirapina Ecological Station (22°00'S 47°45'W) and the Itirapina Experimental Station (22°15'S 48°00'W), in São Paulo State, southeastern Brazil. These two areas together cover around 5,500 ha and are crossed by several surveillance dirty roads and firebreaks (hereafter firebreaks). These areas have a subtropical dry winter climate (Cwa according to the Koppen classification), with an altitude of 770m asl, average annual rainfall of 1,320mm, average annual temperature of 22.2°C and a well-defined dry (April to September) and rainy (October to March) seasons (Bueno et al. 2002; São Paulo 2006). The vegetation of the sites is Cerrado, a savanna-like vegetation occurring along gradients from grasslands to open- and closed savannas and gallery forests (Bueno et al. 2002; São Paulo 2006).

A pre-existing path (~6km each) (Figure 1S) crossing each site was walked biweekly from December 2022 to January 2024 by one of us (RDF), searching for Maned wolf feces. A total of 279.8 km was covered on the trails, with a sampling effort of 252 hours. The samples were identified based on morphology (shape, color, size), smell, the presence of footprints in the surroundings and the presence of hairs in the feces, the dung, footprints and hairs where identified with the aid of a reference collection (Bueno et al. 2002; Miranda et al. 2014). The feces were stored separately in plastic jars and labelled according to the species and geographic coordinates of collection. In the laboratory, the samples were washed in running water using a fine mesh sieve (1mm) (Emmons 1987) and then examined individually to record the ingested items.

The materials found in the feces, such as bones, claws, hairs, scales, leaves, seeds and shells, were identified by comparing them with reference collections, identification guides and the help of specialists. The plant and animal contents of the samples were weighed separately on a precision analytical balance (Radwag AS.R2 plus Series, Synergy Lab, Brazil). At the same time, we estimated the minimum number of individuals of animal prey consumed by counting specific body parts found in the samples (such as mandibles, skulls, tails, claws) (Emmons 1987). The biomass consumed was then estimated by multiplying the minimum number of individuals found in the samples by the average mass of the species obtained in the literature (Emmons 1987; Bueno et al. 2002). In cases where it was not possible to identify the species, the estimate of biomass consumed was based on the average body mass of species that occur in the study area with measurements similar to those found in the bones/fragments of the samples

(Bueno and Motta-Junior 2004). For the plant content in diet, we estimated the minimum number of fruits, as well as the biomass ingested, based on the average number of seeds per fruit (following Bueno and Motta-Junior 2004) based on a database of fruits from the study sites.

To estimate fruit availability in the study area, data on fruiting plants was collected monthly for a year in six 0.1 ha plots (100 m x 10 m) haphazardly established in the study sites from ca. 500 m to 4.1 km distance among them, and close to the transects used to sample feces. In addition, 14 individuals of wolf-fruit (*Solanum lycocarpum*) were monitored during the same period, as this species is often recorded in Maned wolf's diet (Bueno and Motta-Junior 2004; Motta-Junior et al. 2014). To estimate if Maned wolf consumes food items based on availability, we calculated Ivlev's selectivity index (D; Ivlev 1961) including species recorded in diet and for which we obtained data on availability in the community. To do this, we applied the formula, $D = (r_i - p_i)/(r_i + p_i)$ where, "r_i" is the proportion of resource "i" consumed out of the total resources consumed, and "p_i" is the proportion of resource "i" available in the environment out of the total resources available in the environment (Lyngdoh et al., 2020). The index ranges from -1 to +1. Following Lyngdoh et al. (2020), we classified resources as avoided if values of $D < -0.2$, used according to availability as those falling between $D = -0.2$ to 0.2, and positively selected if $D > 0.2$. Since not all the plant species present in the wolf's diet occurred in the plots, we evaluated the selectivity of inclusion in diet for 14 plant species, of which we had data on occurrence in the diet and abundance in the study area.

Regarding animal items, Ivlev's index was obtained for rodent and marsupial species, the animal items most commonly found in fecal samples. We separated the rodents into three species identified (*Clyomys laticeps*, *Necromys lasiurus* and *Calomys tener*) and a group for unidentified rodents (Rodentia spp.). Marsupials were grouped as Didelphimorphia. Since there is no recent detailed data about the abundance of rodents and marsupials in our study site, we used abundance data for a nearby Cerrado site with similar vegetation and small mammal's species (Furtado et al. 2021), assuming similar distributions of species abundance between sites. To apply Ivlev index to these small mammals' groups we added up the abundance of the *C. laticeps* to compare with the occurrence of *C. laticeps* in feces, just as we did for the *N. lasiurus* and *C. tener*. For marsupials, we added up the abundance of Didelphidae, since we did not identify the marsupial genus in our samples and, finally, for unidentified rodents, we added up the abundance of the other rodent genera (excluding *C. laticeps*, *N. lasiurus* and *C. tener* used previously), always based on Furtado et al. (2021).

We also calculated the niche breadth of the Maned wolf as a way of understanding whether this animal plays a generalist or specialist role in relation to dietary items. We used the calculation of the standardized Levins index by the number of samples with each food item, according to the formula: $BA = (B - 1)/n - 1$, where "BA" is the standardized Levins index, "n" is the number of food categories and "B" is given by $B = 1/\Sigma pi^2$, where "pi" is the frequency of each category used (Krebs 1998). In this index 1 represents extreme generalist and 0 extreme specialist, with values >0.6 considered high, from 0.4 to 0.6 as moderate and <0.4 as low (Sá Oliveira et al. 2014). To calculate this index, we segregated the Maned wolf's food items into eight different categories (wolf fruit, other fruits and grasses, rodents, other mammals, reptiles, insects and birds).

To test whether fruit colors influences its choice by Maned wolf, we compared the number of fruit species of each color that occurred in the maned wolf's diet with the availability of fruit species of those colors in the community. In other words, fruit occurrence (presence of a fruit species in the study sites) *versus* use by this canid (presence of the same fruit species in their diet) by a χ^2 test. To find out which fruits were available in the area, we used a survey of plant species in the sampled sites (São Paulo 2006). The test was carried out aggregating the fruits by color (green, red, yellow, orange, brown, purple, black, white and blue fruits) (Figure 4).

To test whether there was a difference between the estimated total biomass (in grams) ingested between dry and rainy seasons, we applied a Generalized linear mixed-effects models (Gaussian distribution) (GLMM) carried out using the "glmmTMB" package (Brooks et al. 2017) in the RStudio (R Core Team 2024). In this test, the response variable was the biomass consumed, and the explanatory variables were the food item group ("animal" or "plant"), and the season in which the item was consumed ("dry" – April to September, or "rainy" – October to March), considering interactions between these variables in the model. We also considered each sample as a random factor. We checked the normality and homoscedasticity of residuals using RStudio's own functions ("hist", "qqnorm", "qqline" and "residuals"). We removed two outliers from our samples (the data relating to the two armadillo consumptions, with very difscrepant biomass in relation to the biomass of the other groups consumed) (7.7 and 6.3 standard deviations away from mean), to produce more robust GLMM estimates.

To assess the difference in the occurrence of food item groups in Maned wolf feces in the different seasons, we performed a G-test using the "DescTools" package (Signorell 2024) based on the presence and absence of each food item groups in each fecal sample from the dry season or the rainy season. To do this, we used the eight grouping categories from the niche breadth calculation.

2.3.RESULTS

We obtained a total of 97 Maned wolf samples and 39 different food items identified, 23 of which were of plant origin and 16 of animal origin. The Maned wolf showed an omnivorous diet, with a balance between the biomass consumed of plant (57.5%) and animal items (42.5%), with *S.* (26.2%), *Annona crassiflora* (14.4%) standing out among plant items, and armadillos (Cingulata, 24.5%) and rodents (12.4%) among animal items. We found plant items were in 61.4% of the samples, compared to 38.6% of the samples for animal items. Fruits were present in 98.2% of the samples obtained during the rainy season and 100% of the samples from in dry season. Seeds from *S. lycocarpum* fruits were present in 61.4% of the rainy season samples and 97.5% of the dry season samples. Finally, among the predominant food items in the samples, fruit from *S. lycocarpum* (75.3% out of the samples), grasses (24.7%) and *A. crassiflora* (14.4%) stood out among food of plant origin (mostly fruits). Regarding items of animal origin, rodents (43.3%), birds (41.2%) and Coleoptera (29.9%) stood out (Table 1S).

There was a difference between the biomass of plant and animal items consumed between seasons (GLMM test: $Z = 3.58$, $p < 0.001$) (Figure 1- B,C). Also, the season influenced the consumed biomass of plant or animal items ($Z = -2.7$, $p = 0.029$), and the consumption of plant items was positively affected by the rainy season ($Z = 2.43$, $p = 0.015$) (Figure 2). There were differences between seasons for *'S. lycocarpum*' ($G = 20.879$, $p = 4.9e\text{-}06$), and 'rodents' ($G = 10.33$, $p = 0.001$) most consumed in the dry season, and 'Other fruits' ($G = 32.722$, $p = 1.1e\text{-}08$), most consumed in the rainy season (Figure 1 - A).

The analysis of the frequency of occurrence of food items and the analysis of biomass in studies of an animal's diet are two distinct but complementary approaches. Frequency of occurrence refers to the number of times a food item appears in the animal's diet, regardless of the amount consumed. In this way, it is a measure of the regularity or incidence of food in the diet. On the other hand, biomass refers to the total amount of food consumed, based on the mass of the items ingested. This measure reflects nutritional importance, or contribution in terms of quantity ingested. These two approaches are complementary, providing different information covering the preference or availability of food items (frequency of occurrence), or how much each item contributes to the diet in terms of mass or energy (biomass). In general, considering together frequency and % biomass consumed respectively, the most important items in the Maned wolf's diet were wolf fruit (75.2% and 26.2%), rodents (43.3% and 12.3%), birds (41.2% and 4.7%), and large fruits such as *A. crassiflora* (14.4% and 14.4%), *Pouteria torta* (13.4% and 4.3%) and *Pradosia brevipes* (13.4% and 4.3%).

We were able to identify nine new fruit species explored in the Maned wolf's diet (see table 1S and 2S), while only the consumption of Lepidoptera larvae was a novelty among animal items. The Maned wolf's showed a broad niche (Levins index = 0.66, e.g. > 0.6) based on the eight food items groups tested, and a positive selection for most fruit species, with emphasis on *S. lycocarpum* (0.74), *Campomanesia adamantium* (0.83), *Hancornia speciosa* (0.84) and *Psidium grandifolium* (0.95). On the other hand, two species were avoided: *Miconia* spp. (-0.23) and *Xylopia aromatica* (-0.7) (Figure 3 – A). For small mammals, the Ivlev index showed positive selection for the rodent species *N. lasiurus* and *C. laticeps*, neutral effect for *C. tener* and unidentified Rodentia (Rodentia spp.), and a negative selection for the marsupials Didelphimorphia. (Figure 3 – B).

Although there was a greater recurrence of green, yellow and orange fruits in the diet of this canid (Figure 4), there was no selection for fruit consumption based on the colors of fruits available ($X^2 = 6.4$, $p = 0.27$).

2.4.DISCUSSION

The Maned wolf has an omnivorous diet, with a tendency to consume more food from plant than animal origin in frequency and biomass. Rodents and *S. lycocarpum* were more consumed during the dry season, while other fruits were more consumed during the rainy season. Maned wolf positively selected some rodents (*N. lasiurus*, *C. laticeps*) and fruits (*C. adamantium*, *H. speciosa*, *P. grandifolium* and *S. lycocarpum*) as food items, but consume less opossums, and fruits from *Miconia* spp. and *X. aromatica* than expected on availability. This canid had a high occurrence of medium/large fruits of orange to green colors in diet, although not deviating from colors available in the plant community.

Regarding the frequency of occurrence, most studies point to a diet with similar proportions of animal and plant origin, with both food groups ranging from 45% to 55% (See table 1). In the current study, there was a slightly higher frequency of food from plant rather than animal origin, 61.4% and 38.6% respectively, what make Maned wolves meso-carnivores (Van

Valkenburgh 2007). These values are in line with those found by Rodrigues et al. (2007), Bueno and Motta-Junior (2004), and Motta-Junior (2000) (Table 1). The variation observed among studies (from 29.1% to 61.4% of frequency of occurrence of plant items, and 38.6% to 71.8% of animal items) and sites may suggest an ecological plasticity of Maned wolf (Table 1), with the ability to exploit different food items and in different proportions to overcome diet constraints, including in modified landscapes (Motta-Junior 2000; Massara et al. 2012).

In the diet of the Maned wolf, some food items stood out in terms of frequency of occurrence, such as rodents (Motta-Junior 2000; Bueno et al. 2002; Juarez and Marinho-Filho 2002; Massara et al. 2012) (Figure 2S), birds (Motta-Junior et al. 1996; Aragona and Setz 2001) and wolf-fruit (*S. lycocarpum*) (Lombardi and Motta-Junior 1993; Motta-Junior et al. 1996; Bueno et al. 2002; Massara et al. 2012) (Figure 3S). Rodents showed a higher frequency of occurrence in the samples during the dry season in this study (~63%), as expected based on other studies (Motta-Junior et al. 1996). Several rodent species show peaks in abundance during the dry seasons in Cerrado (Alho and Pereira 1985; Vieira 1997; Vieira et al. 2010), what may contribute to a higher consumption of rodents at this time given that these preys are consumed based on its availability (Fig. 3B). In addition, the lower availability of fruits of most plant species in dry season (see Kuhlmann and Ribeiro 2016), may result in the Maned wolf actively searching for animal prey rather than fruits. Giving the scarcity of fruits and insects in dry season (Kuhlmann and Ribeiro, 2016; Ramos-Robles et al. 2023; Van Dijk et al. 2024), rodents and marsupials probably wander more away from their shelters in search of food, making them more exposed to predators than during the rainy season (Rodrigues et al. 2007). Bird consumption was similar between the two seasons (see also Motta-Junior et al. 1996; Aragona and Setz 2001). The wolf-fruit was the most recurrent food in the samples across the year (present in 75% of samples), but in especial in dry season (97.5%), demonstrating the importance of *S. lycocarpum* as a year-round resource for Maned wolf, including in the shortage period of dry season (see also Motta-Junior et al. 1996; Aragona and Setz 2001). Although *S. lycocarpum* and rodents are present in feces at a high frequency, the biomass analysis showed that armadillos (Bueno et al. 2002; Bueno and Motta-Junior 2004; Queirolo and Motta-Junior 2007; Rodrigues et al. 2007) and large fruits (>4cm) (Aragona and Setz 2001; Rodrigues et al. 2007), may have similar or greater importance to items that appear more frequently in the Maned wolf's diet (Bueno and Motta-Junior 2004; Rodrigues et al. 2007). In our study armadillos had a very low frequency of occurrence (occurred twice in the samples, 2.1%), so even though they are important for the biomass consumed, they may not be an essential resource for the Maned wolf diet.

Maned wolf's diet is affected by seasonality in terms of the frequency and biomass of food items. In the dry season some resources, like rodents and wolf fruit are consumed to a greater extent and are considered important for overcoming the adversities imposed by drought. On the other hand, other fruits are especially eaten in the rainy season (Motta-Junior et al. 1996; Aragona and Setz 2001; Bueno et al. 2002). This can be explained by the availability of these resources in the different seasons, since most species fruit during the rainy season (Kuhlmann and Ribeiro 2016), while rodents and *S. lycocarpum* are available, and sometimes more abundant, in the dry season (Alho and Pereira 1985; Motta-Junior et al. 1996; Aragona and Setz 2001; Vieira et al. 2010).

The Levin’s niche breadth index showed a value of 0.6, which represents generalist diet tendencies for Maned wolf (Bueno et al. 2002; Jácomo et al. 2009; Paula et al. 2013) and is in line with values found by other studies (0.4 to 0.6, Motta-Junior et al. 1996; Motta-Junior 1997; Aragona and Setz 2001; Rodrigues et al. 2007). The Ivlev’s selectivity index showed that the fruits consumed are, mostly, actively sought out and selected by the Maned wolf. *Attalea geraensis* and *Diospyros lasiocalyx* appear to be consumed opportunistically, according to availability, while small fruits consumed by birds (*Miconia* spp. and *X. aromatica*) are avoided, as they are likely to have a low energy contribution based on Maned wolf's size (Motta-Junior 2000). In this case, the higher consumption of medium and large fruits, as opposed to the low consumption of small fruits, may also be related to the optimal foraging theory, as it is more advantageous for the maned wolf to consume fewer fruits that provide a higher energy intake, rather than consuming many small fruits each with a low energy reward (MacArthur and Pianka, 1966; King and Marshall 2022). The higher consumption of *S. lycocarpum* in the season of lower fruit availability (Figure 5S-8S) is also demonstrated by the high rate of selection by the Maned wolf for this fruit (Motta-Junior et al. 1996; Motta-Junior 2000) and may be related to the concept of prey substitution (White et al. 1996), so that it replaces other fruits with *S. lycocarpum* and rodents in the dry season (Queirolo and Motta-Junior 2007). This is because, while many plant species do not produce fruit during the dry season, *S. lycocarpum* produces fruit all year round (Figure 7S,8S) (Lombardi and Motta-Junior 1993; Motta-Junior and Martins, 2002). Positive selection for *S. lycocarpum* fruits was also found by Motta-Junior and Martins (2002), which reinforces the importance of this resource for the Maned wolf's diet. However, our study pointed out a positive selection for various fruit species by the Maned wolf, while Motta-Junior and Martins (2002) obtained results that point out mostly to inclusion in diet according to availability.

In relation to small mammals, the Maned wolf showed positive selection of the species *N. lasiurus* and *C. laticeps*, corroborating the findings of Queirolo and Motta-Junior (2007) and Bueno and Motta-Junior (2006), who observed a positive correlation of selection for *N. lasiurus* and *C. laticeps* by Maned wolves, respectively. The genus *C. tener* was positively selected in the studies by Motta-Junior (2000) and Motta-Junior and Talamoni (2005), while in the current study the results pointed to the consumption of this genus according to availability, this may suggest that the Maned wolf may change its prey selectivity according to the availability of resources and the area in which it lives. This result may have been influenced by the fact that rodent abundance was based on secondary data (Furtado et al. 2021), with some unidentified specimens collected in the feces grouped together as "Rodentia spp.", or by occasional differences between the diet of Maned wolf at different sites. All these identified rodents genera have terrestrial habits, or semi-fossorial in the case of *C. laticeps* (Alho and Pereira 1985; Bonvicino et al. 2008; Furtado et al. 2021) and inhabit mostly open areas (Bueno and Motta-Junior 2006). Furthermore, *C. laticeps* is a nocturnal species (Ferrando and Leiner 2017), and although *N. lasiurus* is known as predominant diurnal, in the dry season this rodent seems to change its activity patterns to more crepuscular (Vieira et al. 2010), which combined with the previous cited characteristics makes it easier for Maned wolf to prey on these organisms, specially at the dry season, when it seems to increase animal consumption. (Motta-Junior 2000; Bueno and Motta-Junior 2004; Motta-Junior and Talamoni 2005; Bueno and Motta-Junior 2006).

