

UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM ENTOMOLOGIA

“Natural history and phenotypic variation of *Metaphotina brevipennis*
(Sassure 1872) (Acontistidae, Mantodea)”

“História Natural e Variação Fenotípica de *Metaphotina brevipennis* (Sassure 1872)
(Acontistidae, Mantodea)”

Drielly da Silveira Queiroga

Tese apresentada à Faculdade de Filosofia,
Ciências e Letras de Ribeirão Preto da
Universidade de São Paulo, como parte das
exigências para obtenção do título de
Doutor em Ciências, obtido no Programa
de Pós-Graduação em Entomologia

Ribeirão Preto - SP

(2022)

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Orientador: Kleber Del Claro

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DEDICATÓRIA

Dedico essa tese, assim como tudo que hoje sou capaz de fazer, à memória de minha querida vó Nilza. Obrigada pelos olhos que me deu para enxergar a vida e a beleza na natureza.

Agradecimentos

Essa tese é muito mais o fruto de toda uma trajetória do que dos últimos quatro anos, então não teria como eu deixar de agradecer a quem me deu a base para trilhar esse caminho com os próprios pés. Por isso, primeiramente eu quero agradecer às mulheres da minha vida: A minha avó Nilza (in memória), minha mãe Rosi, minha tia Tereza e minha dinda Simone. Mulheres que são a minha família, que me criaram e educaram para que eu tivesse liberdade de buscar meus sonhos. Delas eu herdo o valor mais importante que nos foi passado pela minha avó: a educação. Minha avó analfabeta, me repetia todas as vezes “a sua única obrigação é estudar”. Ela que não teve essa oportunidade na vida, junto com minha mãe, tia e dinda, me deram todas as ferramentas para alçar meus voos e, com isso, a oportunidade de me apaixonar pela carreira de bióloga e cientista. Dessa forma, nada do que eu seja ou produza tem sentido se não for dedicado a elas.

Nessa caminhada não posso esquecer de agradecer ao meu parceiro Renan Moura, quem tem me dado apoio e incentivo em todos os aspectos dessa vida que partilhamos há 10 anos. Obrigada por todos os momentos em que você foi minha rocha, que me ergueu e entendeu minhas fraquezas. Para além do nosso relacionamento, eu também te admiro como cientista e tenho em você um dos exemplos que busco ser. Obrigada por estar comigo durante essa tese, seja no suporte emocional ou no suporte científico que me deu.

Eu vou agradecer brevemente aqui à minha maior fonte de estresse e prejuízo financeiro, que não vai ler essa tese, mas também que pouco se importa se eu tenho um doutorado ou não porque vai me amar de qualquer jeito: Tau. Assim como Renan, esse ser de quatro patas com a ficha médica veterinária mais longa que você provavelmente já viu, está comigo há 10 anos. Mesmo sem palavras, sua companhia foi fundamental para que eu me mantivesse firme todo esse tempo. Eu adoraria que você não tivesse arrumado

problema e passado por uma cirurgia na semana que eu tinha que entregar essa tese, mas também sei que sem você talvez eu não tivesse tido forças para chegar tão longe. Afinal, quem pode se dar ao luxo de desistir tendo que sustentar um cachorro gastão desses? É por isso que eu dedico essa tese a você também, Tau, meu pedacinho mais puro de amor.

Também é impossível não agradecer à uma das surpresas mais lindas que me mudar para o interior de Minas propiciou: conhecer a menina do sorriso doce e mão pesada que se tornou a melhor parceira de campo que eu poderia ter. Claire, obrigada pela força nas coletas, por não me deixar desanimar e bater puçá no mato para mim quando eu estava chorando depois de cinco dias sem pegar nenhum louva-a-deus. A gente compartilhou muito desespero, mas também risadas e amizade. Obrigada Renan por me apresentar à Claire e obrigada Claire por nunca mais ter saído da minha vida.

Vou mencionar aqui também a ajuda fundamental que tive dos colegas de laboratório Vitor Miguel, Iasmim, Danilo, Isa, Fernando e tantos outros pela ajuda em cuidar dos louva-a-deus quando tinha campo ou que me ausentar e a toda a galera do LECI. Principalmente Vitor e Iasmim, que foram os mais requisitados ao longo desses quatro anos. Obrigada por disporem do seu tempo e carinho com os meus bebês.

Agradeço aqui a professora Maura que sempre me atendeu com o maior carinho e paciência. Mesmo nas perguntas mais simples ou dúvidas mais bobas, você sempre me forneceu a mais paciente e detalhada das explicações. Também à professora Vanessa Sul Moreira, por toda a sua empolgação, ideias e tutoria. Trocar ideia com você sempre foi uma porta de inspiração e fôlego novo. Cada uma a seu jeito, ambas são inspirações para mim na carreira de cientista.

Agradeço também as minhas amigas Fabi, Gabi, Pamella e aos amigos do “Bertelas United” Arthur, Egon, Ruthe e Lino pelas risadas, jogos de RPG e debates sobre quem tem a vida mais complicada ou está mais duro de dinheiro. Aos amigos do “Uai, Sô

tô sem assunto”, pelas conversas mais aleatórias e sem sentido que me faziam relaxar nos momentos de surto.

Quero agradecer ao professor Nathan Morehouse pela tutoria durante o intercâmbio, as conversas instigadoras e inspiradoras que me fizeram apaixonar pela área de ecologia sensorial. Obrigada por receber de braços abertos alguém que você se quer conhecia e ter dedicado seu tempo à minha formação.

Em conjunto, quero agradecer aos folks do Morehouse Lab, em especial Jenny, Olivia, David e Dennis, pelas conversas, risadas e por me acolherem tão bem durante o tempo que estive aí. It was awesome to spend this time with you guys. Thank you for having me and make it a wonderful time. Send my regards to Yumi, Maple and Shirley too.

Gostaria de agradecer também ao Dr. Antônio Agudelo por me receber no INPA e me ensinar os conceitos chaves que necessitaria para identificação de Mantodea, à Cesar Favacho pela identificação de alguns táxons e ao Dr. Júlio Rivera pelas discussões e ideias que agregaram na tese.

Nessa trajetória, não posso esquecer de incluir aqui os colegas do curso de Pós-graduação em Entomologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, ao professor Eduardo Almeida pela pronta ajuda em todas as questões que solicitei, principalmente no período do intercâmbio. Também agradeço ao professor Fabio Nascimento pela ajuda durante a formação de parceria entre a USP e a University of Cincinnati, onde realizei meu intercâmbio.

Também na USP tem uma pessoa que é impossível não agradecer, pois sem ela dificilmente eu teria conseguido realizar o sonho do intercâmbio e ter passado por esse doutorado da melhor forma possível. Por isso, eu quero agradecer à Renata Cavallari, secretária do PPG em Entomologia. Rê, eu nunca vou ter palavras para agradecer a todo

o seu carinho, atenção e dedicação comigo e com todos na Entomologia. Eu te disse uma vez e repito: você é uma daquelas poucas pessoas que fazem a diferença de verdade. Ter cruzado meu caminho com o seu foi uma das maiores loterias que ganhei. Sou muito grata por toda a ajuda que me estendeu.

Gostaria de agradecer às administrações dos lugares em que coletei, o clube Caça e Pesca Itororó de Uberlândia, ao Parque Estadual Serra de Caldas Novas, administrado pela Secretaria de Meio Ambiente de Goiás, por me fornecerem as permissões de acesso e coleta nas reservas.

Agradeço também à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) e ao seu Programa de Internacionalização (PrInt) pelas bolsas concedidas para a execução dessa tese e intercâmbio.

Por último e não menos (na verdade, muito importante, por isso que deixei por último para fazer mistério), gostaria de agradecer ao meu professor e orientador Kleber Del Claro. Kleber é uma das poucas pessoas que conheci que, ao invés de lhe cortar as asas, te dá o impulso para voar mais longe. Me orientou no mestrado, em um projeto que não era usual do seu campo, mas nunca me impediu de fazer o que eu acreditava, sempre topando as minhas empreitadas doidas. No doutorado não foi diferente. Eu havia me encantado com louva-a-deus e Kleber não só nunca tinha trabalhado com esses bichos, como sabia que seria muito difícil encontrar alguma parceria para me ajudar. Ele viu meu projeto, explicou as limitações e ao invés de dizer um “não”, ele me disse “vai pra casa, pensa nisso e semana que vem a gente conversa”. Na semana seguinte eu voltei com um projeto sobre a comunidade de louva-a-deus no Cerrado e apresentei para ele. Qualquer outro orientador teria olhado para a minha cara, me chamado de doida e me dado só duas opções: troca de projeto ou troca de orientador, mas Kleber me ofereceu a terceira, que foi: “Se é isso que você realmente quer, vamos fazer”. Eu nunca vou esquecer esse dia,

esse voto de confiança, que se traduziu não só nessa tese, mas em um intercâmbio e uma oportunidade de carreira no exterior, todos frutos dessa escolha. Mesmo dizendo que não entendia de louva-a-deus, o seu entendimento de história natural, de ecologia, comportamento, de dinâmicas e interações no Cerrado foi mais do que o suficiente para me guiar durante a tese. Por isso, Klebão, eu vou ser eternamente grata a você. Obrigada por me inspirar, por me orientar e por, acima de tudo, acreditar em mim.

FICHA CATALOGRAFICA

Queiroga, Drielly da Silveira

Natural history and phenotypic variation of *Metaphotina brevipennis* (Sassure 1872) (Acontistidae, Mantodea) , 2022.
80 p.: il.; 30 cm

Tese, apresentada à Faculdade de Filosofia, Ciências e Letras de
Ribeirão Preto. Área de concentração: Entomologia.

Orientador: Del Claro, Kleber

1. Mantodea, 2. Camuflagem, 3. Biology, 4. Tropical Savannah

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RESUMO

Queiroga, D. **História Natural e Variação Fenotípica de *Metaphotina brevipennis* (Sassure 1872) (Acontistidae, Mantodea)**. 2022. Tese (Doutorado em Ciências – Pós-Graduação em Entomologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto Universidade de São Paulo), 2022.

As forças seletivas que moldam a evolução das espécies variam entre ambientes e táxons, propulsionando a biodiversidade. Ambientes altamente sazonais conferem uma pressão seletiva particular ao exigir que os táxons lidem com a inconstância das condições do meio. Nesses ambientes é comum que as espécies exibam algum grau de plasticidade, podendo essa se refletir na mudança do tempo de desenvolvimento, mudanças comportamentais e até mesmo mudanças morfológicas, como a variação na coloração. Louva-a-deus (Mantodea) são conhecidos por suas estratégias envolvendo coloração, tanto de forma agressiva quanto protetiva. Assim como muitos insetos, seu desenvolvimento e expressão dessas e outras características pode variar com mudanças no ambiente, como a sazonalidade. O Cerrado é uma savana com sazonalidade demarcada por um longo período de seca (maio a outubro), onde as comunidades se alteram fortemente em resposta a esse fenômeno. Dessa forma, essa tese investigou como uma espécie de louva-a-deus do Cerrado, *Metaphotina brevipennis* responde à essas variações temporais e usa seus atributos morfológicos em favor da sua sobrevivência. Nós analisamos diversos fatores relacionados à história de vida dessa espécie, como desenvolvimento, fenologia, comportamento, reprodução e o impacto de inimigos naturais. Também analisamos como a variação na coloração dos indivíduos está distribuída ao longo das estações, a influência dos morfos no comportamento e seu potencial para camuflagem. Nossos resultados indicam que *M. brevipennis* possui estratégias plásticas, com populações variando fenologicamente entre locais e ao longo do tempo, mostrando alta adaptação à sazonalidade do Cerrado. Ao descrever pela primeira vez a história natural de um louva-a-deus do Cerrado, nós esperamos que este estudo sirva de inspirações para outros futuros, abordando questões sobre a regulação dessa plasticidade e os mecanismos chaves que a desencadeiam.

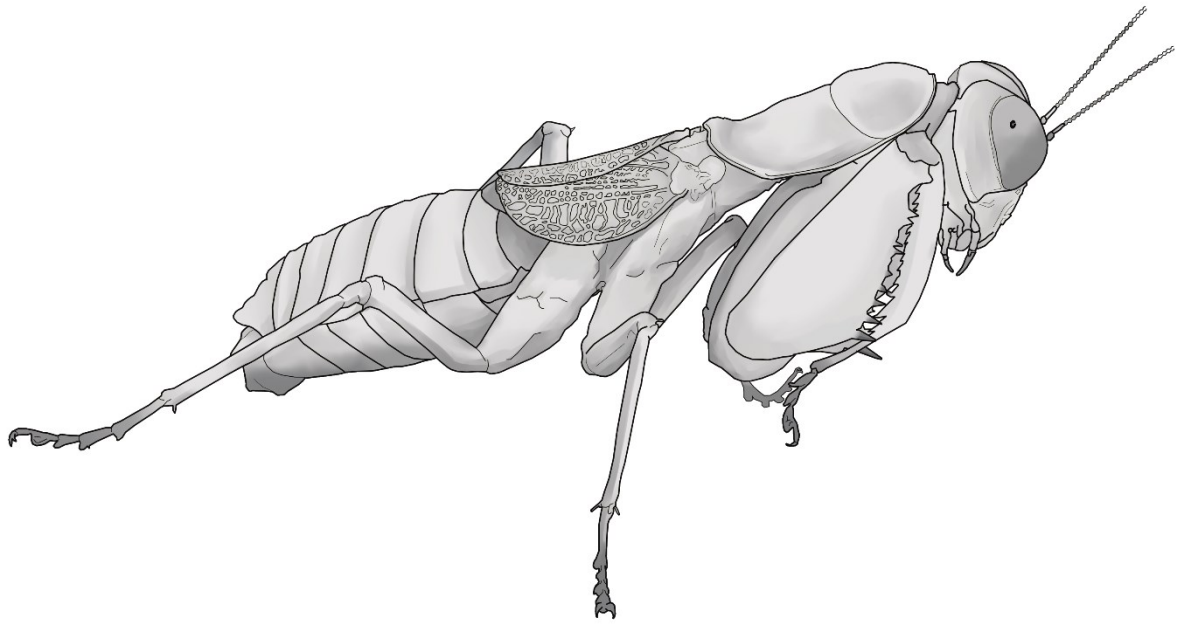
Palavras Chaves: Mantodea, camuflagem, biologia, savana tropical

ABSTRACT

Queiroga, D. **Natural history and phenotypic variation of *Metaphotina brevipennis* (Sassure 1872) (Acontistidae, Mantodea)**. 2022. Tese (Doutorado em Ciências – Pós-Graduação em Entomologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão preto Universidade de São Paulo), 2022.

