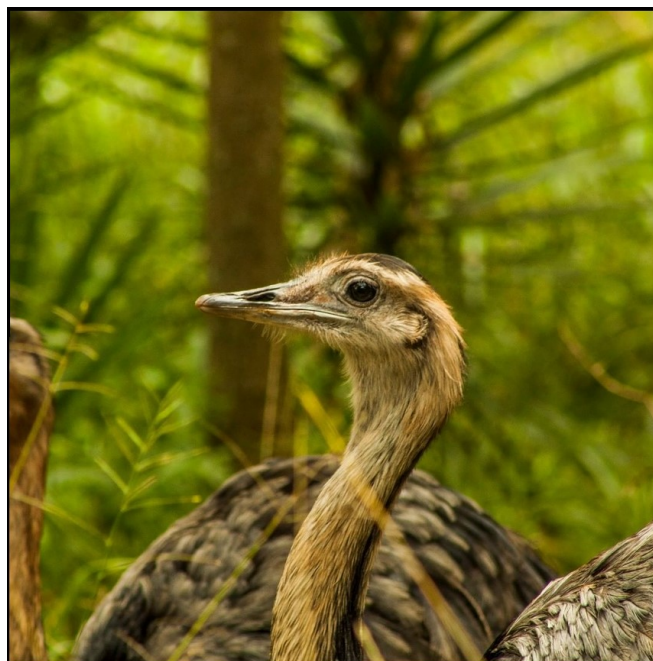


UNIVERSIDADE FEDERAL DE SÃO CARLOS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

Dieta e ecologia funcional da ema (*Rhea americana*) no Pantanal e Cerrado

Cauê Lazareth Balassa Jacques



São Carlos - SP

2024

UNIVERSIDADE FEDERAL DE SÃO CARLOS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

Dieta e ecologia funcional da ema (*Rhea americana*) no Pantanal e Cerrado

Dissertação ao Programa de Pós-graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos como requisito parcial para obtenção do título de mestre.

Área de atuação: Aplicações Ecológicas

Orientador: Prof. Dr. Alexander Vicente Christianini

São Carlos - SP

2024



UNIVERSIDADE FEDERAL DE SÃO CARLOS

Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Folha de Aprovação

Defesa de Dissertação de Mestrado do candidato Cauê Lazareth Balassa Jacques, realizada em 09/05/2024.

Comissão Julgadora:

Prof. Dr. Alexander Vicente Christianini (UFSCar)

Prof. Dr. Augusto João Piratelli (UFSCar)

Profa. Dra. Érica Hasui (UNIFAL)

O Relatório de Defesa assinado pelos membros da Comissão Julgadora encontra-se arquivado junto ao Programa de Pós-Graduação em Ecologia e Recursos Naturais.

Agradecimentos

Agradeço primeiramente ao Prof. Dr. Alexander Vicente Christianini pela constante orientação, paciência e parceria nestes 2 anos.

Agradeço ao meu laboratório de Interações Ecológicas, em conjunto com os meus colegas de pesquisa: Liliane, Mariana, Renato e Guilherme. Obrigado por cada parceria e ajuda durante esta trajetória. São amigos que vou levar comigo, sempre. Agradeço à Mariana Campagnoli por fornecer as medidas de largura e comprimento do bico das emas obtidas no MZUSP, ao qual também agradeço. Foram dados essenciais para o desenvolvimento do meu trabalho.

Agradeço a Universidade Federal de São Carlos-SP e a Secretaria e Coordenação do Programa de Pós-Graduação em Ecologia e Recursos Naturais pela atenção e por me proporcionar a oportunidade de realizar esta jornada de pesquisa e aprendizado em meu mestrado. Agradeço ao Parque Ecológico de São Carlos, SP, por permitir desenvolver os experimentos com as emas em cativeiro. Muito obrigado a todos os funcionários do parque. Rogério, Fernando, Samanta, Renan, Kainan, Balbino e Moacir por me ajudarem durante toda trajetória da pesquisa. Sem vocês, eu não conseguiria.

Agradeço pela concessão da bolsa de mestrado pela CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior do Ministério da Educação) ao longo destes dois anos. Em conjunto, agradeço ao PROAP (Programa de Apoio a Pós-Graduação) da Capes (código de financiamento 01) por custear, e assim, permitir minha ida para o Congresso de Ornitologia das Américas, e também por auxiliar na compra de reagentes empregados nas análises em laboratório.

Gostaria de expressar minha profunda gratidão à minha família Lazareth, Balassa e Jacques, pelo constante apoio, amor e compreensão durante os processos. Aos meus pais, Marco S. Jacques e Katia L. Balassa, e ao meu irmão, Luan L. B. Jacques, que sempre estiveram presentes, incentivando e acreditando em mim e nas minhas escolhas. Agradeço à Denise pelos conselhos e cuidados comigo. Amo vocês! Aos meus amigos, verdadeiros irmãos de alma, Garbola, Bbax, Tsuruda, Nakapa, Okada, Dudu, Jimi, PA, Ratão, Magaia, Aaron, Luisa, Thiago, Pilz, Gui (Canastra), Guy (Ilha Anchieta), Paulinha, Lucas T., Fernanda, Xandão, Bidico, Heitor, Alex, Nélio, Priscila, pelo apoio

incondicional e momentos compartilhados que tornaram esta jornada mais leve e significativa. Um agradecimento especial também à minha filhinha-pet, Luna (pokis) Jacques, cujos abraços foram essenciais nos momentos de necessidade e até hoje em conjunto com a Kiara, o Floquinho e o Scooby. Agradeço também as estrelas que também já me deram muito amor Maylon, Thainá e Mel. Expresso minha gratidão ao universo e a todos os processos que me conduziram até aqui. Sem palavras. Por fim gostaria de agradecer o meio ambiente, à natureza, o oceano de todos os ensinamentos que sempre me passou em cada lugar e momento onde estive. Sem eles, eu não seria nada. Obrigado do fundo do meu coração!

Resumo

A ema (*Rhea americana*) é a maior ave da América do Sul, habitando, por exemplo, as planícies alagáveis do Pantanal e as savanas conhecidas como Cerrado no Brasil. Nesse estudo, a dieta da ema foi avaliada no Pantanal, revelando uma variedade de alimentos, com destaque para folhas, frutos/sementes, invertebrados e pequenos vertebrados. A diversidade de plantas consumidas incluiu leguminosas e espécies com frutos carnosos, como *Psidium* sp. (Myrtaceae) e sementes grandes de palmeiras. Essa alimentação variada sugere um potencial papel na dispersão de sementes, com a presença de sementes aparentemente intactas nas fezes. Numa segunda etapa realizada com emas em cativeiro revelaram que elas possuem um tempo de passagem gastrointestinal longo, permitindo a dispersão de sementes a longas distâncias. As sementes ingeridas pela *R. americana* apresentaram resultados variáveis na germinação, com algumas espécies beneficiadas e outras não. O declínio populacional das emas pode afetar a regeneração de plantas, especialmente quando se pensa no componente quantitativo da dispersão de sementes ou nas distâncias de dispersão. Compreender a relação ecológica entre a *R. americana* e as plantas nativas parece importante para a dinâmica e conservação dos ecossistemas onde a espécie ocorre.

Palavras-chave: Dieta, Dispersão, Frugivoria, Predação, Restauração

Sumário

1. Introdução geral.....	7
2. Referências	19
3. Capítulo 1	27
3.1 Introduction	29
3.2 Materials and Methods	31
3.3 Results	32
3.4 Discussion.....	34
3.5 Acknowledgments	37
3.6 References	38
4.0 Capítulo 2	44
4.1 Introduction	45
4.2 Materials and Methods	47
4.2.1 Feeding experiments with captive Rheas	47
4.2.2 Estimates of GPT and its conditionants.....	48
4.2.3 Comparisons of seed germination	48
4.2.4 Statistical Analysis	49
4.6 Results	50
4.6.1 Estimates of GPT and its conditionants.....	50
4.6.2Comparisons of seed germination	50
4.7 Discussion.....	51
4.8 Acknowledgments	55
4.9 References	56
5.0 Figures	63
5.1 Tables	67
5.2 Supplementary material.....	70
6.0 Conclusão	73

1. Introdução geral

Destruição e degradação dos ecossistemas naturais são as principais causas de declínio da biodiversidade global (Pereira *et al.* 2010). Os biomas brasileiros constituem uma porção significativa da biodiversidade mundial, com altos níveis de riqueza e endemismo de espécies da flora e fauna (Myers *et al.* 2000). Contudo, toda essa biodiversidade observada vem sendo crescentemente ameaçada por ações antrópicas, como a fragmentação, procedimento de divisões de habitats em fragmentos menores, que se tornam isolados e separados por uma matriz, ou seja, ambientes não nativos (Haddad *et al.* 2015). Neste processo, além da alteração dos habitats naturais (Durigan *et al.* 2008; Fahrig, 2003), outras intervenções em vegetações nativas podem ocorrer, tais como, caça, queimadas, extração madeireira e plantio de monoculturas, alterando toda a paisagem nativa da região, consequentemente diminuindo a biodiversidade (Laurance *et al.* 2012; Tabarelli *et al.* 2004). No Brasil, este processo de fragmentação tem sido uma das causas da diminuição da diversidade biológica (Machado *et al.* Filho, 2010), como o efeito de várias mudanças na estrutura e dinâmica da diversidade e abundância da fauna e na comunidade vegetal (Rausch, *et al.* 2019). Enormes alterações paisagísticas e ambientais já colocaram determinados biomas como principais vítimas deste processo, como no caso do Cerrado e do Pantanal (Strassburg *et al.* 2017).

O Cerrado, considerado a savana brasileira, predomina na região no Planalto Central do Brasil, classificado como *hotspot* de biodiversidade com mais de 10.000 espécies de plantas, onde engloba as três maiores bacias hidrográficas da América do Sul, distribuindo 43% das águas superficiais brasileiras e prestando serviços ecossistêmicos essenciais (Strassburg, *et al.* 2017). Para mais, este bioma atua na conservação das espécies dos diferentes grupos faunísticos, atingindo aproximadamente 837 espécies de avifauna (Silva, 1995), 199 espécies de mamíferos, centenas de espécies de répteis e anfíbios e 1.200 espécies de peixes (MMA, 2021b).

Já o Pantanal é considerada a maior planície alagável do mundo, ocupando uma área de 210.000 Km² entre o Brasil, Bolívia e Paraguai. Sua biodiversidade é constituída por 3.500 espécies de plantas, 124 espécies de mamíferos, 463 espécies de aves e 325 espécies de peixes (Júnior *et al.*, 2014). Neste bioma a dinâmica das comunidades de aves está intimamente relacionada à heterogeneidade do ambiente e aos eventos de inundação (Figueira *et al.* 2006)

O grupo das aves é uma das peças fundamentais para o bom funcionamento e dinâmica dos ecossistemas brasileiros. Por meio de interações tróficas, as aves participam das interações com a comunidade, como as plantas, onde podem influenciar a distribuição de espécies ao longo de um ambiente ou região por meio de frugivoria e dispersão de sementes (Sekercioglu *et al.* 2016). A dispersão de sementes, processo pelo qual os diásporos são retirados de alguma distância além do limite da copa da planta-mãe (Christianini e Martins, 2015), está associada ao final do ciclo reprodutivo de plantas adultas com o estabelecimento de seus descendentes em novos ambientes, influenciando em muitos aspectos chave para a biologia das espécies de plantas (Nathan e Muller-Landau, 2000, Wilson e Traveset, 2000). A maioria das árvores encontradas em florestas tropicais possuem sementes dispersas por animais (Jordano, 2000; Nathan e Muller-Landau, 2000, Wilson e Traveset, 2000). De 80% a 95% das árvores destas florestas produzem diásporos com adaptações aparentes à dispersão de sementes por animais (zoocóricos). Isto indica que animais frugívoros devem ter um papel funcional formidável na dispersão de sementes de diversas espécies de plantas, influenciando à dinâmica espacial e sobrevivência dos regenerantes (Christianini e Martins, 2015). As aves têm o maior número de espécies de vertebrados frugívoros nestes ambientes tropicais, contribuindo de forma significativa no papel funcional de dispersores de sementes (Jordano, 2000). A dispersão de sementes molda a estrutura espacial e a composição de espécies das comunidades vegetais (Nathan e Muller-Landau, 2000; Levine e Murrell, 2003; Snell *et al.* 2019). Portanto, esta funcionalidade torna-se essencial para toda a estrutura ecossistêmica na paisagem natural.

As plantas podem se beneficiar da dispersão de sementes mediada por animais, uma vez que a chance de serem depositadas em ambientes com as condições favoráveis aumenta, pois, o dispersor pode garantir maior distanciamento da semente com a planta-mãe (planta que produz os diásporos), facilitando a sua chance de colonização em um novo ambiente sem a presença de outros indivíduos da mesma espécie, diminuindo assim, a competitividade intraespecífica (Janzen, 1970; Connell, 1971). Sendo assim, a contribuição dos dispersores pode se dar pelo transporte de sementes para longe da planta-mãe e/ou sua deposição em microsítios, que oferecem condições favoráveis e potencialmente ambientes seguros para o estabelecimento da prole e o desenvolvimento da plântula (Primack e Miao 1992; Howe e Miriti 2000; Herrera 2002).

Além disso, outra contribuição das aves é a qualidade de tratamento, onde, elas influenciam no sucesso da germinação após a passagem da semente pelo sistema digestório do animal (Schupp, 1993). Vertebrados frugívoros podem afetar a aptidão das plantas dispersando as sementes para locais favoráveis ao estabelecimento e passando pelo seu intestino, alterando assim os padrões de germinação, melhorando a taxa de germinação e/ou sucesso de colonização. Um dos principais benefícios que as sementes obtêm dos animais frugívoros, é a retirada da polpa, após a passagem intestinal do fruto no animal (Levey, 1986; Schupp *et al.* 2010; Fricke *et al.* 2019). Além da remoção da polpa pelo trato digestório do animal, pode ocorrer o processo de escarificação física e/ou química na semente, pelo qual a semente altera seu tempo de germinação, podendo melhorar ainda mais a qualidade da dispersão das sementes (Levey, 1986; Schupp *et al.* 2010). Deste modo, as aves podem ter funções significativas, em que, além de carregar as sementes possivelmente para locais propícios (microsítios) também podem induzir a germinação das sementes, após a passagem das mesmas pelo trato digestivo (Samuels e Levey, 2005).

O tempo de passagem, isto é, o tempo entre a ingestão e a regurgitação ou defecação (TPD) por um animal frugívoro, é um componente essencial para avaliar a eficácia da dispersão de sementes (Gasperin e Pizo, 2012). Para mais, o tamanho da semente é especialmente importante, pois determina em grande parte se a semente será defecada ou regurgitada. Sabendo o TPD e combinando esta informação com a movimentação das aves, pode-se estimar a distribuição espacial das sementes ingeridas (Westcott *et al.*, 2008). No caso das aves, o TPD das sementes é influenciado por diversos fatores como: taxa de ingestão, massa corporal, dieta (quantidade de frutos consumidos), tamanho do fruto, a química e textura do fruto (Herrera 1984, Levey 1986, Worthington 1989, Schabaker e Curio 2000). Os frutos são constituídos por diferentes nutrientes ou substâncias adstringentes que podem reter a sementes por maior tempo, como os lipídeos e carboidratos (Traveset, 1998); outras, podem acelerar a defecação, dependendo da espécie. Sementes defecadas costumam ter um TPD mais longo do que as regurgitadas, devido ao tempo retido no estômago do animal, o que pode influenciar na escarificação do tegumento e na distância da dispersão das mesmas (Traveset e Verdú, 2002). Embora as aves contribuam para a manutenção das comunidades vegetais, muitas espécies de aves encontram-se ameaçadas de extinção (Rogers *et al.*, 2021). E uma delas, sendo o enfoque do nosso estudo, é a ema (*Rhea americana*).

A ausência de animais de maior porte em ambientes naturais, como as emas, pode gerar grandes consequências para todo o contexto dinâmico de um ecossistema. Existem diversas plantas que exibem estruturas carnosas como polpa, arilo, carúncula que revestem e protegem as sementes. Estas estruturas além de abrigar o embrião da semente, também atuam como atrativos e recompensas alimentares para animais frugívoros (Christianini e Martins, 2015). Plantas com diásporos maiores impedem que muitos animais menores os engulam; assim, frugívoros com maior porte, acabam desempenhando a função de dispersar sementes maiores, por terem condições morfológicas e anatômicas ideais para tal função, ajudando a moldar comunidades de plantas através da capacidade de dispersarem sementes grandes (Lord, 2004). O tamanho do fruto pode ser uma variável significativa na habilidade alimentar ou preferências para os frugívoros. A massa corporal e o tamanho do bico se correlacionam positivamente com o tamanho/diâmetro do fruto consumido (Pratt e Stiles 1985; Wheelwright 1985; Williams e Karl 1996). A morfologia das aves tende a ser associada ao tipo de fruto consumido, onde o bico é uma estrutura diretamente relacionada à obtenção destes recursos (Wheelwright, 1985), e seu tamanho influencia no tipo de dieta e alimento que o animal consome, ou seja, se ele é capaz de engolir frutos maiores ou menores dependendo do tamanho de seu bico e capacidade de ingestão (figura 1). Infelizmente, quando se fala de extinções e declínios populacionais, os frugívoros de maior tamanho são os primeiros a serem citados (Méndez *et al.*, 2018). Com ausência de frugívoros de grande porte em ambientes naturais, o recrutamento de plantas com frutos carnosos de todos os tamanhos de sementes deixa de ocorrer e consequentemente efeitos drásticos no fluxo gênico, a composição e estruturação espacial das espécies de plantas (Bagchi *et al.*, 2018). A eficácia na dispersão de semente pode estar positivamente relacionada com a massa corporal das aves, grandes aves, como as emas (*Rhea americana*) removem maior número de frutos/sementes, e conseguem reter por maior tempo intestinal do que aves menores (Jordano, 2000; 2016; Nathan *et al.* 2008; Schurr *et al.* 2009). Deste modo, a capacidade de reter sementes em seu intestino por mais tempo comparado aos animais menores, a sua área de vida grande, com alta capacidade de deslocamento, fazem com que as emas possam ser boas dispersores de sementes por longas distâncias, o que aumenta a possibilidade de sucesso das sementes na colonização de novas áreas, através da redução da competição com a planta-mãe ou com outros indivíduos da mesma espécie (Alcántara *et al.* 2000; Pakeman 2001; Aerts *et al.* 2006). Se as emas são dispersoras

eficazes de sementes, elas podem ser uma espécie-chave como agentes na restauração ou regeneração de vegetação. Devido a sua capacidade em consumir frutos maiores, sendo uma barreira para pequenos frugívoros. Além disso, as emas apresentam alta mobilidade, fornecendo oportunidades de alcance das sementes em longas distâncias em média de 60 Km/h, dependendo das condições ambientais (Azevedo, 2010).