It is also argued that the great local abundance of *C. laticeps* and *C. tener*, as well as their low escape capacity, with few strategies for erratic movements and jumping, in the case of the first, and low locomotion capacity, in the case of the second, may facilitate predation by Maned wolf (Vieira 1997; Bueno and Motta-Junior 2006). The Maned wolf probably plays a role in regulating the populations of these rodents, in a characteristic top-down process (Bueno and Motta-Junior 2006; Flemming et al. 2017). Finally, the negative selection for marsupials was observed. Although the genus *Didelphis* is commonly found in Maned wolf diets (Bueno and Motta-Junior 2004; Queirolo and Motta-Junior 2007; Rodrigues et al. 2007), they are usually larger than rodents and have scansorial habits, sheltering in trees in threatening situations (Motta-Junior 2000; Almeida et al. 2008). In addition, didelphids have various defense mechanisms, from active forms such as showing their teeth, biting, ruffling their fur and different vocalizations, as well as passive forms of defense, such as defecation and flatulation, secretion of a viscous liquid and death feigning (McManus, 1970). In this way *Didelphis* may require physical confrontation, greater energy expenditure or a greater challenge to the Maned wolf to prey on them (Ortiz et al. 2023). In this case, the consumption of small mammals suggests that, for the Maned wolf, the optimal foraging favors the consumption of rodents, as opposed to the predation of larger mammals, such as didelphids, which likely require greater energy expenditure to be preyed upon (Bueno and Motta-Junior, 2006; King and Marshall, 2022; Vettorazzi et al. 2022).

We identified for the first time the consumption of nine out of 23 identified fruit species (table 1S). Despite that, many of the genera of the same fruit species have already been recorded in the literature as being part of the Maned wolf diet, such as *Byrsonima* (Motta-Junior and Martins 2002; Queirolo and Motta-Junior 2007), *Campomanesia* (Bueno and Motta-Junior 2004; Rodriges et al. 2007), *Myrcia* (Aragona and Setz 2001) and *Cordiera* (Motta-Junior and Martins 2002; Belantani et al. 2005). Some of the new records in the Maned wolf's diet include fruits that are usually consumed by birds (*X. aromatica* and *Myrcia guianensis*), wich suggests that the Maned wolf can exploit fruits other than those most associated with mammals. The consumption and dispersal of *Bidens* sp. suggests Maned wolf also play a role in diplochory (Vander Wall and Longland 2004), since it uses two different dispersal strategies, epizoochory and then endocory for the same plant species. For large fruit species (> 4 cm in length), such as *P. brevipes* and the palm *A. geraensis*, the Maned wolf may represent one of the few remaining seed dispersers (table 1S), considering that other large mammals have become locally extinct in Itirapina, such as tapirs (Pires et al. 2018; Ong et al. 2021).

The prospect that larger animals than rodents would be present in the Maned wolf's diet was fulfilled, given the occurrence of armadillos (Figure 4S – C) and opossums (Bueno and Motta-Junior 2004; Cruz et al. 2021). Finally, reptiles, like lizards (Figure 4S - A), seem to contribute less to its diet, when compared to mammals or birds (see also Bueno and Motta-Junior 2004; Bueno and Motta-Junior 2006), probably representing an alternative resource. Insects are commonly associated as important complements of the diet of smaller canids, such as *Cerdocyon* and *Lycalopex* (Motta-Junior et al. 1994; Rocha et al. 2008; Cruz et al. 2021). However, Maned wolves are also able to exploit a great diversity of invertebrates to supplement their diet, even if their contribution is low for the wolfs diet in terms of biomass (Figure 4S – C), consuming manly orthopterans and coleopterans in this and other studies (Aragona and Setz 2001; Bueno et al. 2002; Bueno and Motta-Junior 2004), but also lepidopterans, hymenopterans (bees, wasps and ants) and termites (Figure 4S - B). Motta-Junior (2000) and Bueno and Motta-Junior (2004) discuss the possibility of Maned wolf exploiting wasp and bee honey as a resource, which may explain the presence of Apoidea in our samples. The consumption of termites by Maned wolf is not commonly reported (Bueno et al. 2002; Bueno and Motta-Junior 2004) and may not be a widely exploited resource. However, it is possible that termites are part of the diet of the Maned wolf, even if to a lesser extent or influenced by seasonality, since samples with termites were restricted to the dry season, which may be related to the exploitation as an alternative resource given the scarcity of other preferred resources such as fruits. In the same way, the consumption of Lepidoptera larvae may be infrequent and an alternative resource, since we found no previous records in the literature of Maned wolf consuming them.

In this study, the Maned wolf mostly consumed medium or large fruits, as expected for mammals (Bueno and Motta-Junior 2004; Fedriani et al. 2024). We also found fruits from other dispersal syndromes in its diet. Small and bright colored bird-dispersed fruits like *Miconia* spp., *M. guianensis* and *X. aromatica* and the sticky *Bidens* sp. often dispersed by epizoochory in the fur of mammals were also found in feces. In our study site there is no selection of fruit color by the Maned wolf. Fruit color selection tends to be associated with groups that have well-developed vision to distinguish colors, such as birds (Duan et al. 2014; Fedriani et al. 2024) and primates (Melin et al. 2019). For mammals with dichromatic vision, such as canids (Siniscalchi et al. 2017), coloration may be a less important selection factor than aroma. In these cases, the most consumed fruits tend to have opaque, unflashy colors (Valenta and Nevo 2020; Fedriani et al. 2024). In addition, many of the fruits found in the Maned wolf's diet have a strong and characteristic aroma when ripe (personal observation), such as *H. speciosa*, *Duguetia frufuracea*, *S. lycocarpum* and *P. brevipes*. In terms of occurrence, less eye-catching colored fruits such as brown, orange, yellow and green were the most recurrent in the canids' samples, like in other studies (Bueno and Motta-Junior 2004; Valenta and Nevo 2020).

The presence of various fruits in the diet of the Maned wolf's and other carnivores may be related to the high nutritional value and availability of this resource (Koike & Massaki 2019; Draper et al. 2021), as well as the cost-benefit ratio balance, given that some fruits are easy to obtain and have a high energy content (MacArthur and Pianka, 1966; King and Marshall 2022). Because they are rich in carbohydrates, vitamins and minerals, fruits represent important resources for these specific components, with great energy availability (Quintero et al. 2020; Rojas et al. 2021) and of great contribution for carnivorous mammals (Draper et al. 2021), and for the Maned wolf. In addition, fruits such as *S. lycocarpum* may have a vermifuge effect

(Miranda et al. 2013), protecting the Maned wolf against some infections. In this way, *S. lycocarpum* can be understood not only as one of the main food resources for the Maned wolf, being essential especially during the dry season, but also an important source for maintaining the wolf's health and overcoming diseases.

This study enhances our understanding of the feeding ecology of the Maned wolf. It highlights the significance of fruit in the rainy season and rodents in the dry season, illustrating the species' omnivorous and generalist feeding habits. The Maned wolf selectively incorporates certain fruits into its diet. In addition, the work allows us to draw parallels between which resources are key to the existence of the Maned wolf in an area and to perform its ecological roles and can help with future conservation or reintroduction projects for these animals. Also provide new information's about its diet and the seeds that it potentially disperses, which can be used for natural restoration planning that includes the Maned wolf. Finally, it promotes an understanding of which species and ecological dynamics may be affected by the reduction or local extinction of Maned wolf populations in the Cerrado, given their potential role in controlling prey populations and in frugivory and seed dispersal. That is, which species are associated with the Maned wolf in such a way that the local extinction of this canid would result in a cascade effect of suppression of dispersal and consequent increase in inbreeding or, on the other hand, an explosion in populations due to the absence of predation, as occurred in Yellowstone with the reduction of the grey wolf populations.

2.5.ACKNOWLEDGMENTS

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Figure 1

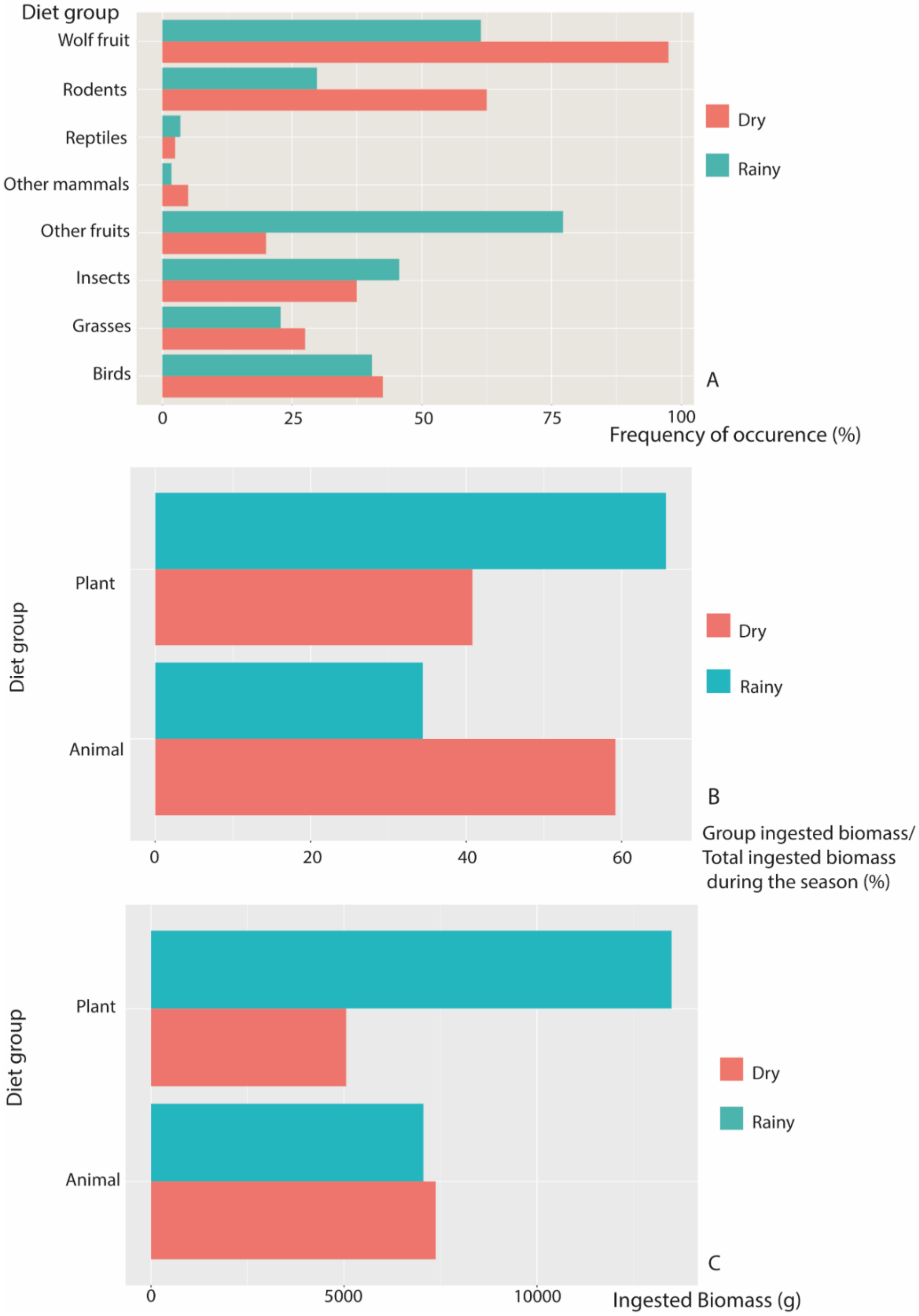

Figure 1: **(A)** Frequency of occurrence (%) of diet groups in the samples (n = 97) of Maned wolf in different seasons (dry and rainy); **(B)** Contribution of biomass ingested (%) of animal or plant origin in the diet of the Maned wolf in different seasons (dry and rainy); **(C)** Animal or plant ingested biomass (g) by the Maned wolf in the different seasons (dry and rainy).

Figure 2

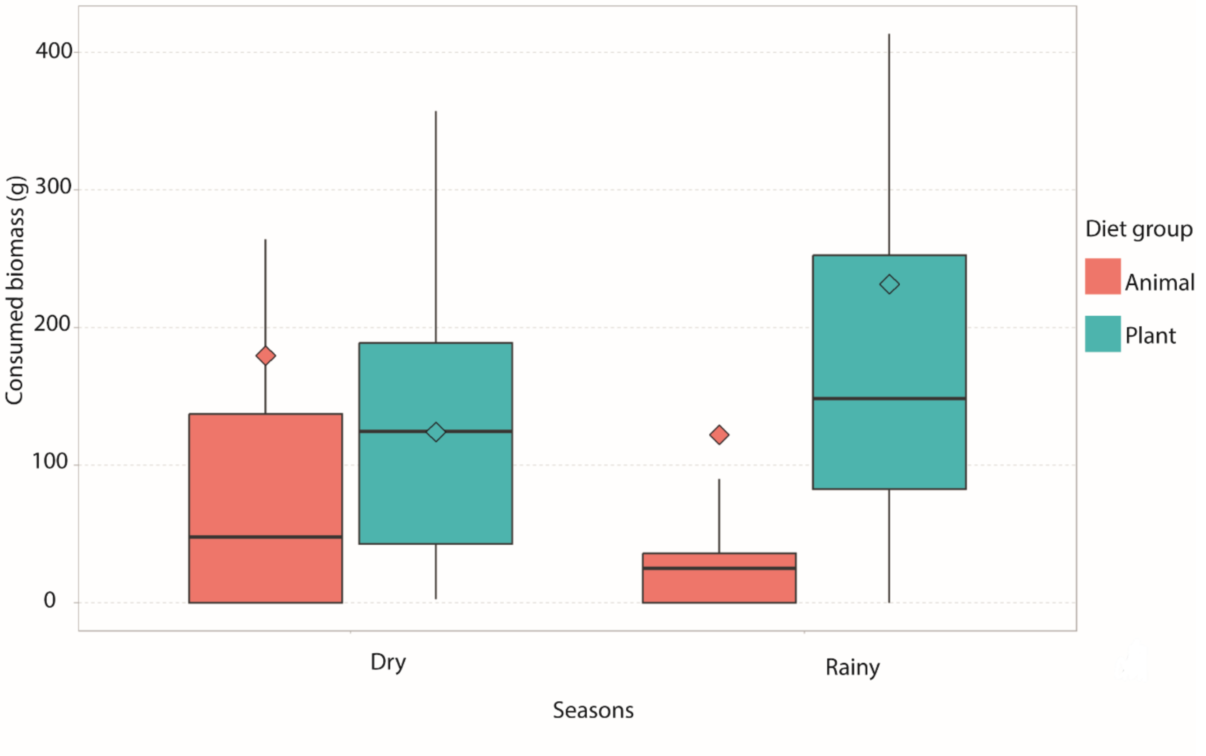

Figure 2: Boxplot of animal and plant consumed biomass by Maned wolf in the different seasons (dry and rainy).

Figure 3

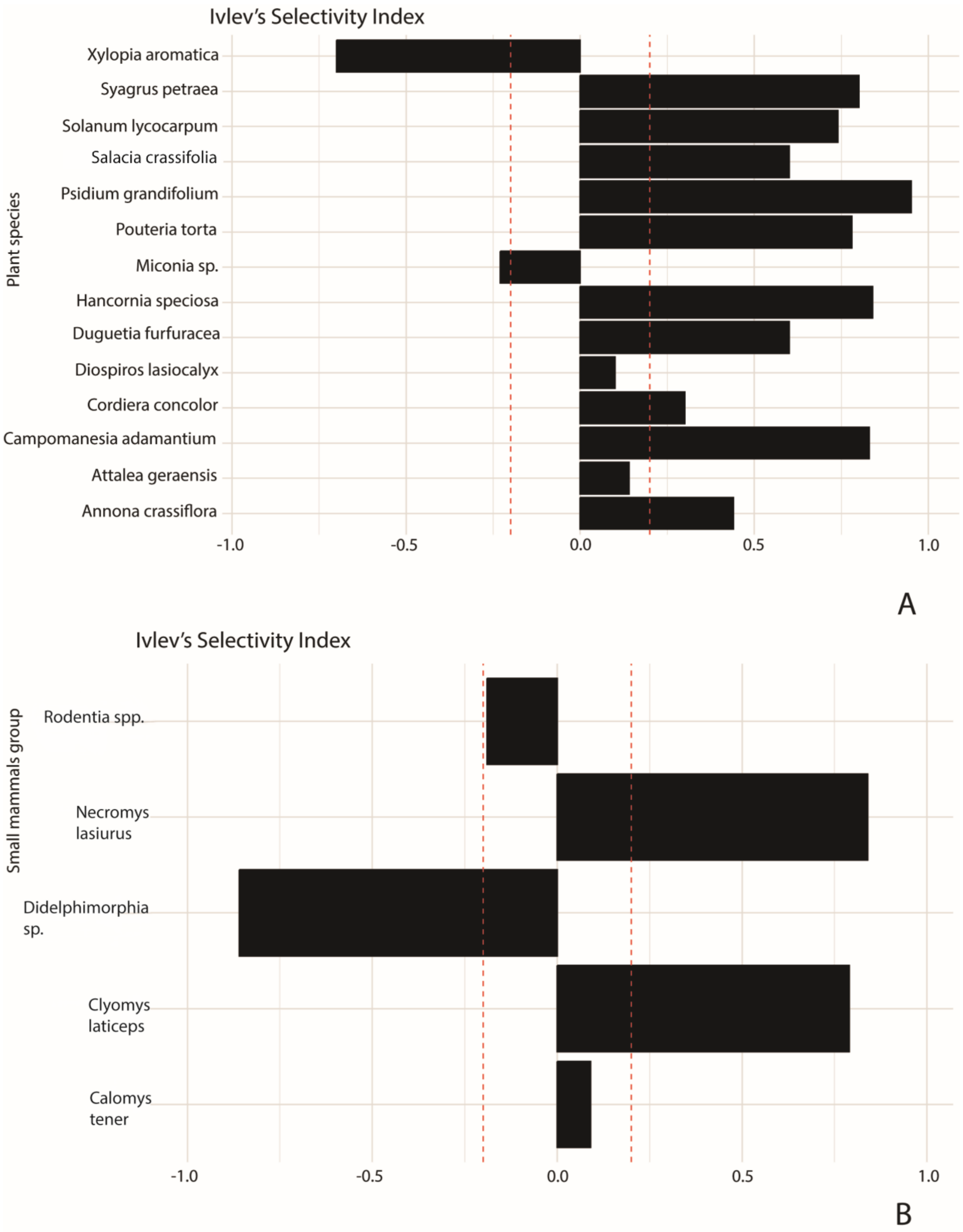

Figure 3: **(A)** Ivlev's selectivity index for some of plant species consumed by Maned wolf. *Xylopia aromatica* and *Miconia* sp. are negatively selected, *Diospyros lasiocalyx* and *Attalea geraensis* are consumed according to availability, and the other fruits are positively selected; **(B)** Ivlev's selectivity index for small mammals consumed by Maned wolf. Didelphimorphia sp. are negatively selected, Rodentia spp. and *Calomys tener* are consumed according to availability, and *Necromys lasiurus* and *Clyomys laticeps* are positively selected. The red lines delimit the tolerance values from -0.2 to 0.2,

which determine the fruits that are consumed according to availability, neither negatively nor positively selected

Figure 4

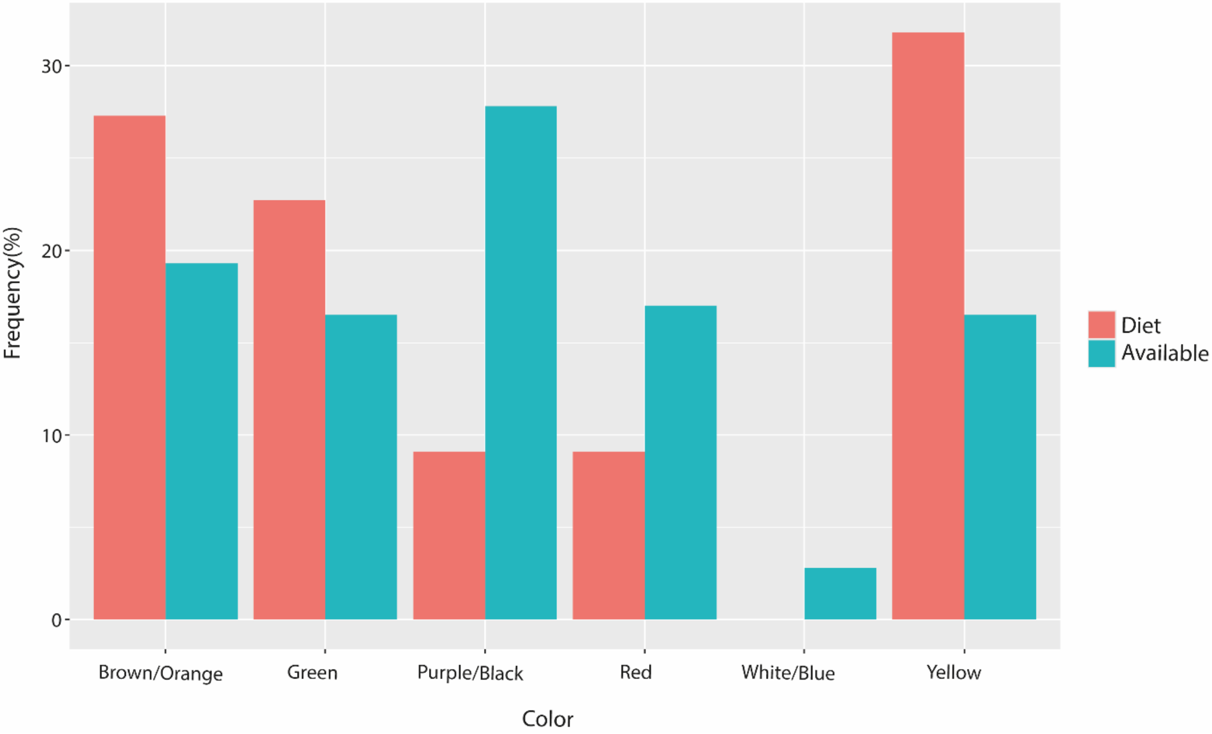

Figure 4: Percentage (n° color/n° total) of plant species with fleshy fruits grouped into color groups consumed by the Maned wolf (22) and those that occur in the study area (176), in Itirapina. Fruits of red/orange, yellow and green color are more common in Maned wolf diet, while purple/black and white/blue fruits (commonly associated with ornithocory) aren't.