Selective forces that shape the evolution of species vary between environments and taxa, being a key driver of biodiversity. Highly seasonal environments provide additional selective pressure by requiring taxa to cope with changes in environmental conditions. In such environments, it is common for species to exhibit some degree of plasticity, which might reflect changes in developmental time, behavior, and morphological changes, such as color variation. Praying mantises (Mantodea) are known for their strategies involving color in aggressive and protective behaviors. Like many insects, their development and other traits can be affected by changes in the environment, such as seasonality. The Cerrado is a savanna with a remarkable dry season (May to October), where plants and animals respond by altering a variety of life traits to deal with its seasonality. Thus, this thesis investigated how a species of Cerrado mantis, *Metaphotina brevipennis* responds to these temporal variations and uses its morphological attributes in favor of its survival. We analyzed several factors related to the life history of this species, such as development, phenology, behavior, reproduction, and the impact of natural enemies. We also analyzed how the variation in the color of individuals is distributed over the seasons, whether their color leads to behavioral differences in habitat choice, and whether it enhances their camouflage. Our results indicate that *M. brevipennis* is highly plastic in its strategies, and populations vary phenologically between locations and over time, showing high adaptation to Cerrado seasonality. By describing for the first time the natural history of a Cerrado mantis, we hope this study serves as inspiration for future ones, addressing questions about the regulation of this plasticity and the key mechanisms behind it.

Keywords: Mantodea, camuflagem, Biology, tropical Savannah



INTRODUÇÃO GERAL

Os insetos predominam em quase todos os habitats terrestres, tanto no número de táxons, quanto na diversidade de ambientes e funções que podem desempenhar, ocupando diversos níveis nas cadeias tróficas (Stork 1988, Price et al. 2011). Quando tratamos de organismos predadores, os insetos se destacam por sua participação nos processos evolutivos e na funcionalidade de praticamente todos os ecossistemas (Grimaldi and Engel 2005). Em especial, os insetos predadores generalistas desempenham um papel ainda maior nas teias alimentares, podendo se envolver na competição por recursos, predação intra-guilda e canibalismo (para exemplos ver Fagan et al. 2002). Assim, acabam pertencendo simultaneamente à mais de um nível trófico, o que colabora para a estabilidade das redes ecológicas (Gullan and Cranston 2012).

Um dos exemplos mais clássicos e carismáticos de predadores generalistas entre os insetos são os mantódeos (Beckman and Hurd 2003). Como para a maioria dos predadores, a principal pressão seletiva sobre os mantódeos é a limitação alimentar, ditada pela disponibilidade de presas no ambiente (Hurd 1999). Esses organismos desenvolveram ao longo da evolução estratégias comportamentais e morfológicas para lidarem com a diversidade de presas, colonizando ambientes temperados e tropicais (Loxton and Nicholls 1979; Svenson and Whiting 2004). O valor e o impacto das diferentes estratégias do grupo têm sido estudados principalmente quanto à sua camuflagem agressiva (Barabás and Hancock 1999; O'Hanlon et al. 2014; Agudelo and Rafael 2014) e agressividade intraespecífica (Barry 2015). Outros estudos abordam a sua taxonomia e as relações filogenéticas das espécies (Ippolito et al. 2015; Svenson et al. 2015; Agudelo et al. 2015), porém pouco se aborda sobre o papel da sua morfologia (Loxton and Nicholls 1979) e mecanismos de seleção de presas (Nelson et al. 2006).

A maior parte das informações tidas a respeito de mantódeos refletem apenas as características de algumas poucas espécies estudadas mais profundamente (Rivera and

Svenson 2014). O canibalismo, por exemplo, é um evento incomum e registrado majoritariamente para espécies em ambientes temperados (Barry 2015; Raut and Gaikwad 2016; Kadoi et al. 2017), assim como o uso de pólen na alimentação (Beckman and Hurd 2003). Por outro lado, algumas estratégias são comuns na ordem e estão relacionadas filogeneticamente, como o comportamento de busca de presas (Svenson and Whiting 2004). Enquanto o hábito cursorial é comum em espécies de ambiente aberto (Milledge 1990) e parece ser uma característica plesiomórfica do grupo, a estratégia de espreita (Matsura and Inoue 1999) surgiu como uma especialização em táxons mais recentes, muito provavelmente junto com a ornamentação corporal para a camuflagem (Vidal-García et al. 2020). Essas características refletem adaptações que, muito provavelmente, podem influenciar na seleção de presas e de habitats que irão ocupar.

A maioria dos animais se distribui de forma aleatória no espaço, mas sua prevalência em determinados ambientes está relacionada com características bióticas e abióticas em seu micro-habitat (Pennings et al. 1998). As características bióticas incluem a diversidade de organismos com quais os animais estudados se relacionam (Mangel 1990; Martín and Salvador 1997), enquanto as características abióticas incluem a complexidade de fatores do ambiente (Hill et al. 2004; Perea et al. 2007). O termo estrutura de habitat se refere às variações que podem ser encontradas naquele ambiente estudado, que ocorrem principalmente quanto à forma, cor, textura e tamanho (Eterovick et al. 1997). Assim, a seleção de habitat em animais funciona através de decisões comportamentais do indivíduo baseadas na qualidade dos diferentes habitats disponíveis (Brown and Orians 1970).

Para mantídeos, estudos apontavam a preferência para ambientes complexos estruturalmente (Prete 1999). Entretanto, Hill et al. (2004) encontraram resultados

inversos em uma espécie cursorial, sugerindo que a escolha do habitat pode estar ligada principalmente à estratégia de forrageio adotada. Em uma outra via, Brown e Orians (1970) discutem que essas decisões podem ser alteradas devido à presença dos componentes bióticos, como quando os coespecíficos funcionam como sinalizadores da qualidade do habitat em locais onde a disponibilidade é variável (Stamps 1987, 1988). Essa forma de sinalização também pode ser benéfica ao prevenir encontros não desejáveis, evitando os custos da competição em ambientes com maior disponibilidade de habitats (Castelo et al. 2003). Ainda há a possibilidade de que as escolhas sejam influenciadas pelas variações individuais na personalidade dos animais (Gosling 2008), embora esse campo não tenha sido explorado em muitos táxons.

Experimentos que investigam a influência do componente biótico nas escolhas de habitat são raros em mantódeos. Um dos poucos exemplos é o de O'Hanlon (2011) que testou a interferência coespecífica em *Ciulfina biseriata*, uma espécie australiana, que habita troncos onde geralmente é encontrado apenas um indivíduo (Holwell 2006). Nesta espécie, machos tendem a preferir troncos de árvores onde há uma parceira potencial, evitando troncos ocupados por outros machos, enquanto fêmeas tendem a evitar troncos ocupados por qualquer um dos sexos (O'Hanlon 2011). Em uma outra forma de explorar sinais bióticos, ninfas de *Tenodera ardifolia sinensis* usam pistas químicas de presas e complexidade visual do habitat para orientar seus padrões de movimento e micro-habitats escolhidos (Wilder 2005). A escolha do micro-habitat pode variar de acordo com fase da vida e atividade desempenhada. (Lin and Grieleber 2016), e muitas vezes os mantódeos irão ter escolhas específicas por um fundo ambiental, independente da disponibilidade dele no local (Lin and Grieleber 2016). É possível que esse comportamento de escolha específica por um habitat, ou “fundo”, independente da

disponibilidade deste, confira vantagens na sobrevivência dos louva-a-deus, sendo um tópico que merece atenção.

Um outro fator importante para muitos animais é a cor. A coloração animal tem diversas funções, como termorregulação e comunicação (Cott 1940). Estes mecanismos de seleção estão relacionados com a evolução da comunicação, através da sinalização e do desenvolvimento dos sistemas sensoriais (Stevens et al. 2009). São resultado de diversas formas de seleção, principalmente a seleção natural e a seleção sexual (Zamora-Camacho e Comas 2019).

Além de ser uma forma de atrair ou alertar, as cores também podem funcionar de forma oposta, escondendo o organismo no processo de camuflagem (Cott 1940, Stevens and Merilaita 2009). Podemos dizer que um animal está críptico ou camuflado, quando este se confunde com o pano de fundo ambiental onde se encontra (“background matching”), do ponto de vista de um predador orientado visualmente (Endler 1988, Merilaita and Dimitrova 2014. Figura 1). Dessa forma a camuflagem pode ser entendida como uma defesa distal, um mecanismo usado para dificultar a detecção dos organismos, podendo envolver a coloração corporal, estruturas morfológicas, compostos químicos, comportamento e material encontrado no ambiente (Dettner 1994; Nakahira and Arakawa 2006; Ruxton 2009; Silveira et al. 2010).

Uma das características mais notáveis em mantódeos é sua capacidade de camuflagem (Prete 1999). Seus padrões de coloração e forma podem envolver a camuflagem por semelhança ou disruptiva (Prete 1999, Stevens 2009). Na coloração disruptiva, cores e formas (tais como manchas), produzem uma quebra nos contornos do corpo do animal tornando difícil sua identificação por predadores visuais (Barabás and Hancock 1999; O’Hanlon et al. 2014, Videl-García et al. 2020). No grupo há espécies possivelmente miméticas de formigas (Scherrer and Aguiar 2021), além das que exibem

semelhanças protetivas especiais (*sensu* Cott 1940) se assemelhando a flores, como forma de camuflagem ofensiva (Agudelo and Rafael 2014, O'Hanlon et al. 2014, Svenson et al. 2015).

Nos louva-a-deus a camuflagem se apresenta em diferentes níveis de complexidade, a depender de cada tipo de presa ou predador alvo (Agudelo Rondón et al. 2007). O'Hanlon et al. (2014), ao estudarem o louva-a-deus orquídea *Hymenopus coronatus*, encontraram pela primeira vez um caso de “camuflagem”¹ floral em mantódeos. Segundo este estudo, *H. coronatus* apresenta o mesmo padrão de reflectância de orquídeas locais, além de atrair polinizadores sem a necessidade do fundo ambiental para a camuflagem. Este estudo é apenas um exemplo de como as estratégias de cripticidade do grupo podem ser refinadas.



Figura 1: Exemplo de camuflagem em Mantodea. Quando o padrão de coloração do animal o confunde com o plano de fundo ambiental onde está inserido, dificultando sua identificação por um predador orientado visualmente. Foto: Kleber Del Claro

¹ Apesar do autor se referir à mimetismo floral, na maioria das definições o termo mimetismos deve ser empregado apenas quando um animal imita outro animal. Se parecer com qualquer outra estrutura do habitat, mesmo que de forma impressionante, trata-se de semelhanças protetivas especiais (*sensu* Cott 1940)

Apesar de uma das habilidades mais notáveis sobre mantódeos ser relacionada à camuflagem (Svenson and Whiting 2009; Fatimah et al. 2016; Raut and Gaikwad 2016), poucos estudos tem investigado a eficiência e os diferentes níveis de complexidade dessa estratégia encontrados no grupo (Barabás and Hancock 1999; O’Hanlon et al. 2014).

Apesar das estratégias envolvendo coloração serem as mais chamativas, informações básicas de história natural ainda são escarças para o grupo (Rivera and Svenson 2020). Com cerca de 2.300 espécies agrupadas em 434 gêneros, os Louva-a-deus *Praying mantids*, *mantis* (eng.), e tantos outros nomes, referem-se à animais da subordem Mantodea, filogeneticamente relacionados com baratas (Blattodeas) e cupins (Isoptera) dentro do clado Dictyoptera. São encontrados em uma ampla variedade de ambientes (Hurd 1999) e exibem uma ampla diversificação morfológica, de estratégias de predação e especialização de habitat (Svenson and Whiting 2004).

Para a região neotropical são descritas cerca de 474 espécies agrupadas em 91 gêneros e seis famílias, sendo para o Brasil registada 251 espécies, em 69 gêneros (Agudelo Rondón et al. 2007). Nem todas as espécies registradas para o Brasil possuem a região de coleta ou o bioma pertencente, sendo difícil estimar a riqueza do táxon pelos biomas e regiões do país. Esses dados ainda podem estar subestimados devido ao número de estudos desbalanceados entre os biomas, com a maior parte deles acontecendo na região amazônica e da Mata Atlântica, deixando as outras regiões com alguns poucos registros (Figura 2). O Cerrado, em especial, é um dos ambientes mais diversos do Brasil, porém o número de espécies de louva-a-deus atribuídas a esse bioma é baixo (Figura 2). As espécies de mantódeos que ocorrem nesse ambiente devem estar adaptadas à sua marcante sazonalidade e longos períodos de seca (sazonalidade cerrado). Essas condições podem ter atado como pressões seletivas sobre a ordem,

propiciando o surgimento de estratégias novas e únicas, que só poderão ser entendidas através do estudo da história de vida desses organismos (Del-Claro et al. 2013).