Devido as alterações nos habitats, algumas espécies vegetais do Cerrado enfrentam risco de extinção pela falta de dispersores de sementes, uma vez que suas sementes muito grandes dependem de frugívoros maiores para serem dispersas no ambiente (Guimarães *et al.* 2008). As alterações na qualidade de sistemas e perda de habitat podem determinar um processo seletivo de perda no geral de espécies da fauna e flora (MacArthur *et al.* 1972). Espécies de maior porte estão sofrendo mais com a caça e perdas de hábitat, onde dependem de maiores áreas para obtenção de recursos (Dirzo *et al.* 2014). Isto leva a um impacto seletivo, pelo qual os impactos antrópicos ocasionam primeiro a perda de aves frugívoras de maior tamanho corporal que dispersam sementes de maior tamanho (Silva e Tabarelli 2000, Bleher e Böhning-Gaese 2001). Por conseguinte, a ausência de grandes frugívoros, como as emas, podem trazer problemas para as populações de plantas, uma vez que a dispersão de sementes diminuiria, por serem uma das poucas aves que possivelmente disperse grandes sementes e que além disso, também disperse grandes quantidade de sementes menores, devido a sua morfologia e capacidade de ingerir e reter uma quantidade alta no volume de sementes quando comparado aos frugívoros menores, consequência também de sua morfologia e fisiologia (Chen, 2015). Além disso, as espécies de aves maiores são geralmente mais eficazes como dispersores de sementes, pois conseguem percorrer maiores distâncias, com um tempo de retenção intestinal mais longo; entretanto, essa eficácia normalmente depende do tamanho das sementes consumidas (Godínez Alvarez *et al.* 2020).

A *Rhea americana*, uma vez já vista como uma ave comum, facilmente observada em toda a sua extensão territorial, atualmente e infelizmente, está sendo intensamente ameaçada de extinção. Exibindo enorme declínio populacional observado nos últimos anos nos estados brasileiros, é classificada como quase ameaçada de extinção segundo a União Internacional para Conservação da Natureza (*International Union for Conservation of Nature; IUCN, 2016*). Ações antrópicas como a caça, queimadas, perda de habitat para agricultura, como também a eliminação de ovos por maquinários agrícola

(Dani 1993; Giannoni 1996) contribuem para a diminuição das populações da espécie. O manejo inadequado e falhas de reintrodução também contribuem para tal diminuição da população. Animais domésticos podem preda as espécies nativas após a soltura sem o devido estudo detalhado (Short *et al.* 1992; Miller *et al.* 1994). O objetivo de salvar uma espécie está diretamente relacionado à conservação e proteção de seu habitat (Bergel, 2018). Por isso, a importância de um estudo biológico, detalhado e prévio, possibilita a reintrodução da espécie em seu ambiente natural.

A *Rhea americana* considerada oportunista em seus hábitos alimentares (Azevedo, 2010) é uma espécie que demonstra especializações morfológicas e comportamentais, onívora, consome uma grande variedade de matéria vegetal disponíveis no ambiente, como frutos, folhas, flores e sementes, embora também consumam pequenos vertebrados e invertebrados (Azevedo *et al.* 2006; Comparatore e yageddú 2007). Sua pastagem é de forma lenta, ingerindo pedras e areia que auxiliam a trituração dos alimentos (Sick, 1997). A morfologia é diferente quando comparada as outras espécies de aves, ela apresenta um bico de tamanho grande chato e largo, um tipo de bico adequado para engolir alimentos inteiros e não os triturar (figura 1) (Lima *et al.* 2014). A ema não é seletiva durante o forrageamento. Para mais, seu comportamento alimentar é um típico comportamento do “*pegue e jogue*” (Figura 2), onde no momento da ingestão o assoalho da boca e sua faringe alteram, possibilitando o aumento de volume total da cavidade bucal, sendo capaz de consumir uma carga alta de frutos/sementes (Gussekkloo, 2000).

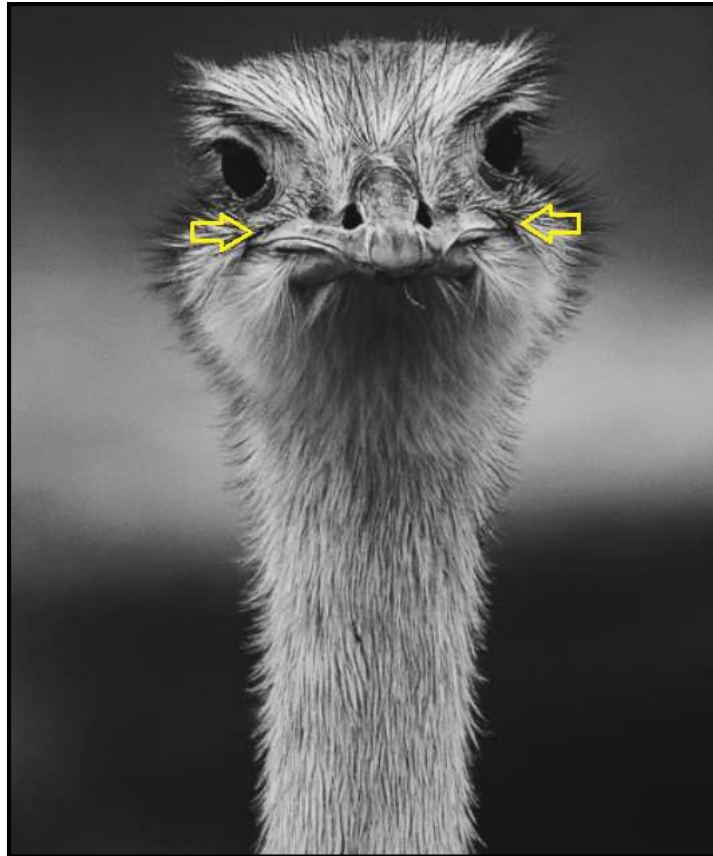


Figura 1: Setas indicando a largura do bico em *Rhea americana* (imagem modificada pelo autor, fonte: Flickr)

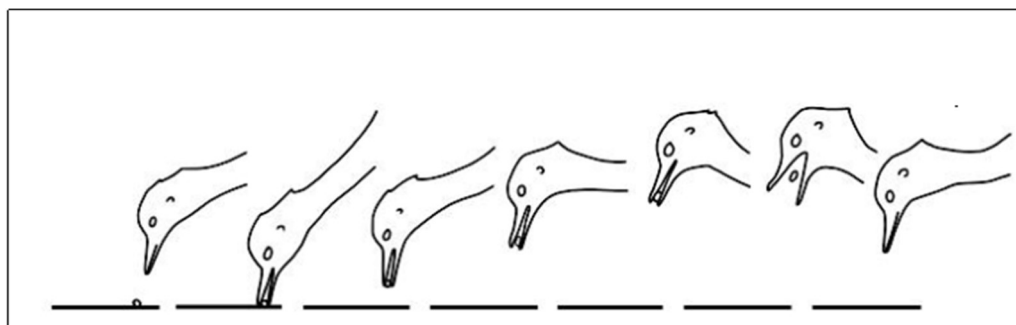


Figura 2: Comportamento alimentar de ingestão de fruto de *Rhea americana*. As linhas horizontais representam o nível do solo. (Fonte: Gussekloo, 2000)

A ema (*Rhea americana*) é uma das maiores espécies de frugívoros da fauna existentes no cerrado, sendo a maior ave da América do Sul (Schauensee, 1982). O macho e a fêmea podem atingir 35 Kg e 32 Kg e 170 e 134 cm de altura respectivamente (Sick, 1997). Sua anatomia digestória é constituída por um cólon curto com cecos compridos emparelhados, onde ocorrem fermentações microbianas, com altas concentrações de ácidos graxos voláteis, o que ajuda na digestão de celulose (Stevens e Hume, 2004). Isso se assemelha à fisiologia digestiva dos cavalos (Skadhauge *et al.* 1996).

Além disso, elas apresentam dimorfismo sexual: o macho é mais robusto, com pescoço mais grosso com base preta, tem a cabeça perfilada e o restante da plumagem é acinzentada, já a fêmea um pouco mais clara de modo geral e com o tamanho de corpo um pouco menos robusto (Brandt & Neto, 1997), (Figura 3). A ema como outras ratitas por não voar, não precisam evitar o excesso de peso, o que possibilita ter uma dieta diversificada com alto volume no consumo de alimentos (Wright e Bowmaker 2001). Para mais, as ratitas substituíram efetivamente a capacidade de execução de voo, diminuindo sua asa, pelo tamanho de sua perna, exibindo alta capacidade em correr em altas velocidades. Isto não é só um mecanismo de defesa conveniente de predadores, mas também permite que essas aves percorram grandes distâncias (Noble, 1991). As emas, como outras aves, possuem adaptações morfofisiológicas em sua anatomia, tais como a presença de moela e o proventrículo, cujas funções estão relacionadas ao armazenamento de alimentos.

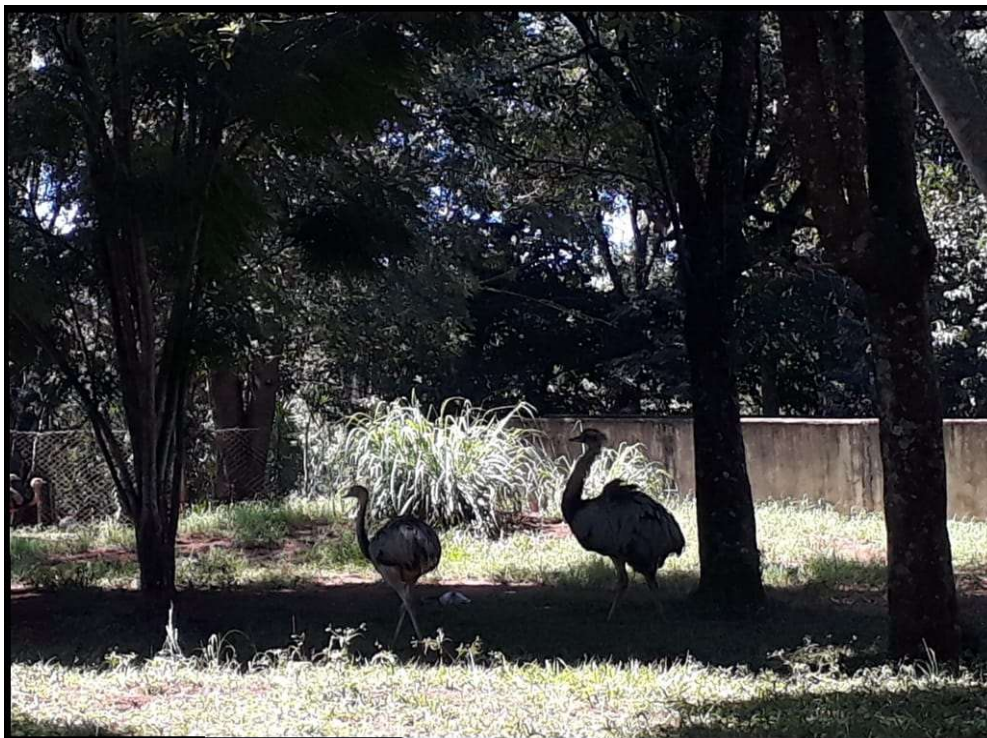


Figura 3: Dimorfismo sexual entre macho (lado direito) e fêmea (lado esquerdo) de emas (*Rhea americana*) (foto: autor)

As emas (*Rhea americana*), vivem em regiões campestres e Cerrados, distribuindo-se pelo Brasil, Uruguai, Argentina e Sul da Bolívia (Giannoni, 1996). No Brasil encontram-se nas regiões sul do Pará, além do nordeste, centro-oeste, sudeste e sul do País (Sick, 1997) (figura 4), sempre em vegetações abertas, em campos e savanas. Como já foi citado anteriormente é uma boa dispersora de sementes de algumas espécies de plantas do cerrado (Azevedo, 2013). São animais terrestres que conseguem alcançar grandes velocidades em média de 60 Km/h, correndo em ziguezagues ou linhas retas como forma de estratégia de escape de predadores (Codonotti *et al.* 1995). É uma ave que vive em grupos de 5 a 30 indivíduos mistos de machos e fêmeas, jovens e adultos (Bruning, 1974).

Na Argentina, a espécie tem o hábito de se alimentar de gramíneas de maior porte, presentes no bioma Pampa (Folch, 1992). Infelizmente, estas áreas estão sendo fortemente modificadas pelas práticas de uso da terra (Bilenca e Minarro, 2004; Viglizzo *et al.* 2011). Alterações do ambiente natural devido a pastagens, fragmentação de habitat, aumento da população humana, construção de estradas e caça por sua pele, carne e

plumas, além da coleta de ovos afetou de forma significativa as populações de emas (*Rhea americana*) (Sick 1997)). Por mais que as emas sejam encontradas em diferentes regiões do continente, particularmente em áreas protegidas e em algumas fazendas, o número populacional foi bastante reduzido, a ponto de ocorrer extinções locais em muitas áreas.

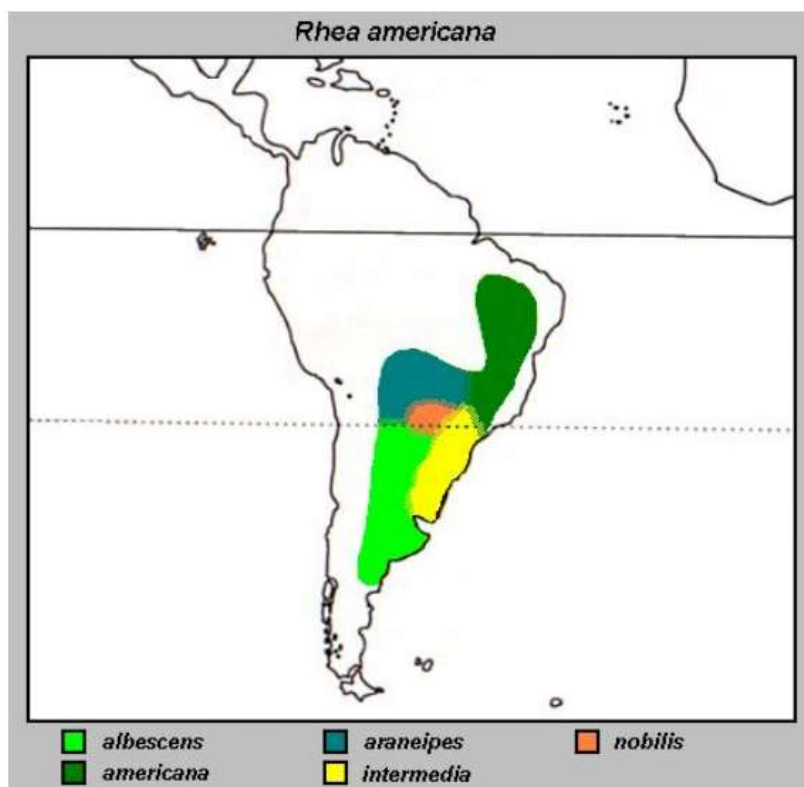


Figura 4: Distribuição da ema *Rhea americana* e suas cinco Subespécies na América do Sul (fonte: Azevedo, 2010).

Em relação ao papel funcional das emas, estudos que incluem elas como dispersoras de sementes são bastante recentes. O trabalho do Azevedo (2010), desenvolvido em Minas Gerais, conseguiu indicar que a ema atua como eficiente dispersor de sementes dependendo da espécie de planta; seu hábito de ir andando e forrageando em grandes áreas (Davies, 2002) e sua capacidade de engolir grandes frutos (Renison *et al.* 2010) aumentam seu papel na dispersão de sementes e restauração de habitats. Estudos com outras Ratitas, do mesmo grupo que as emas (*Rhea americana*), já mostraram que estes animais, considerados “aves terrestres gigantes” tem um importante papel funcional na dinâmica e distribuição das sementes. Como outro exemplo, Stocker

e Irvine (1983) conseguiram observar e registrar durante o período de dois anos, que as aves Casuar (*Casuarius casuarius*) espécie do mesmo grupo (ratitas) são as únicas frugívoras existentes grandes o suficiente para dispersar efetivamente muitas espécies de plantas encontradas nas florestas tropicais australianas. Nas fezes do animal foram encontradas 78 espécies de diásporos de plantas, o que mostra a eficácia no papel funcional como dispersor de sementes. Outro estudo na savana africana, observou que, com a presença dos frugívoros como os avestruzes (*Struthio camelus*), as sementes das diferentes espécies de acácia africana (*Acacia* spp.) estavam sendo dispersas e depositadas em ambientes abertos em condições físicas mais ideais para sobrevivência e desenvolvimento do embrião do que. Quando comparado à ausência dos frugívoros, as sementes caíam em ambientes sem as condições ideais para o desenvolvimento das espécies de plantas (Miller, 1996). Para mais, as emas (*Rhea americana*) e os emus (*Dromaius novaehollandiae*) podem desempenhar um papel semelhante dos avestruzes (*Struthio camelus*) na dispersão de uma ampla variedade de diásporos (Calviño-Cancela *et al.* 2006). Deste modo, o grupo das ratitas pode desempenhar o importante papel funcional como dispersores eficazes de sementes em ambientes naturais, contribuindo com a dinâmica das comunidades ecológicas. De qualquer forma, existem poucos trabalhos que investigaram o papel das Ratitas, como as emas, na dispersão e germinação de sementes. Grandes vertebrados em sistemas neotropicais, como ungulados, primatas, tucanos e as emas, são capazes de dispersar sementes grandes e tendem a dispersar sementes por longas distâncias, o que os torna influentes na manutenção da diversidade do ecossistema e na dinâmica da paisagem natural (Levey, 1987; Vidal *et al.* 2013; Andresen *et al.* 2018; Fuzessy *et al.* 2018).