Table 1 – Diet diversity, frequency of occurrence and ingested biomass between this study and studies carried out in other years and areas of the Brazilian Cerrado. Sample size is the number of analyzed scats. n.d. – not determined.

		Items on diet		**Occurrence (%)**		**Biomass (%)**		
Source	**Sample size**	**Plant**	**Animal**	**Plant**	**Animal**	**Plant**	**Animal**	**Site**
This study	97	23	16	61.4	38.6	57.5	42.5	Itirapina - SP (22°15'S; 47°49'W)
Motta-Junior, 2000	191	17	38	60.3	39.7	33.7	66.3	Luís Antônio – SP (21°35’S; 47°46’W)
Rodrigues et al., 2007	328	24	39	59.7	40.3	32.1	67.8	Águas Emendadas - DF (15°32'S; 47°33'W)
Bueno and Motta-Junior, 2004	483	22	52	57.4	42.6	21.9	78.1	Itapetininga - SP (23°42'S; 47°57'W)
Bueno and Motta-Junior, 2009	614	18	52	57	43	n.d.	n.d.	Itapetininga - SP (23°42'S; 47°57'W)
Santos et al., 2003	150	11	18	53.9	46.1	43.1	56.9	Matias Barbosa - MG (21°51'S; 43°19'W)
Dietz, 1984	740	20	20	51	49	n.d.	n.d.	Serra da Canastra - MG (20°20'S; 46°40'W)
Juarez and Marinho-Filho, 2002	70	13	20	50.4	49.6	54.6	45.4	Jaborandi - BA (14°14'S; 45°56'W)
Queirolo and Motta-Junior, 2007	400	26	43	49.5	50.5	43.2	56.8	Serra da Canastra - MG (20°20'S; 46°40'W)
Bueno et al., 2002	325	24	44	49.3	50.7	31.8	68.2	Itirapina - SP (22°15'S; 47°49'W)
Motta-Junior et al., 1996	105	10	34	46.7	53.3	43.5	56.5	Brasília - DF (15°57'S; 47°56'W)
Belentani et al., 2005	46	5	25	42.4	57.6	44.3	55.7	Parque Florestal Salto e Ponte - MG (19°12'S; 48°08'W)
Silva and Talamoni, 2003	230	13	41	29.1	56.8	3.7	88.1	Serra do Caraça - MG (20°05'S; 43°29'W)
Massara et al., 2012	95	5	17	21.1	78.5	49.2	50.7	Serra da Calçada - MG (20°06'S; 43°58'W)
Mean	276.7	16.5	32.8	49.2	49.7	38.2	61.1	
Standard deviation	216.2	7.1	13.1	11.7	10.3	14.9	13.2	

Legend: In Occurrence values represent the percentage of frequency of occurrence of plant or animal items in the samples; for Biomass the values represent the percentage of animal or vegetal items ingested in relation to the total biomass ingested in the diet.

2.7.SUPPLEMENTARY MATERIALS CHAPTER 1

Figure 1S

Figure 1S: A view of some paths used to sample fecal samples of Maned wolf in Cerrado from Itirapina Ecological Station, southeast Brazil. R.D. Feliciano.

Figure 2S

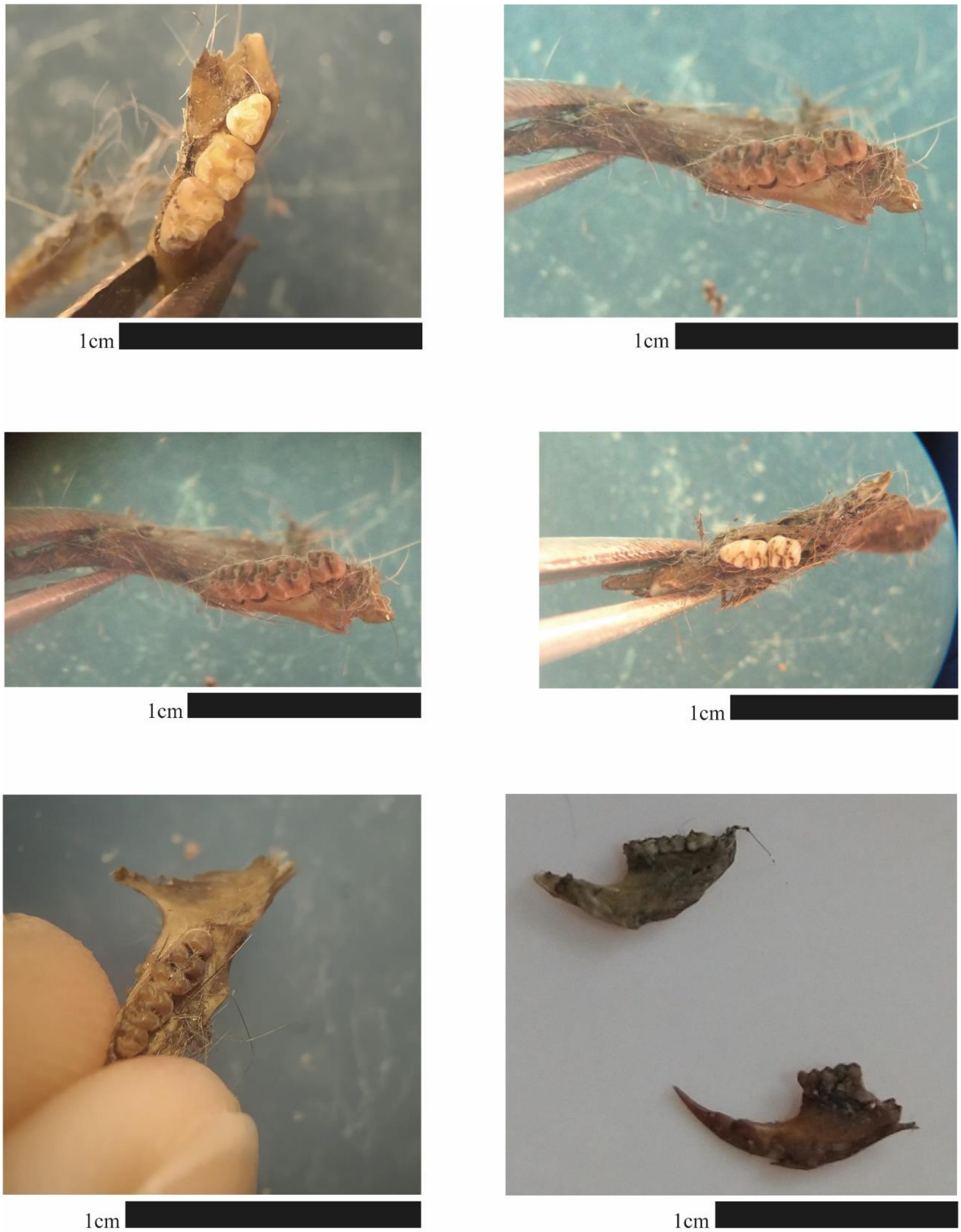

Figure 2S: Rodents jaw obtained in Maned wolf fox samples.

Figure 3S

Figure 3S: Maned wolf feces with *Solanum lycocarpum* seeds. R.D. Feliciano, 2023.

Figure 4S

Figure 4S: Animal remains found in Maned wolf feces. **(A)** Lizard; **(B)** Termites; **(C)** Fragment of insect pupae and armadillo osteoderms; **(D)** Eggshell fragments. R.D. Feliciano.

Figure 5S

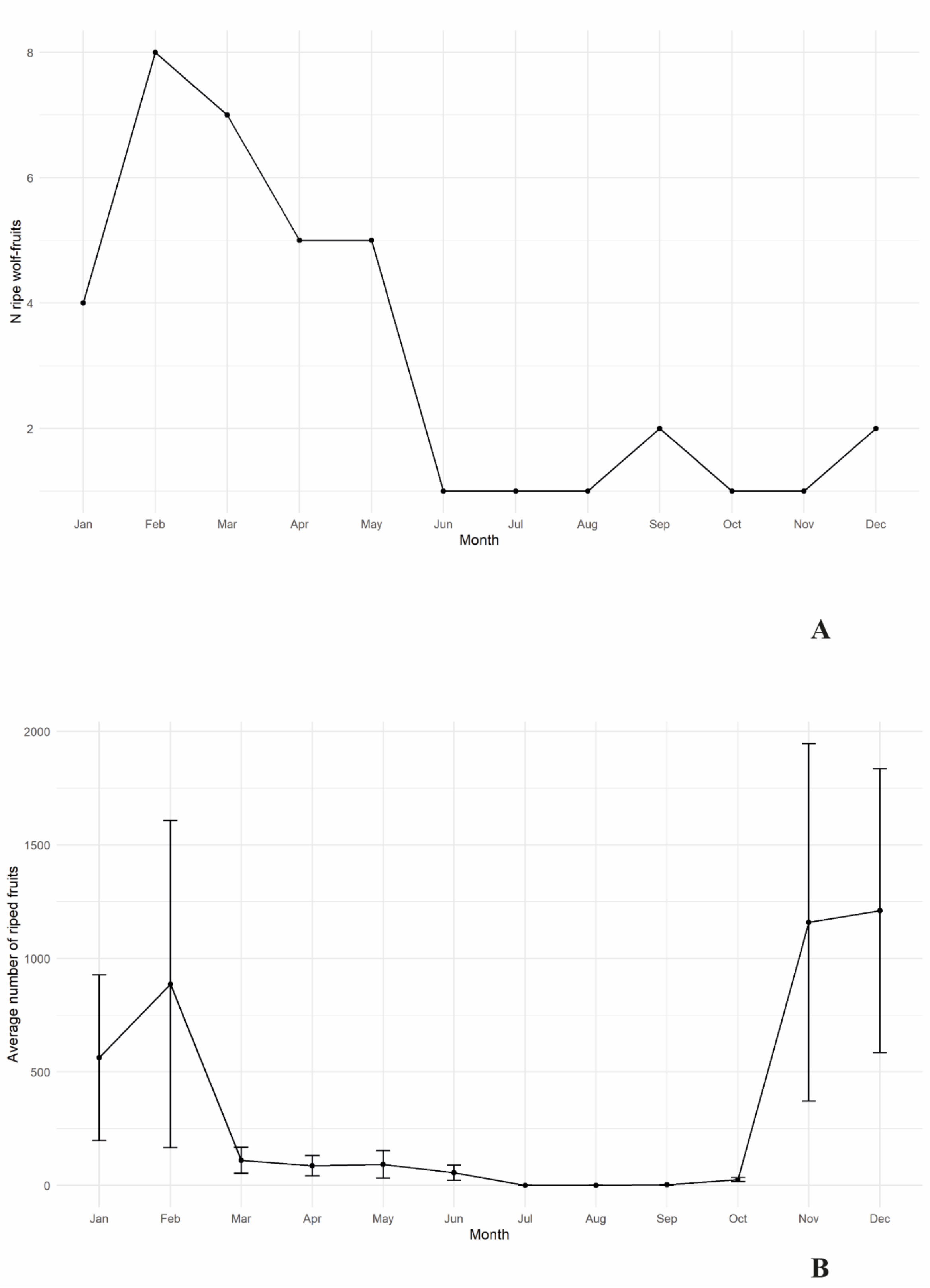

Figure 5S: **(A)** Total number of ripe *Solanum lycocarpum* fruits per month, based on a pool of 14 individual plants; **(B)** Average number (±SE) of ripe fruits of other fleshy fruited species per 0.1 ha plot and month.

Figure 6S

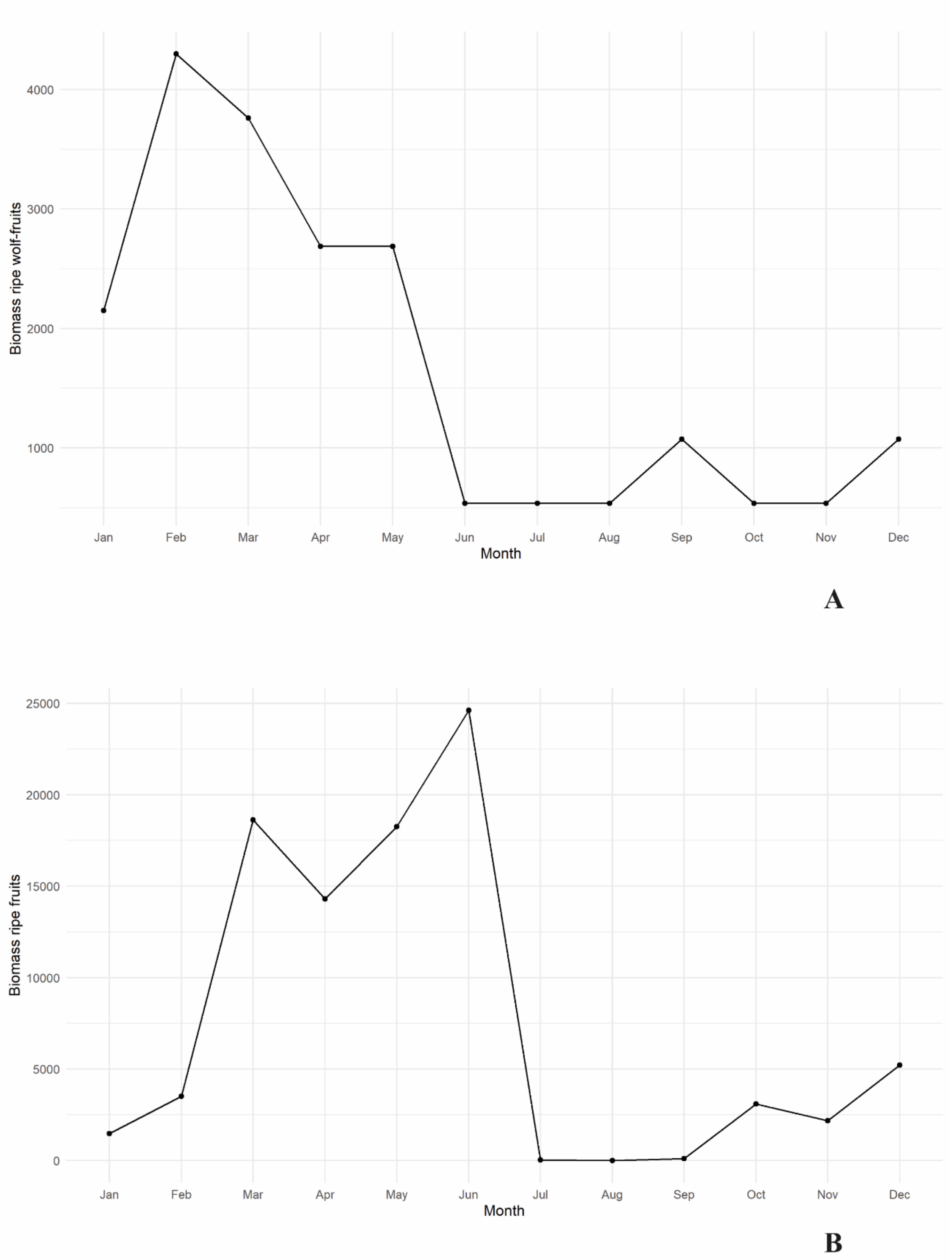

Figure 6S: **(A)** Biomass of ripe fruit of *Solanum lycocarpum* per month; **(B)** Biomass of ripe fruit of the other fleshy fruited species per 0.1 ha plot and month.