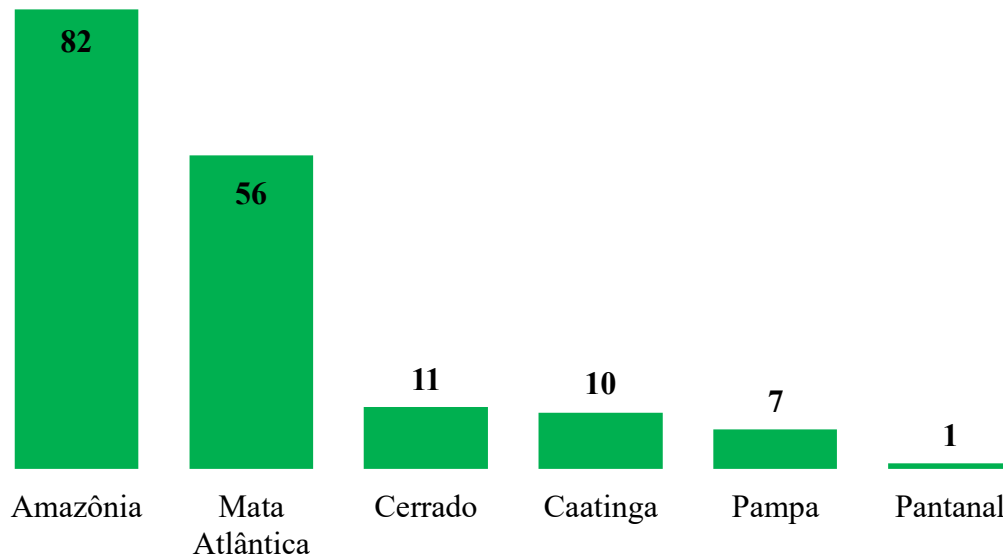


Figura 2: Riqueza de espécies de mantódeos registradas para cada bioma brasileiro. Fonte: Agudelo AA 2022. Mantodea in Catálogo Taxonômico da Fauna do Brasil. PNUD. Disponível em: <<http://fauna.jbrj.gov.br/fauna/faunadobrasil/348>>. Acesso em: 10 Out. 2022

Dessa forma, a presente tese tem como objetivo elucidar alguns dos caminhos evolutivos e estratégias adotadas por uma espécie de louva-a-deus no Cerrado através da descrição da sua biologia e história natural. Utilizamos *Metaphotina brevipennis* (Acontistida, Mantodea), uma espécie de Mantodea, para testar hipóteses relacionadas à sua distribuição temporal, preferência por habitat e como um dos atributos mais marcantes em louva-a-deus, a cor, é explorada em um ambiente sazonal como o Cerrado.

No capítulo 1, **Natural History and Biology of *Metaphotina brevipennis* (Sassure 1872) (Acontistidae, Mantodea) in Cerrado**, discutimos aspectos da história natural de *M. brevipennis*, como a flutuação populacional dessa espécie em duas áreas de Cerrado, sua fenologia e período reprodutivo. Partindo de observações em

laboratório, pudemos estimar o tempo de vida dos sexos, o número de instares pelos quais essa espécie passa até a fase adulta e seu comportamento. Fornecemos dados também dos seus inimigos naturais e nota sobre os efeitos do fogo no Cerrado sobre a dinâmica dessa espécie.

No capítulo 2, **Seasonal color variation and camouflage in a praying mantis from the Brazilian**, nós abordamos como que a variação na coloração das fêmeas se dá ao longo das estações do ano no Cerrado. Utilizamos de experimentos em laboratório para avaliar se essa espécie possui preferências em relação ao seu micro-habitat e se essas preferências são preditas pela cor. Finalmente, usamos dados de refletância de machos e fêmeas de *M. brevipennis* para entender o quão crípticos eles podem estar sob a visão das suas principais presas e predadores no ambiente natural.

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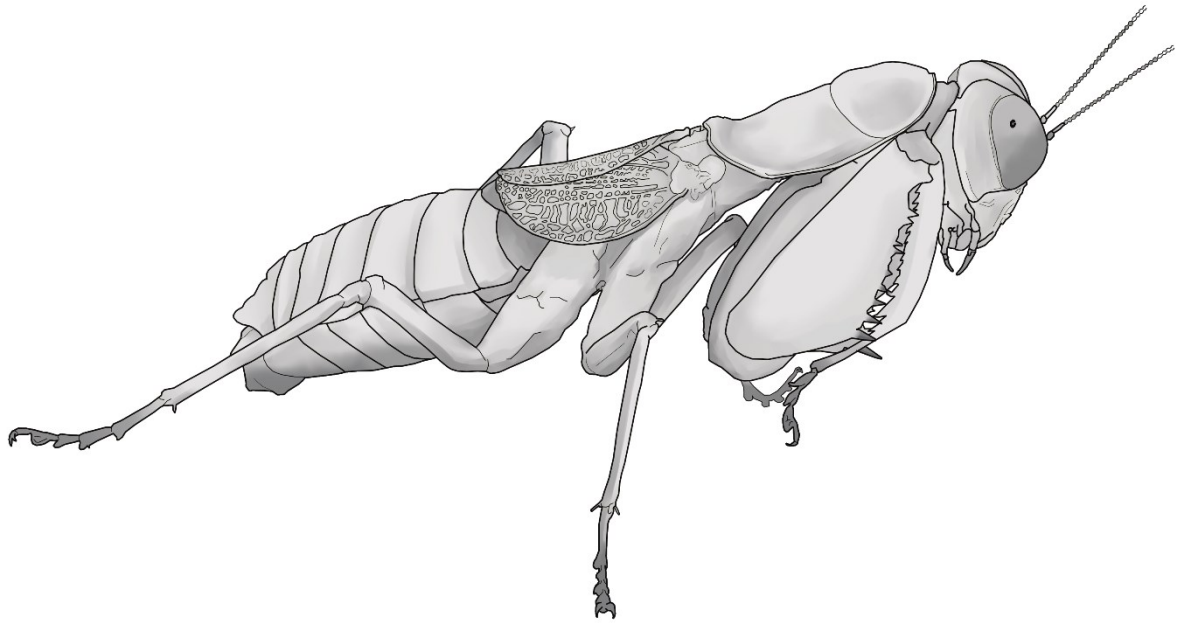
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CAPÍTULO I

Natural History and Biology of *Metaphotina brevipennis* (Sassure 1872)

(Acontistidae, Mantodea) in Cerrado.

Drielly Queiroga and Kleber Del-Claro

Abstract

description of a praying mantis in the Cerrado biome. We studied two independent populations of *Metaphotina brevipennis* and described aspects of their population dynamics, phenology, development, reproduction, and natural enemies. We found that *M. brevipennis* adults and nymphs are present the entire year, however the phenology varies between populations, and none of the environmental variables we investigated were related to it. This species has between six to seven molts, and in the first three, they resemble an ant, having the potential to be myrmecomorphic. Female aggressiveness prevented mate in most trials, and no courtship behavior was observed. Tachinid flies were important enemies and parasitized *M. brevipennis* significantly more than other mantis species. We also provided notes on the effect of wildfires in one of the studied populations.

Keywords: Mantid, Phenology, Savanna, Seasonality, Population fluctuation

Introduction

Life history is often influenced by temporal dynamics (Chase 2011, Chesson 2000), which ultimately promotes diversity, by the species turnover over time or by affecting interspecific interactions (Shimadzu et al. 2013). These temporal dynamics are more pronounced in seasonal environments, where the cyclic effects of droughts and wet seasons often rule species traits, such as growth, mortality, and reproduction (McNamara et al. 2008, Tonkin et al. 2017). Species in environments with strong seasonality (e.g., repeatability) of disturbances such as droughts, floods, wildfires (such as savannas), and others, usually undergo selection to synchronism their life-history traits with these disturbance regimes (Cohen 1966, Lytle 2001, Tonkin et al. 2017).

The Cerrado, a Brazilian savanna, is an extremely diverse and endangered environment (Myers 1988). Species adapted to Cerrado (and other strongly seasonal environments), usually are specialized in one season (e.g., wet or dry), which ultimately enhances the turnover of species, by constantly changing the dominant species across seasons (Tonkin et al. 2017). However, how strongly a species will respond to seasonality is also related to its lifespan. According to the propositions of Iwasa and Levin (1995) and Lytle (2001), if a given species has a lifespan that takes around the same time as the seasonal fluctuations of the environment, it is more likely that it will be adapted to the seasonality, synchronizing its development (Tonkin et al. 2017). On other hand, if a species has a too discrepant lifespan than the fluctuation in the environment, seasonality might not strongly influence its life-history traits (Lytle and Poff 2004).

There is a large literature about how taxa deal with seasonality in Cerrado, especially insects (de Resende et al. 2021, Oliveira et al. 2021, Silva et al. 2011, Silva et al. 2015, Queiroz et al. 2022). However, this knowledge is not balanced, with some

orders being well sampled, such as Hymenoptera (Queiroz et al. 2022), while others with almost no information exist. Some cryptic orders are, in fact, poorly studied in any kind of environment (Mashimo et al. 2014), but it is not the case for one of the most charismatic insects: The praying mantis. Mantodeans are insects well widespread, occurring in all continents but Antarctica (Prete et al. 1999). They are often remembered for their remarkable camouflage and big eyes that, thanks to their pseudo pupil, seem to be always looking back at the viewer (Greyvenstein et al. 2020).

Mantises have received little attention in the Neotropics despite the high proportion of known species and little is known about their biology, natural history, behavior, and ecology (Rivera and Svenson 2014). Of all 2.400 known species, 531 occur in the Neotropics and 251, almost half of them, in Brazil (Agudelo 2022, Agudelo et al. 2007, Rivera and Svenson 2020). Although a big part of the Neotropical diversity of praying mantis can be found in Brazil, little is known about their life history and biology. As far we are aware, there is no study about the natural history of mantis in Cerrado, despite the size of this biome and its importance to Brazil's biodiversity.

There are general aspects of mantis that remains unclear, for example, how they interact with other animals. They are, at the same time, predators, and prey for a variety of animals and may play a significant role in shaping communities, by exerting top-down control on their prey and hosts. Mantis can be eaten by a variety of animals, from vertebrates to invertebrates and the opposite is also true (Nyffeler et al. 2017, Reitze and Nentwig 1991). Interestingly, mantises have been reported to even prey on toxic animals (Mebs et al. 2017), evidencing their role as generalist predators.

There are a lot of mantis species that could be studied in Cerrado to start answering these questions. The best candidate among them is, nonetheless, *Metaphotina brevipennis* (Saussure, 1872), a small mantis species from the family Acontistidae

(Giglio-Tos, 1915). This species is well spread in seasonal environments (Rivera and Svenson 2020) and had recently been replaced in the *Metaphotina* genus by Rivera and Svenson (2020). Authors remark that it is unclear what put *M. brevipennis* apart from a sympatric species, *M. bimaculata*, once morphological variation between these two species is extensive and could be an artifact of morphological plasticity rather than characters exclusive from each one (Rivera and Svenson 2020). Currently, both species are separated based on their distribution, with *M. brevipennis* populations occurring from Paraguay to southern Brazil and *M. bimaculata* from Argentina and Bolivia (Rivera and Svenson 2020). Thus, using *M. brevipennis* as a model could help in understanding if exist variation between the biology of these two species or if they behave as one. Besides that, *M. brevipennis* shows some interesting morphological features, such as brachypterous female (Fig. 1) while males have fully developed wings (Heitzman-Fontenelle 1968) and color variation between individuals (Heitzman-Fontenelle 1968). Combined, these traits can lead to a variety of outcomes to deal with a highly seasonal environment.

Our goal was to describe for the first time several aspects of the natural history and population dynamics of Mantodea in two preserved sites in the Cerrado biome. We chose as a model *M. brevipennis* to provide data about how environmental variables affect mantis' species population dynamics and reproduction, their pattern of development, reproductive behavior, and antagonistic pressures.



Figure 1: Female of *M. brevipennis*. It has short wings (brachypterous) with tegminas usually resembling the overall body color while the second pair of wings is brightly colored in red and black

Materials and Methods

Study Sites

We carried out the study between January 2019 and February 2020, every two months, at two different natural reserves in the Cerrado biome: the Clube Caça e Pesca Itororó de Uberlândia (CCPIU; 18°59'08.1"S 48°18'03.5"W) in Minas Gerais state (Fig. 2-B) and the Parque Estadual Serra de Caldas Novas (PESCAN; 17°48'23.7"S 48°42'07.4"W) in Goiás state (Fig. 2-C). The reserves are 190 km apart, separated by their distance and by the Paranaíba river, characterizing two different studied populations for our interest species. The landscape of both sites is composed of typical savanna-like vegetation, with small trees and an abundance of shrubs and grasses (see Lopes et al., 2009; Reu & Del-Claro, 2005 for more details about the reserves). The

climate is tropical Aw type, megathermic, with a rainy season in summer (October to March) and a dry season in winter (April to September) (see Alves-Martins et al. 2012 and Ferrando and Leiner 2017).

Population dynamics and Phenology

We searched individuals of *M. brevipennis* between 06h00 and 18h00 by visual search and using an entomological hand net. We performed visual search by actively looking for mantises on shrubs, small trees (up to 1.90m) and tall grass, and then we used a hand-net on the same areas where we performed visual search, aiming to catch any missed individuals. As mantis are usually scattered through the environment and vegetation can be denser (thus creating more searching areas) across sampling points, we decided to estimate our sampling effort by time. Sampling effort was around 18h per site (2) per campaign (6), totalizing 216h of effort. This effort was employed in an area of approximately 7.9km² in CCPIU and 9.8km² in PESCAN along all samples.

Once an individual was spotted by visual search, it was captured gently by hand or using small plastic vials. We took notes on location and any interactions the individuals would be performing at the time of capture. Individuals caught by hand net were placed in plastic vials and notes on the kind of vegetation we were sampling (grass, shrub, or trees) were taken.

We obtained hourly data on temperature (°C), rainfall (mm), and humidity (%) between 2019 and 2020 for both sites on the webpage of the Instituto Nacional de Meteorologia (INMET). Data about temperature was averaged by month and for rainfall we used accumulated precipitation in each month.