Sua influência na dispersão de sementes pode afetar a diversidade de espécies, as taxas de migração, a dinâmica de metapopulações e o fluxo gênico. Desta forma, o presente estudo busca pesquisar e compreender a ecologia da *Rhea americana* para a conservação e preservação dos ecossistemas onde estão presentes.

Para isso esse trabalho se divide em dois capítulos. O capítulo 1 é sobre a dieta e o papel da Ema (*Rhea americana*) no Pantanal. O capítulo 1 oferece insights valiosos sobre a dieta da Ema durante a estação seca no Pantanal, uma região de extrema importância ecológica e de biodiversidade. Compreender o que essa espécie consome é fundamental para entender suas necessidades nutricionais e sua importância nas

interações ecológicas e serviços ecossistêmicos. A ema inclui grande variedade e quantidade de frutos na dieta. Com base nessas informações no capítulo 2 investigamos o papel funcional da ema como dispersora ou predadora de sementes de plantas nativas do Cerrado. Encontramos papéis variáveis para as emas, de acordo com a espécie consumida, e um potencial de dispersão de sementes em distâncias bastante longas, dado o longo tempo de passagem dos itens ingeridos no aparelho digestivo. Investigar o papel funcional da ema com as sementes parece essencial para compreender sua contribuição para as relações ecológicas que afetam a manutenção da diversidade de plantas no Cerrado.

2. Referências

- Aerts, R., Maes, W., November, E., Negussie, A., Hermy, M., & Muys, B. (2006). Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp. *cuspidata* seeds. *Forest Ecology and Management*, 230(1-3), 23-31.
- Aerts, Raf *et al.* Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp. *cuspidata* seeds. *Forest Ecology and Management*, v. 230, n. 1-3, p. 23-31, 2006.
- Alcántara, J. M., Rey, P. J., Valera, F., & Sánchez-Lafuente, A. M. (2000). Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology*, 81(7), 1937-1950.
- Andresen, E., Arroyo-Rodríguez, V., & Ramos-Robles, M. (2018). Primate seed dispersal: old and new challenges. *International Journal of Primatology*, 39, 443-465.
- Atienza, J. C., Illera, J. C., Richard, E., Julia, J. P., Aceñolaza, P. G., Zapata, S. C., ... & Bertolero, A. (1995). Doñana. *Acta vertebrata*. vol 22 (1/2).
- Bagchi, R., Swamy, V., Latorre Farfan, J. P., Terborgh, J., Vela, C. I., Pitman, N. C., & Sanchez, W. G. (2018). Defaunation increases the spatial clustering of lowland Western Amazonian tree communities. *Journal of Ecology*, 106(4), 1470-1482.
- Bilenca, D. (2004). Identificación de áreas valiosas de pastizal en las pampas y campos de Argentina, Uruguay y sur de Brasil (AVPs). Fundación Vida Silvestre Argentina.
- Bleher, B., & Böhning-Gaese, K. (2001). Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia*, 129, 385-394.
- Brandt, L. F. S., & Neto, A. S. (1999). Introdução e monitoramento de *Rhea americana* na EPDA Galheiro (Perdizes, MG). *CEMIG, Belo Horizonte*.
- Calviño-Cancela, M., R. Dunn, R., Van Etten, E. J., & B. Lamont, B. (2006). Emus as non-standard seed dispersers and their potential for long-distance dispersal. *Ecography*, 29(4), 632-640.
- Christianini, A. V., & Martins, M. M. (2015). 1.2. Frugivoria e dispersão de sementes. *Sementes Florestais Tropicais: da ecologia à produção*, 81-101.
- Comparatore, V., & Yagueddú, C. (2007). Diet of the Greater Rhea (*Rhea americana*) in an agroecosystem of the Flooding Pampa, Argentina. *Ornitologia Neotropical*, 18(2), 187-194.

- Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations*, 298(312).
- Da Silva, J. M. C., & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature*, 404(6773), 72-74.
- Da Silva, J. M. C., & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature*, 404(6773), 72-74.
- Damasceno Júnior, G. A., Simões, M. G., Trevelin, C. C., Manoel, P. S., Guimarães, E., Freitas, A. C. D., ... & Niero, I. R. D. A. (2014). Pantanal: fauna, flora e paisagens.
- Dani, S. (1993). A ema (*Rhea americana*): biologia, manejo e conservação. Fundação Acangaú. Belo Horizonte: Q21 Fundação Acangaú. 136 p..
- De Azevedo, C. S. D., & Young, R. J. (2006). Behavioural responses of captive-born greater rheas *Rhea americana* Linnaeus (Rheiformes, Rheidae) submitted to antipredator training. *Revista Brasileira de Zoologia*, 23, 186-193.
- De Azevedo, C. S., da Silva, M. C., Teixeira, T. P., Young, R. J., Garcia, Q. S., & Rodrigues, M. (2013). Effect of passage through the gut of Greater Rheas on the germination of seeds of plants of cerrado and caatinga grasslands. *Emu*, 113(2), 177-182.
- De Azevedo, C. S., da Silva, M. C., Teixeira, T. P., Young, R. J., Garcia, Q. S., & Rodrigues, M. (2013). Effect of passage through the gut of Greater Rheas on the germination of seeds of plants of cerrado and caatinga grasslands. *Emu*, 113(2), 177-182.
- Dde Azevedo, C., Tinoco, H., Ferraz, J., & Young, R. J. (2006). The fishing rhea: a new food item in the diet of wild greater rheas (*Rhea americana*, Rheidae, Aves). *Revista Brasileira de Ornitologia-Brazilian Journal of Ornithology*, 14(3).
- Del Hoyo, J., Elliot, A., & Sargatal, J. (1992). Order Struthioniformes. *Handbook of the Birds of the World. Lynx Edicions, Barcelona*, 1, 76-89.
- et alDirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J., & Collen, B. (2014). Defaunation in the Anthropocene. *science*, 345(6195), 401-406.
- Durigan, G., Bernacci, L. C., Franco, G. A. D. C., Arbocz, G. D. F., Metzger, J. P., & Catharino, E. L. M. (2008). Estádio sucessional e fatores geográficos como determinantes da similaridade florística entre comunidades florestais no Planalto Atlântico, Estado de São Paulo, Brasil. *Acta Botanica Brasilica*, 22, 51-62.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*, 34(1), 487-515.

- Figueira, J. E. C., Cintra, R., Viana, L. R., & Yamashita, C. (2006). Spatial and temporal patterns of bird species diversity in the Pantanal of Mato Grosso, Brazil: implications for conservation. *Brazilian Journal of Biology*, 66, 393-404.
- Fricke, E. C., Bender, J., Rehm, E. M., & Rogers, H. S. (2019). Functional outcomes of mutualistic network interactions: a community-scale study of frugivore gut passage on germination. *Journal of Ecology*, 107(2), 757-767.
- Fuzessy, L. F., Janson, C., & Silveira, F. A. (2018). Effects of seed size and frugivory degree on dispersal by Neotropical frugivores. *Acta Oecologica*, 93, 41-47.
- Gasperin, G., & Pizo, M. A. (2012). Passage time of seeds through the guts of frugivorous birds, a first assessment in Brazil. *Revista Brasileira de Ornitologia*, 20(1), 48-51.
- Giannoni, M. L. (1996). *Emas & avestruzes: uma alternativa para o produtor rural*. Funep.
- Godínez-Alvarez, H., Ríos-Casanova, L., & Peco, B. (2020). Are large frugivorous birds better seed dispersers than medium-and small-sized ones? Effect of body mass on seed dispersal effectiveness. *Ecology and Evolution*, 10(12), 6136-6143.
- Guimarães Jr, P. R., Galetti, M., & Jordano, P. (2008). Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PloS one*, 3(3), e1745.
- Gusseklou, S. W. S. (2000). *The evolution of the palaeognathous birds*. Leiden University.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... & Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advances*, 1(2), e1500052.
- Haddad, N. M., Brudvig, L., Clobert, J., Davies, K., Gonzalez, A., Holt, R., & TOWNSHEND, J. (2015). Fragmentação de Habitat e seu Impacto Duradouro nos Ecossistemas da Terra. *Science Advances*, 1(2), 8-17.
- Herrera, C. M. (2002). Seed dispersal by vertebrates. Plant–animal interactions: an evolutionary approach, 185-208.
- Howe, H. F., & Miriti, M. N. (2000). No question: seed dispersal matters. *Trends in ecology & evolution*, 15(11), 434-436.
- Inc., Philadelphia, USA.
- IUCN Red List of Threatened species. Versão 2015.4 Disponível em <http://iucnredlist.org>. Acesso em: julho 2022, 2016.

- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104(940), 501-528.
- Jordano, P. (2014). Fruits and frugivory. *Seeds: the ecology of regeneration in plant communities*, 3, 18-61.
- Jordano, P. (2014). Fruits and frugivory. *Seeds: the ecology of regeneration in plant communities*, 3, 18-61.
- Laurance, W. F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C. J., Sloan, S. P., ... & Scott McGraw, W. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489(7415), 290-294.
- Laurance, W. F., Pérez-Salicrup, D., Delamônica, P., Fearnside, P. M., D'Angelo, S., Jerozolinski, A., ... & Lovejoy, T. E. (2001). Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology*, 82(1), 105-116.
- De Azevedo, C. S. (2010). Ecologia, comportamento e manejo de emas (*Rhea americana*, Rheidae, Aves).
- Levey, D. J. (1986). Methods of seed processing by birds and seed deposition patterns. *Frugivores and seed dispersal*, 147-158.
- Levine, J. M., & Murrell, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 549-574.
- Herrera, C. M. (1984). Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology*, 65(2), 609-617.
- Lima, D., Lima, W., Rodrigues, M., Abreu, L., & Barbosa, Y. G. (2014). Corpo estranho esofágico em ema (*Rhea americana*). *Enciclopédia Biosfera*, 10(19).
- MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, 53(2), 330-342.
- Machado, E. L. M., & Oliveira-Filho, A. T. D. (2010). Spatial patterns of tree community dynamics are detectable in a small (4 ha) and disturbed fragment of the Brazilian Atlantic forest. *Acta Botanica Brasilica*, 24, 250-261.
- Machado, E. L. M., Oliveira-Filho, A. T. D., Carvalho, W. A. C., Souza, J. S., Borém, R. A. T., & Botezelli, L. (2004). Análise comparativa da estrutura e flora do compartimento arbóreo-arbustivo de um remanescente florestal na fazenda Beira Lago, Lavras, MG. *Revista Árvore*, 28, 499-516.

- Miller, B., Biggins, D., Hanebury, L., & Vargas, A. (1994). Reintroduction of the black-footed ferret (*Mustela nigripes*). In *Creative conservation: interactive management of wild and captive animals* (pp. 455-464). Dordrecht: Springer Netherlands.
- Miller, M. F. (1996). Dispersal of Acacia seeds by ungulates and ostriches in an African savanna. *Journal of Tropical Ecology*, 12(3), 345-356.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853-858.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853-858.
- Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in ecology & evolution*, 15(7), 278-285.
- Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in ecology & evolution*, 23(11), 638-647.
- Noble, J. C. (1991). On ratites and their interactions with plants. *Revista Chilena de Historia Natural*, 64(1), 85-118.
- Pakeman. (2001). Plant migration rates and seed dispersal mechanisms. *Journal of biogeography*, 28(6), 795-800.
- Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P., Fernandez-Manjarrés, J. F., ... & Walpole, M. (2010). Scenarios for global biodiversity in the 21st century. *Science*, 330(6010), 1496-1501.
- Pratt, T. K., & Stiles, E. W. (1985). The influence of fruit size and structure on composition of frugivore assemblages in New Guinea. *Biotropica*, 314-321.
- Primack, R. B., & Miao, S. L. (1992). Dispersal can limit local plant distribution. *Conservation Biology*, 6(4), 513-519.
- Rausch, L. L., Gibbs, H. K., Schelly, I., Brandão Jr, A., Morton, D. C., Filho, A. C., ... & Meyer, D. (2019). Soy expansion in Brazil's Cerrado. *Conservation letters*, 12(6), e12671.
- Renison, D., Valladares, G., & Martella, M. B. (2010). The effect of passage through the gut of the Greater Rhea (*Rhea americana*) on germination of tree seeds: implications for forest restoration. *Emu-Austral Ornithology*, 110(2), 125-131.

- Ribeiro, E. S., Souza, R. S., Moreira, E. L., Pasa, M. C., & de Souza, R. A. T. M. (2013). Contribuição das plantas frutíferas do cerrado na dieta das aves e a importância das aves no processo de dispersão de sementes. *Biodiversidade*, 12(1).
- Rogers, H. S., Donoso, I., Traveset, A., & Fricke, E. C. (2021). Cascading impacts of seed disperser loss on plant communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 52, 641-666.
- Schauensee, R.M. (1982). A Guide to the Birds of South America. Inter Collegiate PressInc., Philadelphia, USA.
- Schauensee, R.M. (1982). A Guide to the Birds of South America. Inter Collegiate Press
- Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: a conceptual review. *New phytologist*, 188(2), 333-353.
- Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., & Nathan, R. (2009). Long-distance seed dispersal. *Annual Plant Reviews Volume 38: Fruit Development and Seed Dispersal*, 38, 204-237.
- Sekercioglu, Çagan H.; Wenny, Daniel G.; Whelan, Christopher J., Why Birds Matter: Avian Ecological Function and Ecosystem Services, [s.l.]: University of Chicago Press. Pag 49-72, 2016.
- Short, J., Bradshaw, S. D., Giles, J., Prince, R. I. T., & Wilson, G. R. (1992). Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia—a review. *Biological conservation*, 62(3), 189-204.
- Sick H. (1997). Ornitologia Brasileira. Editora Nova Fronteira: Rio de Janeiro, Rio de Janeiro, Brazil.
- Silva, J. D. (1995). Birds of the cerrado region, South America. *Steenstrupia*, 21(1), 69-92.
- Skadhauge, E., Dawson, T.J., Prys-Jones, R., Warüi, C.N. The role of the kidney and gut in osmoregulation. (1996) In: Deeming, D.C. (Ed.), Improving our understanding of ratites in a farming environment. Ratite Conference, Oxfordshire, UK, pp. 115–122..
- Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., ... & Schupp, E. W. (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants*, 11(4), plz016.

- Stevens, C. E., & Hume, I. D. (2004). *Comparative physiology of the vertebrate digestive system*. Cambridge University Press.
- Stocker, G. C., & Irvine, A. K. (1983). Seed dispersal by cassowaries (*Casuarius casuarius*) in North Queensland's rainforests. *Biotropica*, 170-176.
- Strassburg, B. B., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., ... & Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, 1(4), 0099.
- Strassburg, B. B., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., ... & Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, 1(4), 0099.
- Tabarelli, M., Cardoso da Silva, J. M., & Gascon, C. (2004). Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity & Conservation*, 13, 1419-1425.
- Traveset, A. (1998). Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant ecology, evolution and systematics*, 1(2), 151-190.
- Traveset, A., & Verdú, M. (2002). 22 A meta-analysis of the effect of gut treatment on seed germination. In *Seed dispersal and frugivory: Ecology, evolution, and conservation* (pp. 339-350). New York: CABI Pub.
- Vidal, M. M., Pires, M. M., & Guimaraes Jr, P. R. (2013). Large vertebrates as the missing components of seed-dispersal networks. *Biological Conservation*, 163, 42-48.
- Viglizzo, E. F., Frank, F. C., Carreño, L. V., Jobbagy, E. G., Pereyra, H., Clatt, J., ... & Ricard, M. F. (2011). Ecological and environmental footprint of 50 years of agricultural expansion in Argentina. *Global change biology*, 17(2), 959-973.
- Westcott, D. A., Setter, M., Bradford, M. G., McKeown, A., & Setter, S. (2008). Cassowary dispersal of the invasive pond apple in a tropical rainforest: the contribution of subordinate dispersal modes in invasion. *Diversity and Distributions*, 14(2), 432-439.
- Wheelwright, N. T. (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology*, 66(3), 808-818.
- Williams, P. A., & Karl, B. J. (1996). Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand journal of ecology*, 127-145.

- Willson, M. F., & Traveset, A. (2000). The ecology of seed dispersal. In *Seeds: the ecology of regeneration in plant communities* (pp. 85-110). Wallingford UK: CABI.
- Worthington, A. H. (1989). Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*. *Oecologia*, 80, 381-389.
- Wright, M. W., & Bowmaker, J. K. (2001). Retinal photoreceptors of paleognathous birds: the ostrich (*Struthio camelus*) and rhea (*Rhea americana*). *Vision Research*, 41(1), 1-12.

3. Capítulo 1

Dry Season Diet of the Greater Rhea (*Rhea Ameriana*) in the Pantanal, western Brazil: A fecal-based approach

Cauê Lazareth Balassa Jacques¹, Beatriz Pereira Peixoto² e Alexander Vicente Christianini³

¹ Programa de Pós-graduação em Ecologia e Recursos Naturais - UFSCar-Universidade Federal de São Carlos, Rod. Washington Luís, s/n – Monjolinho, 13165-905; São Carlos – SP, Brazil

²Bacharelado em Ciências Biológicas, Universidade Federal de São Carlos, Campus Sorocaba, Rod. João Leme dos Santos, Km 110,, 18052-780, Sorocaba – SP, Brazil

³Departamento de Ciências Ambientais UFSCar - Universidade Federal de São Carlos, Sorocaba, SP, Rod. João Leme dos Santos, Km 110,, 18052-780, Sorocaba – SP, Brazil

Summary:

The Greater Rhea (*Rhea americana*) is the largest extant bird in South America (32kg - 35kg) and may potentially play a significant role in interactions with plants. However, little is known about its diet in the wild. We investigated the Greater Rhea's diet in the world's largest wetland, the Pantanal in western Brazil, during the dry season (April-July). We collected 61 fecal samples (ranging from 1.9 g to 96.7 g dry weight each) which were sorted in the laboratory. The items were classified and their dry biomass measured. The Greater Rhea's diet was composed of a variety of foods, especially leaves, found in all samples (1.97 g to 62.5 g per sample), followed by fruits/seeds (0g to 47.1 g), invertebrates (0g to 0.06 g), and vertebrates (0g to 0.3 g). We recorded fruits/seeds from 32 species/morphospecies of plants. Common species were from Leguminosae and plants with fleshy fruits, such as *Psidium* sp. and *Ximenea americana*. Large seeds from palms,

such as *Attalea phalerata*, *Acrocomia aculeata*, and *Copernicia alba*, were also commonly found. Greater Rheas exhibited a diet dominated by plant material (leaves, fruits, and seeds), with occasional presence of animal prey, therefore, a folivore-frugivore based diet. Their robust body and wide gape width enable them to ingest large-sized fruits. The presence of many apparently intact seeds in the feces suggests the potential role of the Greater Rhea in seed dispersal, likely contributing to gene flow among plant populations in the Pantanal. The decline of Greater Rhea populations throughout their range may affect long-distance plant dispersal, given their ability to carry seeds over long distances.