Figure 7S

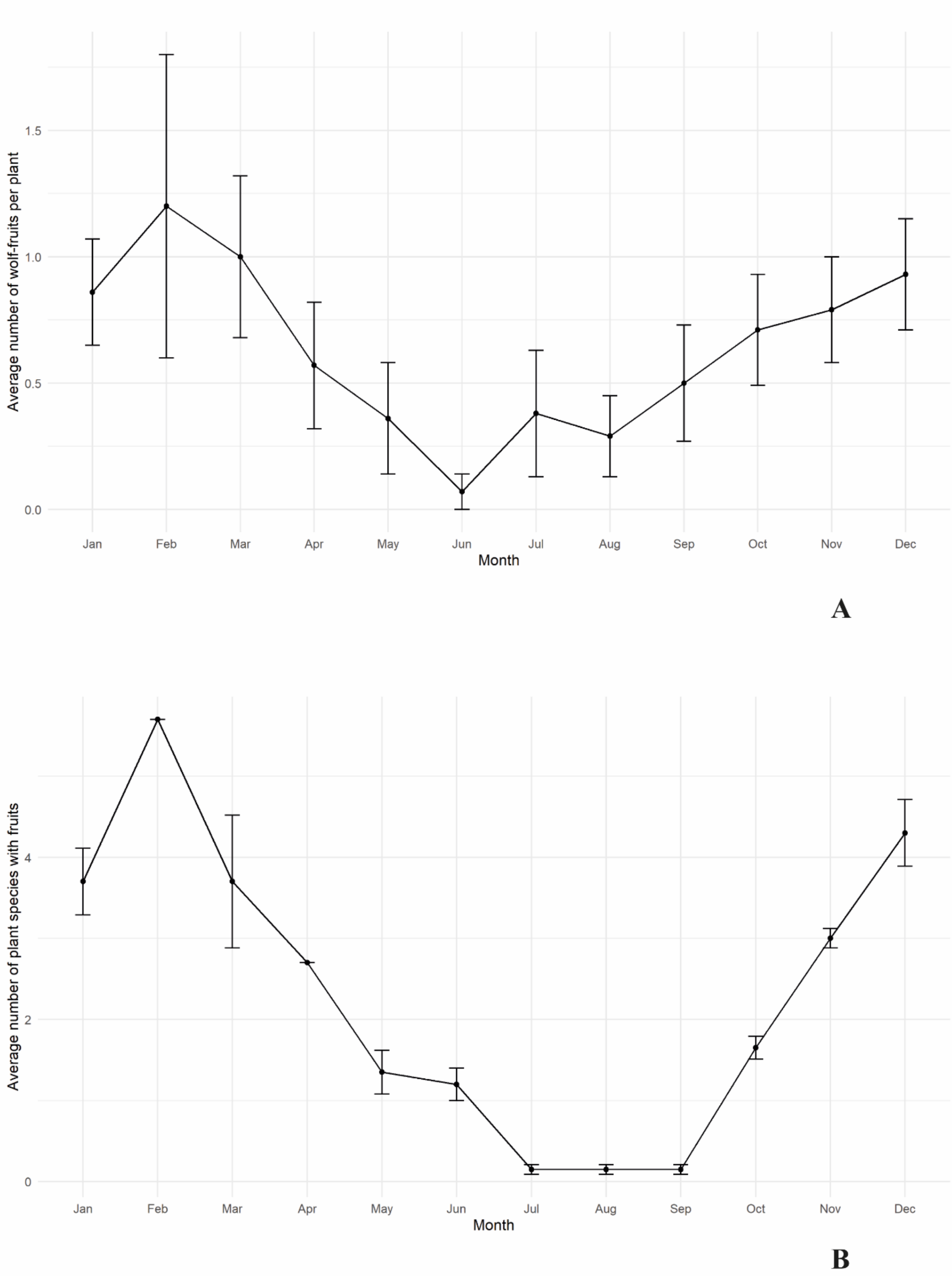

Figure 7S: **(A)** Average number (±SE) of fruits per *Solanum lycocarpum* plant (N=14) per month; **(B)** Average number (±SE) of other fleshy fruited species with fruits per 0.1 ha plot and month

Figure 8S

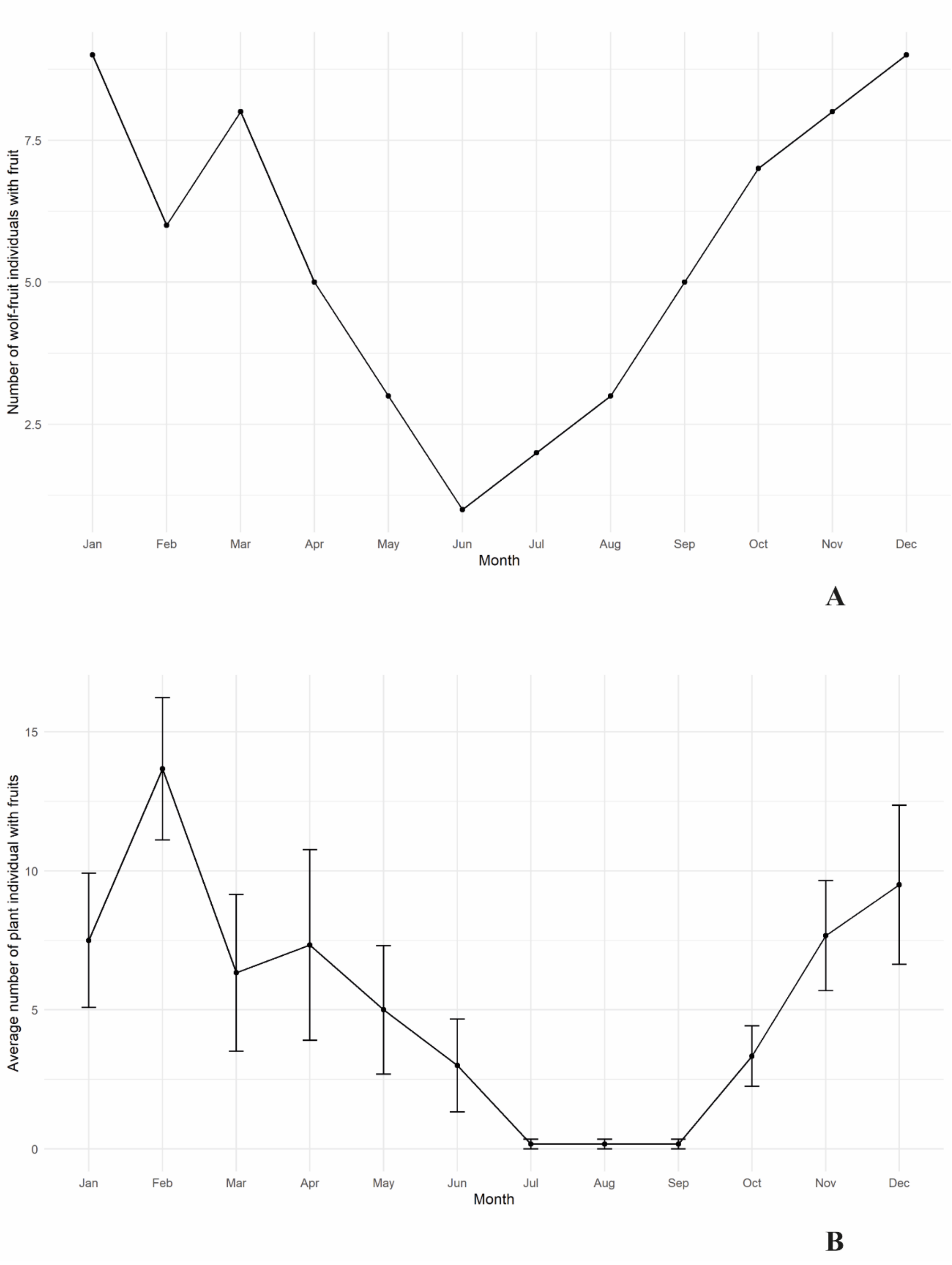

Figure 8S: **(A)** Number of individuals of *Solanum lycocarpum* with fruit per month (based on N=14 plants); **(B)** Average number (±SE) of individuals of other fleshy fruited plants per 0.1 ha plot and month.

Figure 9S

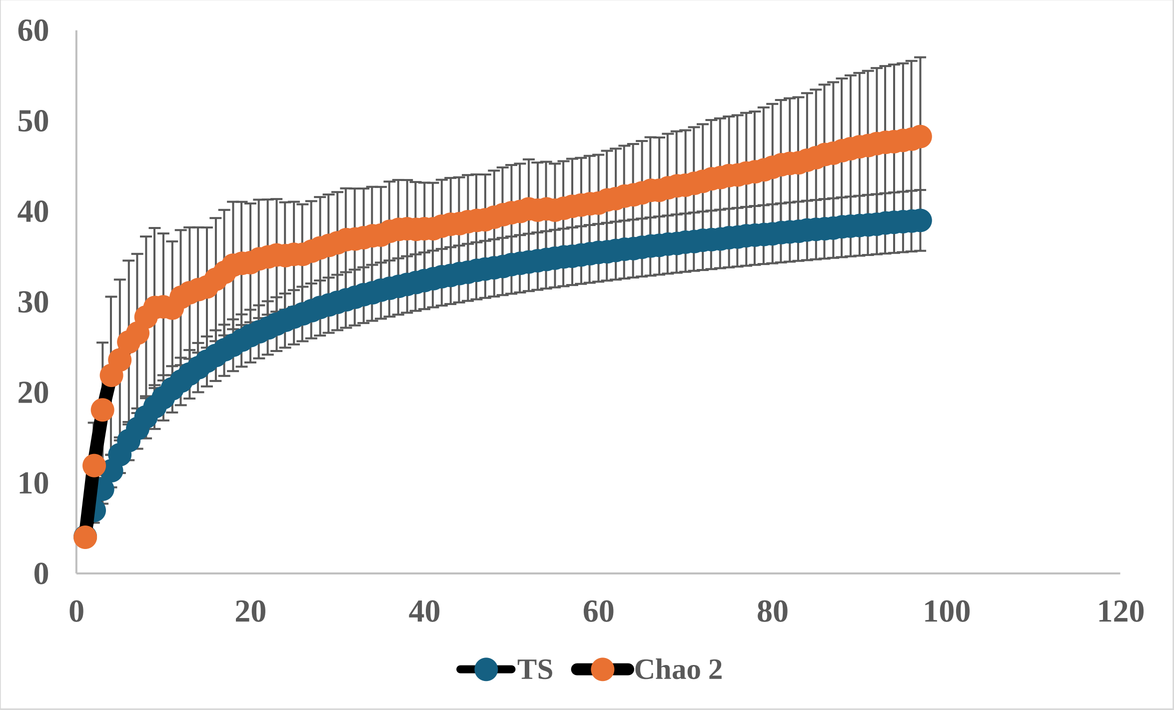

Figure 9S: Rarefaction curve of the food items identified in the Maned wolf diet. TS – Curve found in the study; Chao 2 - Expected curve based on the Chao 2 estimate. Points are mean and deviations are the standard deviation.

Table 1S – Maned wolf frequency of occurrence and estimated consumed biomass of diet items in samples. Scientific nomenclature according to Flora e Funga do Brasil (2024) for plants and IUCN (2024) and Abreu et al. (2023) for animals

	Frequency (N° of samples with the specie)	**Relative frequency (%)**	**Consumed biomass (g)**	**Proportion of consumed biomass (%)**
Plant				
Annonaceae				
Annona crassiflora	14	14.43	4710	14.4
Duguetia furfuracea	7	7.21	112.8	0.35
Xylopia aromatica°	2	2.06	6.51	0.02
Apocynaceae				
Hancornia speciosa	6	6.18	138.2	0.42
Arecaceae				
Attalea geraensis°	1	1.03	42.7	0.13
Syagrus petraea	10	10.3	176.1	0.54
Syagrus romanzoffiana	6	6.18	185.5	0.57
Asteraceae				
Bidens sp.°	7	7.21	n.d.	n.d.
Celastraceae				
Salacia crassifolia	4	4.12	33.2	0.10
Ebenaceae				
Diospyros lasiocalyx	3	3.09	178.9	0.55
Malpighiaceae				
Byrsonima crassifolia°	4	4.12	24	0.07

Melastomataceae				
Miconia sp.	2	2.06	54.6	0.17
Myrtaceae				
Campomanesia adamantium°	13	13.40	701.7	2.15
Myrcia guianensis°	4	4.12	19.3	0.06
Psidium grandifolium	7	7.21	257.8	0.79
Passifloraceae				
Passiflora cincinnata°	1	1.03	4.5	0.01
Poaceae				
Poaceae sp.	24	24.74	2.6	0.008
Rubiaceae				
Cordiera concolor°	3	3.09	40.9	0.13
Rutaceae				
Citrus x Sinensis	5	5.15	684.7	2.10
Sapindaceae				
Talisia angustifolia	9	9.27	288	0.88
Sapotaceae				
Pouteria torta	13	13.40	1409.4	4.31
Pradosia brevipes°	10	10.31	1136.4	3.48
Solanaceae				
Solanum lycocarpum	73	75.25	8566.4	26.22
Undefined seeds	9	9.27	n.d.	n.d.
Animal				

Reptilia				
Squamata *(Ameiva* sp.*)*	3	3.09	147	0.45
Mammalia				
Didelphimorphia *(Didelphidae* sp.*)*	1	1.03	60	0.18
Cingulata				
Dasypus sp.	1	1.03	4500	13.77
Cabassous sp.	1	1.03	3500	10.71
Rodentia	42			
Clyomys laticeps		11.34	1895.3	5.80
Necromys lasiurus		17.52	1020	3.12
Calomys tener		13.40	188.5	0.58
Rodentia spp.		31.96	930	2.85
Birds				
Undefined birds*	40	41.23	1530	4.68
Egg	1	1.03	10	0.03
Arthropoda				
Apoidea	1	1.03	0.1	0.0003
Coleoptera *	29	29.89	70	0.21
Formicidae *	5	5.15	2.9	0.009
Isoptera *	5	5.15	3.9	0.01
Lepidoptera	1	1.03	2	0.006
Ortoptera*	19	19.58	33	0.1
Plant total		61.4	18774.4	57.5

Animal total	38.6	14243.1	42.5

Legend: *Groups that more than 1 morphospecies was identified, but without identification of Genus or Specie; ° Denotes species recorded for the first time in Maned-wolf diet; n.d. = Not determined; Proportion of biomass consumed is based on the relation of the biomass ingested for one item in relation to the total biomass ingested.

3. CHAPTER II: THE TWO LARGEST CANIDS OF THE BRAZILIAN CERRADO ARE LEGITIMATE SEED DISPERSERS.

Abstract

Mammalian carnivores may play an important role in seed dispersal, but their quantitative and qualitative contributions are often not explored, in special for tropical species. Here we investigated the potential impact of fruit consumption by two canids (Crab-eating fox *Cerdocyon thous* and Maned wolf *Chrysocyon brachyurus*) in seed germination and dispersal. We collected seeds from fresh dung samples from wild *C. brachyurus* (N=97, 98% with seeds) and *C. thous* (N=13, 92% with seeds) in two contiguous protected sites of Cerrado in southeastern Brazil. We performed germination trials with seeds defecated by them and compared results obtained for seeds embedded in fruit pulp and with pulp removed by us (cleaned seeds) for 15 plant species. To estimate gut passage time (GPT) for *C. thou*s, we feed a captive individual with fruits from seven species. We found 23 seed species in dung samples of *C. brachyurus*, of which 18 germinated successfully. For *C. thous*, we found 12 seed species in dung samples, of which eight germinated. Both canids ingest and disperse seeds of plants with medium to large fruits (>1cm), but also bird-dispersed plants (such as *Miconia*) and *Bidens pilosa*, the later primarily dispersed by epizoochory. There were no differences in the germination percentage between seeds consumed by canids and cleaned seeds for eight species, suggesting the main effect of canids is due to fruit pulp removal. However, canids increased seed germination for five plants (*Solanum lycocarpum*, *Cordiera concolor*, *Psidium grandifolium*, *Diospyros lasiocalyx* and *Syagrus romanzoffiana)* compared to the other two treatments. For two other species the germination percentage of defecated seeds was lower compared to seeds cleaned up, suggesting canids decreased germination percentage. GPT in *C. thous* ranged from 12 to 25 hours (17.8 ± 5.14 hours, n ≥ 20 seeds per species), allowing them to deposit seeds far away. We conclude that canids are legitimate seed dispersers in Cerrado and probably play an important and overlooked role in seed dispersal in this species-rich savanna.

Key-words: *Cerdocyon thous*, *Chrysocyon brachyurus*, Savanna, Seed germination, Zoochory

3.1. INTRODUCTION

Seed dispersal is a key demographic and ecological process influencing the ecology, evolution and diversity of species of plants and animals (Van der Pijl, 192; Howe, 1989; Galetti, 2013). This process occurs at the level of the individual, the population, the community and the landscape (Van der Pijl, 1982; Howe, 1989; Levine and Murell, 2003; Jordano et al., 2007; Galetti et al., 2013; Rogers et al., 2021; Villar et al., 2021). The main agents of seed dispersal in tropical regions are animals, mostly birds and mammals, via frugivory (Traveset et al., 2007; Jordano 2000). Indeed, around 40% to 70% of woody plants in tropical savannas (Jordano, 2000; Kuhlmann and Ribeiro, 2016) and up to 90% in humid forests (Howe and Smallwood, 1982; Fleming et al., 1987; Jordano, 2000) are adapted to dispersal by frugivores, showing how important this mutualistic relationship is for the maintenance of plant regeneration and recruitment in tropical ecosystems (Janzen, 1970; Van der Pijl, 1982).

Seed dispersal by animals can be influenced by characteristics of the plant and the animal itself. Animal's body size is usually correlated with the maximum size of the fruit/seed able to be consumed, as well as the number of seeds that can be ingested and carried in a visit to a fruiting plant, or gut passage time (GPT) and distance these seeds will be deposited after passing through the digestive tract (Levin et al., 2003; Nathan et al., 2008; González-Varo et al., 2013). In addition, GPT can be affected by physiological factors of the frugivore, but also characteristics related to the seed, such as seed size, weight and thickness, as well as factors such as the composition of the fruit pulp and diet (Traveset, 1998).

The effectiveness of seed dispersal by frugivores (i.e. the chance to recruit a new individual plant, Schupp, 1993) can be influenced by quantitative factors, such as the number of seeds ingested per visit to a fruiting plant, and qualitative factors, such as the treatment given to the seeds during seed handling and digestion (Schupp et al., 2010). The quantitative or qualitative components will influence the likelihood of seed germination, the germination speed that is important for the establishment of the seedling, especially under adverse environmental conditions, where time windows favorable for seedling establishment and survival are short or unpredictable (Kandereit et al., 2017; Reed et al., 2022), and also the distances and places of seed deposition, that will influence the odds of seedling survival and recruitment (Schupp, 1993; Schupp et al., 2010). Effectiveness is also affected by internal and external factors (Nathan, et al., 2008; Schupp, et al., 2010), such as the animal’s jaw opening capacity, GPT (Traveset and Verdú, 2002) or the ability to move between habitats (Delciellos et al., 2017). In relation to plants, apart from the size of the fruit/seeds, the chemical composition of the fruit pulp (Howe, 1984; Howe, 1993; Herrera, 1995), the availability or seasonality of fruit production (Fenner, 1998; Jordano, 2000) and how important fruits are to the animal's diet (Howe, 1977; Mills et al., 1993), can influence foraging decisions and, consequently, seed dispersal. However, most studies focus on quantitative aspects, only listing the number of viable seeds after consumption by frugivores or stopping at the type of treatment the seed is receiving in the animal's gut (chemical or mechanical). This often means that some qualitative factors are overlooked, such as the role of seed cleaning in removing inhibitors of seed germination (Samuels and Levey, 2005).

Fruits are included in the diet of many mammalian carnivores and these animals may play an important role in seed dispersal (Herrera, 1989; Willson, 1993; Jordano et al., 2007; González-Varo et al., 2013; Draper et al., 2022). In northern hemisphere foxes (*Vulpes vulpes)*, ferrets (*Mustela* spp.), weasels (*Martes foina*), badgers (*Meles meles* or *Taxidea taxus*) and bears (*Ursus arctos*) may play an important role dispersing seeds of several plants (Herrera, 1989; Jordano et al., 2007; González-Varo et al., 2013; García-Rodriguez et al., 2021). Information about the role of mammalian carnivores in seed dispersal in the Neotropics is much more restricted, although it is known that coatis (*Nasua nasua*), Maned wolves (*Chrysocyon brachyurus*), Crab-eating foxes (*Cerdocyon thous*) and Tayras (*Eira barbara*) can often consume fruit (Bueno and Motta-Junior, 2004; Alves-Costa and Eterovick, 2007; Bezerra et al., 2009). Mammalian carnivores can swallow seeds as a whole (including medium and large seeds >1cm) (Kuhlmann and Ribeiro, 2016; Nakashima and Do Linh San, 2022), either by eating the fruit directly or by eating an animal that had the seeds in its digestive tract (secondary dispersal) (Hämäläinen et al., 2017). Because they have large living areas, they transport these seeds away from the mother plant (Draper et al., 2021). It is known that the passage through the digestive tract of carnivores has mostly a positive or neutral effect on the final amount and percentage of seed germination and also on the speed of germination, by removing the inhibitory germination components present in the fruit pulp (Traveset, 1998; Traveset et al., 2007; Draper et al., 2022). Furthermore, frugivorous carnivores tend to defecate in places with little vegetation cover, and such deposition in specific microsites may be of great importance for the colonization of open sites by plants (Nakashima and Do Linh San, 2022). In this way, fruit-eating carnivores largely play the role of legitimate seed dispersers, meaning that they affect seed dispersal by combining high quality and quantity of dispersed seeds, strongly impacting the regeneration and population dynamics of the dispersed seeds (Herrera, 1989; Bustamante et al., 1992; Draper et al., 2022).