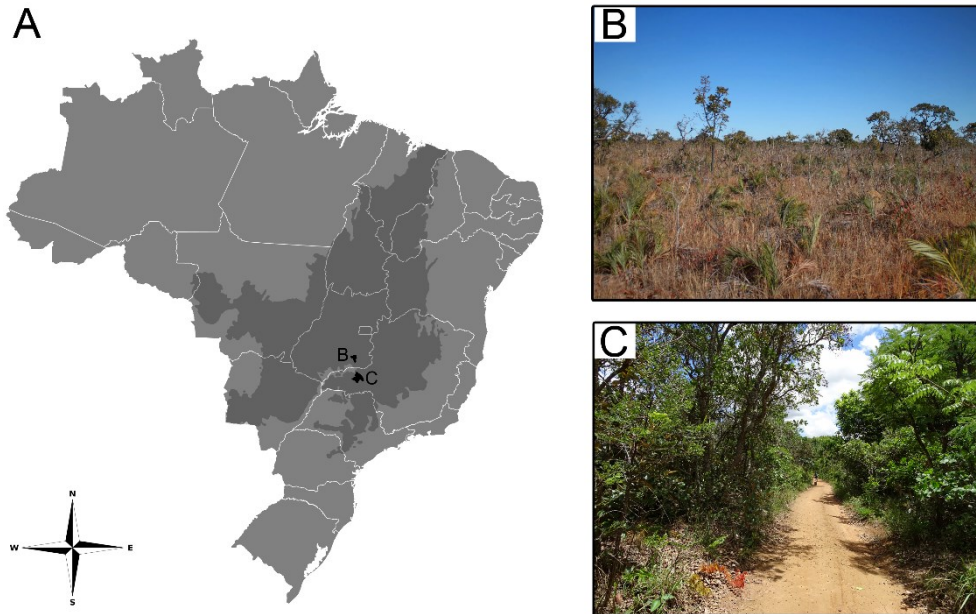


Figure 2: Location of sample sites. Shaded area (A) represents the distribution of Cerrado in Brazil. Sites are represented by letters: B for PESCAN in Goiás state and C for CCPIU in Minas Gerais state.

Biology and development

We labeled individuals according to their life stage (e.g., nymphs, sub-adults or adults) (Fig. 3). Adults and sub-adults were labeled according to their sexes, once it is easy to tell males and females of *M. brevipennis* apart (Fig. 3). They were kept at the lab in plastic vials with artificial plants, and placed inside a B.O.D., with temperature and photoperiod controlled (25°C, 12h/12h). Vials were cleaned with a dry brush after each meal and washed every two weeks. Humidity was provided by spraying water three times a week inside the vials. Individuals were fed three times a week according to their size, using a variety of prey items (e.g., flies, and beetles). We achieved this feeding regime after several trials where we utilized the abdomen size as a proxy for hunger. We recorded the date of each molt, ootheca laying day, and how many oothecae each female laid. For the fertilized ootheca, we recorded how many days it took from laying

to hatch, how many days it took to emerge all individuals, and how many emerged. Additional individuals were obtained at Fazenda Experimental do Glória in February and March of 2021, an experimental site of the University of Uberlândia, also in Uberlândia city, for reproductive analysis (table 1, Q5 and Q6).

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Behavioral observations

We only used adults and subs-adults individuals (from both sexes) for behavioral observations. We performed two distinct types of observation regarding to our goals: Hunting behavior and Reproductive behavior. All observations were made in a glass aquarium (15x10x20cm), ad libitum sense (Altmann 1974).

Once there is no available information about female receptivity, we used for reproductive behavior five days old adult males and females (when adults came from

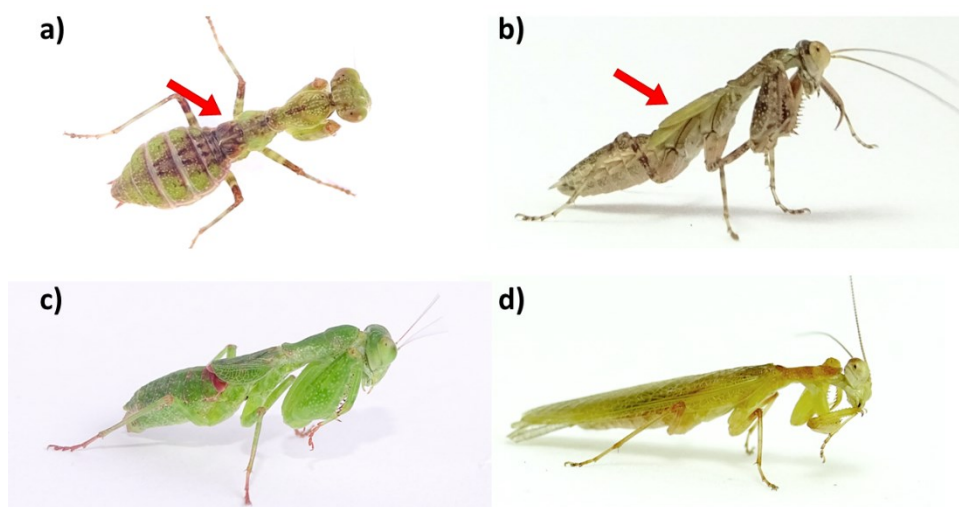


Figure 3: Females (a and c) and Males (b and d) of *M. brevipennis*. Red arrows indicate the wing buds, indicative of subadult forms (a and b), while adult forms have brachypterous wings (female, c) or fully developed wings (males, d).

nymphs raised in the lab), or as soon as possible when we got wild individuals. Trial experiments were unsuccessful when performed during the day, so most mating interactions were observed during the night. Between 19h and 22h, one individual of each sex was placed inside an aquarium on opposite sides. A white foam separated them for approximately 15 minutes for acclimatization. After that, we removed them and monitored them every 15 minutes through a small hole for one hour (ad libitum, sensu Altman 1974). Mutual aggression always happened in the first minutes; thus, we could stay away to not interfere in their behavior.

Natural Enemies

As the pressures exerted by predation are difficult to observe and analyzed in field conditions, we evaluated the impact of parasites on *M. brevipennis*. Through the year of 2019-2020, we sampled all mantis in both sites and kept them in the lab regardless of developmental stage. Then we observe and note all individuals parasitized, their species and the type of parasite when it emerged.

In September of 2021, the CCPIU site went under a huge wildfire that spread all over the reserve. In some visits to inspect the site and how the mantis community dealt with it, we observed some different dynamics and interactions that did not occur before. We provide these as notes on the effect of the fire.

Data Analysis

To investigate if there is a synchronism in the development of *M. brevipennis* and if it has a defined reproductive period, we used data about female oviposition and adult presence throughout the year in both CCPIU and PESCAN sites (table 1, Q1 and Q2). We performed two separated Circular statistical analysis through the package “circular”

(Agostinelli and Lund 2017) setting the number of adults and ootheca at each month as response variable and the months converted in angles as explanatory variables. As samples occurred in alternated months, each month represents an angle of 60° for the first question. For ootheca, we used all months since we only included in the analysis only the oothecas laid at the lab, thus, each month represents a 30° angle in the reproductive circular analysis (table 1).

It is known that temperature, nutritional state, day-light duration, and a series of other factors can influence the developmental time of insects and, ultimately, their survival (Miki et al. 2020). For this reason, we investigated if the variation in abiotic variables is related to the abundance of individuals by a Pearson Correlation test (table 1, Q3). We used adult individuals at the time of capture as explanatory variables and monthly averages in temperature, humidity, and accumulated rainfall as explanatory variables. We also analyzed delayed correlations, through a procedure called time lag with one and two months of lag (De-Freitas et al. 2022, Messas et al. 2017).

We compared the frequency of behaviors exhibited by males and females during the hunting experiments by chi-square test, along with behavior descriptions (table 1, Q3). We set sex (male or female) as columns and the frequency of each behavior as a row to compare expected and obtained frequencies.

To investigate the proportion of parasites in *M. brevipennis* and in all mantises (table 1, Q5), we performed a chi-square test, setting the individuals parasites of *M. brevipennis*, individuals parasitized of all other mantis species together, all other mantis species with no parasites, and *M. brevipennis* without parasites as variables.

We also provided descriptive aspects of the development and reproduction of *M. brevipennis*. We analyzed the survivorship of offspring from hatch to adults and reported the expected instars for this species (table 1. Q6). We describe female and male

longevity, days an ootheca takes to hatch (table 1. Q7), offspring means and deviations (table 1. Q8), how many oothecae are expected by a single female, and laying behavior (table 1. Q9). We compared the lifespan of females and males by a t-test with Welch correction.

All graphs were made using `ggplot2` (Wickham 2016) and plots available in the respective packages. All analyses were performed in the R environment (R core team 2021).

Table 1: Description of the main questions, the approach and data used to answer them, and the origin (site) of the data. Q refers to the identification as referred in the main text.

Q	Question	Test	Data	N	Site
Q1	Are <i>Metaphotina brevipennis</i> individuals distributed equally along the year in both reserves?	Circular Analysis	Adults of <i>M. brevipennis</i> at the time of sampling	196	CCPIU + PESCAN
Q2	Does <i>M. brevipennis</i> has a defined reproductive period?	Circular Analysis	Oothecas obtained from adult females in the lab	58	CCPIU + PESCAN
Q3	Do abiotic variables influence the abundance of <i>M. brevipennis</i> ?	Time-lag Pearson correlation	Adults of <i>M. brevipennis</i> at the time of sampling + Rainfall + Humidity + Temperature	196	CCPIU + PESCAN
Q4	Are females more aggressive than males toward their preys?	Chi-square	Frequency of hunting behaviors	18	CCPIU+PESCAN
Q5	Who are the natural enemies of <i>M. brevipennis</i> and their prevalence?	Chi-square	Mantis community from 2019-2020. Frequency of healthy and parasitized individuals	365	CCPIU + PESCAN
Q6	How many individuals reach adulthood?	Descriptive	Number of individuals from each instar born in the lab	248	CCPIU + PESCAN + GLORIA
Q7	How many days an ootheca takes to hatch?	Descriptive	Oothecas obtained from fertilized females obtained in the field	12	CCPIU + PESCAN + GLORIA
Q8	How many nymphs can be born from a single ootheca?	Descriptive	Oothecas fertilized obtained in the field	12	CCPIU + PESCAN + GLORIA
Q9	How many oothecas a female usually lays?	Descriptive	Oothecas laid in the lab	88	CCPIU + PESCAN
Q10	Do Females live longer than males?	T-test	Days from molting to adult instar to natural death. Lifespan inferior to 13 days were excluded	42	CCPIU + PESCAN

Results

We collected a total of 365 mantodeans between 2019 and 2020, were 212 belonged to *M. brevipennis* species. Individuals were more abundant at PESCAN along the year, but specially in June (Fig. 4), when we captured 55 individuals, most of them nymphs (Table 2). From all, only 43 individuals were captured by visually searching in the environment and individuals were usually spotted on inflorescences and the tip of branches, especially on Malpigiaceae plants, mainly of the genus *Banisteriopsis* (Fig. 5).

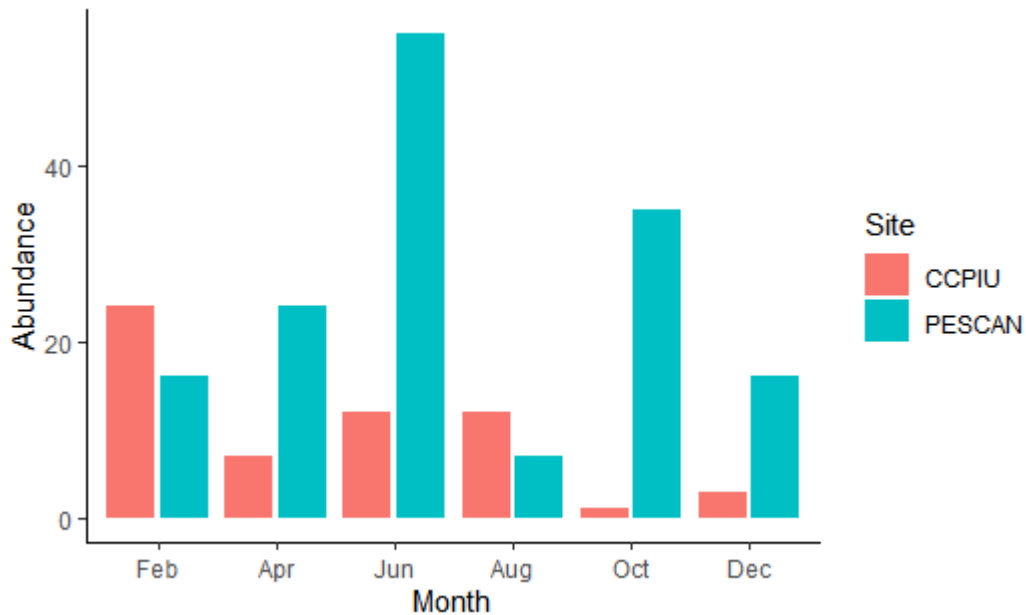


Figure 4: Abundance of *M. brevipennis* (adults and nymphs) in both Cerrado reserves (PESCAN and CCPIU) along the year of 2019.

Circular analysis showed and homogeneous distribution of adult forms in PESCAN (Table 4, Fig. 6 b), but a concentrated distribution in CCPIU (Tabel 4, Fig. 6 a). Adults were more abundant between February and April in CCPIU, coinciding with the middle and the end of wet season, while in PESCAN they were more abundant in October, the end of the dry season. Also, no adult form was caught in PESCAN during December.

Table 2 : Captures of nymphs and adults in both sites throughout the study

Month	CCPIU		PESCAN	
	Nymph	Adult	Nymph	Adult
February	16	8	10	6
April	3	4	15	9
June	10	2	51	4
August	12	0	5	2
October	0	1	24	11
December	0	3	16	0

Females obtained from both sites laid a total of 88 oothecas in laboratory conditions. However, we included only 58 oothecas in the circular analysis (Table 3) once some of them we could not precisely determine the laid date. There was a significant pattern in the distribution of oothecas laid by females from both sites along the year (Table 3). Although the distribution is not random, the strength seasonality in adult forms varies between sites, being weaker in CCPIU than in PESCAN (Table 3, Fig. 6)

Table 3: Circular statistical analyses testing for seasonal prevalence of oothecas and adult individuals of *M. brevipennis*. Significant ($p < 0.05$) effects are in bold.