Keywords: defaunation; frugivory; herbivory seed dispersal; palms.

3.1 Introduction

The Greater Rhea, *Rhea americana* (Rheiformes, Rheidae), is the largest extant bird in South America, found in grasslands and savannas in Brazil, Argentina, Bolivia, Paraguay, and Uruguay (Schauensee, 1982). Males and females can reach weights of 35 kg and 32 kg, and heights of 170 cm and 134 cm, respectively (Sick, 1997). The Greater Rhea has a very wide gape width (54.3 mm, Mariana L. Campgnolli, unpublished data), enabling it to swallow large items that smaller birds could not (Wheelwright 1985).

Little is known about the Greater Rhea's diet in the wild. Most of the available information on its diet comes from opportunistic anecdotal observations (Sick 1997; Azevedo *et al.*, 2006), with few studies systematically investigating the diet (Martella *et al.*, 1996; Comparatore and Yagueddú, 2007; Puig *et al.*, 2011; Comparatore and Yagueddú, 2016). Available data suggest a diet consisting of fruits, seeds, leaves, insects, and small vertebrates (Martella *et al.*, 1996; Sick 1997; Azevedo *et al.*, 2006). Some studies mention a diet more focused on dicotyledonous leaves (mainly legumes) when food availability is abundant and diversified (Comparatore and Yagueddú, 2007). The Greater Rhea may also opportunistically consume other types of food, such as small vertebrates (Azevedo, 2006; Comparatore and Yagueddú, 2016). Rheas also ingest stones and hard items probably to aid in food grinding in their very large gizzards (Sick, 1997). Rheas do not have a crop, but they have a large cecum that aids in food digestion (Angel, 1996). Due to their large body size, *R. americana* likely plays an important role in maintaining ecosystem services such as long-distance seed dispersal for a variety of plant species, likely promoting gene flow at further distances than smaller bird species (Azevedo 2013; Valladares & Martella, 2010; Campos *et al.*, 2020).

The Greater Rhea has unfortunately experienced a significant population decline in recent years. It is currently classified as near threatened by the International Union for Conservation of Nature (IUCN, 2016). Hunting, extensive uncontrolled wildfires, habitat loss due to agricultural activities, as well as the destruction of eggs by agricultural machinery (Dani, 1993; Giannoni, 1996) all contribute to the decrease in the species' populations. The implications of defaunation, the rapid and drastic decline of animal species in natural ecosystems, have not been fully understood yet. Some studies indicate that population declines of frugivorous animals can negatively impact seed dispersal,

causing changes in plant regeneration and vegetation diversity (Dirzo 2010; Wilkie *et al.*, 2011; Effiom *et al.*, 2013; Gutiérrez-Granados; Harrison *et al.*, 2013). The extinction of fauna species with large mass may have more significant impacts for plants with larger fruits and seeds, as they depend on larger animals to disperse their seeds (Chen and Moles, 2015).

The Pantanal, located in the center of South America, spans an area of 150,355 km² across Brazil, Paraguay, and Bolivia. It is a seasonally flooded plain, with the main water source being the Paraguay River and its tributaries (Alho, *et al.*, 2019). Comprising approximately 2,000 plant species, the Pantanal exhibits strong influences from neighboring vegetation domains: the Amazon Rainforest to the north, the Cerrado to the east, the Atlantic Forest to the central-south, and the Chaco of Bolivia and Paraguay to the west (Alho, 2005; Pott *et al.*, 2011a). The Pantanal included seasonally flooded grasslands, savannas (Cerrado), and forested environments (patches of forest, ridges, riparian forests, and cerradões) (Pott and Adámoli 1999, Silva *et al.* 2000; Alho, *et al.*, 2019). In the Pantanal, bird community dynamics are closely related to environmental heterogeneity and flooding events (Figueira *et al.*, 2006). The Pantanal plain serves as a wintering region for various bird species from different regions of the Northern and Southern Hemispheres, as well as from the northern region of South America, Bolivia, and Paraguay (Nunes and Tomas, 2004), being considered important habitat for Brazilian birds (Nunes, *et al.*, 2006). The bird fauna of the Pantanal comprises 580 species, among which considerable populations of Greater Rheas (*Rhea americana*) can still be found (Hasenclever *et al.*, 2004; Nunes, 2011). Approximately bird species facing risks of extinction at global and regional levels in the Pantanal are the Hyacinth Macaw (*Anodorhynchus hyacinthinus*) and the Greater Rheas (*Rhea americana*), both presenting reasonable wealthy populations (Nunes *et al.*, 2008).

Despite previous research efforts on Greater Rheas (Sick, 1997; Azevedo, 2006; Navarro and Martella, 2009; Azevedo, 2010; Comparatore and Yagueddú, 2007 and 2016; Bazzano), little is known about their ecological significance in natural ecosystems (Nunes *et al.*, 2008). This is especially true for the Pantanal region, characterized by annual cycles of flooding and a severe dry season, leading to variations in food resource availability. We investigate the diet of *R. americana* with the aim of describing its diet and assessing its potential role in interactions with native plant species.

3.2 Materials and Methods

The study was conducted at Fazenda Rio Negro (FRN hereafter) (19°34'30.60"S; 56°14'44.79"W), located in the Nhecolandia region, Municipality of Aquidauana, MS, Western Brazil. The farm is composed of a mosaic of different vegetation types, representative of the main phytophysiognomies of the Pantanal (according to Prance and Schaller, 1982), including semideciduous forests, grasslands, and savannas (Cerrado). The region's climate is classified a tropical sub-humid, with average temperatures ranging from 20°C to 27°C (Tarifa, 1984). The annual rainfall ranges between 1000 and 1400 mm, with 80% of the rain concentrated in the summer (Allem and Valls, 1987). In FRN, it is possible to observe distinct groups of Rheas (*Rhea americana*), and at least one group regularly visits the surroundings of the farm's headquarters (AV Christianini, personal observation).

To describe the diet of the Greater rheas, we opportunistically collected 61 fresh feces between April and July 2002 during the dry season in the region. During this period, rheas expand their habitat use to areas previously covered by water during the flooding season, including grasslands near the headquarters of FRN (AV Christianini, personal observation). The feces were recognizable by their large size, presence of uric acid, and abundant plant material. Once collected, the samples were dried in an oven (approximately 60°C) for 48 hours and stored in paper bags at room temperature. The samples were later sorted in the laboratory, and their contents were separated into animal and plant components with the aid of a stereomicroscope. We classified the contents in leaves, seeds, vertebrates, and invertebrates present in the 61 fecal samples of *Rhea americana* and quantified the mass of each item separately using a precision balance (Shimadzu). The quantification of items was performed based on the frequency of occurrence and the percentage of mass the item represents per sample (Herrera, 1998). We counted the seeds in each sample and identified them to the lowest possible taxonomic level based on a reference collection and specialized literature (Pott and Pott, 2007; Kuhlmann, 2012 and 2018). To test if Greater rheas included more leaves or fruits in diet we compared the mass of leaves and seeds found in sample with a Kruskal-Wallis test, because data was not normaly distributed. Due to the low record of invertebrates and vertebrates in the feces, their comparisons with other food items were only qualitative.

3.3 Results

In the fecal samples analyzed ($n = 61$), we observed a predominance of plant material (100 % of the samples), mainly leaves, with a notable presence of grasses that were not identified at species level (Table 1). We were able to identify the consumption of various fruit species through the seeds found in the feces, as well as the presence of invertebrates and vertebrates (Table 1). The mass of plant material (leaves) was higher than the seeds found in the Rheas' feces (Kruskal Wallis: $H = 13$; $GL = 1$; $P = 0.0003$). Leaves presented an average of 11 ± 10 g (mean $\pm$ standard deviation) per fecal sample, while seeds (8 ± 10 g), and arthropods (0.003 ± 0.004 g) attained lower values. Seeds were found in almost all feces (95% of the samples), with a high variation in the quantity of seeds from different plant species ($CV = 190\%$). Invertebrates accounted for $16 \pm 0.37\%$ present in feces, and vertebrates had only one record in all fecal samples (1%) (Figure 1). In total, seeds from 32 species/morphospecies of plants were observed. *Psidium* (Myrtaceae) contributed the most to the number of seeds found (a total of 141 seeds), distributed in 11 feces (18%) out of the 61 fecal samples analyzed. Seeds of Leguminosae sp. 1 had the highest distribution among all the fecal samples analyzed with 24.5%. On the other hand, plants such as *Psycotria* sp., Myrtaceae, Meliaceae, Lauraceae, Leguminosae sp. 2, and unidentified species were found in only one sample each (1%) (Table 1).

In addition to plants, there was ingestion of some invertebrates, always in small quantities, such as Coleoptera ($n=1$ sample), Hemiptera ($n=1$), Hymenoptera ($n=5$), and Lepidoptera ($n=1$). Traces of vertebrates (fish scales) were observed in one of the analyzed fecal samples (Table 1). Thus, items of animal-origin contributed only a very small fraction of the biomass ingested by the Greater Rheas (Table 1).

Table 1: Total number, frequency, and mass of seeds observed in the feces of *Rhea americana*. Number, percentage, mean, and standard deviation of each seed species in the feces (n=61). For plant species recorded in three or more samples, the mean and standard deviation of the numbers are presented, otherwise absolute values are presented.

Item identified	Total number of items in the feces (n=61)	Frequency of each item present in all feces (n=61) (%)	Mean and standard deviation quantity of item distributed in feces (n =61) (%)
MATERIAL		61 (100)	-
VEGETAL	-		
PLANTAE			
<i>Psidium</i> sp.	141	11 (18)	13 ± 16
<i>Copernicia alba</i>	116	12 (19)	10 ± 8
<i>Ximenea americana</i>	20	2 (3)	19; 1
<i>Malpighia emarginata</i>	48	9 (15.)	5 ± 7
<i>Acrocomia aculeata</i>	18	14 (23.)	2 ± 1
<i>Bactris setosa</i>	14	9 (15.)	1 ± 1
<i>Licania</i> sp.	11	3 (5.)	5 ± 6
<i>Attalea phalerata</i>	8	4 (6)	2 ± 1
<i>Guazuma ulmifolia</i>	6	4 (6)	1 ± 0.6
<i>Miconia</i> sp.	5	3 (5)	1 ± 0.6
<i>Vitex cymosa</i>	3	3 (5)	1 ± 0
<i>Psycotria</i> sp.	2	1 (1)	2
<i>Rheedia gardneriana</i>	2	2 (3)	1; 1
	It was not possible		
<i>Ficus</i> sp.	to count	6 (10)	13 ± 20
Rutaceae	15	5 (8)	3 ± 1
Rubiaceae	14	7 (11)	2 ± 1
Annonaceae	11	5 (8)	2 ± 2
Myrtaceae	2	1 (1)	2
Meliaceae	1	1 (1)	1

Lauraceae	1	1 (1)	1
Sapotaceae	Broken seeds		-
Leguminosae sp. 3	3	2 (3)	1 ± 1
Leguminosae sp. 1	55	15 (24)	3 ± 4
Leguminosae sp. 2	2	1 (1)	2
Graminea sp. 1	1	1 (1)	1
Graminea sp. 2	11	3 (5)	3 ± 4
Unidentified 1	4	4 (6)	1 ± 0
Unidentified 2	1	1 (1)	1
Unidentified 3	1	1 (1)	1
Unidentifies 4	2	1 (1)	1
Unidentified 5	2	1 (1)	2
Unidentified 6	2	2 (3)	1 ± 0
INVERTEBRATES			
Coleoptera	1	1 (1)	1
Hemiptera	1	1 (1)	1
Hymenoptera	5	5 (8)	1
Lepidoptera		1 (1)	
(caterpillar)	1		1
VERTEBRATES			
Fish scale	1	1 (1)	1
Total	530	-	-

3.4 Discussion

We found a predominance of plant material in the diet of Greater Rheas, either in the form of leaves or fruits/seeds. Invertebrates and vertebrates seem to be consumed opportunistically. Although *R. americana* has been classified as omnivorous (Azevedo, 2010; Masat *et al.*, 2011), our study suggests that Greater Rheas has a predominantly folivore-frugivore diet, at least during the dry season in the Pantanal. These results support the findings of Azevedo (2006); Pereira *et al.* (2003) and Moojen *et al.* (1941)

(Table 2), which found that the diet of *R. americana* consisted mainly of plant material, and items of animal origin were only occasionally found, as observed in our study.

Table 2: Frequency of items in the ratite diet based on different studies available. Other items include stones and small rocks.

Authors	Ratite	plant leaf%	Seeds%	Vertebrates%	Invertebrates%	items %
This study	<i>Rhea americana</i>	100	96	1.63	3.24	absence
Moojen <i>et al.</i> 1941	<i>Rhea americana</i>	presence	absence	absence	presence	absence
Martella, 1965	<i>Rhea americana</i>	90	8.9	0	0.1	0.1
Pereira, 2003	<i>Rhea americana</i>	presence	absence	absence	presence	absence
Azevedo, 2006	<i>Rhea americana</i>	60.3	48.2	4.72	17	13.7
Puig <i>et al.</i> , 2013	<i>Rhea pennata</i>	93.61	6.12	0	0.06	0.2

The consumption of certain food may be associated with the availability and abundance of resources in the environment. Depending on the seasons, *R. americana* appears to be more selective in including items in its diet (Comparatore and Yagueddú, 2016). It is likely that seasonal variations in the availability of fruits from certain species may explain the predominance of fruits from some plant species in the feces during the study. Additionally, it was observed that Greater Rheas also consume invertebrates

(Coleoptera, Hemiptera, Hymenoptera, and Lepidoptera) and vertebrates, such as fish scales found in the feces (also see Azevedo, 2006), perhaps taking advantage of dead fish or fish present in shallow waters as natural pools shrink and recede during the dry season in the region. Other studies on ratites such as *R. pennata* (Bonino *et al.*, 1986; Cajal, 1988; Paoletti and Puig, 2007; Echaccaya *et al.*, 2017; Marinero *et al.*, 2017), reveal a selective feeding behavior, favoring leaves, but also incorporating a variety of other foods such as fruits and seeds depending on their availability in the habitat.

The large number of seeds found in the feces of *R. americana* demonstrates the bird's ability to ingest a large quantity of fruits/seeds, including those of large size, such as palm fruits. Although larger frugivorous birds in a community are often less abundant and make less frequent visits to fruiting plants compared to smaller frugivorous birds, larger birds also disperse a substantial number of smaller seeds (Chen & Moles, 2015), compensating for their lower visitation frequency with a greater volume of fruit intake per visit (Campagnoli & Christianini, 2021). Seed dispersal is influenced by various factors, with the size of the agents interacting with the plants being a crucial element (Carvalho *et al.*, 2023). Plants that produce large diaspores, such as larger fruits, have their ingestion by smaller birds restricted due to narrow gape width of their beaks. Thus, it is likely that Rheas can perform seed dispersal of some plants not attended by smaller frugivorous birds (e.g. large seeded palms).

In relation to the frequency of plant species found in the feces (Table 1), the predominance of legumes may be associated with the high nitrogen (N) content in the seeds, a vital element for the morphological and physiological formation of animals (Matsson, 1980). Additionally, *R. americana* reproduces in the dry season (Pinto, 1964) and likely consumes more protein-rich items as a source of nutritional reserves to account for the physiological stress of egg production and nesting (Robbins, 1981; Camparatore and Yagueddú, 2007). Other carbohydrate-rich fruit species, such as *Psidium* sp. (*Psidium guineense*: $4.74 \pm 0.259\text{g}/100\text{g}$ carbohydrate content in the fruit; Caldeira *et al.*, 2004), also contribute to the diet of *R. americana* in smaller proportions. Studies have revealed that young *R. americana* consume more items of animal origin (Azevedo, 2006). The differences in the diet of young and adult individuals may be related to the energy and protein needs of the chicks for proper development. Thus, some feces of smaller mass (for example, samples of 15.13 g and 18.35 g obtained by us) containing legume seeds

may be associated with young individuals requiring more protein for morphological development, while larger feces (38.54 g and 44.35 g) are likely from adults associated with the reproductive period when there is also a higher demand for protein.

Although there is currently no study on seed dispersal by *Rhea americana* including plants from the Pantanal, its diet can be considered as an indicative of seed dispersal effectiveness, as whole seeds of various species were found and are therefore likely viable for germination (De Azevedo et al., 2013). Moreover, seeds of different sizes were found in the feces, revealing the ability of the Greater Rheas to consume seeds of various dimensions, for example, from palms like *Attalea phalerata* (8 – 11 cm in length; 3.5 – 5 cm in diameter and 57.1 – 91.7 g in weight; Negrelle, 2015; Lima, 2010) or *Bactris grassipes* (1.6 cm in length; 1.53 cm in width and 2.1 g in weight, unpublished data). Indeed, there are correlations between the body size of dispersers, such as Greater Rheas, and fruit size (especially diameter and mass) (Donatti *et al.*, 2011). Furthermore, *R. americana*, due to its robust body, allows for a prolonged retention of seeds in its digestive tract (61.6 ± 13.5 hours, average of eleven species (CLBJ, unpublished data, Capítulo 2)) and also because it can cover large areas (453 hectares over three months; Juan *et al.*, 2013), potentially play a crucial role as seed dispersers over longer distances. Indeed, due to their morphology, behavior, and interactions with fruits the Greater Rhea is considered functionally similar to mammals as seed dispersers (Donatti *et al.*, 2011).