Canids are medium to large sized mammalian carnivore, generally with generalist habits, large living areas and long digestion times (Wang and Tedford, 2007; Jácomo et al., 2009; Price et al., 2015; Reis et al., 2023). Several studies already recorded fruits in the diet of Neotropical canids (genera *Cerdocyon*, *Lycalopex*, *Chrysocyon*, *Atelocynus*, *Urocyon*), based on the collection of feces or analysis of stomach contents (Motta-Junior and Martins, 2002; Bueno and Motta-Junior, 2004; Rocha et al., 2004; Draper et al., 2022). However, studies detailing the functional role of canids in seed dispersal (quantitative and qualitative components of seed dispersal effectiveness) are still scarce, especially in tropical regions (Draper et al., 2022; Reis et al., 2023). Thus, there are few studies covering a wide range of seeds species and the qualitative and quantitative components of canids in seed dispersal. Also, few studies compared seed germination of gut passed seeds with both cleaned seeds and seeds still embedded in fruit pulp as controls, precluding a detailed understanding of the role of canids in seed germination (i.e. if they only remove germination inhibitors in fruit pulp or scarify seeds and trigger germination; Samuels and Levey, 2005). Finally, there is a poor understanding of GPT in canids (only for three species in this group, see Draper et al., 2022). This also limits knowledge about seed dispersal by canids, as these the GPT and dispersal distances are correlated processes.

Canids such as Maned wolves and Crab-eating foxes are found inhabiting the savannas from Central South America (Cerrado), consuming a large amount of fruit and potentially acting as seed dispersers (Bueno and Motta-Junior, 2004; Reis et al., 2023). Since the Maned wolf and the Crab-eating fox have broad ecological plasticity and exploit natural and human-modified environments, they can potentially link plant populations by transporting propagules between isolated natural patches (Coelho et al., 2008; Silva et al., 2020). Those two canids may also be fulfilling the role of large-bodied frugivores that are currently extinct, or present in very small populations in remnants, such as tapirs and rheas (Kuhlmann and Ribeiro, 2016).

Here we investigate the role of fruit ingestion in seed germination percentage and speed by the two largest canids of the Cerrado, the Maned-wolf *Chrysocyon brachyurus* and the Crab-eating fox *Cerdocyon thous*, using experimental trials that include seeds ingested by the canids, seeds manually cleaned, and seeds embedded in fruit pulp. We sought to investigate the morphometric characteristics of the fruits consumed by canids in the Cerrado and to estimate the proportion of fruits present in the study site that are dispersed by the two canids, based on the seed species in our samples. We also described the GPT of seven species of seeds whose fruits are ingested by *C. thous* and the influence of seed mass and size in this process. We expect that they are legitimate seed dispersers of most of the plant species they consume, improving germination in relation to the treatment of cleaned seeds and of seeds with pulp. About GPT, we expect that they will have a longer passage time than other groups of typical frugivores, such as birds.

3.2. MATERIALS AND METHODS

3.2.1. Study area

The Cerrado contains a species-rich tropical savanna considered a worldwide biodiversity hotspot (Myers et al., 2000), covering around 2 million km^2 in Central South America (Oliveira-Filho and Ratter, 2002). Cerrado contains approximately 10,000 plant species, 40% of them endemic (Myers et al., 2000). The Cerrado has been converted to cropland at fast rates in last decades (Sano et al., 2008). Because of this process, most of Southeastern Brazilian Cerrado's areas no longer shelter large frugivores species, such as the Rhea (*Rhea americana*) and Tapir (*Tapirus terrestris*), but may still contain more resilient species such as Maned-wolves and Crab-eating foxes (Ferreira et al., 2022).

We performed field sampling in two contiguous protected areas of Cerrado in southeastern Brazil, the Itirapina Ecological Station (22°00'S 47°45'W) and Itirapina Experimental Station (22°15'S 48°00'W) both with altitude of 770m asl, with a total of 5,512 ha in size (Bueno et al., 2002). The region's climate is characterized, according to Koppen, as Cwa (subtropical with a dry winter), with average annual rainfall of 1,320 mm and average annual temperature of 22.2°C. The dry season runs from April to September and the rainy season from October to March (São Paulo, 2006). Sites contain well conserved tracts of open savannas, as well as woodlands and forest patches near streams (São Paulo, 2006).

3.2.2. Canids studied

The Maned wolf is the largest canid in South America, weighing between 20 to 33 kg. It inhabits savannas and grasslands, and its distribution spans Paraguay, Uruguay, Argentina, Brazil, Bolivia and Peru (Dietz, 1985, Bueno et al., 2002). This species is most active during the crepuscular and nocturnal periods, has a solitary behavior (except during the breeding season) and has large home ranges, varying from 21 to 115 km² (Dietz, 1985; Bandeira de Melo et al., 2007; Jácomo et al., 2009). It is currently classified as near threatened globally (NT - IUCN, 2024). The Crab-eating fox is a medium-sized canid, weighing between 4 to 8.5 kg. It lives in forests, savannas and grasslands, with a distribution that included Colombia, Venezuela, Guyana, Suriname, Bolivia, Paraguay, Uruguay, Argentina and Brazil. (Bueno and Motta-Junior, 2004). It has mostly nocturnal and crepuscular habits, commonly aggregating in pairs or small family groups, and has a home range that could vary from 0.5 to 12.8 km² (Juarez and Marinho-Filho, 2002; Rocha et al., 2004). Both canids have generalist and omnivorous diets, consuming a wide variety of fruits, vertebrates and invertebrates (Motta-Junior et al., 1994; Bueno et al., 2002; Bueno and Motta-Júnior, 2004; Reis et al., 2023). As other Neotropical canids, detailed quantification about their role in seed dispersal is lacking (reviewed in Drapper et al. 2022).

3.2.3. Collecting feces and obtaining seeds

Seeds defecated by canids were retrieved from fresh fecal samples obtained in the field. These samples were collected between December-2022 and January-2024, with biweekly collection every month. Feces were sampled along predetermined routes, mainly walking through firebreaks where tracks of both canids are often found, covering approximately 12 km long each field expedition (Figure 1S). Additionally, in September 2023 and January 2024 extensive car drives were conducted around both protected areas to cover larger areas and increase sample sizes. Total sampling effort covered 279.8 km of firebreaks during 252 hours of sampling effort.

The samples were collected with gloves on and stored in individually labeled sterilized plastic jars with GPS information. The feces were identified by their size, shape, color, smell, presence of hairs and nearby footprints, following Bueno and Motta-Junior (2004) and Chame (2003). We also extracted hair samples from feces that could originate after grooming by canids and used them to produce slides that were compared with the "Guide to Brazilian Mammal Hair" (Miranda, 2014). To understand the sufficiency of our sampling effort, we made a collector's curve for Maned wolf and another for Crab-eating fox, based on the species of seeds found in the samples. In this way, we compared our collector curve with a curve based on the Jackknife 1 estimate.

In the laboratory, the fresh fecal samples were washed through a fine mesh sieve (1 mm). The seeds were identified to species or genus level using herbarium collections, plant guides (Souza et al., 2018; Kuhlmann, 2021) and help of specialists. We classified seeds found in samples as intact or damaged based on their characteristics (e.g whole seed or broken seed/seed fragments). The undamaged and damaged seeds were separated and quantified (Schlautmann et al., 2021). We assumed that the total amount of seeds ingested equals intact plus damaged seeds in samples. Then we calculated the proportion of seeds damaged in samples by dividing damaged seeds by total number of seeds found in the sample.

To estimate GPT of the Crab-eating fox, we offered manually depulped seeds of seven species to a female Crab-eating fox in a zoo, the São Carlos Ecological Park. These fruits (*Bromelia balansae*, *Campomanesia adamantium*, *Citrus* x *sinensis*, *Cordiera concolor*, *Hancornia speciosa*, *Psidium grandifolium* and *Solanum lycocarpum*) were often consumed by free-living canids and were available in Cerrado (except *Citrus* x *sinensis*, which were available on a plantation near the study area). The seeds (n ≥ 20 per species) were offered together with the usual food in the captive individual's diet (mostly meat and common fruits). Only one seed species was offered at a time, with a different species being offered each week, with a one-week break between offerings. The food with the seeds inserted was offered between 6:30 to 9:00 am, and the feeding time was recorded. To record the day and time of defecation of each species offered, a camera trap active 24 hours a day was installed in the Crab-eating fox enclosure (Srbek-Araújo and Chiarello, 2007). During the next five days, we made visits twice a day (morning and afternoon) to the Crab-eating foxes to monitor defecation, to collect the animal's feces and check the camera. The feces were collected and sorted at the lab in search for the seeds offered, and the time and day on which the seeds were defecated were recorded. To obtain an estimate of the time taken for the seeds to pass through the Crab-eating fox digestive tract (gut passage time - GPT), we calculated the time of seed consumption, concentrated in a short time interval, minus the time of defecation for each seed, after which we did the average GPT for each seed species offered (Varela and Bucher, 2006). The individual calculation for each seed was possible because all the seeds were consumed simultaneously and defecated at different times, so we had the exact time of consumption and defecation for each one. Daily monitoring was discontinued when no seeds were recorded in the feces after one full day, or after the total number of seeds offered had been found in feces. The experiment complies with the guidelines for experiments with captive animals following the rules laid down by the São Carlos Zoo.

To test the influence of seed size (mass and lenght) in mean GPT and investigate the morphometric characteristics of the fruits and seeds that are consumed by the Cerrado's canids, we collected and measured a sample of at least 30 fruits from Cerrado's that are part of the diet of Maned wolf and Crab-eating fox (Table 1S). The collection of fruits also helped us to obtain the seeds for treatments C1 and C2 of the germination experiment.

To estimate what proportion of local fruit species are being consumed and dispersed by wild canids, we divided the number of species dispersed by canids by the number of species of fruit plants recorded in the study area (obtained in São Paulo, 2006).

3.2.4. Seed germination trials

In order to understand how consumption by canids affected seed dispersal effectiveness compared to fruits that fall naturally from the mother plant and the role of gut-passage in seed scarification in relation to pulp removal, we carried out seed germination tests. For this experiment we used seeds found in the feces of *C. brachyurus* and *C. thous* in the field and from the captive Crab-eating fox experiment. The seeds ($N \geq 12$ per treatment) were arranged in plastic seedbeds (eight boxes x eight columns), filled with vermiculite, moistened daily with distilled water, placed under natural light conditions (sunlight during the day and no light at night), and protected from rain. The seeds were monitored daily, for 120 days, to check the number of germinated seeds and the time they took to germinate (in days). Germination was recorded by the protrusion of the radicle. The germination experiment was based on three treatments: 1) defecated seeds; 2) control 1 (C1): whole fruits planted, as a way of simulating fruits that fall from the mother-plant (Rocha et al., 2004); 3) control 2 (C2): seeds whose pulp was removed manually by us and cleaned with water, to test the "dehinibition effect" (Samuels & Levey, 2005). These tests allowed us to analyze the effect of canid consumption on seed germination, observing whether chemical scarification, physical scarification and seed cleaning act as inhibitors, promoters or non-interfering agents of germination (Samuels and Levey, 2005). If the germination of consumed $\leq$ C2 $>$ C1, it would mean that the most important role of seed ingestion in the germination is the removal of fruit pulp covering the seed (i.e. dehinibition effect); If the germination percentage of seeds extracted from feces was higher than that of the other controls, it would mean that scarification in the digestive tract plays an important role in triggering the germination; If the germination of seeds passed through the gut was lower than that of the other treatments, it would mean that scarification after passing through the digestive tract has a negative effect on seed germination; if the germination percentages are the same between the treatments, it would mean seed ingestion is not needed for seeds to germinate.

To understand the speed of germination between treatments, we monitored the seeds daily to observe germination (radicle protrusion). When germination was confirmed, the number of days each seed took to germinate from planting was counted. In this way, the germination time was estimated on a time scale in days, based on the exact day of planting and the exact day of germination of each seed.

3.2.5. Statistical analysis

To test the influence of canids on seed germination we compared the percentage (number of germinated seeds/total number of seeds sown) of seeds germinated between treatments (canids, C1 and C2) with G-tests. To evaluate if canids influence the speed of seed germination, survival analyses were carried out using the "Survdiff" tool from "Survival" package in RStudio (R Core Team, 2023; Therneau, 2023). In both cases, p-values were corrected due to multiple comparisons (Bonferroni correction; Rice, 1989).

To analyze how the size and mass of seeds ingested by the Crab-eating fox may influence GPT, we used a multiple linear regression (mean mass (g) and length (mm) of the seeds ingested x mean GPT (hours)). Graphical analysis was carried out using RStudio's GGPlot and DescTools Package (Wickham, 2016; Signorell, 2024). To test whether there is a difference in average GPT between the species, we carried out an one-way ANOVA and then a Tukey test. We also calculated the coefficient of variation of GPT between species to obtain a measure of relative variation between them.

3.3. RESULTS

We obtained 97 samples of Maned wolf, from which 95 contained seeds from 23 plant species (16 families) in samples (Table 2S). For the Maned wolf we observed an average of 122.2±739.1 seeds of 2.3±1.4 plant species per sample, with minimum and maximum of zero and eight species per sample. The cumulative number of species sampled and comparison with estimates from Jackknife 1 (Figure 2S) indicated collection effort was enough to characterize species ingested at the site. For the Crab-eating fox, in the 13 samples obtained (12 with seeds), 12 distinct species were identified (Table 3S) with an average of 21.5±34.6 seeds per sample was observed. The mean number of species of seeds found in Crab-eating fox samples were 1.4±0.5, with minimum and maximum of zero and two species per sample. For Crab-eating fox the cumulative number of species sampled did not reach a plateau, showing that more samples would be needed to provide a more complete sample of species consumed by the fox (Figure 2S).

From the 23 species found in Maned wolf feces, 78.3% (N=18) germinated after passing through the animal's digestive tract (Table 2S), while for the Crab-eating fox, from the 12 species found in the feces, 66.7% (N=8) germinated after passing through their digestive tract (Table 3S). For the Maned wolf, the most recurrent plants in the feces were: *Solanum lycocarpum*, present in 75.3% of the samples; Poaceae sp., (24.7%); *Annona crassiflora* (14.4%); *Campomanesia adamantium* and *Pouteria torta* (both 13.4%). The seeds that were found less frequently were *Passiflora cincinnata* and *Attalea geraensis*, both present in 1.0% of the samples (Table 4S). In turn, the most recurrent species in the feces of the Crab-eating fox were *S. lycocarpum* and *C. adamantium*, both with a 23.1% frequency of occurrence (Table 4S). Seeds from eight species were also found damaged in the Maned wolf samples, but in none the percentage of damaged seeds was larger than 4.2% (Table 4S). For the Crab-eating fox only two species showed damaged seeds after ingestion, with the values of damaged seeds compared to the total ingested in these species not exceeding 13% (Table 4S).

The germination and survival tests showed that the Maned wolf played a positive role, increasing germination, in relation to the C2 treatment of five species, a neutral role in the germination of seven species and a negative role in the germination percentage of two species. Regarding germination speed, two species (*S. lycocarpum* and *Cordiera concolor*) germinated faster after passing through the Maned wolf's digestive tract compared to the treatments (on average 69 and 16 days earlier, respectively), 10 others showed no differences in speed of seed germination between wolf and cleaned seeds treatments, and two (*Annona crassiflora* and *Myrcia guianensis*) took longer to germinate than the control C2 (Table 1; figure 1-3; table 2S,7S). As for the Crab-eating fox, the results showed that one species had a higher germination percentage after passing through the animal's digestive tract, five species showed no significant differences between the Crab-eating fox treatment and the C2 treatment (cleaned seeds) and two species had a reduction in their germination percentage after passing through the digestive tract (Table 1; Figure 4; Table 3S,7S). In relation to the C1 and C2 controls, the experiments showed that of the 14 species tested, eight had seeds from the C2 germinating to a greater extent than C1, while the other six had similar proportions between these two treatments. Furthermore, from the point of view of germination speed, 10 species from the C2 germinated faster than the C1, while the remaining four had no difference in germination speed between the treatments.

The GPT in Crab-eating fox was 17.8 ± 5.14 hours, considering all plant species (figure 5). The mean GPT differed among the seven species ($F = 18.66$, $p < 0.05$) (Table 5S, 6S) but was not related to the mass ($F = 0.7$, $p = 0.44$) or length of the seeds ($F = 0.39$, $p = 0.56$) (Figure 3S). The coefficient of variation was 27.3% of the GPT comparing each species (Table 5S). In addition, we observed that the seed species consumed at the same time were defecated at different times for all the seed species, in at least two different moments (Figure 6).

3.4. DISCUSSION

We showed that most fruit species consumed by the two canids remain viable after passing through the digestive tract and can be dispersed by them. The percentage of seeds destroyed by both the Maned wolf and the Crab-eating fox is minimal. For most of the seed species, those that had passed through the canids' digestive tract showed a germination percentage and speed similar to seeds from treatment C2 (cleaned seeds) and higher than from treatment C1 (seeds with fruit pulp). Nevertheless, for some species, we observed that canids can increase or decrease germination speed and percentage compared to the C2 control. Finally, the passage time in the digestive tract of the Crab-eating fox was long, with an average GPT of 17.8 hours.

Both canids showed a low percentage of seed damage (ca. 1% to 13% depending on the seed species), and most seeds were able to germinate after passing the gut, indicating that the Maned-wolf and Crab-eating fox are legitimate seed dispersers (Herrera, 1989; Motta-Junior et al., 1994; Motta-Junior and Martins, 2002; Souza et al., 2021; Draper et al., 2022; Reis et al., 2023). Seeds were probably damaged during fruit chewing, as most seeds found in feces were still able to germinate. These percentages are in line with the low percentage of seed damage among those consumed by carnivorous mammals in general (~10%) (Motta-Junior and Martins, 2002; Draper et al., 2022).

The fact that 78% and 61% of the species consumed by the Maned wolf and the Crab-eating fox, respectively, have germinated, and knowing they consume seeds from ca. 10 to 15% of the local flora producing fleshy fruits show that they could disperse around 18 to 25 species from the area. The Maned wolf's broad dispersal potential, maintaining the viability of approximately 80% of the seeds species it ingests, is reinforced by literature (Motta-Junior and Martins, 2002). We may extrapolate the number of seeds moved by the canids to obtain an estimate of their quantitative contribution to seed dispersal. Considering 279.8 km of sampling and that fire breaks sampled have ca. 3 m wide, our sampling covered 839,400 m^2. For the Maned wolf, considering each sample contains an average 122.2 seeds and that 95 feces were obtained during samples (totaling 11,609 seeds), Wolves contributed to the deposition of ca. 1.4 seeds at each 100 m^2. This estimate is likely conservative, since we sampled only fresh dung and did not considered feces decay, removal by secondary seed dispersers (Christianini et al. 2012) or burying by the local traffic of vehicles between the biweekly surveys. Therefore, these canids are probably much more important to seed dispersal at community level in Cerrado than suggested so far (Draper et al., 2022; Carvalho et al., 2023).