Analysed factors	Site	N	Angular Mean	Circular SD	Length of mean vector (r)	Rayleigh's test (Z)	P
Adults	CCPIU	25	39.82643	61.02597	0.5638273	0.5638	0.0023
	PESCAN	32	90	134.9213	0.0625	0.0625	0.8841
Oothecas	CCPIU	40	19.21175	80.8292	0.369691	0.3697	0.0037
	PESCAN	18	338.3612	65.34192	0.521893	0.5219	0.0059

Females raised in captivity laid approximately three oothecas during their lifespan (\bar{x} : 2.378, sd:1.55) but a few of them laid up to eight. We obtained 12 ootheca fecundated from

nature and/or from captured pregnant females. Oothecas took around 20 days to hatch (\bar{x} : 19.67, SD: 2.424621).



Figure 5: Male (a) and female (b) sub-adults of *M. brevipennis* on a Malpigiaceae plant.

A total of 248 nymphs were obtained from all of them. The number of offspring from a single ootheca was highly variable, ranging from five to 55 (\bar{x} : 20.6, sd: 14.58). As a note, one virgin female laid an ootheca which hatched five individuals, but all died without molting. Also, some oothecas laid by virgin females appear to bear some underdeveloped offspring, but it needs further investigation to be confirmed (Fig. 7).

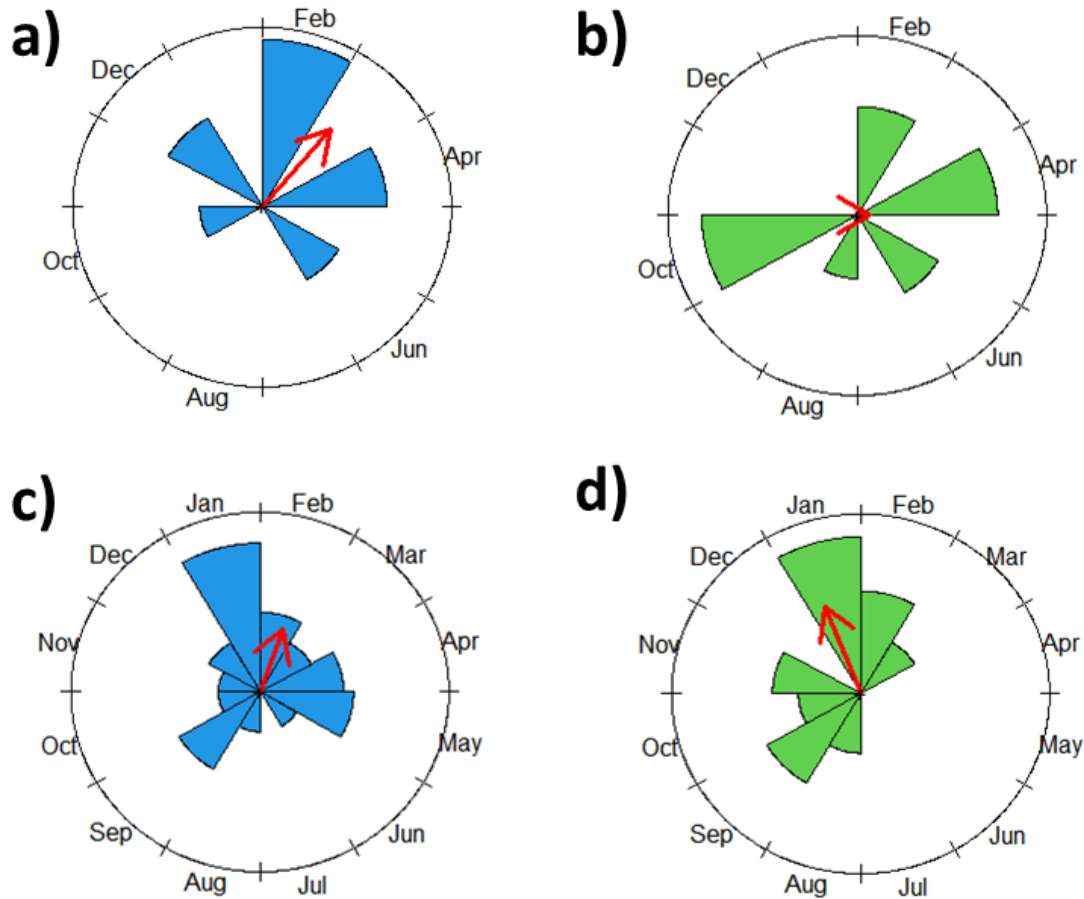


Figure 6: Annual peaks in the presence of *M. brevipennis* adults (a and b) and ootheca (c and d) in CCPIU (blue) and PESCAN (green). Arrow position represents the mean angle (mean month) where arrow length represents the length of mean vector (r). Statistical results are in table 3.

From all 248 individuals that were born in the lab, only five become mature. While females ($n=2$) had seven instars, two males become adults after six and one male with seven (as females did). Also, females lived longer than males ($t_{(37,674)}=4.7083$, $P<0.001$, ♀ days $\bar{x}=70.03$, ♂ days $\bar{x}=28.86$), around 2.5 months after becoming mature, while males had a short lifespan, being around for up to a month. Thus, females had a lifespan, in average, 2.5 higher than males.

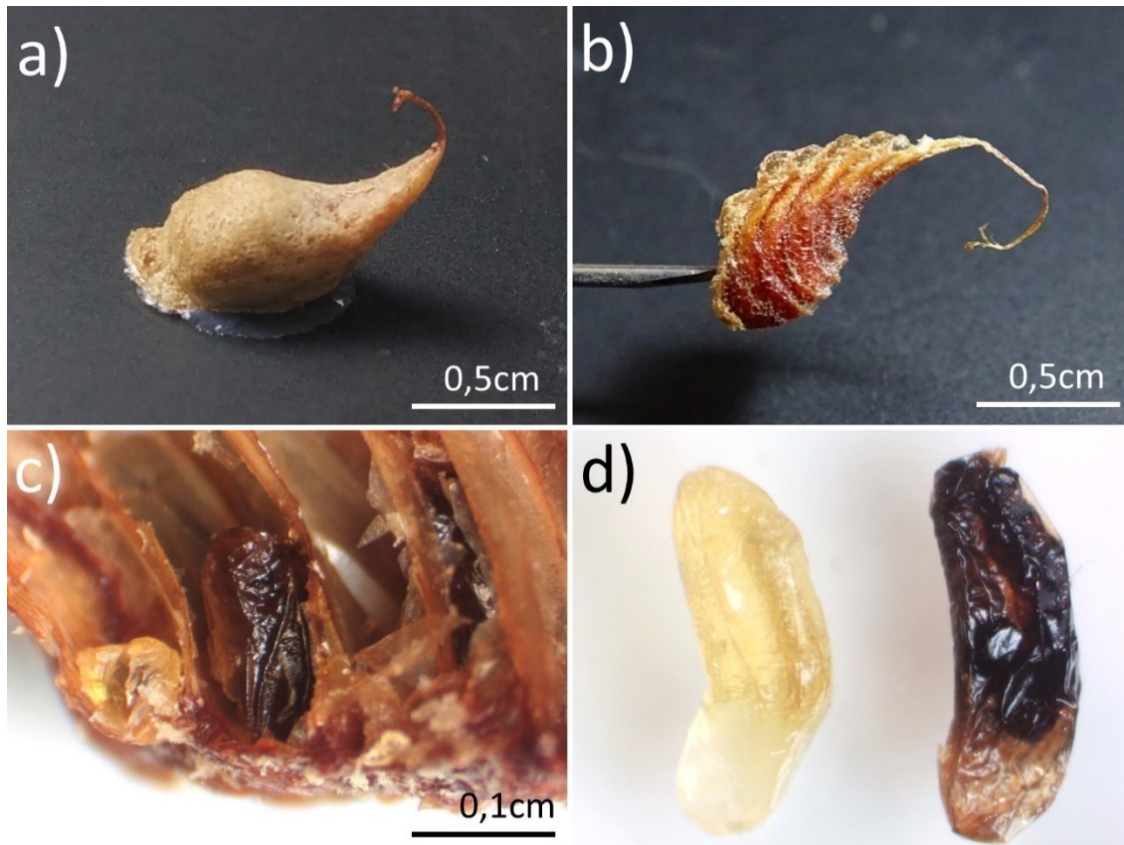


Figure 7: Ootheca and eggs of *M. brevipennis*. a) an ootheca laid by a virgem female before and (b) after coat removal. c) Histological cut, lateral view of egg chambers and eggs. d) two different eggs collected from the same ootheca. The dark one appears to bear unborn mantis inside.

There was a high mortality in the first instars (Fig. 8, Table 4), most between the first and second, where only about 35% survived. From all oothecas, only three individuals make it to the last instar, representing 1.21% of all offspring together. Individuals varied from six to seven instars total (Table 4), and males becomes mature earlier than females.

Nymphs from first to third instar have a strong resemblance of ants (myrmecomorphy), possible of the genus *Camponotus* (Fig. 9). From the fourth instar forward, they start to exhibit a wide variety of colors, ranging from the bright green to the reddish brown, with a lot of intermediate colors and combinations of colors between them.

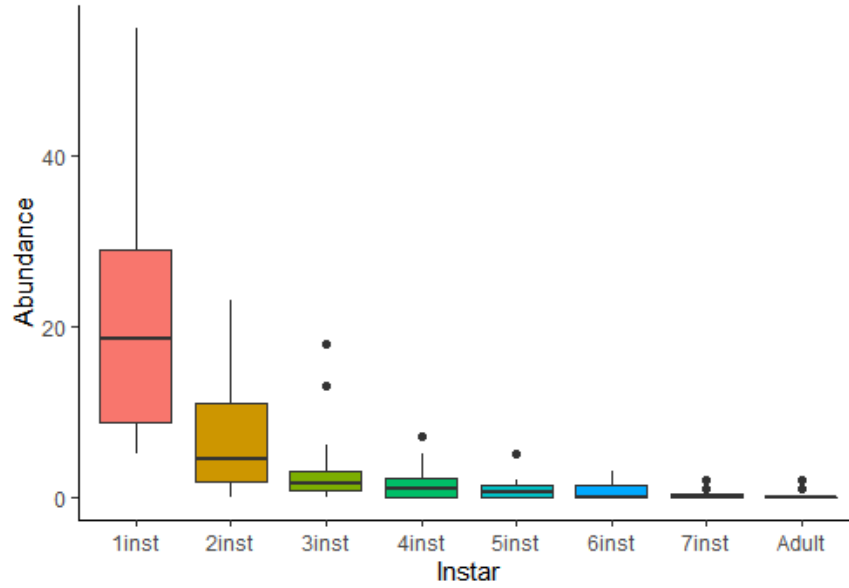


Figure 8: Survivorship of *M. brevipennis* individuals through the instars.

Table 4: The survivor frequency through instars. From 248 individuals born from 12 ootheca, only 1.21% reached the last instar. Mean (\bar{x}) and standard deviation (SD) are provided along with the total and the percentage (%). * Two individuals male from the same ootheca became adults on the seventh instar.

Instar	Survivor	
	N ($\bar{x} \pm SD$)	%
1inst	248 (20.67 \pm 14.58)	100
2inst	89 (7.417 \pm 8.11)	35.89
3inst	46 (3.833 \pm 5.78)	18.55
4inst	21 (1.75 \pm 2.22)	8.47
5inst	12 (1 \pm 1.47)	4.84
6inst	8 (0.6667 \pm 1.07)	3.23
7inst*	5 (0.4167 \pm 0.79)	2.02
Adult	3 (0.25 \pm 0.621)	1.21

Pearson correlations did not find a relationship between abundance of adults of *M. brevipennis* and abiotic variables (Table 5). Abiotic factors did not influence the pattern observed

in the circular analysis, as none of the factors were significant, even with two months lag (Table 6).



Figure 9: Second instar nymph of *M. brevipennis*. Black bar represents 0.5 cm in length. Pictures of other instars are available in the supplementary material B.

Table 5: Pearson linear correlation coefficient and time lag between abundance of *M. brevipennis* and abiotic variables. Time-lag represented at times 0 (present), 1 and 2 (month lag). No significant abiotic variables were observed ($p > 0.05$)

Variable	Lag	Df	t	Cor.	P
<i>Temperature</i>	0	10	-2.0141	-0.5372	0.07169
	1	10	0.96832	-0.29279	0.3557
	2	9	0.70375	-0.22839	0.4994
<i>Humidity</i>	0	10	1.9708	0.549058	0.08024
	1	10	1.7776	0.49002	0.1058
	2	9	1.6042	0.471551	0.1431
<i>Rainfall</i>	0	10	-0.37883	-0.11895	0.7127
	1	10	0.41304	0.129513	0.6883
	2	9	0.80437	0.258977	0.4419

Natural enemies keep preys' populations under control and shape their distribution along the time. Once quantify the predation pressure on *M. brevipennis* could be infeasible, we decided to investigate the frequency of one well-known parasite of praying mantis: the Tachinidae flies. By comparing the frequency in which parasites emerged from *M. brevipennis* and other mantis species caught, we observed a significant predominance of parasites in this species over the total (Table 6). Surprisingly, only one of the 134 praying mantis specimens captured had parasite, while 13 out of 231 individuals of *M. brevipennis* had parasites.

Table 6: Frequency of *M. brevipennis* parasite by Tachinidae flies, All other mantis species individual's parasite by the same fly and individuals without parasitic flies. Values inside parentheses () represent the expected totals, while inside brackets [] represent the chi-square statistic for each level.

	Parasited	Non-Parasited	Row Totals
All	1 (5.14) [3.33]	133 (128.86) [0.13]	134
<i>M. brevipennis</i>	13 (8.86) [1.93]	218 (222.14) [0.08]	231
Column Totals	14	351	365

Female-male interactions ended in female killing or heavily injuring the male in five out of our six attempts to mate them. Despite of the aggressiveness that happened in our mating behavior trials, females did not wait males or inspected them (facing them while still and shaking the antenna in their direction). We believe that it implies that they did not engage in copulatory ritual, thus, we will not classify these events as mating cannibalism. In the only succeed mating, the female did not move while waiting for male to approach. She remained still, with forelegs folded near the body and face toward the male, while shaking her antenna also towards him. The male approached slowly, few steps each time, while also keeping his face and antenna toward the female. He approached by her back and stayed for about five minutes still.