The understanding of the rhea's diet in the environment reveal the potential important functional role that this species plays in natural ecosystems and the potential consequences of its absence. Therefore, further investigations about the role of the Greater Rhea in seed dispersal will likely provide valuable insights into the contribution of the species to ecological processes that sustain the dynamics of natural ecosystems.

3.5 Acknowledgments

We would like to thank the Federal University of São Carlos, SP (UFSCar), for providing facilities to develop this research. We also thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for the financial support through the PROAP-CAPES program, Financial Code 001. AVC acknowledges the support of the Neotropical Grassland Conservancy and the Rufford Foundation.

3.6 References

- Alho, C. J. R. (2005). Universidade para o Desenvolvimento do Estado e para a Região do Pantanal (UNIDERP). *The world's largest wetlands: ecology and conservation*, 203.
- Alho, C. J., Mamede, S. B., Benites, M., Andrade, B. S., & Sepúlveda, J. J. (2019). Threats to the biodiversity of the Brazilian Pantanal due to land use and occupation. *Ambiente & Sociedade*, 22, e01891.
- Allem, A. C., & Valls, J. F. M. (1987). Recursos forrageiros nativos do Pantanal Mato-grossense. (Vol. 8, p. 339). Departamento de Difusão de Tecnologia, Vol. 8, p. 339.
- Angel, C. R. (1996). A review of ratite nutrition. *Animal Feed Science and Technology*, 60(3-4), 241-246.
- Bariani, A. (2007). Propriedades bioquímicas e biológicas de proteínas de sementes de leguminosas arbóreas da Amazônia. Dissertação de Mestrado.
- Bazzo, J. C., De Freitas, D. A. F., Silva, M. L. N., Cardoso, E. L., & Santos, S. A. (2012). Aspectos geofísicos e ambientais do pantanal da Nhecolândia. *Revista de Geografia (UFPE)*, 29(1).
- Bonino, N., Bonvissuto, G., Pelliza de Sbriller, A., & Somlo, R. (1986). Hábitos alimentarios de los herbívoros en la zona central del área ecológica Sierras y Mesetas Occidentales de Patagonia.
- Britski, H. A. (1999). Peixes do Pantanal. Manual de identificação. *Brasília: Embrapa-SPI; Corumbá: Embrapa-CPAP.*, 184.
- BROWN JR, K. S. (1986). Zoogeografia da região do Pantanal Mato-grossense. In *Simposio sobre recursos naturais e socio economico do Pantanal, 1986* (pp. 137-179).
- Cajal, J. L. (1988). The Lesser Rhea in the Argentine Puna region: present situation. *Biological Conservation*, 45(2), 81-91.
- Caldeira, S. D., Hiane, P. A., Ramos, M. I. L., & Ramos Filho, M. M. (2004). Physical-chemical characterization of araçá (*Psidium guineense* SW.) and tarumã (*Vitex cymosa* Bert.) of Mato Grosso do Sul State (Brazil), vol. 22, 145-154.
- Campagnoli, M. L., and Christianini, A. V (2022). Temporal consistency in interactions among birds, ants, and plants in a neotropical savanna, *Oikos*, 1-13.

- Campos, C. M., Ramos, L., Manrique, N., Cona, M. I., Sartor, C., De Los Ríos, C., & Cappa, F. M. (2020). Filling gaps in the seed dispersal effectiveness model for *Prosopis flexuosa*: quality of seed treatment in the digestive tract of native animals. *Seed Science Research*, 30(3), 215-223.
- Chen, S. C., & Moles, A. T. (2015). A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. *Global Ecology and Biogeography*, 24(11), 1269-1280.
- Comparatore, V., & Yagueddú, C. (2007). Diet of the Greater Rhea (*Rhea americana*) in an agroecosystem of the Flooding Pampa, Argentina. *Ornitologia Neotropical*, 18(2), 187-194.
- Comparatore, V., & Yagueddú, C. (2016). Diet preference and density of the Greater Rhea (*Rhea americana*) in grasslands of the Flooding Pampa, Argentina. *Revista Brasileira de Ornitologia*, 24, 13-20.
- Da Silva, J. M. C. (1995). Avian inventory of the Cerrado region, South America: implications for biological conservation. *Bird Conservation International*, 5(2-3), 291-304.
- De Azevedo, C. S., da Silva, M. C., Teixeira, T. P., Young, R. J., Garcia, Q. S., & Rodrigues, M. (2013). Effect of passage through the gut of Greater Rheas on the germination of seeds of plants of cerrado and caatinga grasslands. *Emu*, 113(2), 177-182.
- De Azevedo, C., Tinoco, H., Ferraz, J., & Young, R. J. (2006). The fishing rhea: a new food item in the diet of wild greater rheas (*Rhea americana*, Rheidae, Aves). *Revista Brasileira de Ornitologia-Brazilian Journal of Ornithology*, 14(3).
- De Schauensee, R. M., Poole, E. L., Quinn, J. R., & Sutton, G. M. (1970). A guide to the birds of South America.
- Del Hoyo, J., A. Elliot and J. A. Sargatal (eds.) (1992) A Hand-book of the Birds of the World, v.1. Barcelona: Lynx Edi-tions. *Ecology*, 66(3), 808-818.
- Donatti, C. I., Guimarães, P. R., Galetti, M., Pizo, M. A., Marquitti, F. M., & Dirzo, R. (2011). Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology letters*, 14(8), 773-781.
- Echaccaya, M., Arana, C., & Salinas, L. (2017). Dieta del Suri, *Rhea pennata* (Orbigny, 1834) (Aves: Rheidae), en ecosistemas altoandinos de Moquegua, Perú. *Revista peruana de biología*, 24(2), 139-144.

- Effiom, E. O., Nuñez-Iturri, G., Smith, H. G., Ottosson, U., & Olsson, O. (2013). Bushmeat hunting changes regeneration of African rainforests. *Proceedings of the Royal Society B: Biological Sciences*, 280(1759), 20130246.
- Gräbin, D. M., Tomas, M. A., & Tomas, W. M. (2012). Densidade de Rhea americana em três paisagens diferentes do Pantanal da Nhecolândia, MS. *Oecologia Australis*, 16(4), 905-913.
- Gutiérrez-Granados, G., & Dirzo, R. (2010). Indirect effects of timber extraction on plant recruitment and diversity via reductions in abundance of frugivorous spider monkeys. *Journal of Tropical Ecology*, 26(1), 45-52.
- Harrison, R. D., Tan, S., Plotkin, J. B., Slik, F., Detto, M., Brenes, T., ... & Davies, S. J. (2013). Consequences of defaunation for a tropical tree community. *Ecology letters*, 16(5), 687-694.
- Hasenclever, L., Reiman, C., Mourão, G. D. M., & Campos, Z. D. S. (2004). Densidades, tamanho de grupo e reprodução de emas no Pantanal Sul. Inc., Philadelphia, USA.
- Schubart, O., Aguirre, Á. C., & Sick, H. (1965). Contribuição para o conhecimento da alimentação das aves brasileiras. *Arquivos de Zoologia*, 12, 95-249.
- IUCN, 2016. BirdLife International. The IUCN Red List of Threatened. <https://www.iucnredlist.org/> (accessed 21 january 2024).
- Jordano, P. (2000). Fruits and frugivory. In M. Fenner (Ed.), *Seeds: The ecology of regeneration in plant communities*. Wallingford, UK: CAB International, (pp. 125–166).
- Jordano, P., García, C., Godoy, J. A., & Garcia-Castaño, J. (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences*, 104(9), 3278-3282.
- Juan, E. E., Bazzano, G., Navarro, J. L., & Martella, M. B. (2013). Space use by wild Greater Rhea (*Rhea americana*) in a relict grassland of central Argentina during the non-breeding season. *El hornero*, 28(1), 01-06.
- Klink, C. A., & Machado, R. B. (2005). Conservation of the Brazilian cerrado. *Conservation biology*, 19(3), 707-713.
- Kuhlmann, M. (2018). *Frutos e sementes do Cerrado: espécies atrativas para fauna* (Vol. 2). Frutos Atrativos do Cerrado.

- Levey, D. J. (1987). Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist*, 129(4), 471-485.
- Levine, J. M., & Murrell, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 549-574.
- Lima, J. M. T. (2010). *Ecology of native oil-producing palms and their potential for biofuel production in southwestern Amazonia*. University of Florida.
- Marinero, N. V., Navarro, J. L., & Martella, M. B. (2017). Does food abundance determine the diet of the Puna Rhea (*Rhea tarapacensis*) in the Austral Puna desert in Argentina? *Emu-Austral Ornithology*, 117(2), 199-206.
- Martella, M. B., Navarro, J. L., Gonnet, J. M., & Monge, S. A. (1996). Diet of greater rheas in an agroecosystem of central Argentina. *The Journal of wildlife management*, 586-592.
- Martins, V., & Chaves, ó. M. (2020). Efeito da defaunação na diversidade e regeneração florística das florestas. *Revista Interdisciplinar de Ensino, Pesquisa e Extensão*, 8(1), 374-389.
- Masat, O. M. O., Chatellenaz, M. L., & Fontana, J. L. (2011). Dieta del Ñandú, Rhea americana (Aves: Rheidae), en en el Parque Nacional Mburucuyá, Argentina. *Brenesia*, 83-89.
- Mattson, W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual review of ecology and systematics*, 11, 119-161.
- Moojen, J., Carvalho, J., & Lopes, H. (1941). Observações sobre o conteúdo gástrico das aves brasileiras. *Memórias do Instituto Oswaldo Cruz*, 36, 405-444.
- Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in ecology & evolution*, 15(7), 278-285.
- Negrelle, R. R. B. (2015). *Attalea phalerata* Mart. ex Spreng.: aspectos botânicos, ecológicos, etnobotânicos e agronômicos. *Ciência Florestal*, 25, 1061-1066.
- Nunes, A. P., & Tomas, W. M. (2004). Análise preliminar das relações biogeográficas da avifauna do Pantanal com biomas adjacentes. *Simpósio sobre Recursos Naturais E Sócio-Econômicos Do Pantanal*, 8.
- Nunes, A. P., Silva, P. A., & Tomas, W. M. (2008). Novos registros de aves para o Pantanal, Brasil. *Revista Brasileira de Ornitologia*, 16(2), 160-164.

- Nunes, A. P.; Ticianeli, F. A. T. e Tomas, W. M. (2006). Aves ameaçadas ocorrentes no Pantanal. Série Documentos, *Embrapacpap*, 83:1-47.
- Paoletti, G., & Puig, S. (2007). Diet of the Lesser Rhea (*Pterocnemia pennata*) and availability of food in the Andean Precordillera (Mendoza, Argentina). *Emu-Austral Ornithology*, 107(1), 52-58.
- Pereira, J. A., Quintana, R. D., & Monge, S. (2003). Diets of plains vizcacha, greater rhea and cattle in Argentina. *Rangeland Ecology & Management/Journal of Range Management Archives*, 56(1), 13-20.
- Pinto, O. M. D. O. (1964). Ornitologia Brasileira: Catálogo descritivo e ilustrado das aves do Brasil. In *Ornitologia brasileira: catálogo descritivo e ilustrado das aves do Brasil* (pp. 182-182).
- Pizo, M. A., & Galetti, M. (2010). Métodos e perspectivas da frugivoria e dispersão de sementes por aves. *Ornitologia e conservação: ciência aplicada, técnicas de pesquisa e levantamento*, 493-506.
- Pizo, M. A., Donatti, C. I., Guedes, N. M. R., & Galetti, M. (2008). Conservation puzzle: Endangered hyacinth macaw depends on its nest predator for reproduction. *Biological Conservation*, 141(3), 792-796.
- Pott, A. e Adámoli, J. (1996). Unidades de vegetação do Pantanal dos Paiaguás. In: II Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal: manejo e conservação. Embrapa Pantanal, Corumbá.
- Pott, A., & Adámoli, J. (1999). Unidades de vegetação do Pantanal dos Paiaguás. Simpósio sobre Recursos Naturais e Socio-Econômicos do Pantanal, Manejo e Conservação, Corumbá, 2, 183-202.
- Pott, A., & Pott, V. J. (1994). *Plantas do Pantanal*. Brasília: *Embrapa-Spi*, 1994.
- Pott, A., Oliveira, A. K., Damasceno-Junior, G. A., & Silva, J. S. (2011). Plant diversity of the Pantanal wetland. *Brazilian Journal of Biology*, 71, 265-273.
- Prance, G. T., & Schaller, G. B. (1982). Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. *Brittonia*, 228-251.
- Puig, S., Cona, M. I., Videla, F., & Mendez, E. (2013). Diet selection by the lesser rhea (*Rhea pennata pennata*) in Payunia, Northern Patagonia (Mendoza, Argentina). *Revista de la Facultad de Ciencias Agrarias UNCuyo*, 45(1), 211-224.

- Renison, D., Valladares, G., & Martella, M. B. (2010). The effect of passage through the gut of the Greater Rhea (*Rhea americana*) on germination of tree seeds: implications for forest restoration. *Emu-Austral Ornithology*, 110(2), 125-131.
- Schupp, E. W. (1993). Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, 107, 15-29.
- Sick, H. (1997). *Ornitologia brasileira* [Brazilian ornithology]. Rio de Janeiro (Brasil): *Editora Nova Fronteira. Portuguese*.
- Silva, J.M.C. (1995^a). Avian inventory of the Cerrado region, South America: implications for biological conservation. *Bird Conservation International*, 5: 291-304.
- Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., ... & Schupp, E. W. (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants*, 11(4), plz016.
- Sparks, D. R., & Malechek, J. C. (1968). Estimating percentage dry weight in diets using a microscopic technique. *Rangeland Ecology & Management/Journal of Range Management Archives*, 21(4), 264-265.
- Strassburg, B. B., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., ... & Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, 1(4), 0099.
- Wheelwright, N. T. (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology*, 66(3), 808-818.
- Wilkie, D. S., Bennett, E. L., Peres, C. A., & Cunningham, A. A. (2011). The empty forest revisited. *Annals of the New York Academy of Sciences*, 1223(1), 120-128.

4.0 Capítulo 2

Seed predator or disperser? The role of the Greater Rhea (*Rhea americana*) in the Brazilian Cerrado

Abstract

The Greater rhea (*Rhea americana*) is the largest (32-35 kg) flightless bird that inhabits the grasslands and savannas of South America. Rheas likely play important ecological roles in these ecosystems (e.g. seed dispersal or predation) but the outcome of fruit ingestion by Rheas is largely unknown. We investigated the potential role of Greater rheas in seed dispersal using fruit feeding trials with captive animals and seed germination experiments for 11 plant species from the Brazilian savannas (Cerrado). Rheas have a long gut passage time (GPT) (mean $\pm$ SD: 61.6 $\pm$ 13.5 hours), allowing them to carry seeds to long distances. Seeds within heavier fruits and those with lipid-rich fruit pulp had shorter and longer GPT, respectively, which influences the potential distances of seed dispersal achieved. The impact of seed ingestion varied from seed destruction (for *Myrsine guianensis*, *Amaioua guianensis* and *Ocotea pulchella*) to successful (*Erythroxylum pelleterianum*, *Campomanesia adamantium*, *Schinus terebinthifolia*) or improved germination (*Myrcia guianensis*, *Alibertia concolor*) compared to controls. The impact of Rheas on seed germination was inconclusive for other three species. Dispersal is done at the cost of some seed losses probably due to prolonged abrasion inside gut. Rheas perform different ecological roles depending on the fruits consumed and their characteristics. Given the consumption of a great quantity and diversity of fruits combined with a long GPT and large home range, Rheas may influence the fate of a great amount of seeds. Current pervasive population declines of Rheas can disrupt these processes, affecting plant regeneration, particularly for species that depend on them for long-distance seed dispersal.

Keywords: ratites, retention capacity, savanna, seed dispersal, seed predation.

4.1 Introduction

Birds play important roles in ecosystems, many of them while interacting with plants, including pollination, herbivory, seed dispersal and seed predation (Sekercioglu 2006). Seed dispersal and predation are linked to the reproductive cycle of plants and the establishment of their subsequent generations, influencing several aspects of plant species biology, the spatial distribution of individuals and species composition of plant communities (Nathan and Muller-Landau, 2000; Levine and Murrell, 2003; Jordano *et al.* 2007; Snell *et al.* 2019). The potential importance of animals for seed dispersal of plants is exemplified by the reliance of the vast majority of tropical shrubs and trees on seed dispersal by animals, notably birds and mammals (Jordano, 2000; Willson and Traveset, 2000).

Animal characteristics may influence seed dispersal, and one of the primary elements is the body size of the animals that interact with plants (Jordano *et al.* 2007). For instance, birds of large body size have also a large gape width that allow them to swallow large diaspores (i.e. fruits and seeds) and disperse the seeds from those plants by endozoochory (Pratt and Stiles, 1985; Wheelwright, 1985; Williams and Karl, 1996; Jordano 2000; Godínez-Álvarez *et al.* 2020). In the absence of such large birds, most of the large seeds would achieve no dispersal away from parental plants, which often translate into very small probabilities of recruitment (Galetti *et al.* 2013; Pérez-Méndez *et al.* 2018). Large frugivores can also be important dispersers of smaller seeds due to their great gut capacity to ingest a larger quantity of fruits and seeds when compared to smaller frugivores (Chen and Moles 2015; Godínez-Álvarez *et al.* 2020). Indeed, in spite large frugivorous birds are often less abundant compared to smaller birds - and thus perform less frequent visits to fruiting plants - larger birds may disperse a great number of smaller seeds, compensating for their lower visitation frequency with a higher volume of fruit intake per visit (Campagnoli and Christianini, 2021).

Large-bodied frugivores also retain seeds for longer periods in their guts compared to relatively small body-sized frugivores (Jordano *et al.* 2007; Westcott *et al.* 2005). Data on gut passage time of seeds (GPT) combined to bird movements allow researchers to estimate the potential spatial distribution of defecated seeds (Westcott and Graham 2000; Westcott *et al.* 2005; Donoso *et al.* 2020). Frugivore GPT may also

be influenced chemical components in fruit pulp that affect the speed of seed passage through the bird gut and the potential distances achieved through dispersal (Murray *et al.* 1994; Traveset 1998; Donoso *et al.* 2020). An extended GPT, combined with the typical large home range and high mobility of animals with large body size, make larger frugivores effective long-distance seed dispersers (Westcott *et al.* 2005, Jordano *et al.* 2007, Donoso *et al.* 2020). Consequently, large birds are often more effective seed dispersers, increasing the likelihood of plant colonization/recolonization of new sites, influencing metapopulation dynamics, and often reducing parent-offspring competition and negative density-dependent effects near parental plants (Alcántara *et al.* 2000; Pakeman, 2001; Aerts *et al.* 2006; Calviño-Cancela *et al.* 2008; Godínez-Alvarez *et al.* 2020).