For the Maned wolf, five plant species (from 23 species tested) showed a higher germination percentage after passing through the digestive tract compared to the other treatments, and for the Crab-eating fox, just one plant species (from 12 species tested). This shows that, for these seed species, canids play an important role in both dispersal and in increasing germination success (Rocha et al., 2004; Varela and Bucher, 2006; Souza et al., 2021; Draper et al., 2022; Reis et al., 2023). For other seven and five seed species (Maned wolf and Crab-eating fox respectively), there were no differences between the treatment of cleaned seeds (C2) and seeds that had passed through their digestive tracts. In the case of equal germination percentage between treatments C2 and canid seeds, the role of these canids is more related to the removal of seed pulp rather than to chemical scarification processes in the digestive tract (Table 1). The importance of seed cleaning for plant germination is evident, considering that seeds with pulp tend to have lower germination and take longer to germinate (Traveset, 1998; Moore, 2001). Fruit pulp often contains germination inhibitors (Ribeiro, 2016), and seeds with pulp can be more easily attacked by pathogenic fungi or microorganisms (Traveset, 1998; Martín et al., 2022). In addition, for two species for Maned wolf and two species for Crab-eating fox the germination percentage of seeds from the C2 treatment was higher than that of the canid's seeds. For these few species, a long retention time in digestive track and excessive scarification probably damaged the embryo and constrained germination (Traveset, 1998; Jordano, 1992) (see Table 1, Figure 1 to 4).

With regard to germination speed, two species (*Cordiera concolor* and *Solanum lycocarpum*) that passed through the Maned wolf's and Crab-eating fox tracts had their seeds germinating in less time compared to the other treatments. Passage through the digestive tract can influence germination through the removal of pulp and chemical and physical scarification of the seed coat, which facilitates the exchange of water and gases between the seed and the environment, triggering and accelerating germination (Traveset et al., 2007). For 10 species with the Maned wolf treatment (*Duguetia furfuracea*, *Hancornia speciosa*, *Syagrus romanzofianna*, *Salacia crassifolia*, *Diospyros lasiocalyx*, *Miconia* sp., *Campomanesia adamantium*, *Psidium grandifolium*, *Citrus* x *sinensis* and *Pradosia brevipes*) and four species with the Crab-eating fox treatment (*H. speciosa*, *Bromelia balansae*, *Miconia* sp., *P. grandifolium*), there was no difference in germination speed compared to the C2 treatment (See Figure 1 to 4; Table 7S), but seeds in these two treatments showed a higher germination speed compared to C1. For the plant species whose seeds showed a germination speed equal to C2 (clean seeds), and higher than C1 (seeds with pulp), the removal of the pulp seems to have been the determining factor in reducing the germination speed of the seeds. Especially because the two treatments without pulp (Canids and C2) showed faster germination compared to seeds with pulp (C1) (Ribeiro, 2016) (See Figure 1 to 4; Table 7S).

Where and under what conditions a seed will be deposited after ingestion are determinants to seed fate. The GPT of Crab-eating fox ranged from 11 to 25 hours, in line with the long GPTs often observed in carnivores (Draper et al., 2021; 2022) and relatively longer than that of birds (which usually varies from a few minutes to up to 12 hours) (Clench and Mathias, 1992). A long GPT can be important for a seed to find available microsites for germination and seedling establishment (Green, 1983) and to reduce negative density-dependent effects often found near parental plants (Janzen 1970). However, our values are slightly higher than values reported in the literature for Crab-eating foxes (between 4.5 and 13 hours: Smith et al., 2003; Varela and Bucher, 2006). The study by Smith et al. (2003) was based on estimates of body mass, while Varela and Bucher (2006) used some seeds from species in the Argentine Chaco. This variation suggests foxes may retain seeds from Cerrado for longer periods and probably defecate them farther away than species from other sites. These results may also be related to the animal's activity pattern (Tsuji et al., 2015), diet, the difference in follow-up time for each experiment, and the low number of studies carried out with this species, once only the study by Varela and Bucher (2006) carried out tests of GPT on animals, while other studies have made estimates based on body mass (Smith et al., 2003). Varela and Bucher (2006) monitored the Crab-eating fox for 14 hours after offering the seeds, while in the current study we monitored it for five days (120 hours), in addition they tested four native species from Argentina and three sizes of crafted seeds, thus none of the species between works (Varela and Bucher and our study) are the same. Crab-eating fox also defecates at different times seeds consumed together, ranging from 2 to 5 defecations, between 11 and 25 hours after ingestion (Figure 6). Thus, a set of seeds of the same species consumed at a time can be spread in up to five different times and places of seed deposition. Given the broad plasticity in habitat use by Crab-eating foxes seeds can be deposited in a diversity of habitats, even in degraded lands, reducing dispersal limitation to those sites and favoring natural restoration (Campos et al., 2012).

This study demonstrates the important role of these two canids in seed dispersal in the Cerrado. The role of canids had a negative effect on the percentage of seed germination for only two species of maned wolf and two species of crab-eating fox. In most cases, the role was similar to that of the treatment of clean seeds (C2) and greater than that of the treatment of seeds with fruit pulp (C1). However, even this neutral effect still has benefits from the point of view of the seed, since it is being dispersed by the canids with a high degree of integrity and viability. Both canids play a role as seed dispersers of mostly medium and large fruits (>1cm; 0.84 to 17.37cm, see Table 1S) (Kuhlmann, 2021; Reis et al., 2023), and also of fruits typically dispersed by birds (*Miconia* sp. and *Myrcia guianensis*) (Allenspach and Dias, 2012; Vogado et al., 2016), and by epizoochory, exemplified by the germination of *Bidens pilosa* after ingestion by the Maned wolf. At the same time, many of the seeds that have been consumed by the Maned wolf and germinated are large (length>1.5cm) (Table 1S) and probably depend exclusively on large-bodied vertebrates no longer occurring in most sites of Cerrado (such as tapirs) for their dispersal (Donatti et al. 2011). Thus, the maintenance of the both canids, especially the Maned wolf, a near-threatened species, significantly contributes for the maintenance of seed dispersal for several plant species, in special of some large-seeded species that smaller frugivores, like birds, cannot disperse in Cerrado remnants.

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Table 1: Influence of the passage through the digestive tract of the Maned wolf and Crab eating fox on the germination percentage and germination speed of different Cerrado plant species: positive (+), neutral (0) or negative (-) influence in relation to treatment C2 - clean seeds.

	Maned wolf (*Chrysocyon brachyurus*)		**Crab-eating fox (*Cerdocyon thous*)**	
	Germination percentage	Germination speed	Germination percentage	Germination speed
Annona crassiflora	0	-	n.d.	n.d.
Duguetia furfuracea	0	0	n.d.	n.d.
Hancornia speciosa	0	0	0	0
Syagrus romanzoffiana	+	0	n.d.	n.d.
Bromelia balansae	. n.d.	n.d.	0	0
Salacia crassifolia	0	0	n.d.	n.d.
Diospyros lasiocalyx	+	0	n.d.	n.d.
Miconia sp.	0	0	0	0
Campomanesia adamantium	-	0	-	-
Myrcia guianensis	-	-	n.d.	n.d.
Psidium grandifolium	+	0	+	0

Cordiera concolor	+	+	0	+
Citrus x Sinensis	0	0	-	-
Pradosia brevipes	0	0	n.d.	n.d.
Solanum lycocarpum	+	+	0	+

Legend: Positive - percentages showed significantly higher values after passing through the digestive tract compared to C2; Neutral - percentages did not show significantly different values after passing through the digestive tract compared to C2; Negative - percentages showed significantly lower values after passing through the digestive tract compared to C2; n.d. – not determined.

Figure 1

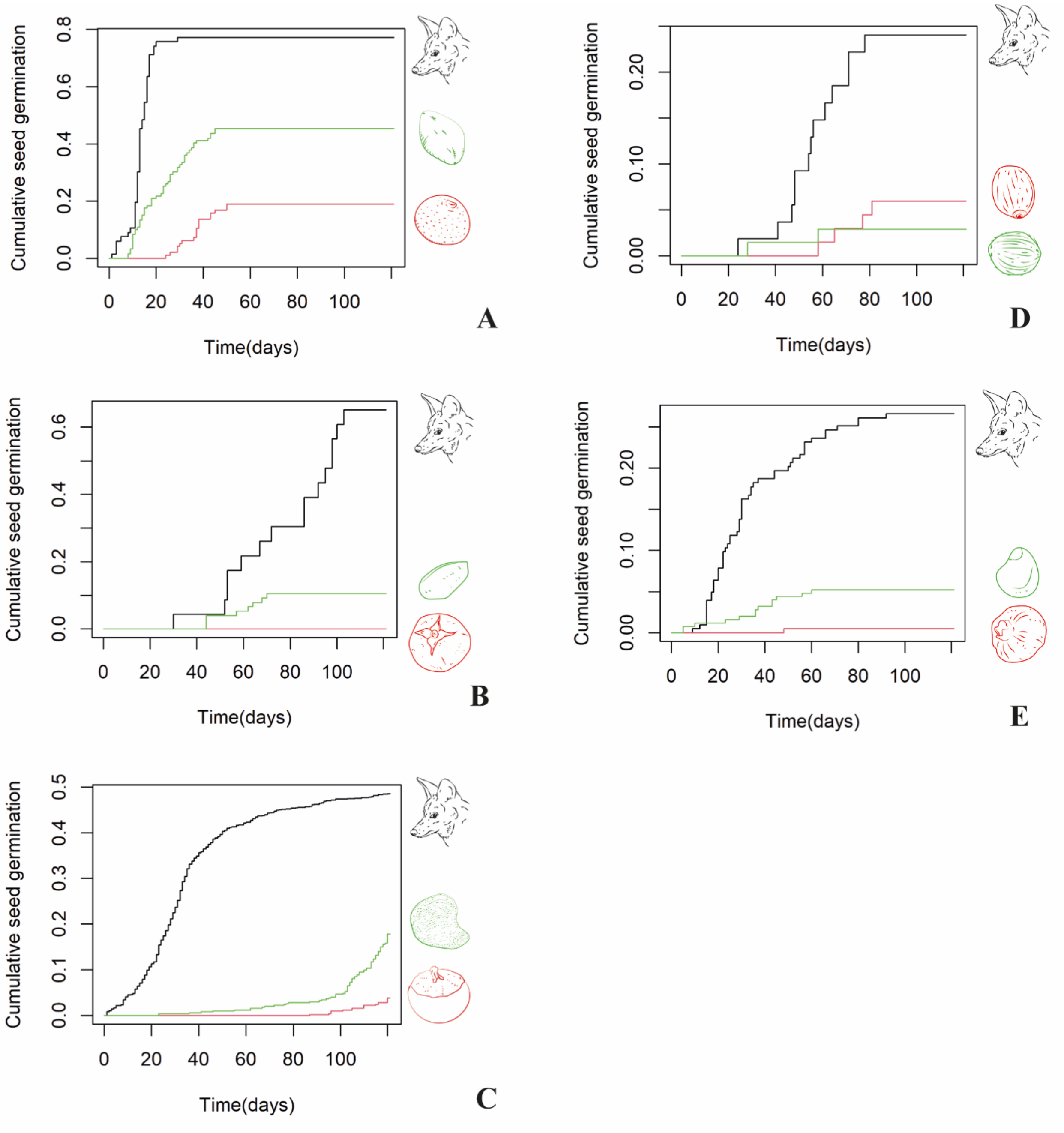


Figure 1: Time of seed germination of species for which seeds extracted from Maned wolf feces showed a higher germination. A- *Cordiera concolor*; B- *Diospyros lasiocalyx*; C- *Solanum lycocarpum*; D- *Syagrus romanzoffiana*; E - *Psidium grandifolium;* Black – Maned wolf seeds (the illustration shows an image of the Maned wolf); Green - C2 seeds (the image represents the morphology of the seeds of the specie tested); Red - C1 seeds (the image represents the morphology of the fruit of the specie tested).

Figure 2

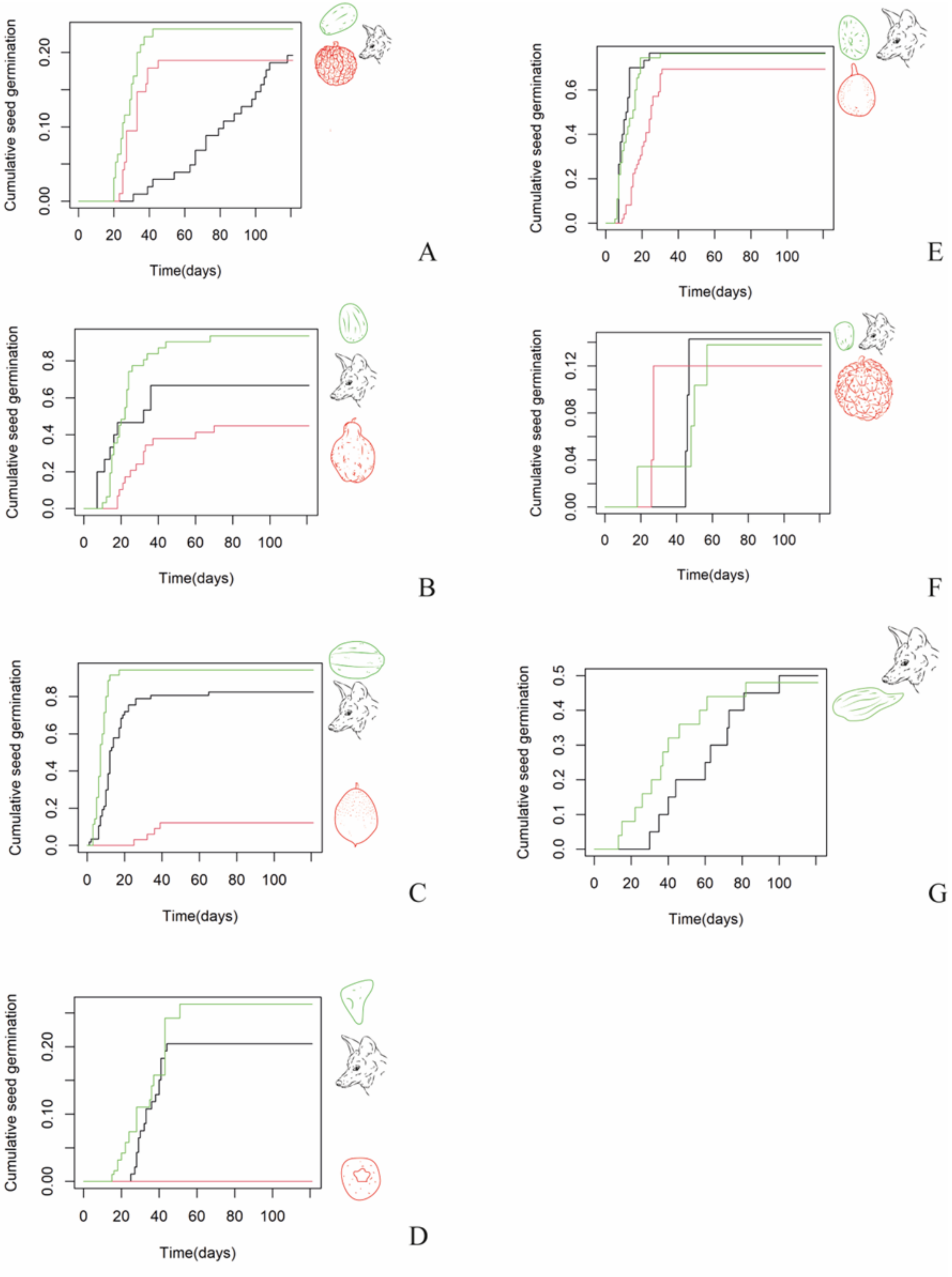


Figure 2: Time of seed germination of species for which seeds from C2 treatment showed a bigger or equal germination compared to Maned wolf treatment. Legend: A - *Annona crassiflora*; B - *Salacia crassifolia*; C - *Pradosia brevipes*; D - *Miconia* sp.; E - *Hancornia speciosa*; F - *Duguetia furfuracea*; G - *Citrus x sinensis*; Black – Maned wolf seeds (the illustration shows an image of the Maned wolf); Green - C2 seeds (the image

represents the morphology of the seeds of the specie tested); Red - C1 seeds (the image represents the morphology of the fruit of the specie tested).

Figure 3

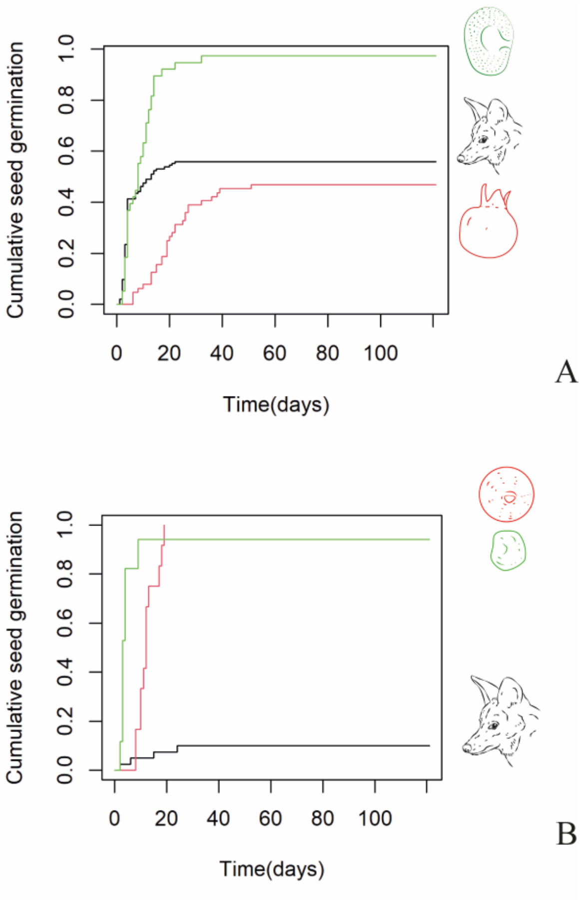


Figure 3: Time of seed germination of species for which seeds extracted from Maned wolf feces showed a similar germination compared to C1. Legend: A - *Campomanesia adamantium*; B - *Myrcia guianensis*; Black – Maned wolf seeds (the illustration shows an image of the Maned wolf); Green - C2 seeds (the image represents the morphology of the seeds of the specie tested); Red - C1 seeds (the image represent the morphology of the fruit of the specie tested).