The female faced him for few seconds, three times in this period. Then the male approached the female by her back and stepped on her abdomen with his forelegs tarsus first, followed by the second pair of legs. The male held the female abdomen with his second and third pairs of legs, and on the base of her thorax with his forelegs. Due to their position (facing the observer) and dim light (required for this experiment) we could not describe precisely how male moved her abdomen to mate. They stayed in this position for one hour and twenty-four minutes, then the female started to move around with the male still mounting her. They moved to the top with mesh that was covering the arena and stayed there for hours. Fearing that the male could be killed, we offered food to the female, which she accepted regardless the presence of the male (Fig. 10). The couple stayed in this position for two days and half. The male survived.



Figure 10: Female (bottom) and male (up) of *M. brevipennis* in their copulatory position. Female was given a piece of meat for preventing her to attack the male.

We visited CCPIU again, between March 2022 and July 2022, after a huge wildfire that take over the entire reserve. During our observations, we collected 18 individuals of *M.*

brevipennis (seven females and 11 males), all of them adults or subadults. We could not find any nymph at initial stages, what would be easier during our samples 2019-2020. Also, from the 11 males, two of them were found parasitized by horsehair worms (Nematomorpha), something that we did not find previously. Another new observation was regarding to ootheca parasites. For the first time we found oothecas parasitized by *Podagrion* sp. wasps. After the fire, we collected nine oothecas, but eight of them harbored *Podagrion* wasps or had the visual marks (Fig. 11) of them and the only one ootheca that was not parasitized did not hatch.



Figure 11: Ootheca of *M. brevipennis* parasitized by *Podagrion* sp wasps. This ootheca was attached to *Banisteriopsis laevifolia* (Malpigiaceae). The hole in the base is clear evidence of parasitism.

Discussion

We described for the first time aspects of the natural history and population dynamics of a Cerrado mantis, *Metaphotina brevipennis*. The species present adults and nymphs during the entire year, but the phenology can vary between populations, and no environmental variables were related to it. In Cerrado, insect communities' abundance usually change along the year, mainly because its seasonality (Marquis et al. 2002, Pinheiro et al. 2002, Silva et al. 2011). During the dry season, the diversity and abundance of most orders tend to be low, while in the wet season it tends to increase (Queiroz et al. 2022, Silva et al. 2002). The wet season is also the reproductive period for most of the insects in this biome, where many species of herbivores synchronize their development with the flowering period of plants (Oliveira 2008), Silva et al. 2002). This fluctuation represents an increase in prey and predatory arthropods abundance, in a bottom-up effect (Silva et al. 2020, Wu et al. 2018). In this sense, Mantises, as top predators, could also benefit of seasonality as many other predatory arthropods do. While it is true that (at least in CCPIU) *M. brevipennis* population did show a concentration of adults (thus, the reproductive form) in the wet season, we believe that their dynamics could resemble what we found in PESCAN, when mature individuals were spread all throughout the year, even during dry season. In August, the CCPIU went under atypical extreme low temperatures, which caused vegetation to suffer severe cold burn and the overall arthropod diversity decrease dramatically (personal observation). The impact on *M. brevipennis* population at the time could lead to underestimate occurrence in the following months, caused by this stochastic event. It is known that stochastic events can lead to changes in phenology of animal population, so we believe that is more dependable to look on the occurrence pattern observed in PESCAN, which did not go under any known whether abnormality. Despite the dry season being known by reduced abundance of arthropods and, consequently, preys (Queiroz et al. 2022), *M. brevipennis* population may be able to go throughout it because of the "storing" from population in the wet season, in an

analogous way to the “Storage effect theory “(Chesson 2000). Mature individuals in the wet season could benefit from more food availability and thus produce a higher enough offspring that population could maintain in a harsh environment.

Notably, the inverse happened when we looked at the distribution of ootheca. While the circular analysis described both populations as expressing a seasonality in the distribution of ootheca (a proxy of the reproductive period), it was more accentuated in PESCAN than in CCPIU. In PESCAN, oothecae were most concentrated in the middle and end of the wet season (between February and March, which supports the hypothesis that individuals who mature in the wet season could reproduce more and, consequently, help the maintenance of the population during the dry season. We suggest that, while the seasonality of adults could be due to the extreme cold event, this species has a strong plasticity in their phenology, allowing them to better adapt to a variety of factors.

Organisms use a variety of environmental cues to regulate their life cycle, reproduction, and many other traits. Temperature and precipitation are some of the best well-known among them (Tonkin et al. 2017). Temperature, for example, can predict the abundance and species richness pattern (Wardhaugh et al. 2018) signaling the period for molting (De-Freitas et al. 2022) or even influencing the voltinism of some insects (Queiroga et al. 2019). Water availability, both from precipitation and humidity, is also a key factor for the prevalence of many species. Especially in the Cerrado, with its long dry season, humidity plays a significant role, being a source of water that condensates during nighttime (Hofmann et al. 2021). Has been reported that some mantis species, especially in temperate climates, respond strongly to these factors (Hurd et al. 1995). However, it seems that *M. brevipennis* populations in both sites are being modulated by none of these. Despite temperature and water availability being important, they are not alone. Factors such as food availability (Pieter et al. 2015), interspecific interactions (Arnoldi et a. 2019, Jocque et al. 2010), and environmental structure (Bowie and Bowie 2003,

Linn and Griebeler 2016) can also shape mantis species' spatial and temporal distribution. We believe that, due to its wide distribution in South American seasonal environments, *M. brevipennis* is not strongly influenced by abiotic variables. They seems to be adapted to these seasonal changes, such as other mantis species that shift their diet according to the most abundant prey on a specific season (Pieter et al. 2015).

We observed cannibalism in the first stage nymphs, which occurred even in the abundance of water and food. Cannibalism is reported in other mantis species, and it is suggested as a defensive behavior of nymphs (Raut and Gaikwad 2016). Cannibalism, along with natural causes, can be one of the major forces in the high mortality of the first instars. Survivor from hatching to adult was low in *M. brevipennis* as expected, since it is a well-known pattern for many arthropod species, including mantis (Hurd et al. 2004).

First to third instar nymphs of *M. brevipennis* seems to be myrmecomorphic. Although we did not evaluate it, ant mimic nymphs are a common occurrence among mantis species (see Scherrer and Aguiar 2021), even though it has never been properly tested (e.g., Pie and Del-Claro 2002). From fourth instar forward, they assumed a variety of colors, ranging from vivid green to deep brown. It is possible that this color variation helps them to being cryptic depend on the background they choose that may be available in each season. This kind of color polymorphism has been widely reported for mantis (O'Hanlon et al. 2013, Raut and Gaikwad 2016, Rathet and Hurd 1983, Rivera and Svenson 2020, Wang et al. 2017) and in some cases associated climate variables and habitat choice (Prete et al. 1999).

Females of *M. brevipennis* live longer than males, an unbalanced lifespan between sexes that was reported previously for some non-related mantis species in temperate climates (Lawrence 1992, Hurd et al. 1994, Maxwell 1998, Raut and Gaikwad 2016), but it seems to repeat even for tropical species. We believe that it can be related to the high female investment on offspring or aggressiveness that leads to an increased lifespan and, consequently, more

chances to mate. Aggressiveness in female mantis is also related to the sexual size dimorphism in orchid mantises (Svenson et al. 2016), so it may be possible that it explains other life-traits for mantis species.

Sexual cannibalism is one of most cited characteristics when it comes to mantids (Prete et al. 1999). Although they can perform cannibalism, we do not believe it is a trait related to sexual behavior, at least in *M. brevipennis*, were females preyed on males without mating. We also did not observe any noticeable behavior of the male (apart from being cautious) that could signalize a courtship behavior to avoid cannibalism. Mantis seem to be plastic regarding to courtship behaviors. In an experiment about courtship display and cannibalism in *Ameles decolor*, Battiston (2008) observed that some males performed a courtship displays while others do not, and they could mate regardless to it. In this sense, besides, we did not observe a courtship display in *M. brevipennis*, we do not discard the possibility that it happens, but we state that males can copulate without it, in the same way that happened in *A. decolor* (Battiston 2008).

Metaphotina brevipennis was the most common mantis species in both sites. It can partially explain why this species was more parasitized than other species, but not in such discrepant way. Tachinidae flies are known as parasites of arthropods, including mantis (Young 2009). However, there is no information about cues or interactions that could make them prefer a specific host. In addition to being abundant compared to other mantis species, it is possible that some behaviors or microhabitats that *M. brevipennis* chose could make them more susceptible to parasites attack. However, further studies are needed to properly infer a reason.

The recent appearance of *Podragion* wasps in *M. brevipennis* is worrying. Parasitic wasps are well-known and widespread (Breland 1941, Sureshan 2009), but we believe that the complexity of the environment, competition, and a higher availability of other ootheca, were factors contributing to low occurrence of parasitized ootheca in our "before-fire" samples. They have been reported to impact the potential offspring in oothecas (Coombs 1994) and, along with

the effects of the fire, could drastically impact the stability and persistence of *M. brevipennis* at CCPIU. Stochastic events can cause deme extinctions on mantis by changes in the environment and food availability, as was reported to *Tenodera ardifolia sinensis* (Hurd et al. 2004). Thus, it is possible that *M. brevipennis* is experiencing such conditions, and we need to keep tracking their populations to understand how they will respond in long-term to it.

Metaphotina brevipennis was not only the most common species in the environment but demonstrated high plasticity, and some remarkable life strategies to persist in the environment. Are an entire world of questions arising from our finds, mostly related to the triggers to their distribution, how exactly their color and form could help them survive and why they are preferred by parasites. We hope that our study can provide the ground for these and more questions to be investigated in the future, helping us to understand a properly quantify their role in shaping arthropod communities in Cerrado.

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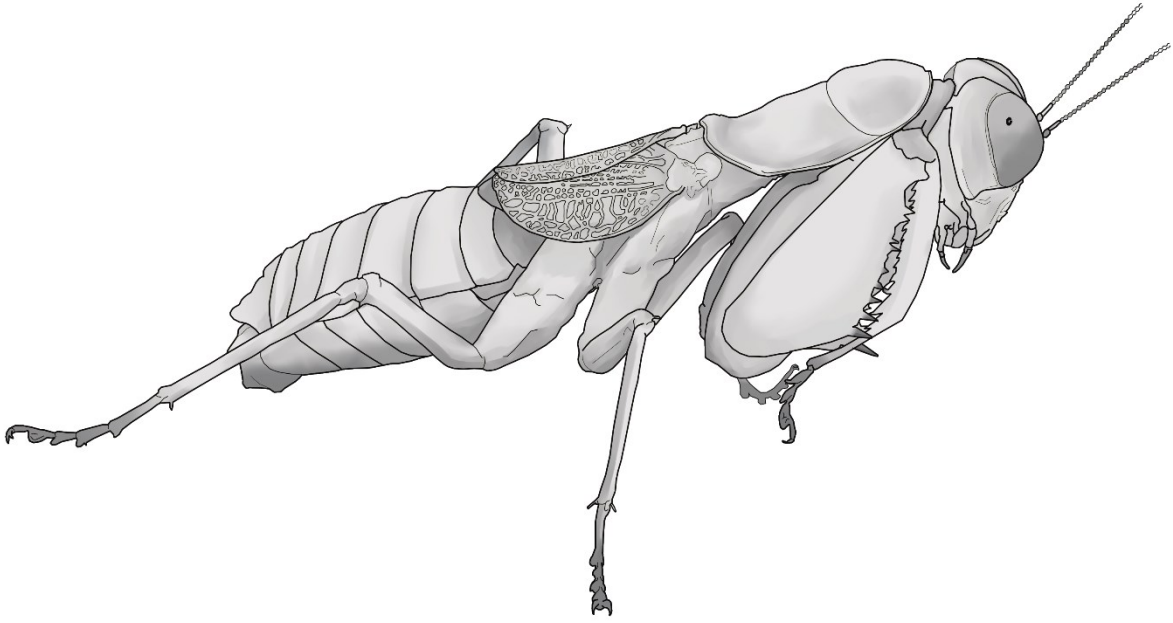
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CAPÍTULO II

Seasonal color variation and camouflage in a praying mantis from the Brazilian savanna

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Abstract

Highly seasonal environments exert strong selective pressures on species that often need plastic strategies to deal with a dynamic environment. Several praying mantis species are polymorphic, varying in color and shape, and it can be related to specific requirements of the habitat they live in. *Metaphotina brevipennis* is a polymorphic mantis species that inhabit the Brazilian savanna, which individuals vary gradually from brown to green forms, with a wider diversity of tones between these two extrema. We hypothesized that *M. brevipennis* color morphs will be unequally distributed along the year, with green forms more abundant in the rainy season and brown ones in the dry season. We also consider that they will have morpho-specific microhabitats preferences, which could enhance camouflage. We tracked a population in a Cerrado reserve for one year to evaluate how color morphs were distributed over seasons. We also performed background choice experiments to evaluate preferred backgrounds for each morph and compared camouflage through the visual system of their main predators and prey using natural observation data. Results confirmed our hypothesis that color morphs were distributed along the year with green forms more abundant in the rainy season and brown ones in the dry season, and at least the green morph shows microhabitat preferences regarding color matching. Mantises were also camouflaged in their natural background against their main predators and prey. We provided for the first time a description of the color role of praying mantis in the Cerrado biome.

Keywords: Polymorphenism, crypsis, Mantodea, Seasonality, Phenotypic variation

Introduction

Animal coloration is a subject that has fascinated naturalists for a long time (Merilaita et al 2017). It is possible to record the essays of Darwin and Wallace about the function of colors, their expression in animals, and how selective forces shape them (Smith and Beccaloni 2010). Wallace in special had a perception of animal coloration as being more a biological feature of an organism than merely a physical phenomenon (Caro et al. 2008). For the last century, animal coloration has been investigated under the light of sexual selection and warning coloration, while camouflage had little progress in the last century as its function was thought to be self-explanatory (Merilaita et al. 2017, Stevens and Merilaita 2011).