Seed ingestion and gut treatment by birds often also influence the success of seed germination (Traveset 1998; Traveset and Verdu 2002). This benefit may be due to the simple removal of fruit pulp covering the seed, that sometimes harbors inhibitors of seed germination (Samuels and Levey 2005), or due to seed scarification in the gut that facilitates water intake and triggers germination (Traveset 1998; Traveset and Verdu 2002; Samuels and Levey 2005; Fricke *et al.* 2019). Seed scarification can increase germination percentage and speed, further enhancing seed dispersal effectiveness (Levey, 1987; Samuels and Levey 2005; Schupp *et al.* 2010; Fricke *et al.* 2019). When frugivores do not interact with fruits, seeds remain embedded in fruit pulp after fruit falls to the ground and are subjected to a higher risk of pathogenic attack that decrease survival and germination (Traveset, 1998; Traveset and Verdu 2002).

The Brazilian savanna, known as the Cerrado, is a predominant vegetation once covering more than 2 million km² in the Central Plateau of Brazil. It is recognized as a biodiversity hotspot, harboring a diversity of over 10,000 plant species, of which more than 40% are endemic (Klink and Machado, 2005, Strassburg *et al.* 2017). The Cerrado also hosts approximately 837 avian species (Silva, 1995), 199 mammal species, a variety of reptiles and amphibians, as well as 1,200 fish species (Klink and Machado, 2005). These animals perform intricate interactions with fruiting plants in Cerrado (Carvalho *et al.* 2023). Among them are Greater rheas (*Rhea americana*; Rheidae), the largest non-flying extant bird in South America. Female and male Rheas can reach 32-35 kg and heights of 134-170 cm, respectively (Sick, 1997). Greater rheas have also a

large gape width (54.3 mm; N = 3; unpubl. data), enabling them to swallow large fruits and seeds that otherwise could not be eaten and dispersed by endozoochory by smaller frugivores due to gape width limitation. However, *R. americana* has been facing a significant population decline in recent years, and it is currently, classified as near threatened (IUCN, 2016). There is evidence that Greater Rheas may behave as seed dispersers, but only a few plant species were tested so far (Azevedo, 2013). Given its large body size, it is likely that Greater rheas may disperse seeds farther than other birds, but no data about GPT in Rheas is available (Azevedo, 2013; Renison *et al.* 2010; Campos *et al.* 2020). The passage of seeds through the Greater Rhea's digestive tract may increase the germination rate of some plants, inducing dormancy break after gut passage. For example, seeds of *Solanum palinacanthum* (Solanaceae) germinate more quickly after being ingested by *R. americana*, a similar result found for *Ziziphus mistol*, which has large seeds (Azevedo, 2013). However, the potential granivorous role of Greather rhea was not investigated so far.

The objectives of this study were to describe, for the first time, the gut passage time of seeds after ingestion by Greather rheas and estimate the impact of seed ingestion on the number and speed of seeds germinating compared to uningested seeds used as controls. We show that the Greather rhea performs different roles, behaving as a seed predator for some plants, while providing seed dispersal and increased seed germination for others, with potential quite long distances of seed dispersal thanks to a very long GPT. Furthermore, analyze whether the composition of lipids in the fruit pulp can influence the GPT of the seeds.

4.2 Materials and Methods

4.2.1 Feeding experiments with captive Rheas

This study was conducted with captive Rheas kept in a Zoo located in the municipality of São Carlos, SP, southeast Brazil (21° 59' 16" S and 47° 52' 37" W). The Zoo maintains a group of 27 Greater Rheas (*Rhea americana*). To assess Gut Passage Time (GPT) and the impact of seed ingestion by Greater rheas on germination, we offered fruits from eleven native species from Cerrado (Table 1). The morphological and chemical characteristics of the fruits/seeds used in experiments are found in Table

S1. All individual birds used in the experiments ($N = 12$) were adults, and the tests were conducted with both males and females. For the experiments the GPT, one *R. americana* was isolated at a time in an enclosure measuring 30 m² at around 4:00 PM. The bird was kept fasting until the following morning. At 8:00 AM we offer to the bird some fruits of a selected species. Only one fruit species was used in each feeding trial. After consuming the fruits, the Greater rhea was again provided with the regular diet, including corn, wheat, soybeans, rice husk, and vegetables (leaves and flowers).

4.2.2 Estimates of GPT and its conditionants

We recorded the GPT for each fruit species with the aid of focal observations and remote monitoring using a camera trap. First, we described GPT from the first fruit/seed ingested up to the first seed recovered in feces (Table S1). We also described GPT as the time from ingestion of first fruit of a given species to defecation of the last seed of the same species. We defined the last seed defecated as those seeds that were not followed by subsequent seed defecations up to four days after the last seed was encountered in feces. Since Rheas may defecate seeds in different times after ingestion (see below), we also calculated a mean GPT. In cases where the total number of seeds retrieved from feces did not match the number of seeds ingested by the Greater rhea, we continued to sample feces for seeds for another four consecutive days. We assume that seeds not recovered up to this period were destroyed during gut passage.

4.2.3 Comparisons of seed germination

We collected all feces produced from the Rhea used in experiments at least once a day. Feces were washed in a 5 mm sieve under a constant water flow to separate seeds from the rest of the fecal material. We removed whole seeds and seed fragments and left them to dry in the shade at room temperature. After up to 24 hs the seeds were sowed in vermiculite, kept under regular watering (twice a day), natural temperature and light conditions. To test the influence of Greater rhea in seed germination, we compared the germination of seeds that passed through the digestive tract of the Greater rhea (treatment T) with those obtained from two controls: Control 1 (C1) – seeds embedded in fruit pulp. The fruits were introduced directly into the substrate, simulating a fruit that falls below the crown of the parental plant without interaction with animals;

Control 2 (C2) - seeds extracted from the fruits (de-pulped manually), simulating seeds cleaned by an animal, but not ingested. With those three germination treatments, we were able to test if a potential improvement in seed germination after gut passage would be due to mechanical/chemical abrasion on the seeds (by comparing gut passed versus manually de-pulped seeds), or release from germination inhibitors commonly found in fruit pulp (whole fruits versus manually de-pulped seeds) (Samuels and Levey 2005). Germination tests run for up to 60 days after seed sowing. We monitored seeds daily and recorded germination by the protrusion of the radicle (Borghetti and Ferreira 2004).

4.2.4 Statistical Analysis

To test the influence of fruit and seed traits on the average GPT, we used the weight, width, and length of both the fruit and the seed as independent variables and GPT as our response variable. Given the potential collinearity among morphological variables of fruits and seeds, first we conducted a Spearman correlation ("psych" package: William 2023) in R (R Core Team 2022) among all independent variables. There was a strong correlation between fruit weight, fruit width, and fruit length (all with $r > 0.80$ between each pair of variables compared; supplementary material Table S2). Similarly, seed characteristics, such as weight, also showed a strong correlation with seed width and length (all $r > 0.78$; Table S2). Seed and fruit traits, however, were weakly correlated (Table S2). Therefore, we chose to work with fruit and seed weights as independent variables to test the influence of fruit and seed traits on GPT. Given the exponential nature of GPT values, we performed a regression using log GPT as response variable. To test the influence of fruit chemical content on GPT, we first compiled information on the total amount of lipids in fruit pulp from the literature (Silva and Fonseca, 2016; Camargo 2014; Hosni *et al.* 2011; Vallilo 2006; Otegui *et al.* 1998) and after conducted another logarithmic regression testing the influence of lipid content in fruit pulp on GPT.

To compare seed germination among the treatments (T, C1, and C2), we applied the chi-square test with the "chisq.test ()" function. To test if Rhea ingestion influence germination speed we used survival analysis with the aid package "survival" (Therneau, 2023) in R (R Core Team, 2022).

4.6 Results

4.6.1 Estimates of GPT and its conditionants

The Gut Passage Time (GPT) of Greater rhea was long (often more than two days), with a coefficient of variation of 21.9% among the eleven plants studied (Table 1). The longest GPT was obtained for *Aegiphila lhotzkiana* (81 ± 34 hours; mean $\pm$ SD) and the lowest was *Campomanesia adamantium* (38.3 ± 17.7 hours). Light fruits had a higher GPT ($P = 0.001$, $r^2 = 0.65$; $b = -0.14$) (Figure 1), indicating an inverse relationship between fruit mass and GPT. Seed weight did not influence GPT ($r = 0.17$, $P = 0.50$). Lipid content in fruit pulp had a small but positive effect on GPT ($P = 0.05$, $r^2 = 0.39$, equation: $Y = 47.4022 * X^{0.1070}$) (Figure 3).

Looking at the times of seed defecation for the five plants whose seeds germinated after gut passage, we found that Rheas defecated the seeds at different times after ingestion (Figure 4). Seeds from these five species were defecated everyday up to five days after ingestion. Therefore, Rheas are likely to spread seeds at different times, locations and distances from the same parental plants after feeding, potentially increasing the intraspecific variability in seed conditions and places of seed deposition in the field.

4.6.2 Comparisons of seed germination

Considering seed germination, seeds from six species did not germinate after gut passage: *Aegiphila lhotzkiana*, *Byrsonima intermedia*, *Smilax polyantha*, *Myrsine guianensis*, *Amaioua guianensis*, and *Ocotea pulchella* (Table 2). However, the seeds of the first three species also did not germinate in controls (i.e. seeds not ingested by Rheas). Therefore, we cannot rule out the possibility that some specific triggers for seed germination may be missing, and the role of Rheas in the seed germination of these species was inconclusive. For the last three species, Rheas behave as seed predators, since a low proportion of seeds ingested were retrieved from feces, and seeds germinated only in controls (Table 2). On the other hand, seeds from other five species (*Myrcia guianensis*, *Erythroxylum pelleterianum*, *Campomanesia adamantium*, *Alibertia concolor*, and *Schinus terebinthifolia*) successfully germinated after passing through the Rhea's digestive tract, with considerable variations among them (Table 2).

For instance, only one seed from each *Campomanesia adamantium*, *Erythroxylum pelleterianum* and *Schinus terebinthifolia* germinated among those recovered (from 76 to 3 seeds recovered per species) after passing through the Rhea gut. All seeds that germinated from these three species were obtained from the first defecation after ingestion, i.e. spent less time inside the gut (Figure 4). Given the low sample sizes of germinated seeds, it was not feasible to carry out survival analyzes for these species. However, *Myrcia guianensis* and *Alibertia concolor* had larger sample sizes that allowed statistical comparisons. For *M. guianensis* germination percentages in T (45%) was similar to that found for C1 (seeds within fruits; 54%; $X^2 < 0.1$; $p = 1.0$), while seeds ingested germinated less than C2 (seeds de-pulped manually; 94%; $X^2 = 6.03$; $p = 0.01$). In *M. guianensis* germination speed was higher for seeds ingested by Rheas (T) compared to C1 ($X^2 = 7.27$; $p = 0.006$), while T and C2 did not differ in germination speed ($X^2 = 1.47$; $p = 0.20$) (Figure 5A). For *A. concolor*, germination in T (30%) was smaller than C1 (40%; $X^2 = 22.25$; $p < 0.01$), but showed no difference compared to C2 (100%; $X^2 = 0.01$; $p = 0.91$). Seeds of *A. concolor* ingested by Rheas also showed a faster germination compared to both C1 ($X^2 = 28.34$; test: $p = 0.0001$) and C2 ($X^2 = 9.41$; test: $p = 0.002$) (Figure 5B).

4.7 Discussion

We found a long GPT in Rheas, with an average of 61.6 ± 13.5 hours (mean $\pm$ SD) across the eleven plant species analyzed. Fruits with lower weight have a longer GPT, but seed characteristics do not influence GPT. The Greater rhea defecates the seeds it consumes at considerable different time intervals, and higher lipid content in fruit pulp delay GPT. Five among the eleven seed species tested germinated after passing through the Rhea's digestive tract, with at least two of them showing a higher germination speed compared to controls. These potential benefits came at the cost of some seeds destroyed during gut passage. Indeed, for some species (*Amaioua guianensis*, *Myrsine guianensis* and *Ocotea pulchella*) Rheas behave as seed predators. Taken together these results suggest that Greater rheas play different roles as seed predators or dispersers, depending on the fruit species ingested, and that seeds dispersed by Rheas may be spread up to quite long distances.

When comparing the GPT of *R. americana* with that of other ratites such as Cassowary (*Casuaris casuarius*) (mean GPT = 7.45 ± 6.77 hours for eleven plant

species; Westcott and Bradford, 2005), GPT in Greater rhea is longer, but similar to the Common Emu *Dromaius novaehollandiae* (GPT varies from one to eleven days, depending on the species consumed) (Calviño-Cancela *et al.* 2008). Therefore, a long GPT is common among ratites and much larger than in small-bodied frugivorous birds. For instance, the longest record among forty bird species with body mass up to 300 g is only 73.3 minutes for *Erithacus rubecula* (reviewed in Antoni, 2020). In Argentinean Pampas, Greater rheas have an average home range of 452.8 hectares (Juan *et al.* 2013). Rheas can cover long distances, with mean daily displacement of 1.08 km (Azevedo, 2010). Thus, by combining long seed retention times and long-distance movement patterns, *R. americana* can transport seeds to long distances from parental plants and connect plant populations through seed dispersal, a role often exclusively played by the larger-bodied frugivores (Jordano *et al.* 2007). Long-distance seed dispersal in Cerrado should be useful to allow colonization/recolonization of sites after disturbances. Wildfires, which are common in savannas like the Cerrado, may kill some plants (Hoffmann, 2009) and often triggers increased removal of seeds by some granivorous taxa, potentially decreasing seeds available for recruitment right after fire (Alcolea *et al.* 2022). Rheas can provide seed inputs to those disturbed sites, by defecating seeds ingested far away in spots not hit by fire. This dispersal however, is achieved at the cost of at least some seeds preyed upon during gut passage for the species investigated, a cost that seems to increase with the time the seed is retained in the gut (Figure 4).

Plants with heavier fruits have faster GPT through the Rheas's gut when compared to plants with lighter fruits, consistent with the results from studies with other birds (e.g. Levey and Grajal 1991; Stanley and Lill, 2002). A faster passage of larger fruits perhaps is just the effect of gravity, or serves as a strategy to eliminate seed ballast that hinders the frugivore's movements or further food ingestion (Jordano, 2000). A fast GPT potentially reduces the adverse effects of excessive chemical and abrasive conditions in the frugivore's gizzard which seems to affect seed germination after ingestion of at least some plants by Rheas (Figure 4).

The presence of soluble chemical substances, such as those with a laxative effect, can increase intestinal transit rates in frugivores (Murray *et al.* 1994). In our study, a constipative effect was found for fruits whose pulp is rich in lipids that present

a longer passage time compared to lipid-poor fruit (Figure 3). Lipid-rich fruit often has low water content (Jordano, 2000), which may help explain the constipative effect observed. Seeds from lipid-rich fruits can thus potentially achieve longer distances of seed dispersal by Rheas than lipid-poor fruit, as the first are retained in the gut for longer periods of time enabling long travel distances. Therefore, the effect of seed ingestion by Greater rheas on GPT is complex and related not only to the physical characteristics of fruits, but also to the chemical composition of fruit pulp influencing GPT. More studies on this topic would be worthwhile.

Our results suggest that an excessively long GPT in Rheas can decrease seed viability (Figure 4). This may be due to unfavorable conditions for seed survival over extended periods of exposition to mechanical abrasion and digestive enzymes during GPT (Murray *et al.* 1994, Traveset and Verdu, 2002). This seems to be the case for at least some of our species that did not germinate after gut passage (*Amaioua guianensis*, *Myrsine guianensis* and *Ocotea pulchella*, Table 2) or those species that germinated only from the first defecations after ingestion by Rheas (Figure 4). Seeds that do not germinate after gut passage in Rheas tend to be those retained for longer periods of time (Figure 4). Many species from Cerrado also usually present seed dormancy or low levels of seed viability (Dayrell *et al.* 2016) precluding a detailed evaluation of the effect of gut passage through the Rhea digestive tract on seed germination. This is probably the case of species such as *A. lhotskiana*, *B. intermedia* and *S. polyantha* that did not germinate even in controls (Table 2). For those species, the effect of fruit ingestion by Greater rheas in seed germination was inconclusive. However, in *M. guianensis* and *A. concolor* seeds that germinated after ingestion by Rheas exhibited a faster germination compared to the controls. For *M. guianensis*, the effect of seed ingestion by Greater rhea seems to be mainly removal of fruit pulp, given an increased germination speed of ingested seeds compared to Control 1 (seeds still embedded in fruit pulp), but not to Control 2 (manually de-pulped seeds) (Figure 5A). For *A. concolor*, seed ingestion by Rheas induces faster germination compared to both controls, indicating that seed abrasion in the gut triggered germination (Figure 5B). These results highlight the influence of Greater rheas in promoting germination and an effective dispersal of certain plant species (see also Azevedo, 2013), while behaving as a seed predator for others.

The Greater rheas are also able to distribute the seeds ingested once in 3 to 7 different defecations spread over 17.6 to 88.6 hours (Figure 4). For instance, seeds of *M. guianensis* able to germinate were released by Rheas after 23.0, 46.1 and 70.8 hours. This great variance in GPT means that seeds are likely to be deposited in different locations, increasing their chances of finding favorable microsites for germination and seedling establishment if favorable locations are randomly distributed (Green, 1983). Dispersal at distance is also more likely to decrease negative density dependent effects commonly observed during early stages of plant regeneration. Variance in places of seed deposition should be especially useful for plants dispersed by Rheas given the mosaic-like pattern of vegetation in the Cerrado, the often clustered and limited spatial distribution of seed rain, coupled with the specific germination requirements of different plants (Mariano *et al.* 2019 and references therein).