Figure 4

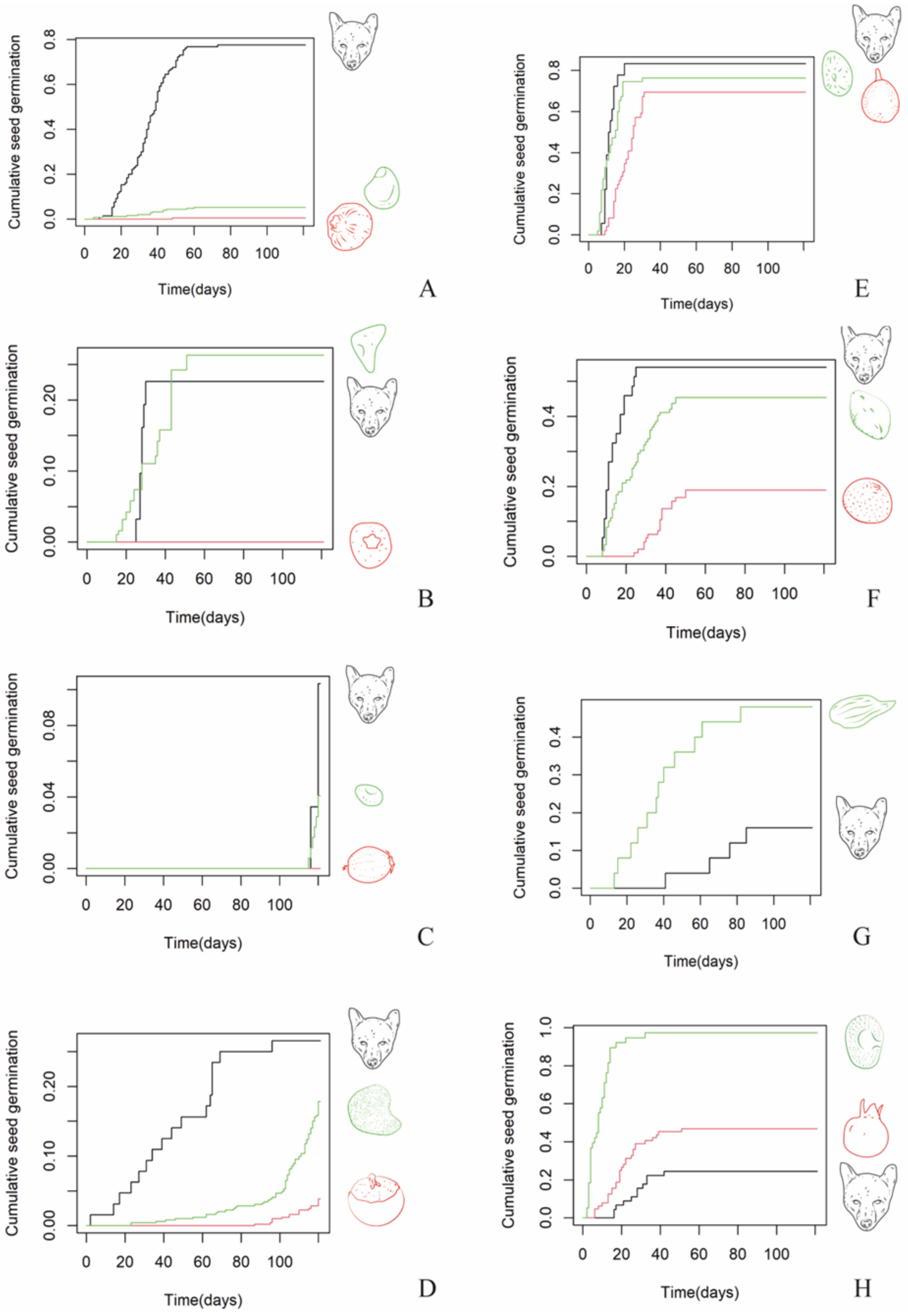


Figure 4: Time of seed germination of species which was extracted from Crab-eating fox feces. Legend: A - *Psidium grandifolium*; B - *Miconia* sp.; C - *Bromelia balansae*; D - *Solanum lycocarpum*; E - *Hancornia speciosa*; F - *Cordiera concolor*; G - *Citrus x sinensis*; H - *Campomanesia adamantium;* Black – Crab-eating fox

seeds (the illustration shows an image of the Crab-eating fox); Green - C2 seeds (the image represents the morphology of the seeds of the specie tested); Red - C1 seeds (the image represents the morphology of the fruit of the specie tested).

Figure 5

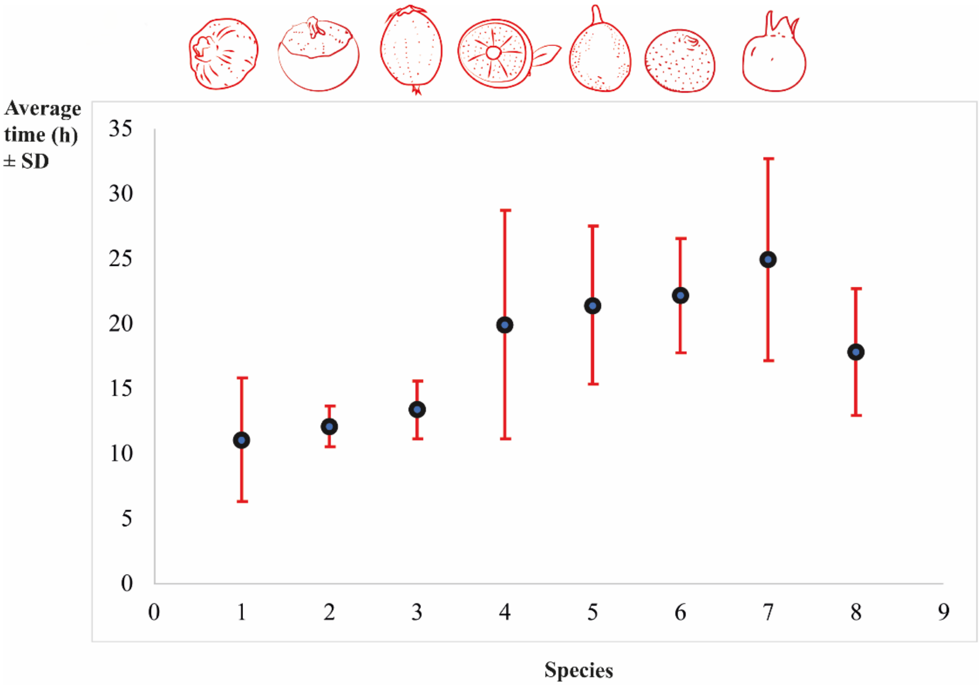


Figure 5: GPT experiment with the Crab-eating fox. Points are mean (GPT in hours), red bars are standard deviation (SD). Legend: Fruit illustrations (in red, above) represent the fruit species of each GPT experiment; Numbers 1 to 8 (x-axis) represents the different species and total: 1- *Psidium grandifolium*, 2- *Solanum lycocarpum*, 3- *Bromelia balansae*, 4- *Citrus* x *sinensis*, 5- *Hancornia speciosa*, 6- *Cordiera concolor*, 7- *Campomanesia adamantium*, 8- Total mean.

Figure 6

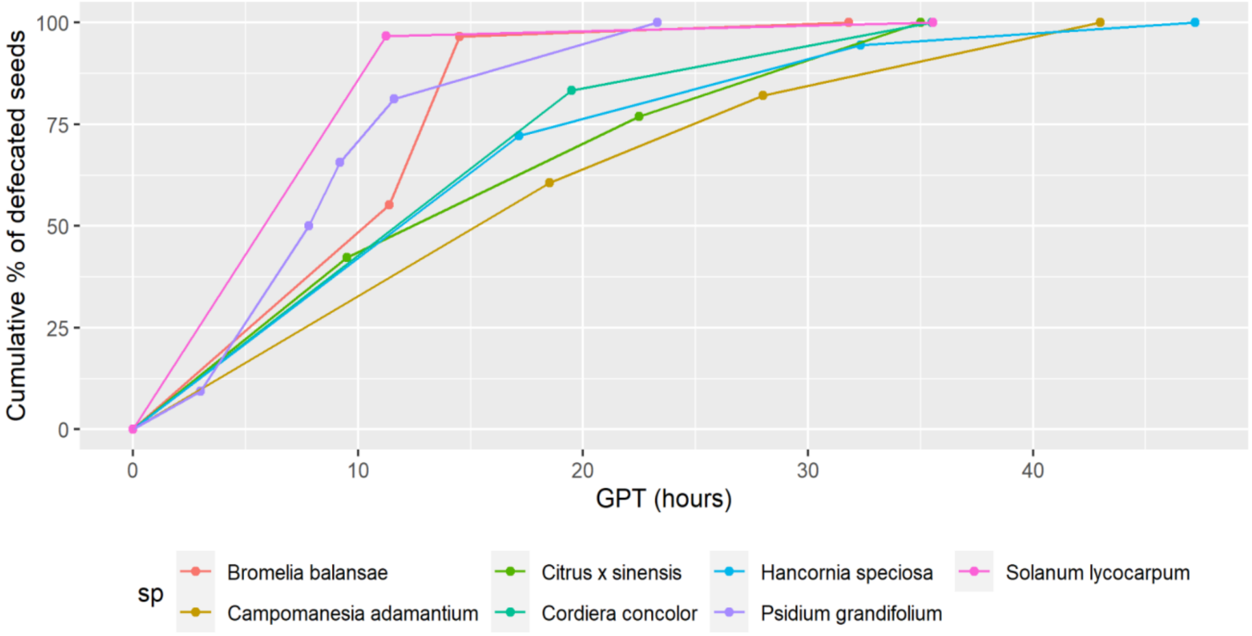


Figure 6: Cumulative percentage of defecated seeds versus GPT (in hours) of seven seed species ingested by the Crab-eating fox (Number of offered seeds that passed through the digestive tract): *Bromelia balansae* (29); *Campomanesia adamantium* (28); *Citrus x sinensis* (26); *Cordiera concolor* (36); *Hancornia speciosa* (18); *Psidium grandifolium* (32); *Solanum lycocarpum* (30).

3.7. SUPPLEMENTARY MATERIAL – Chapter 2

Figure 1S

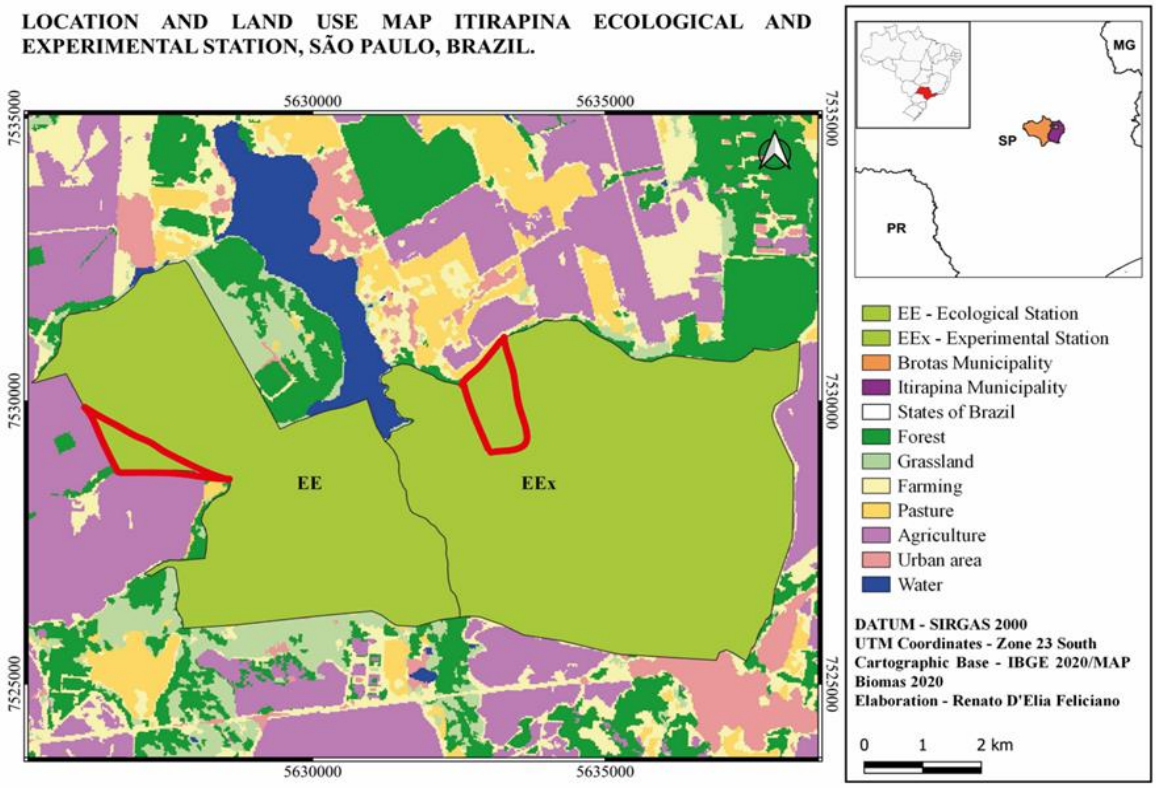
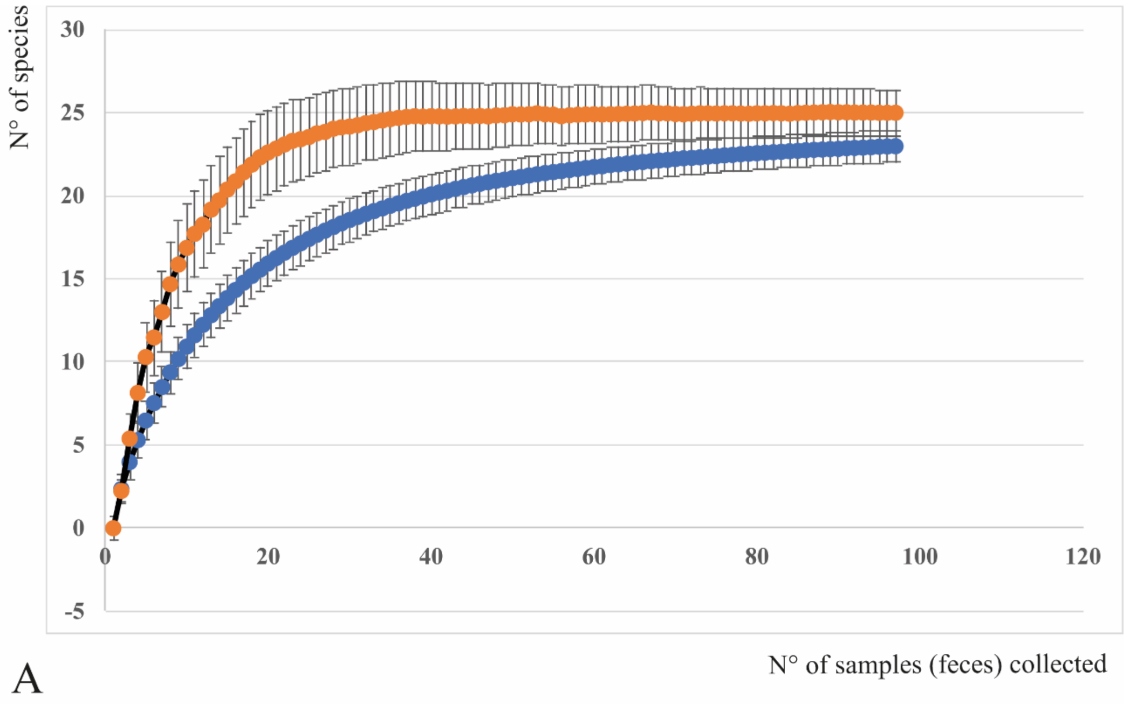


Figure 1S: Map of the study area including the limits of Itirapina Ecological Station (EE) and Itirapina Experimental Station (EEx) and the main vegetation categories of soil use. Transects where feces were collected on foot highlighted in red. Source: Prepared by the authors (2023).

Figure 2S



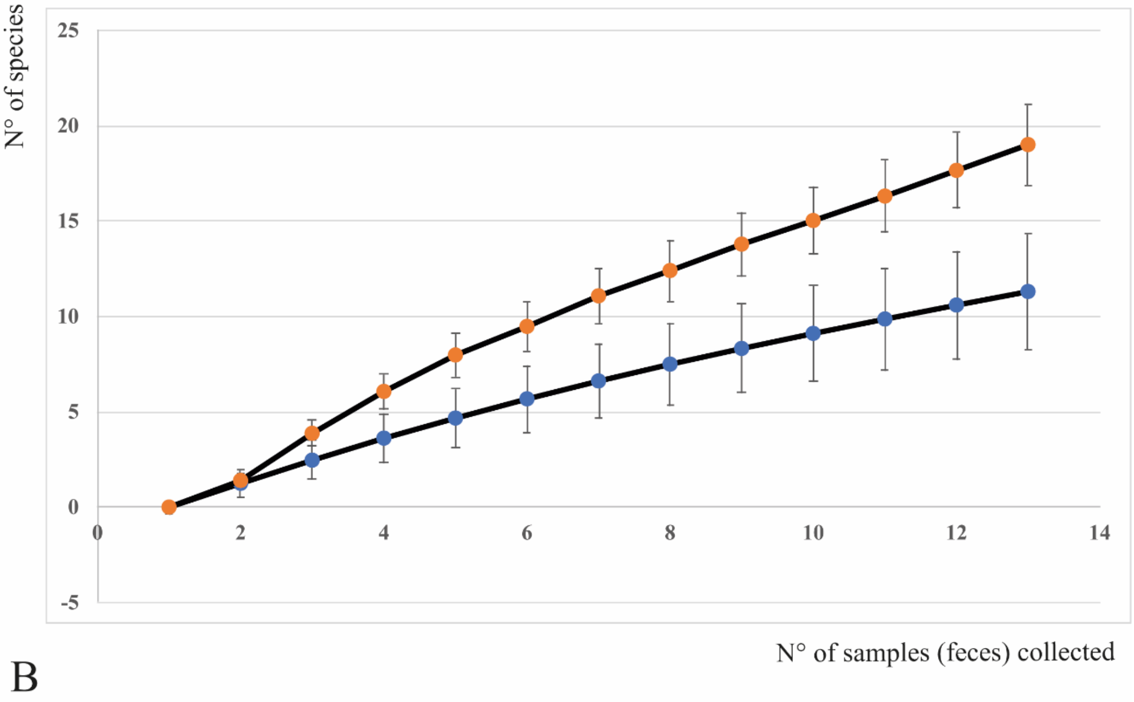


Figure 2S: Cumulative number of plant species sampled (blue) and estimate by Jackknife 1 (orange) for Maned wolf (A) and Crab-eating fox (B); curves represent the mean and the error bars the standard deviation of species.