Perhaps the best definition of camouflage, was that proposed by Endler (1978, 1984, 1991) considering that a colour pattern is cryptic “if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat, where the prey is most vulnerable to visually hunting predators”. This proposal has been used as a basis for quantification of the degree of camouflage, and it assumes that all random samples of a given background are equally cryptic (Endler 1978, 1984).

Camouflage is a primary protection strategy (Cott 1940), and it is achieved by employing morphology and behavior featured together to avoid detection by a predator or prey (Stevens and Merilaita 2009). It is a widespread strategy of concealment, being present in all kinds of environments and animals (Caro et al. 2008, Stevens 2016). Most animals will achieve camouflage through a stationary constant color, which matches a specific background patch. However, the natural background is dynamic and can change along space and time, limiting the range of crypsis work (Cuthill et al. 2019). Some animals are capable to change and adapt their color to the main color in the environment. Most studies focusing on color plasticity in animals

have been performed on a small group capable of rapid changes (Duarte and Stevens 2017, Hanlon et al. 2009), ignoring other slower mechanisms (Stevens 2016), such as phenotypic plasticity in coloration.

Natural selection favors the expression of alternative life histories in highly seasonal environments (Kivelä et al. 2016), allowing species to change strategies as the development time, reproduction, behavior, and morphological features (Kivelä et al. 2016). Seasonal polyphenism is a usual form of phenotypic plasticity that occurs when the different forms of a species occur at different periods of the year (Cosentino et al 2017). It is one of the major features that allowed the colonization and establishment of insects in all kinds of environments (Freitak et al. 2019, Li et al. 2021).

Color polyphenism is the color variation related to environmental changes, and it is particularly widespread in insects (Janzen 1984). It can respond to climatic variables, such as temperature, radiation rainfall, and even, fire frequency (See Clusella-Trullas and Nielsen 2020 for review) or to changes in the background (Janzen 1984, Went et al. 2005). Both climate, and background, are highly variable in seasonal environments such as savannas.

Cerrado is a Brazilian savanna that is the second largest biome in the country and a hotspot of biodiversity. Animals in this savanna are highly adapted to its long dry periods, synchronizing many life traits with the seasons (Pinheiro et al. 2022). Chromatic (i.e., color) polymorphism is not rare in this environment, being a way to increase fitness (Mello et al. 2022, Ximenes and Gawryszewski 2019, Zatz 2002).

One remarkable example of color polymorphism in Cerrado is the praying mantis *Metaphotina brevipennis* (Acontistidae, Mantodea; see Queiroga and Del-Claro unpublished data, Chapter 1). Praying mantis are known for their incredible morphological and color features, often attributed to a strategy to increase camouflage (Agudelo et al. 2019, Greyvenstein et al. 2021, Prete et al. 1999, Rivera and Svenson 2020). *Metaphotina brevipennis* is a small species from the

family Acontistidae, adapted to seasonal environments (Rivera and Svenson 2020). It has been reported their high color variation (Heitzman-Fontenelle 1968, Queiroga and Del-Claro unpublished data, Chapter 1), from brown to green morphs (Fig. 1), that could be an adaptative strategy to camouflage in a seasonal environment. This species occurs all year round and has a lifespan after adult of approximately one month for males and three months for females (Queiroga and Kleber Del-Claro unpublished data, Chapter 1), which means that an individual can experience completely different environmental conditions depending on the season it has born and it could, someway, influence their color plasticity.

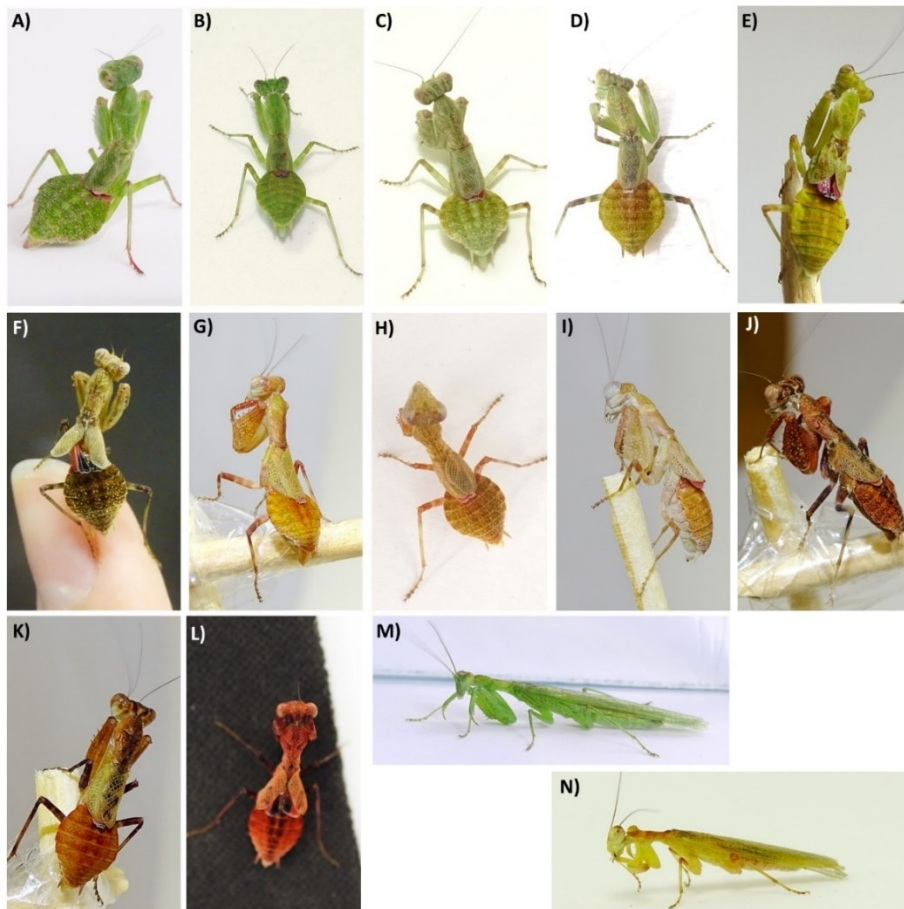


Figure 1: Color variation in *M. brevipennis*. A-M: Females. M-N: Males. Each picture is a different individual

In this sense, we hypothesize that *M. brevipennis* color morphs will be unequally distributed along the year, with green morphs more abundant during wet season and brown morphs in the dry season. We also hypothesize that *M. brevipennis* will prefer backgrounds resembling their main color, favoring camouflage through background matching. We tested our hypothesis through a series of natural observations, behavior experiments and color analysis. Our goal was to provide information about how a mantodean from a seasonal environment uses its color variation to enhance camouflage. As far as we know, this is the first study to test defensive coloration strategies by a mantis in Cerrado biome.

Methods

Study Sites

We carried out the study between January 2019 and February 2020, every two months, at two different natural reserves in the Cerrado biome: the Clube Caça e Pesca Itororó de Uberlândia (CCPIU; 18°59'08.1" S 48°18'03.5" W) in Minas Gerais state (Fig2-B) and the Parque Estadual Serra de Caldas Novas (PESCAN; 17°48'23.7" S 48°42'07.4" W) in Goiás state (Fig 2-C). The reserves are 190 km apart from each other and are separated not only by their distance but also by the Paranaíba river, characterizing two different studied populations for our interest species. The landscape of both sites is composed of typical savanna-like vegetation, with some small trees and an abundance of shrubs and grasses (see Lopes et al., 2009; Reu & Del-Claro, 2005 for more details about the reserves). The climate is tropical Aw type, megathermic, with a rainy season in summer (October to March) and a dry season in winter (April to September) (see Alves-Martins et al. 2012 and Ferrando and Leiner 2017).

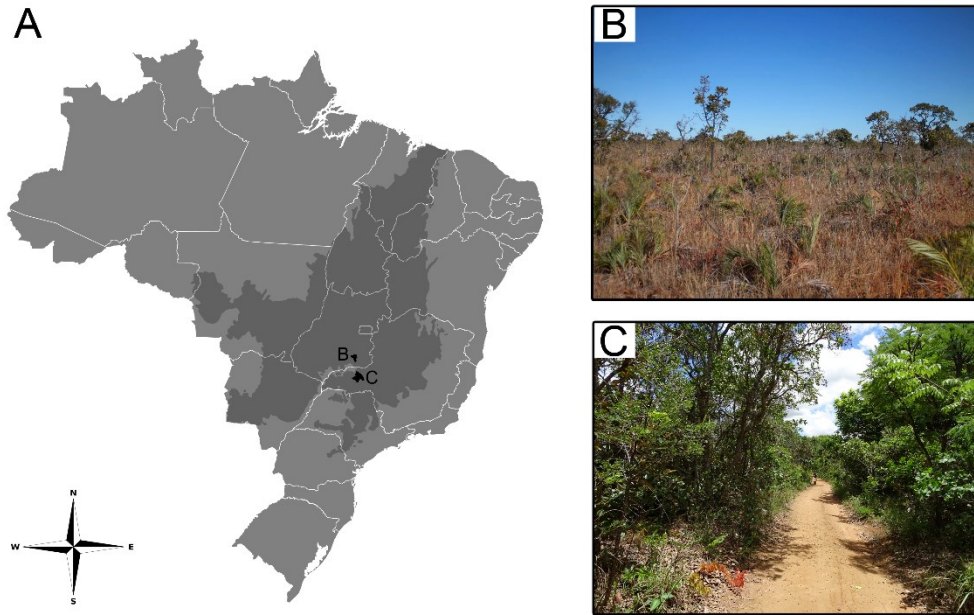


Figure 2: Sampled sites. A) Map of Brazil. Cerrado biome is highlighted in dark green. Letters indicate the sites, “B” for PESCAN and “C” for CCPIU. B) Sampled site at PESCAN and C) CCPIU.

Sampling

Between 2019 and 2020, we searched individuals of *M. brevipennis* between 06h00 and 18h00 by visual search and using an entomological hand net. We performed a visual search by actively looking for mantises on shrubs, small trees (up to 1.90m), and tall grass, and then we used a hand-net on the same areas we performed a visual search to catch any missed individuals. As mantis are usually scattered through the environment and vegetation can be denser (thus creating more searching areas) across sampling points, we decided to estimate our sampling effort by time. The sampling effort was around 18h per site (2) per campaign (6), totalizing 216h of effort. This effort was employed in an area of approximately 7.9km² in CCPIU and 9.8km² in PESCAN along all samples. We obtained the area by using landmarks and sample coordinates on google maps and used the tool “measure distances” to obtain the area.

Seasonal color variation

We establish three color morphs. Two which we attributed to wet (greenish, Fig. 1, A-C) and dry seasons (brownish, Fig. 1, J-L) and one being an intermediated color between them (yellowish, Fig. 1, G-I). We used only females for color categorization, males were rare to find and did not express much color variation as we could see in females (Fig 1. M-N). We tried to classify females that fitted in one of the three morphs, but as color diversity was more variable than we thought, we decided to exclude any ambiguous individuals (Fig 1. D-F) as a conservative approach.

Habitat choice

To understand if females of *M. brevipennis* would prefer green or brown habitats and if this choice is related to their main color, we performed a habitat choice experiment. The experiment was performed in a glass aquarium (15x10x20cm), but outdoors, under the sunlight from 9h-11h and 14h-16h, to mitigate the effects of artificial light on the substrate color and visual perception of the individuals. We provided two types of substrates, a branch full of green leaves and a brown branch of the same size as the green one. Individuals were then left alone inside the arena for 30 minutes. After that time, we registered their chosen substrate by which they were found.

Reflectance measurements

Mature females and males were obtained in CCPIU between February and July of 2022. All of them were found on leaves of *Banisteriopsis laevifolia* (Malpigiaceae), a common plant in the Cerrado, bearing yellow inflorescences, extrafloral nectaries and oil glands, heavily visited by a variety of arthropods of different trophic guilds (Torezan-Silingard 2017, Vilela et al. 2014). Insects were euthanized by cooling and then freezing. The reflectance measures of individuals

were obtained using the optical spectrophotometer JAZ (Ocean Optics Inc, Dunedin, Florida, USA), with illumination provided as an in-built combined deuterium and halogen light source. The Light produced ranged from 200 nm to 1100nm and was guided through a 400 μm diameter glass fiber, positioned at 30 mm above the structures, with the reflected light being collected by the same. Spectra were obtained and processed using the software Spectra Suite (Ocean Optics), with electric dark correction enabled. Each measurement was an average of twenty-five scans obtained for 250ms plus 8 adjacent points (function boxcar width), as a procedure for controlling spectral noise.

Measurements were taken in fresh dead specimens, twice, in standardize body regions (Fig 3): head, thorax, forelegs, wings and abdomen. We did not measure male's abdomen once it is covered by wings and only viewed during flights or deimatic displays (which does not make up crypsis strategies).

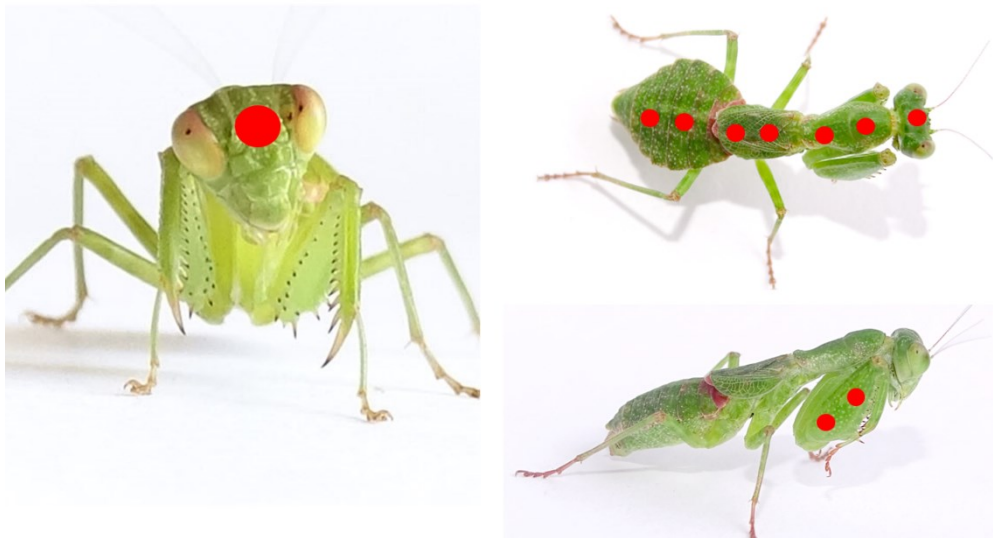


Figure 3: Landmarks pointing out where color was measured. Position was the same for both sexes, excluding male's abdomen. Two measurements were taken on each body part of *M. brevipennis*

Crypsis

To address color discriminability between individuals of *M. brevipennis* and the background, we contrasted their reflectance measurements with the reflectance measurements of *B. laevifolia* leaves, leaves of other plants in the same site, but where no mantises were found, and the mean spectra of the Brazilian Savanna visual background provided by Gawryszewski and Motta (2012).