Indeed, ratites such as Greather rheas, often play crucial roles in seed distribution and vegetation dynamics. For instance, the Cassowary *C. casuarius* found in the tropical forests of Australia effectively disperses seeds from 78 plant species over a two-year period (Stocker and Irvine, 1983). In savannas and sclerophyllous vegetation in Australia, Common Emus *D. novaehollandiae* provide opportunities of very long-distance seed dispersal for myrmecochorous plants that otherwise would reach only small distances of seed dispersal by ants (Calviño-Cancela *et al.* 2008). In African savannas, Ostriches *Struthio camelus* also contribute to the dispersal of seeds from various species of African acacias (*Acacia* spp.) in open environments more favorable for plant development. In the absence of these large terrestrial frugivorous birds, many seeds often fell at shorter distances from parental plants, in less suitable environments for plant growth (Miller, 1996).

Current ecological networks of fruit-frugivore interactions for the Cerrado clearly underestimate the role of large birds, such as Greater rheas, in frugivory, seed dispersal and predation (see Carvalho *et al.* 2023). Given the large body size and gape width of Rheas, and current available data (Renison *et al.* 2010, Azevedo *et al.* 2013, this study), it is likely that the impact of Greater rheas in seed dispersal and predation is considerable. In the field, Rheas ingest very large and hard seeds such as those from the palm *Attalea phalerata* (CLBJ and AVC unpubl. data) that may be more likely to survive long term retention in the gut, as well as other palms reported in their diet

(Carvalho *et al.* 2023). Greater rheas may also disperse seeds of epizoochorous plants attached to their plumage (A.V. Christianini, pers. obs.). Those characteristics, together with a very long GPT, turn Greather rhea's seed dispersal functionally similar to that performed by large mammals, that have been vanishing (Pires, 2023). Unfortunately, Greater Rheas are disappearing from large tracts of Cerrado and grasslands in South America (IUCN, 2016). The rare detection of Greather rheas in interaction networks is probably a reflection of their low occurrence in most landscapes of Cerrado which are defaunated nowadays, leaving many fruits unattended or probably relying on dispersal services performed by species of small sizes which are unlikely to deliver the same services (Galetti *et al.* 2013; Pérez-Méndez *et al.* 2018; Christianini *et al.* 2014). The loss of the seed dispersal services from Greater rheas could have long-term implications, as plants may lose this long-distance dispersal vector and consequently fail to colonize/recolonize new sites and connect plant populations through dispersal (see Jordano *et al.* 2007). The conservation of large birds, such as Greater rheas, is therefore crucial not only for their own survival but likely for maintaining biodiversity and healthy ecosystem processes in South American savannas and grasslands.

4.8 Acknowledgments

We thank Parque Ecológico de São Carlos its staff for their support during feeding trials with captive Rheas. We also thank the Universidade Federal de São Carlos (UFSCar) for providing facilities to the development of this work. CLBJ received a scholarship from the Coordination for the Improvement of Higher Education Personnel (CAPES) and assistance through the PROAP-CAPES program (Finance Code 001). AVC also thanks Neotropical Grassland Conservancy, and the Rufford Foundation small grants.

4.9 References

- Aerts, R., Maes, W., November, E., Negussie, A., Hermy, M., and Muys, B (2006). Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp. *cuspidata* seeds. *Forest Ecology and Management*, 230(1-3), 23-31. <https://doi.org/10.1016/j.foreco.2006.04.001>.
- Alcolea, M., Durigan, G., and Christianini, A. V (2022). Prescribed fire enhances seed removal by ants in a Neotropical savanna. *Biotropica*, 54(1), 125-134. <https://doi.org/10.1111/btp.13036>.
- Alcántara, J. M., Rey, P. J., Valera, F., and Sánchez-Lafuente, A. M (2000). Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology*, 81(7), 1937-1950. <https://doi.org/10.2307/177283>.
- Antoni, G (2020). Tempo de passagem de sementes pelo trato digestório de aves frugívoras. Bachaelor Thesis, Instituto de Biociências, Universidade Estadual Paulista “Júlio de Mesquita Filho”, Rio Claro, Brazil.
- Borghetti F, Ferreira AG., 2000. Germinação: do básico ao aplicado. Porto Alegre: Artmed. 2004; 323.
- Calviño-Cancela, M., He, T., and Lamont, B. B (2008). Distribution of myrmecochorous species over the landscape and their potential long-distance dispersal by emus and kangaroos. *Diversity and Distributions*, 14(1), 11-17. <https://doi.org/10.1111/j.1472-4642.2007.00402.x>.
- Camargo, M. G. G (2014). Padrões de frutificação e diversidade na produção, cor e composição química de frutos no cerrado: Uma visão integrada (Doctoral dissertation, thesis, UNESP, Rio Claro—SP).
- Campagnoli, M. L., and Christianini, A. V (2022). Temporal consistency in interactions among birds, ants, and plants in a neotropical savanna, *Oikos*, 1-13. <https://doi.org/10.1111/oik.08231>.
- Campos, C. M., Ramos, L., Manrique, N., Cona, M. I., Sartor, C., de los Ríos, C., and Cappa, F. M (2020). Filling gaps in the seed dispersal effectiveness model for *Prosopis flexuosa*: quality of seed treatment in the digestive tract of native animals.

- Seed Science Research, 30(3), 215-223.
<https://doi.org/10.1017/S096025852000032X>.
- Carvalho, R.B., Malhi, Y., and Oliveras Menor, I (2023). Frugivory and seed dispersal in the Cerrado: Network structure and defaunation effects. *Biotropica*, 55(4), 729-896. <https://doi.org/10.1111/btp.13234>.
- Chen, S. C., and Moles, A. T (2015). A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. *Global Ecology and Biogeography*, 24(11), 1269-1280. <https://doi.org/10.1111/geb.12346>.
- Christianini, A. V., Oliveira, P. S., Bruna, E. M., and Vasconcelos, H (2014). Fauna in decline: Meek shall inherit. *Science* 345 (6201), 1129.
<https://doi.org/10.1126/science.345.6201.1129-a>.
- Da Silva, J. M. C (1995). Avian inventory of the Cerrado region, South America: implications for biological conservation. *Bird Conservation International*, 5(2-3), 291-304. <https://doi.org/10.1017/S0959270900001052>.
- Dayrell, R. L., Garcia, Q. S., Negreiros, D., Baskin, C. C., Baskin, J. M., and Silveira, F. A (2017). Phylogeny strongly drives seed dormancy and quality in a climatically buffered hotspot for plant endemism. *Annals of Botany*, 119(2), 267-277.
<https://doi.org/10.1093/aob/mcw163>.
- De Azevedo A, C. S., da SilvaB, M. C., TeixeiraB, T. P., YoungC, R. J., GarciaB, Q. S., and RodriguesA, M (2013). Effect of passage through the gut of Greater Rheas on the germination of seeds of plants of cerrado and caatinga grasslands. *Emu*, 113, 177-182. <https://doi.org/10.1071/MU12070>.
- De Andrade Silva, Cinthia Aparecida, and Gustavo Graciano Fonseca (2016). Brazilian savannah fruits: Characteristics, properties, and potential applications. *Food Science and Biotechnology*, 25(5), 1225-1232. <https://doi.org/10.1007/s10068-016-0195-3>.
- Fricke, E. C., Bender, J., Rehm, E. M., and Rogers, H. S (2019). Functional outcomes of mutualistic network interactions: a community-scale study of frugivore gut passage on germination. *Journal of Ecology*, 107(2), 757-767. <https://doi.org/10.1111/1365-2745.13108>.
- Galetti, M., Guevara, R., Côrtes, M. C., Fadini, R., Von Matter, S., Leite, A. B., Labecca, F., Ribeiro, T., Carvalho, C. S., Collevatti, R. G., Pires, M. M., Guimarães, P. R., Brancalion, P. H., Ribeiro, M. C., and Jordano, P (2013). Functional extinction

- of birds drives rapid evolutionary changes in seed size. *Science*, 340(6136), 1086–1090. <https://doi.org/10.1126/science.1233774>.
- Gasperin, G., and Pizo, M. A (2012). Passage time of seeds through the guts of frugivorous birds, a first assessment in Brazil. *Revista Brasileira de Ornitologia*, 20(1), 48-51.
- Godínez-Alvarez, H., Ríos-Casanova, L., and Peco, B (2020). Are large frugivorous birds better seed dispersers than medium-and small-sized ones? Effect of body mass on seed dispersal effectiveness. *Ecology and Evolution*, 10(12), 6136-6143. <https://doi.org/10.1002/ece3.6285>.
- Green, D. S (1983). The efficacy of dispersal in relation to safe site density. *Oecologia* 56, 356-358. <https://doi.org/10.1007/BF00379712>.
- Hoffmann, W. A., Adasme, R., Haridasan, M., T. de Carvalho, M., Geiger, E. L., Pereira, M. A., ... & Franco, A. C (2009). Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology*, 90(5), 1326-1337. <https://doi.org/10.1890/08-0741.1>.
- Hosni, K., Jemli, M., Dziri, S., M'rabet, Y., Ennigrou, A., Sghaier, A., ... & Sebei, H (2011). Changes in phytochemical, antimicrobial and free radical scavenging activities of the Peruvian pepper tree (*Schinus molle* L.) as influenced by fruit maturation. *Industrial Crops and Products*, 34(3), 1622-1628. <https://doi.org/10.1016/j.indcrop.2011.06.004>.
- Howe, H. F., and Primack, R. B (1975). Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica*, 7(4), 278-283. <https://doi.org/10.2307/2989740>.
- IUCN (2016). BirdLife International: *Rhea americana*. The IUCN Red List of Threatened. <https://www.iucnredlist.org/search?query=rhea%20americana&searchType=species>. (accessed 09 october 2023).
- Jordano, P (2000). Fruits and frugivory. In M. Fenner (Ed.), *Seeds: The ecology of regeneration in plant communities*. Wallingford, UK: CAB International. (125–166). <https://doi.org/10.1079/9780851994321.0125>.
- Jordano, P., García, C., Godoy, J. A., and Garcia-Castaño, J (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the*

- National Academy of Sciences, 104(9), 3278-3282.
<https://doi.org/10.1073/pnas.0606793104>.
- Juan, E. E., Bazzano, G., Navarro, J. L., and Martella, M. B (2013). Space use by wild Greater Rhea (*Rhea americana*) in a relict grassland of central Argentina during the non-breeding season. *El Hornero*, 28(1), 01-06.
<https://doi.org/10.56178/eh.v28i1.638>.
- Klink, C. A., and Machado, R. B (2005). Conservation of the Brazilian cerrado. *Conservation Biology*, 19(3), 707-713. <https://doi.org/10.1111/j.1523-1739.2005.00702.x>.
- Levey, D. J (1987). Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist*, 129(4), 471-485. <https://doi.org/10.1086/284652>.
- Levey, D. J., and Grajal, A (1991). Evolutionary implications of fruit-processing limitations in cedar waxwings. *The American Naturalist*, 138(1), 171-189.
<https://doi.org/10.1086/285210>.
- Levine, J. M., and Murrell, D. J (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 549-574. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132400>.
- Lord, J. M (2004). Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. *Austral Ecology*, 29(4), 430-436.
<https://doi.org/10.1111/j.1442-9993.2004.01382.x>.
- Mariano, V., Reboló, I. F., and Christianini, A. V (2019). Fire-sensitive species dominate seed rain after fire suppression: implications for plant community diversity and woody encroachment in the Cerrado. *Biotropica*, 51(1), 5-9.
<https://doi.org/10.1111/btp.12614>.
- Miller, M. F (1996). Dispersal of *Acacia* seeds by ungulates and ostriches in an African savanna. *Journal of Tropical Ecology*, 12(3), 345-356.
<https://doi.org/10.1017/S0266467400009548>.
- Murray, K. G., Russell, S., Picone, C. M., Winnett-Murray, K., Sherwood, W., and Kuhlmann, M. L (1994). Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology*, 75(4), 989-994.
<https://doi.org/10.2307/1939422>.

- Nathan, R., and Muller-Landau, H. C (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, 15(7), 278-285. [https://doi.org/10.1016/S0169-5347\(00\)01874-7](https://doi.org/10.1016/S0169-5347(00)01874-7).
- Obeso, J. R., Martínez, I., and García, D (2011). Seed size is heterogeneously distributed among destination habitats in animal dispersed plants. *Basic and Applied Ecology*, 12(2), 134-140. <https://doi.org/10.1016/j.baae.2011.01.003>.
- Otegui, M. S., *et al* (1998). Studies on tissues associated to hydroxybenzoquinone secretion in *Myrsine laetevirens* (Myrsinaceae). *Nordic Journal of Botany* 18(4), 447-459. <https://doi.org/10.1111/j.1756-1051.1998.tb01522.x>.
- Pakeman, R. J (2001). Plant migration rates and seed dispersal mechanisms. *Journal of Biogeography*, 28(6), 795-800. <https://doi.org/10.1046/j.1365-2699.2001.00581.x>.
- Pérez-Méndez, N., Jordano, P., and Valido, A (2018). Persisting in defaunated landscapes: reduced plant population connectivity after seed dispersal collapse. *Journal of Ecology*, 106(3), 936-947. <https://doi.org/10.1111/1365-2745.12848>.
- Pires, M. M (2023). The restructuring of ecological networks by the Pleistocene extinction. *Annual Review of Earth and Planetary Sciences* (52), 5.1-5.26.
- Pratt, T. K., and Stiles, E. W (1985). The influence of fruit size and structure on composition of frugivore assemblages in New Guinea. *Biotropica*, 314-321. <https://doi.org/10.2307/2388594>.
- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. (accessed 10 October 2023).
- Renison, D., Valladares, G., and Martella, M. B (2010). The effect of passage through the gut of the Greater Rhea (*Rhea americana*) on germination of tree seeds: implications for forest restoration. *Emu-Austral Ornithology*, 110(2), 125-131. <https://doi.org/10.1071/MU12070>.
- Revelle, W (2023). Psych: procedures for psychological, psychometric, and personality research. Northwestern University (2020). Evanston, Illinois, R package.
- Samuels, I. A., and Levey, D. J., 2005. Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology*, 365-368. <https://doi.org/10.1111/j.1365-2435.2005.00973.x>.

- Schupp, E. W., Jordano, P., and Gómez, J. M (2010). Seed dispersal effectiveness revisited: a conceptual review. *New phytologist*, 188(2), 333-353.
<https://doi.org/10.1111/j.1469-8137.2010.03402.x>.
- Sekercioglu, C. H (2006). Increasing awareness of avian ecological function. *Trends Ecol. Evol.*, 21, 464-471. <https://doi.org/10.1016/j.tree.2006.05.007>.
- Sick H (1997). *Ornitologia Brasileira*. Editora Nova Fronteira: Rio de Janeiro, Rio de Janeiro, Brazil.
- Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., ... and Schupp, E. W (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants*, 11(4), plz016. <https://doi.org/10.1093/aobpla/plz016>.
- Stanley, M. C., and Lill, A (2002). Does seed packaging influence fruit consumption and seed passage in an avian frugivore? *The Condor*, 104(1), 136-145.
<https://doi.org/10.1093/condor/104.1.136>.
- Stocker, G. C., and Irvine, A. K (1983). Seed dispersal by cassowaries (*Casuarius casuarius*) in North Queensland's rainforests. *Biotropica*, 170-176.
<https://doi.org/10.2307/2387825>.
- Strassburg, B. B., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., ... and Balmford, A (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology and Evolution*, 1(4), 0099. <https://doi.org/10.1038/s41559-017-0099>.
- Therneau, T (2023). A package for survival analysis in R (R package version 3.5-0).
- Traveset, A (1998). Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, 1(2), 151-190. <https://doi.org/10.1078/1433-8319-00057>.
- Traveset, A., and Verdú, M (2002). A Meta-analysis of the effect of gut treatment on seed germination. In D.J. Levey, W. R. Silva, and M. Galetti (eds), *Frugivores and seed dispersal: ecological, evolutionary and conservation issues* (339–350). CAB International. <https://doi.org/10.1079/9780851995250.0339>.
- Vallilo, M. I., Lamardo, L. C. A., Gaberlotti, M. L., Oliveira, E. D., and Moreno, P. R. H (2006). Composição química dos frutos de *Campomanesia adamantium* (Cambessédes) O. Berg. *Food Science and Technology*, 26, 805-810.
<https://doi.org/10.1590/S0101-20612006000400015>.

- Westcott, D. A., and Graham, D. L (2000). Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, 122(2), 249-257.
<https://doi.org/10.1007/PL00008853>.
- Westcott, D. A., Bentrupperbäumer, J., Bradford, M. G., and McKeown, A (2005). Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, 146, 57-67.
<https://doi.org/10.1007/s00442-005-0178-1>.
- Wheelwright, N. T (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology*, 66(3), 808-818. <https://doi.org/10.2307/1940542>.
- Wickham, H., François, R., Henry, L., and Müller, K (2018). dplyr: A Grammar of Data Manipulation. R package version 0.7. 6. Computer software]. <https://CRAN.R-project.org/package=dplyr>.
- Williams, P. A., and Karl, B. J (1996). Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology*, 20(2), 127-145.
- Willson, M. F., and Traveset, A (2000). The ecology of seed dispersal. In *Seeds: the ecology of regeneration in plant communities* (85-110). Wallingford UK: CAB.
<https://doi.org/10.1079/978117880641836.0062>

5.0 Figures

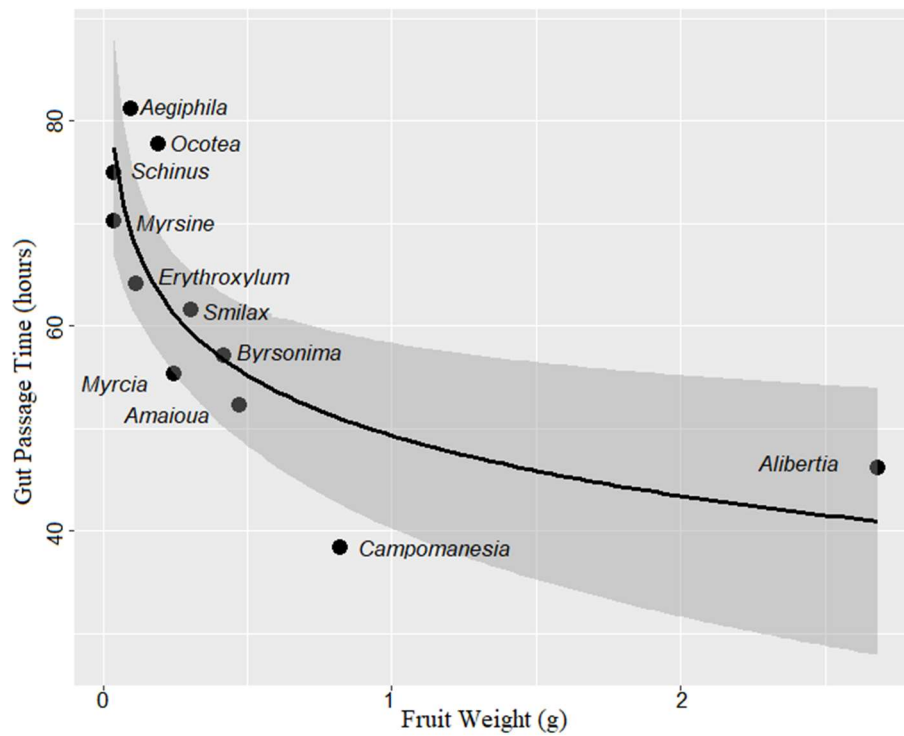


Figure 1: Influence of fruit weight (in g) on the gut passage time of Greater rhea (in average hours). Plant species are indicated by their genera. Shade indicates 95% confidence interval around regression line.