Figure 3S

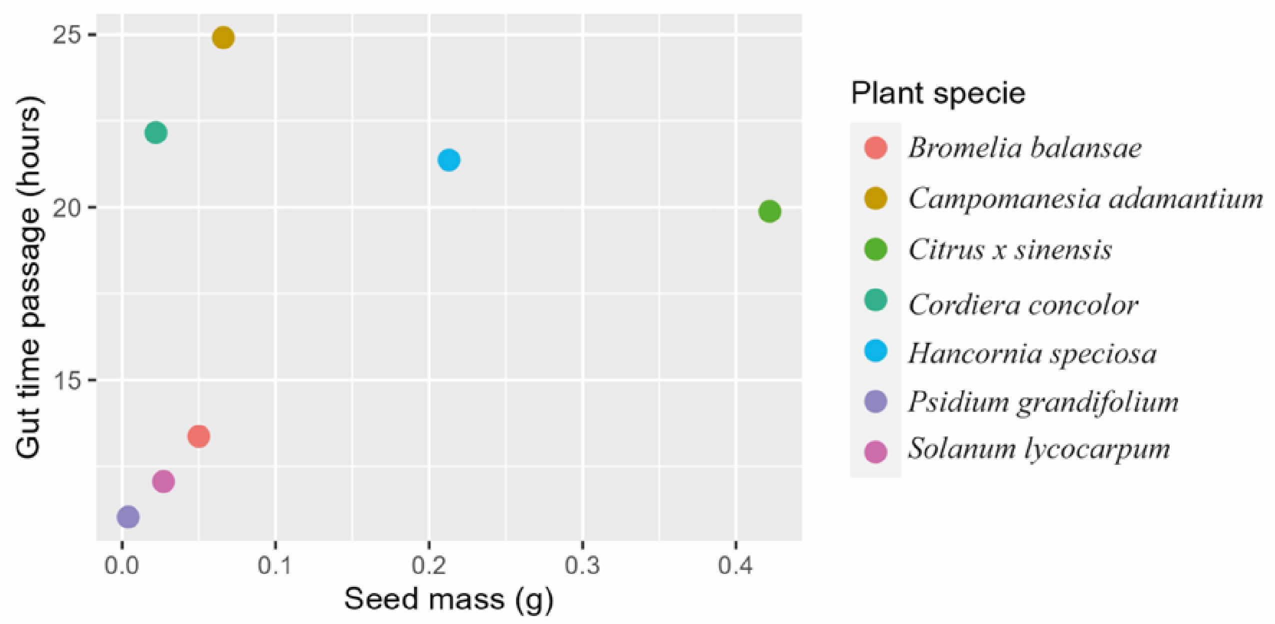


Figure 3S: Simple linear regression between mean GPT Crab-eating fox x seed mass. Legend: Each color represents a different species of plant tested. The variation between GPT and seed mass shows that for these species there is no relationship between gut passage time and seed mass for the Crab-eating fox (F=0.7; p=0.44)

Table 1S: **Characteristics of the fruits and seeds used in germination experiments. Values are means**

Specie	Fruit length (cm)	Fruit height (cm)	Fruit mass (g)	Seed length (cm)	Seed height (cm)	Seed width (cm)	Seed mass (g)
Annona crassiflora	17.37	16.50	2,100	1.60	0.89	0.61	0.67
Duguetia furfuracea	6.66	5.59	37.39	1.38	1.07	0.88	0.67
Hancornia speciosa	3.05	2.67	13.95	0.83	0.76	0.47	0.21
Syagrus petraea	2.44	1.53	3.14	2.12	1.14	1.03	2.14
Syagrus romanzoffiana	2.45	1.98	5.58	2.09	1.28	1.20	2.62
Bromelia balansae	4.42	3.46	30.4	0.63	0.50	0.23	0.05
Salacia crassifolia	2.99	2.32	9.40	1.91	1.51	1.23	2.19
Diospyros lasiocalyx	4.37	3.80	26.82	2.26	1.34	0.96	1.24
Miconia sp.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Campomanesia adamantium	1.80	1.70	3.42	0.62	0.50	0.27	0.07
Myrcia guianensis	0.84	0.73	0.25	0.48	0.44	0.26	0.07
Psidium grandifolium	2.72	2.28	10.34	0.43	0.35	0.24	0.004
Cordiera concolor	1.60	1.38	2.91	0.45	0.34	0.15	0.02

*Citrus x sinensis**	n.d.	n.d.	n.d.	1.19	0.63	0.42	0.42
Pradosia brevipes	3.64	3.21	19.94	1.99	1.48	1.39	2.60
Pouteria torta	5.03	4.47	29.45	2.56	1.55	1.35	2.63
Solanum lycocarpum	10.78	8.31	537.19	0.64	0.50	0.22	0.03

***non-native fruit; nd - no data collected. Source: this study.**

Table 2S: N of seeds tested per treatment, germination percentage and G-test results for maned wolf, C1 = seeds with pulp and C2 = cleaned seeds. n.d. = not determined. *p*-values after Bonferroni correction

Species	**Planted (germinated)**			**Germination percentage (%)**			**G-test (values)**					
							Wolf x C1		**Wolf x C2**		**C1 x C2**	
	wolf	**C1**	**C2**	**wolf**	**C1**	**C2**	**G**	***p***	**G**	***p***	**G**	***p***
Annona crassiflora	102(20)	95(18)	95(22)	19.6	18.9	23.2	0.01	2.72	0.37	1.63	0.51	1.43
Duguetia furfuracea	21(3)	25(3)	29(4)	14.3	12.0	13.8	0.05	2.46	0.002	2.88	0.038	2.53
Xylopia aromatica	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Hancornia speciosa	30(23)	49(34)	55(42)	76.7	69.4	76.4	0.50	1.44	0.001	2.92	0.64	1.27
Attalea geraensis	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Syagrus petraea	46(0)	20(0)	20(0)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Syagrus romanzoffiana	54(13)	67(4)	69(2)	24.1	5.9	2.9	8.30	0.012	13.50	<0.001	0.77	1.1376
Bidens pilosa	21(9)	n.d.	n.d.	42.9	n.d.	n.d.	n.d	n.d.	n.d	n.d.	n.d	n.d.

Salacia crassifolia	15(10)	29(13)	31(29)	66.7	44.8	93.5	1.92	0.50	5.31	0.06	18.58	<0.001
Diospyros lasiocalyx	23(15)	73(0)	76(8)	65.2	0	10.5	53.5	<0.001	26.46	<0.001	11.21	0.002
Byrsonima crassifolia	4(0)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Miconia sp.	93(19)	49(0)	190(50)	20.4	0	26.3	17.6	<0.001	1.20	0.82	26.16	<0.001
Campomanesia adamantium	145(81)	64(30)	38(37)	55.9	46.9	97.4	1.44	0.69	29.86	<0.001	33.47	<0.001
Myrcia guianensis	40(4)	12(12)	17(16)	10.0	100	94.1	38.2	<0.001	40.26	<0.001	1.09	0.89
Psidium grandifolium	203(54)	195(1)	249(13)	26.6	0.51	5.22	72.0	<0.001	42.09	<0.001	9.73	0.005
Passiflora cincinnata	20(4)	n.d.	n.d.	20.0	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Poaceae sp.	10(0)	n.d.	n.d.	0.0	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Cordiera concolor	66(51)	95(18)	119(54)	77.3	18.9	45.4	56.9	<0.001	18.38	<0.001	17.16	<0.001
Citrus x sinensis	20(10)	n.d.	25(12)	50.0	n.d.	48.0	n.d	n.d.	0.02	0.89	n.d	n.d.
Talisia angustifolia	45(37)	n.d.	n.d.	82.2	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Pouteria torta	56(44)	n.d.	n.d.	78.6	n.d.	n.d.	n.d	n.d.	n.d.	n.d.	n.d.	n.d.

Pradosia brevipes	57(47)	33(4)	35(33)	82.5	12.1	94.3	45.8	<0.001	2.97	0.25	54.03	<0.001
Solanum lycocarpum	906(440)	493(19)	493(88)	48.6	3.9	17.8	354.4	<0.001	136.7	<0.001	53.67	<0.001

Table 3S: Number of seeds tested per treatment, germination percentage and G-test results for crab-eating fox. C1 = seeds with pulp and C2 = cleaned seeds. n.d. = not determined. *p*-values after Bonferroni correction.

Species	**Planted (germinated)**			**Germination percentage (%)**			**G-test (Values)**					
							Fox x C1		**Fox x C2**		**C1 x C2**	
	Fox	**C1**	**C2**	**Fox**	**C1**	**C2**	**G**	***p***	**G**	***p***	**G**	***p***
Annona crassiflora	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Hancornia speciosa	18 (15)	49(34)	55(42)	83.3	69.4	76.4	1.39	0.71	0.40	1.58	0.64	1.27
Bidens pilosa	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Bromelia balansae	29(3)	55(0)	172(7)	10.3	n.d.	4.1	6.6	0.03069	1.7	0.5829	4.0	0.14
Miconia sp.	31(7)	49(0)	190(50)	22.6	0	26.3	14.4	<0.001	0.2	1.97	26.2	<0.001
Campomanesia adamantium	45(11)	64(30)	38(37)	24.4	46.9	97.4	5.8	0.047	53.7	<0.001	33.5	<0.001

Psidium grandifolium	130(101)	195(1)	249(13)	77.7	0.51	5.22	253.9	<0.001	223.5	< 0.001	9.7	0.005
Passiflora cincinnata	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Poaceae sp.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Cordiera concolor	37(20)	95(18)	119(54)	54.1	18.9	45.4	15.2	<0.001	0.9	1.07	17.2	<0.001
Citrus x Sinensis	25(4)	0	25(12)	16.0	n.d.	48.0	n.d.	n.d.	6.1	0.01	n.d.	n.d.
Solanum lycocarpum	64(17)	493(19)	493(88)	26.6	3.9	17.8	31.8	<0.001	2.6	0.32	53.7	<0.001

Table 4S: Maned wolf and crab-eating fox number of seeds per sample and damaged seeds. n.d. = not determined

Species	Mean n° of seed per feces (considering all samples) ± SD		N° of seed per feces that contained that plant species (mean) ± SD		% of feces with seeds(n)		% damaged seeds per total seeds (n)	
	Maned wolf (N = 97 samples)	Crab-eating fox (N = 13 samples)	Maned wolf	Crab-eating fox	Maned wolf	Crab-eating fox	Maned wolf	Crab-eating fox
Annona crassiflora	1.6±8.2	0.08±0.3	11.2±19.4	1.0	14.43(14)	7.7 (1)	0	0
Duguetia furfuracea	0.3±1.5	n.d.	4.0±4.2	n.d.	7.21(7)	n.d.	0	n.d.
Xylopia aromatica	0.02±0.1	n.d.	1.0	n.d.	2.06(2)	n.d.	0	n.d.
Hancornia speciosa	0.9±5.6	0.5±1.9	14.8±20.7	7.0	6.18(6)	7.7 (1)	1.12(1)	0
Attalea geraensis	0.01±0.1	n.d.	1.0	n.d.	1.03(1)	n.d.	0	n.d.

Syagrus petraea	0.6±3.4	n.d.	5.6±9.5	n.d.	10.3(10)	n.d.	1.79(1)	n.d.
Syagrus romanzoffiana	0.6±3.8	n.d.	9.5±13.4	n.d.	6.18(6)	n.d.	1.75(1)	n.d.
Bidens pilosa	0.2±0.9	0.2±0.6	2.7±2.5	2.0	7.21(7)	7.7 (1)	0	0
Bromelia balansae	n.d.	0.31±1.1	n.d.	4.0	n.d.	7.7 (1)	n.d.	0
Salacia crassifolia	0.1±0.5	n.d.	2.3±1.5	n.d.	4.12(4)	n.d.	0	n.d.
Diospyros lasiocalyx	0.2±1.6	n.d.	7.0±7.2	n.d.	3.09(3)	n.d.	0	n.d.
Byrsonima crassifolia	0.04±0.2	n.d.	1.0	n.d.	4.12(4)	n.d.	0	n.d.
Miconia sp.	148.5±1461.3	2.5±8.9	7202.5±10167.5	32.0	2.06(2)	7.7 (1)	0	0
Campomanesia	9.4±34.3	5.6±13.2	70.1±69.4	24.3±19.0	13.40(13)	23.1(3)	3.51(32)	2.74(2)

adamantium								
Myrcia guianensis	0.8±6.7	n.d.	19.3±31.3	n.d.	4.12(4)	n.d.	1.30(1)	n.d.
Psidium grandifolium	3.9±20.6	10.1±36.3	53.4±60.8	131.0	7.21(7)	7.7 (1)	0	0
Passiflora cincinnata	0.04±0.4	0.2±0.6	4.0	2.0	1.03(1)	7.7 (1)	0	0
Poaceae sp.	1.7±5.0	0.9±2.3	7.3±8.4	6.0±1.4	24.74(24)	15.4(2)	0	0
Cordiera concolor	0.8±6.4	2.2±8.0	26.7±30.7	29.0	3.09(3)	7.7 (1)	0	0
Citrus x Sinensis	0.2±1.3	0.2±0.8	5.5±4.0	3.0	5.15(5)	7.7 (1)	0	0
Talisia angustifolia	0.5±2.3	n.d.	5.3±5.6	n.d.	9.27(9)	n.d.	4.17(2)	n.d.
Pouteria torta	0.6±1.6	n.d.	4.3±1.8	n.d.	13.40(13)	n.d.	1.79(1)	n.d.

Pradosia brevipes	0.6±2.5	n.d.	5.7±6.0	n.d.	10.31(10)	n.d.	0	n.d.
Solanum lycocarpum	60.4±80.8	3.0±7.3	80.6±84.4	13.0±11.4	75.25(73)	23.1(3)	3.48(202)	12.82(5)

Table 5S: Gut passage time (GPT) of seeds ingested by the Crab-eating fox. Values are mean± standard deviation (GPT, mass and length).

Specie	GPT (hours)	Seed mass (g)	Seed length (cm)
Hancornia speciosa	21.4±6.9	0.21	0.83
Bromelia balansae	13.4±3.9	0.05	0.63
Campomanesia adamantium	24.9±9.4	0.07	0.62
Psidium grandifolium	11.0±6.4	0.004	0.43
Cordiera concolor	22.2±6.1	0.02	0.45
Citrus x sinensis	19.9±10.2	0.42	1.19
Solanum lycocarpum	12.1±4.4	0.03	0.64

Table 6S: Results of Tukey's test after ANOVA for the average GPT of each species in the Crab-eating fox. n.d. = not determined.

Specie	*Hancornia speciosa*	*Bromelia balansae*	*Campomanesia adamantium*	*Psidium grandifolium*	*Cordiera concolor*	*Citrus x sinensis*
Hancornia speciosa	n.d.					
Bromelia balansae	Diff = 8.0, p <0.05	n.d.				
Campomanesia adamantium	Diff = -3.5, p = 0.6	Diff = 11.5, p < 0.05	n.d.			
Psidium grandifolium	Diff = -10.3, p <0.05	Diff = -2.3, p = 0.8	Diff = -13.9, p <0.05	n.d.		
Cordiera concolor	Diff = -0.8, p = 1.0	Diff = 8.8, p < 0.05	Diff = -2.7, p = 0.7	Diff = -11.1, p < 0.05	n.d.	
Citrus x sinensis	Diff = 1.5, p = 1.0	Diff = 6.5, p = 0.01	Diff = -5.03, p = 0.1	Diff = -8.8, p < 0.05	Diff = 2.3, p =0.9	n.d.
Solanum lycocarpum	Diff = -9.3, p < 0.05	Diff = -1.3, p = 0.1	Diff = -12.8, p <0.05	Diff = 1.0, p = 1.0	Diff = -10.1, p < 0.05	Diff = -7.8, p <0.05

Table 7S: Germination time (mean) and Survival tests (considering germination percentage and germination speed) of seeds tested for maned wolf (*Chrysocyon brachyurus*) and crab-eating fox (*Cerdocyon thous*). n.d.= not determined.

	Germination time (mean in days)				**Survival test**					
					***Chrysocyon brachyurus* (*p*-value)**			***Cerdocyon thous* (*p*-value)**		
	Chrysocyon brachyurus	*Cerdocyon thous*	C1	C2	Ingested x C1	Ingested x C2	C1 x C2	Ingested x C1	Ingested x C2	C1 x C2
Annona crassiflora	79.20	n.d.	31.00	27.70	1.00	0.99	1.00	n.d.	n.d.	n.d.
Duguetia furfuracea	46.00	n.d.	26.70	43.30	1.00	1.00	1.00	n.d.	n.d.	n.d.
Hancornia speciosa	10.50	11.70	20.50	12.00	0.02	1.00	0.03	<0.01	1.00	0.03
Syagrus romanzoffiana	55.20	n.d.	70.30	43.00	0.01	<0.01	1.00	n.d.	n.d.	n.d.
Bidens pilosa	54.00	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

Bromelia balansae	n.d.	118.70	n.d.	117.90	n.d.	n.d.	n.d.	0.04	0.47	0.39
Salacia crassifolia	18.40	n.d.	30.90	22.80	0.17	0.35	<0.01	n.d.	n.d.	n.d.
Diospyros lasiocalyx	76.30	n.d.	n.d.	56.60	<0.01	<0.01	0.01	n.d.	n.d.	n.d.
Miconia sp.	34.60	27.70	n.d.	33.80	<0.01	0.91	<0.01	<0.01	1.00	<0.01
Campomanesia adamantium	5.60	26.40	20.90	8.70	0.04	<0.01	<0.01	0.03	<0.01	<0.01
Myrcia guianensis	11.80	n.d.	12.50	3.90	<0.01	<0.01	0.01	n.d.	n.d.	n.d.
Psidium grandifolium	34.50	33.80	48.00	32.90	<0.01	<0.01	0.01	<0.01	<0.01	0.01
Passiflora cincinnata	28.00	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Cordiera concolor	13.10	14.10	36.70	22.60	<0.01	<0.01	<0.01	<0.01	0.34	<0.01

Citrus x sinensis	59.80	66.80	n.d.	38.80	n.d.	0.79	n.d.	n.d	<0.01	n.d
Talisia angustifolia	12.70	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Pouteria torta	37.70	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Pradosia brevipes	14.00	n.d.	33.00	7.50	<0.01	<0.01	<0.01	n.d.	n.d.	n.d.
Solanum lycocarpum	35.60	45.10	108.30	101.10	<0.01	<0.01	<0.01	<0.01	0.07	<0.01

4. CONCLUSÃO

A análise dos papéis desempenhados pelos canídeos *Chrysocyon brachyurus* (lobo guará) e *Cerdocyon thous* (cachorro do mato) na dispersão de sementes e a dieta do lobo-guará nos permite compreender ainda mais sobre a ecologia trófica dessas espécies, a relação entre sua alimentação e as plantas cujas sementes dispersam, além de variações na dieta do lobo-guará frente a alterações sazonais e de disponibilidade de recursos na área em que vivem. A análise dos itens na dieta do lobo-guará possibilitou a identificação de nove novas espécies de frutos consumidos por este canídeo. Além disso, possibilitou entender quais os recursos mais importantes da sua dieta para superar períodos de adversidade climática sazonais, como a estação seca. Por fim, possibilitou aprofundar mais o conhecimento sobre a seletividade de itens alimentares do lobo-guará, principalmente para o Estado de São Paulo e, de Itirapina, sendo um dos poucos a avaliar a seletividade em relação aos frutos para esse sítio.

O lobo-guará e o cachorro-do-mato demonstraram desempenhar papel significativo na dispersão de sementes do Cerrado. A presença de sementes viáveis nas fezes de ambos os canídeos nos prova que são dispersores legítimos no Cerrado, de forma que podem contribuir para a colonização/recolonização de hábitats e regeneração vegetal. A comparação entre as sementes defecadas com os dois tratamentos (sementes limpas e sementes com polpa) indicam que o principal efeito dos canídeos é de remoção da polpa e limpeza das sementes, para a maioria das espécies de plantas estudadas. Contudo para algumas espécies eles podem influenciar nas porcentagens e velocidades de germinação por influência de escarificação química ou mecânica das sementes.

A dieta do lobo-guará revelou diferenças notáveis em termos de frequência e biomassa consumida de itens vegetais e animais. Sua dieta mostrou uma inclinação maior para o consumo de itens vegetais, especialmente frutas. Apesar disso, o lobo-guará demonstra comportamento alimentar com ampla gama de recursos consumidos e seletividade da maior parte dos itens, principalmente de frutos e roedores específicos.

A sazonalidade também se mostrou um importante fator que influencia a composição da dieta e a seleção de alimentos pelos lobo-guará. Sua dieta apresentou maior presença de frutos durante as estações chuvosas, enquanto o fruto da lobeira (*Solanum lycocarpum*) e roedores foram mais consumidos e mais importantes na estação seca. Essas variações podem influenciar diretamente a dispersão de sementes, afetando a distribuição, a germinação e o recrutamento de espécies vegetais ao longo do ano.

Neste estudo, em resumo, tanto o lobo guará quanto o cachorro do mato desempenham papéis significativos na dispersão de sementes que podem se relacionar com a estruturação do ecossistema do Cerrado. Seus comportamentos alimentares demonstram interagirem intensamente com muitas espécies presentes nesse domínio, desempenhando papeis entendidos como de mesopredadores. Além disso, a atuação como dispersores legítimos sugere a necessidade de uma compreensão mais profunda e detalhada sobre as interações entre carnívoros e plantas no Cerrado. Há poucas informações a respeito, por exemplo, para outros carnívoros como quati (*Nasua nasua*), irara (*Eira barbara*) e jaritataca (*Conepatus semistriatus*). Por fim, o estudo possibilita ampliar o entendimento da manutenção destes dois canídeos nos ecossistemas em que estão presentes, tendo em vista que a redução de suas populações ou extinções locais resultariam na perda de diferentes interações tanto com espécies de plantas quanto de animais. Dessa forma, a conservação desses canídeos é importante para a manutenção da biodiversidade dos ecossistemas nos quais eles atuam.

Para trabalhos futuros, é vislumbrada a possibilidade de uma meta-análise das espécies que são dispersas pelo lobo guará e cachorro do mato, com base na literatura. Além disso, a possibilidade de abranger outras partes dos aspectos qualitativos da dispersão de sementes, trabalhando com o recrutamento em campo das sementes dispersas pelos canídeos. Por fim, ampliar os estudos sobre frugivoria e dispersão de sementes para outras espécies de carnívoros que ocorrem no Cerrado.