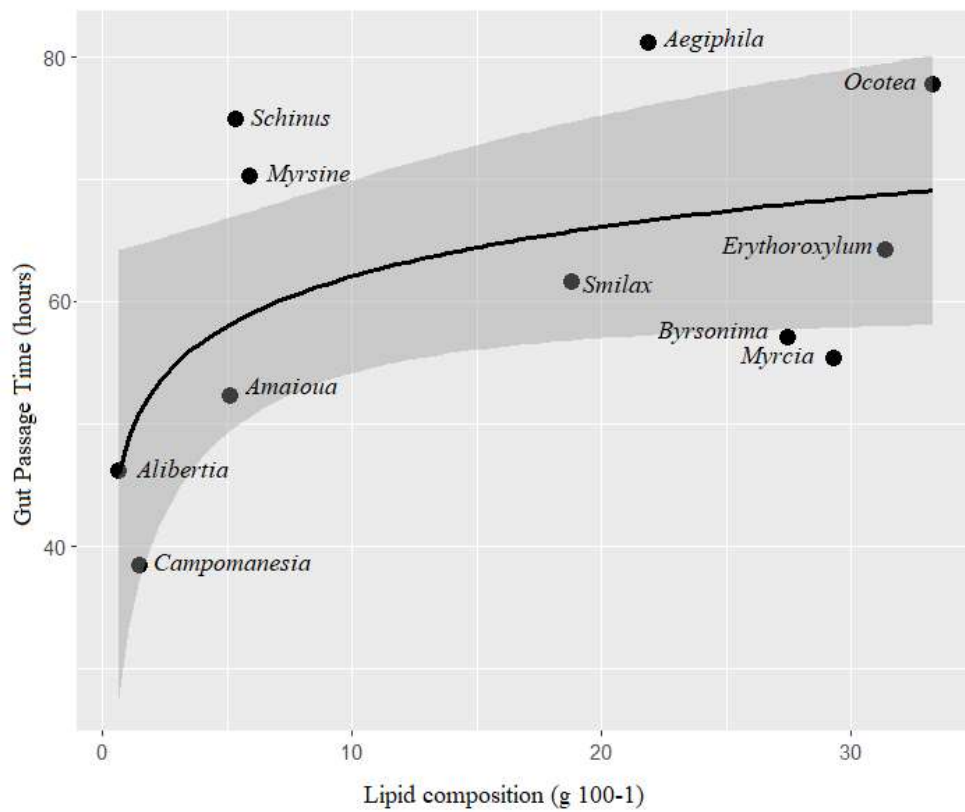


Figure 3: Influence of lipid content in fruit pulp (g 100 g⁻¹) from eleven plants from Cerrado on the average GPT ($P = 0.05$, $r^2 = 0.39$, equation: $Y = 47.4022 \cdot X^{0.1070}$). Plant species are indicated by their genera. Shade indicates 95% confidence interval around regression line.

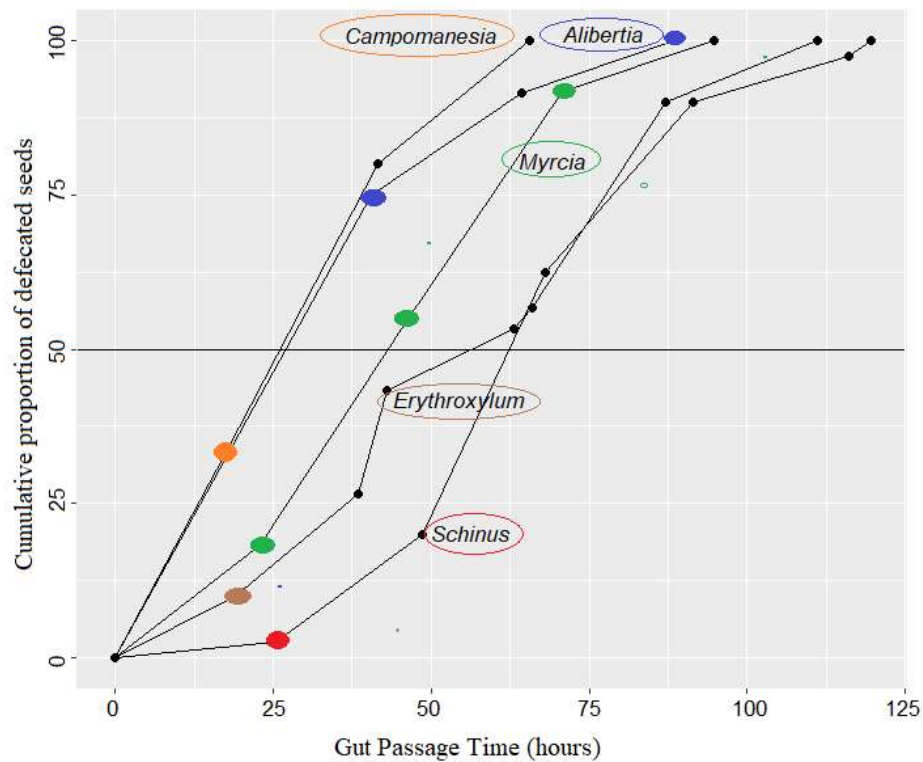


Figure 4: Rheas can spread seeds into different locations after ingestion, given the high within species variation in gut passage time. Cumulative percentage of seeds recovered from feces after ingestion for the five plant species (indicated by their genera, see Table 1) that germinated after gut passage in *Rhea americana*. Large and colored circles (each species depicted in a color) point out the time of defecation that provided seeds that germinate in experiments. Black and small filled circles indicate the times of gut passage when seeds released in feces did not germinate during experiments.

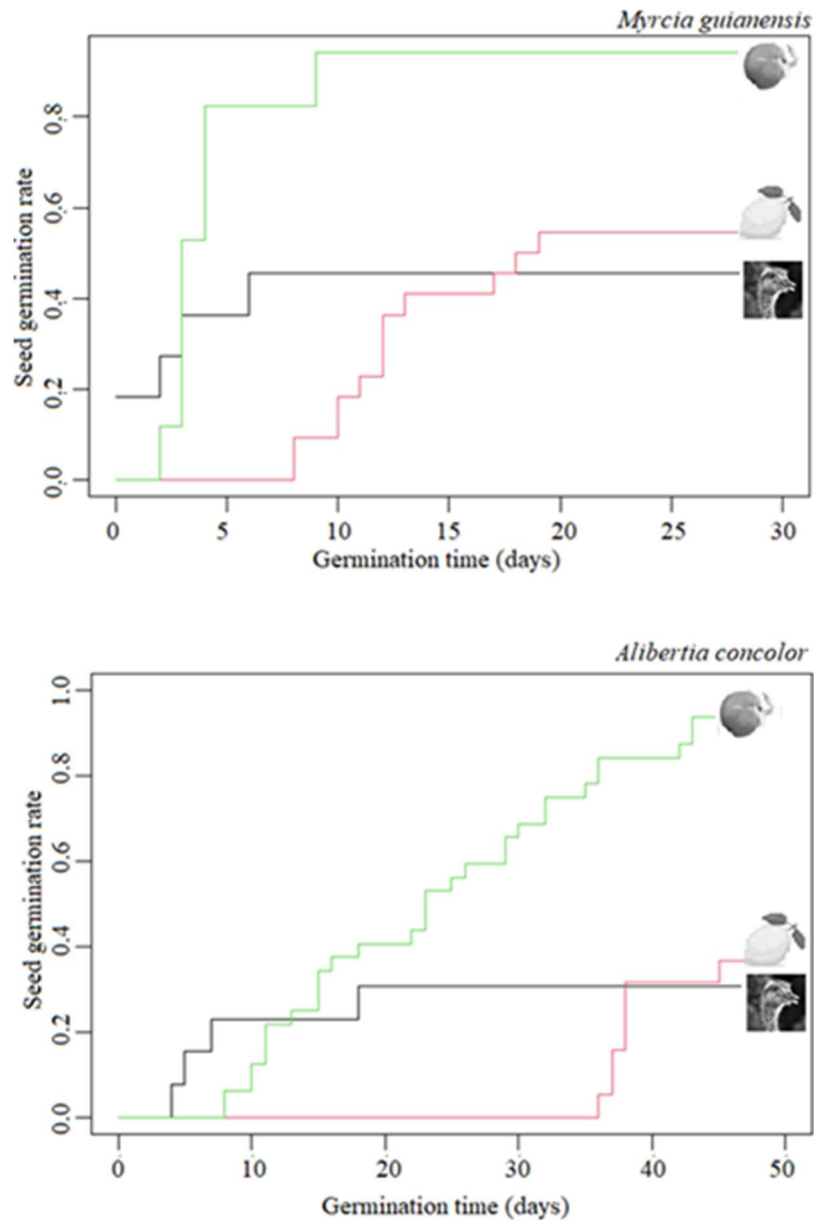


Figure 5: Comparisons of germination speed among seeds ingested by Rheas (T) (design with Rhea), seeds embedded in fruit pulp (C1) (design with the whole fruit and manually de-pulped seeds (C2) (design of the seed only). Speed of seed germination of *Myrcia guianensis* (T versus C1: $X^2 = 7.27$, $p = 0.006$; T versus C2: $X^2 = 1.47$, $p = 0.20$) and *Alibertia concolor* (T versus C1: $X^2 = 28.34$, $p = 0.0001$; T versus C2: $X^2 = 9.41$, $p = 0.002$).

5.1 Tables

Table 1. Fruit species offered to *R. americana* and subsequent output after ingestion. Gut passage time (GPT) is reported as mean $\pm$ SD in hours for each plant species. Results of germination experiments for three treatments: T: ingested by Rheas; C1 and C2 are the seeds embedded in fruit pulp and manually de-pulped seeds that were sowed as controls, respectively. Number of seeds used in each treatment followed by the number of seeds germinated (under parenthesis). The symbol * denotes the species for which it was possible to carry out survival analyzes given sample sizes.

Plant Species	Fruits offered (ingested)	GPT (hours)	T	C1	C2
<i>Aegiphila verticillata</i>	40(40)	81 $\pm$ 34.0	22(0)	10(0)	13(0)
<i>Ocotea pulchella</i>	30(14)	77.7 $\pm$ 43.7	14(0)	15(0)	15 (6)
<i>Erythroxylum pelleterianum</i>	30(25)	64 $\pm$ 28.5	21(1)	24 (6)	24 (13)
<i>Myrcia guianensis</i> *	37(30)	55.3 $\pm$ 22.0	11(5)	22(11)	17(16)
<i>Campomanesia adamantium</i>	10(4)	38.3 $\pm$ 17.7	15(1)	6(5)	14(10)
<i>Alibertia concolor</i> *	20(2)	46 $\pm$ 17.3	13(4)	30 (30)	15 (6)
<i>Myrsine guianensis</i>	15(9)	70.2 $\pm$ 52.0	5(0)	20 (3)	29(17)
<i>Byrsonima intermedia</i>	61(61)	54.5 $\pm$ 30.1	35(0)	10(0)	10(0)

<i>Schinus terenbinthifolia</i>	100(100)	74.8 ± 21.6	40(1)	32(11)	32(26)
<i>Amaioua guianensis</i>	12(8)	52.2 ± 16.0	95(0)	0	92(72)
<i>Smilax polyantha</i>	100(100)	61.3 ± 20.0	67(0)	82(0)	0

Table 2. Final germination (%) and speed (mean in days) of seed germination for the three treatments applied to eleven plant species from Cerrado: T (seeds that passed through *R. americana*), C1 (seeds embedded in fruit pulp) and C2 (manually de-pulped seeds). The symbol * means the values that were possible to carry out survival analyzes because of sample size.

Plant species	% Germination (T)	% Germination (C1)	% Germination (C2)	Germination speed (T)	Germination speed (C1)	Germination speed (C2)
<i>Myrcia guianensis</i>	36	54	94	2.2*	12.5	4
<i>Erythroxylum pelleterianum</i>	2.4	19	40	6	13	11
<i>Campomanesia adamantium</i>	6	83	71	5	34	6
<i>Alibertia concolor</i>	13	37	100	8.5*	37	15
<i>Schinus terebinthifolia</i>	2.5	25	81	5	5.5	29
<i>Ocotea pulchella</i>	0	0	50	0	0	20
<i>Smilax polyantha</i>	0	0	0	0	0	0
<i>Amaioua guianensis</i>	0	0	65	0	0	47
<i>Byrsonima intermedia</i>	0	0	0	0	0	0
<i>Myrsine guianensis</i>	0	0	31	0	57	35
<i>Aegiphila verticillata</i>	0	0	0	0	0	0

5.2 Supplementary material

Table S1: Description of fruit species used in feeding trials with captive Rheas. GPT = gut passage time (in hours). Values refer to fleshy fruits and seeds. Lengths and widths in cm, weights in g and lipid content in g/100g. All values are means, otherwise indicated.

Plant species	Min/max GPT	GPT	Fruit length	Fruit width	Fruit weight	Seed length	Seed width	Seed weight	Lipid content	Number of seeds per fruit
<i>Aegiphila verticillata</i>	22.0/144.3	81.1	0.70	0.49	0.0960	0.56	0.34	0.0350	21.90	1
<i>Ocotea pulchella</i>	23.0/167.4	77.71	1.08	0.62	0.1942	0.91	0.54	0.1396	33.30	1
<i>Schinus terenbinthifolia</i>	25.5/119.5	74.87	0.77	0.92	0.4182	0.54	0.60	0.1107	5.35	1
<i>Myrsine guianensis</i>	41.7/161.6	70.17	0.40	0.39	0.0394	0.37	0.34	0.0251	5.90	1
<i>Erythroxylum pelleterianum</i>	19.0/111.1	64.12	0.68	0.53	0.1173	0.61	0.37	0.0447	31.40	1
<i>Smilax polyantha</i>	22.0/117.5	61.66	0.91	0.84	0.3050	0.53	0.48	0.0613	18.80	1
<i>Byrsonima intermedia</i>	22.0/117.8	54.5	0.77	0.92	0.4182	0.54	0.60	0.1107	27.50	1
<i>Myrcia guianensis</i>	23.0/94.8	55.29	0.84	0.73	0.2480	0.56	0.46	0.0798	29.30	1
<i>Amaioua guianensis</i>	22.0/117.5	52.26	1.75	0.83	0.4740	0.37	0.33	0.0115	5.10	14

<i>Alibertia concolor</i>	16.6/88.6	46.09	2.22	1.56	2.6837	0.52	0.38	0.0267	0.63	15
<i>Campomanesia adamantium</i>	17.6	38.33	1.14	1.15	0.8219	0.50	0.37	0.0360	1.50	4

Table S2: Spearman rank correlations among all variables (dependent and independent). Statistically significant numbers (equal to 1) are in bold.

-	Fruit Length (cm)	Fruit Width (cm)	Fruit Weight (g)	Seed Length (cm)	Seed Width (cm)	Seed Weight (g)	Germination Percentage (%)
GPT	- 0.65	-0.85	-0.88	0.43	0.01	0.16	-0.44
-	Fruit Length (cm)	0.81	0.89	-0.07	0.07	0.00	0.20
-	-	Fruit Width (cm)	0.95	-0.10	0.36	0.17	0.34
-	-	-	Fruit Weight (g)	-0.15	0.12	0.02	0.25
-	-	-	-	Seed Length (cm)	0.41	0.78	-0.02
-	-	-	-	-	Seed Width (cm)	0.81	0.07
-	-	-	-	-	-	Seed Weight (g)	- 0.02
-	-	-	-	-	-	-	Germination Percentage (%)

6.0 Conclusão

A análise da dieta da ema revelou uma diversidade em sua alimentação, incluindo material vegetal, frutos, sementes, invertebrados e vertebrados. Essa variedade reflete a importância da ema como dispersora de sementes de espécies de plantas nativas contribuindo para a regeneração e manutenção das paisagens naturais.

As aves de grande porte, como as emas, são animais importantes nas interações ecológicas e nos processos de dispersão de sementes nos ecossistemas. As características físicas das emas, aliadas ao seu longo tempo de passagem gastrointestinal, tornam-nas agentes eficazes na dispersão de sementes, desempenhando um papel semelhante ao de mamíferos de grande porte. No entanto, o declínio das populações de emas em vastas áreas representa uma ameaça à manutenção da biodiversidade e aos processos ecossistêmicos. A perda dos serviços de dispersão de sementes das emas pode ter consequências de longo prazo, afetando a capacidade das plantas de colonizar novos locais e conectar populações através da dispersão. Portanto, a conservação das emas é crucial não apenas para garantir sua sobrevivência, mas também para a preservação da biodiversidade e da integridade dos ecossistemas como o Cerrado e o Pantanal. Investigações mais aprofundadas sobre o papel das emas na dispersão de sementes, como neste estudo, fornecem *insights* valiosos para a conservação e gestão dos ecossistemas naturais, destacando a necessidade urgente de proteger essas espécies e seus habitat.