We did it by modulating the visual systems of *M. brevipennis*'s predators and prey according to the Receptor Noise Limited model (or just RNL, Vorobyev and Osorio 1998) using the pavo 2.0 package (Maia et al. 2019). We modeled the chromatic perception of Hymenoptera, Diptera and both violet and ultraviolet-sensitive birds. Birds, hymenopterans, and dipterans can be natural enemies of *M. brevipennis* (wasps and parasitic flies) while the last two can be their preys (bees and wandering flies) too.

All models used built-in information about their visual system available in pavo (Maia et al. 2019). For Hymenoptera vision we used “*apis*,” the visual model of the honeybee *Apis mellifera* and “*musca*,” for the visual model of the housefly *Musca domestica*. An average avian violet system was modelled using “*avg. v*” , based on the domestic chicken *Gallus gallus* and for an average ultraviolet avian system we used “*avg.uv*,” based on the visual system of the Blue-tit *Parus caeruleus*.

We used just the spectral information ranging from 300nm to 700 to calculate photoreceptors quantum catch (function *vismodel* in pavo). We set a natural daylight illuminant as this is closest to savanna natural light. Signal-to-noise ratio of 0.13 was established for Diptera and Hymenoptera models, while a signal-to-noise ratio of 0.10 was used for birds. After this we could calculate the chromatic distance (ΔS) between the background and individuals of *M. brevipennis* as a proxy of discriminability through the function *coldist*.

Statistical analysis

To investigate if there is a synchronism in the color morphs of *M. brevipennis* and the seasons of the year, we performed a Circular statistical analysis through the package “circular” (Agostinelli and Lund 2017) for each color morph. We set the number of individuals of each color per month as response variable and the months were converted in angles as explanatory variables. As samples occurred in alternated months, each month represents an angle of 60°. Individuals from both areas were combined to increase our sample per analysis and because areas are climatic similar (chapter 1).

To investigate if the main color of the females influences their habitat choice, we compared the frequencies of the type of patch chose and female main color throughout a chi-square test.

To determine if the chromatic distances (ΔS) between two patches are enough to be noticed or perceived (the concept of Just Noticeable Differences, or JND), we needed to evaluate them against a threshold of discriminability. Despite in theory values above $1\Delta S$ could be considered discriminable; we followed the conservative widespread approach of setting the threshold of 2Δ (2 JND). Thus, we considered chromatic distances above $2\Delta S$ as possible to be discriminate (sometimes hardly discriminate), and as this distance increases, is more likely to a viewer to tell an object and the background apart.

We followed the approach suggested by Maia and White (2018), as it takes account for statistical and physiological significance of chromatic contrast (ΔS). For testing if our samples are statistically distinct, we used the calculated distances between each pair of background-individuals to generate a distance matrix throughout the function *coldist2mat ()* available in *pavo 2.0*. Then we created a vector containing our grouping variables (each type of background, males, and females) to test our color distance matrix throughout a PERMANOVA using the function *adonis ()* in the package *vegan*. Statistical differences between groups were tested using *pairwise.adonis()* function.

To answer if the separation between our groups is perceptually discriminable, we performed a second test independently, by estimating the distance in color space between group's geometric means (Maia and White 2018). For testing for above threshold mean differences between groups, we performed a bootstrap through the function *bootcoldist ()*. This function generates new samples through resampling with replacement of each data in each group, calculating chromatic distances and geometric means (Maia and White 2018). This generates a distribution of mean distances, allowing the creation of confidence intervals for each group (Maia and White 2018). By this two-step approach, if our samples are statistically different and the confidence intervals generated by the bootstrap do not include our theoretical threshold ($2 \Delta S$) of biological significance, we can conclude that our samples (background and individuals) are distinct and likely discriminable by the viewer (Maia and White 2018). We repeated this approach for each visual model calculated.

Results

Results confirmed that females of *M. brevipennis* vary in color, presenting colors from green to brown and with different mixes of color patches. Our circular analysis showed that there is phenology in the distribution of color morphs along the year (Table 1, Fig. 4). The greenish morph prevailed in the wet season, with the peak in the phenophasis in February (Fig. 4). Yellowish females occurred all year round but were more present in the end of the dry season and beginning of the wet season (Fig. 4). On the other hand, brownish females prevailed in the dry season, with a peak of abundance between October and August.

Table 1: Circular analysis results of color morphs of *M. brevipennis* females. Values in bold are significant under 0.05 threshold.

Color morph	N	Angular Mean	Circular sd	Length of mean vector (r)	Rayleigh's test (Z)	P
Greenish	21	26.036	58.2278	0.596665	0.5967	> 0.001
Yellowish	17	286.102	81.0865	0.3673528	0.3674	0.0998
Brownish	23	227.783	56.3624	0.6164107	0.6164	> 0.001

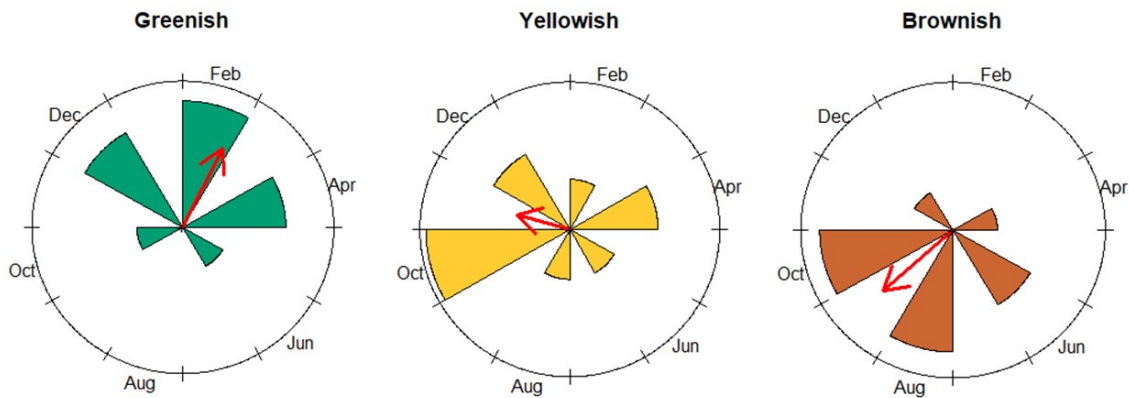


Figure 4: Circular histogram of *M. brevipennis* female's color morphs. Red arrows represent vectors direction (angle) and effect (length).

During de experiments on background choice, females chose differently each background ($\chi^2=5.7228$, $P=0.0167$). Green females chose more the green branches than the brown ones (Table 2), as did brownish females (Tab. 2), but for the second we did not observe a significant difference.

For the color analysis, we could perceive that females and males tend to be chromatic distinct. Females and males differ in the relationship between short-wavelengths (SW) to middle

wavelengths (MW), and from MW to long-wavelengths (LW). This tendency is clear when we remove the three male outliers. We discuss this result further.

Table 2: Frequency of *M. brevipennis* females of three color morphs and their chosen habitat. Values inside parentheses () represent the expected totals, while inside brackets [] represent the chi-square statistic for each level.

	Green branch	Brown Branch	Row Totals
Greenish ♀	12 (8.75) [1.21]	2 (5.25) [2.01]	14
Brownish ♀	8 (11.25) [0.94]	10 (6.75) [1.56]	18
Column Totals	20	12	32

From our background matching analysis, whether animals can see *M. brevipennis* against the background was variable. First, for a hymenopteran viewer, the PERMANOVA was significant for differences dependent on sex ($F_1=114.704$, $P=0.001$) and the background ($F_2=12.431$, $P=0.001$), but these differences were not physiologically significant (<2 JND, Fig 4). The same happened for the vision model of a dipteran viewer. All backgrounds ($F_2=11.895$, $P=0.001$) and sex ($F_1=122.995$, $P=0.001$) were significant different, but they did not attend the discrimination limit (Fig. 4). For the models of a VS and UVS sensitive bird, we found a statistical difference in sexes (VS bird $F_1=219.714$, $P=0.001$; UVS bird $F_1=174.157$, $P=0.001$) and background (VS Bird: $F_2=11.995$, $P=0.001$; UVS bird $F_2=14.245$, $P=0.001$), but the chromatic distances only were above our threshold of $2 \Delta S$ when a female was observed against *B. laevifolia* for a VS and UVS bird, but for the last one, in addition to the contrast female x *B. laevifolia*, they were likely to perceive a *M. brevipennis* male against the other backgrounds

present in the area. It means that individuals were cryptic against most of the backgrounds, except for the two forementioned combinations.

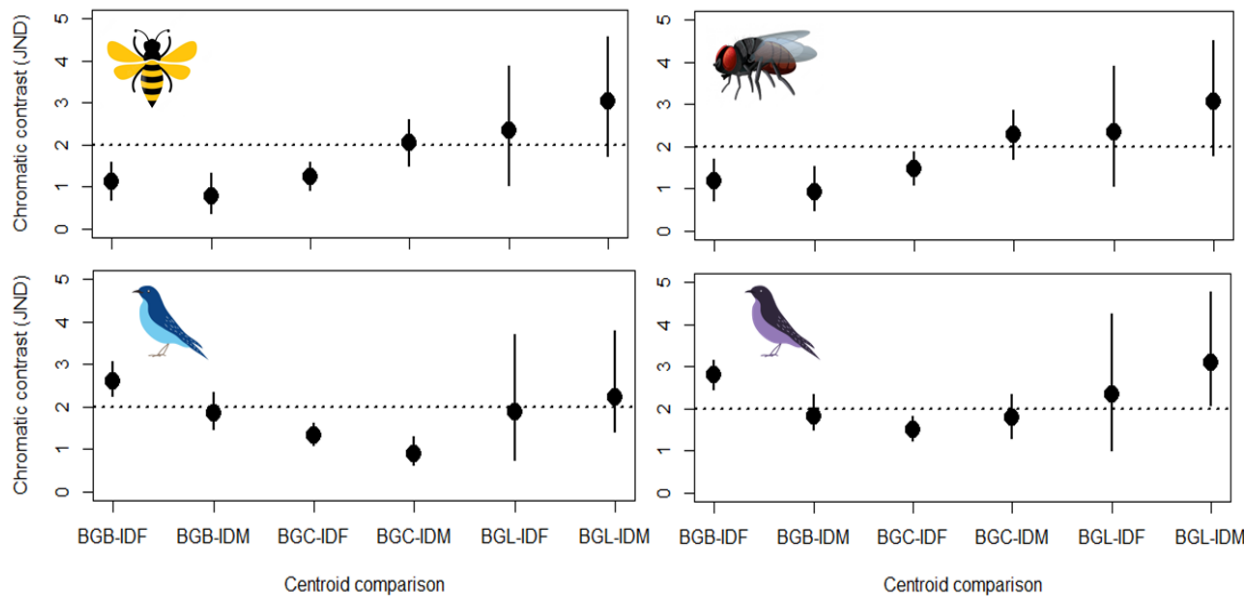


Figure 4: Chromatic contrast expresses as Just Noticeable Differences (JND), between *M. brevipennis* and the background based on different viewers: Hymenoptera (top left), Diptera (top right), Violet sensitive bird (bottom left) and Ultraviolet sensitive bird (bottom right). Dots are the means of each comparison, and vertical lines represents a 95% confidence interval. Dot horizontal lines are our theoretical threshold. Confidence intervals above dotted line are likely to be perceived by the viewer, while the others are cryptic. Legends: BGB: *B. laevifolia* background, BGC: Cerrado Background, BGL: Leafs other than *B. laevifolia* available in the site; IDM: Male; IDF: Female.

Discussion

Our hypothesis of the distribution of the color morphs and optimization of crypsis through background matching was confirmed. Color morphs of *M. brevipennis* were distributed unequally along the seasons, with the green being more abundant in the wet season, the brown in the dry

season, and the yellow as an intermediate color morph, occurring all along the year. Many arthropods express color variation influenced by environmental conditions, especially in seasonal environments such as Cerrado (Mello et al. 2022), such as we found for *M. brevipennis* females. Some climate variables have been reported to trigger color change for better matching to the condition of the environment (Mello et al. 2022, Went et al. 2005), which could also be used by *M. brevipennis*. This has been investigated in vertebrates (Langkilde and Boronow 2012, Walton and Bennette 1993) and invertebrates (Clusella-Trullas and Nielsen 2020) and can occur when environmental factors directly alter gene expression, a case of polyphenism (Evans and Wheeler 2001). For example, Yamamoto et al. (2011) rearing larvae of the butterfly *Byasa alcinous* under different temperature and humidity regimes, found that pupae forms from larvae raised in cold and dry conditions were brown while those from hotter and wetter conditions become yellow. Studies with monarch butterflies showed that colder temperatures induce darker forms in caterpillars, while hotter regimes make them lighter (Davis et al. 2005, Markl et al. 2022), a phenom known as “Thermally melanism”. Although we did not investigate the relationship between such variables and *M. brevipennis*, we believe that it is most likely to happen, as individuals were, indeed darker in the dry and colder seasons, and lighter in the wet season. Experiments raising individuals in different climatic conditions and different backgrounds would be valuable to our understanding of the mechanisms and magnitude of the effects on this species.

Color polymorphism between green and brown forms are understudied, besides being frequently mentioned for arthropods, mostly Polyneopteran insects (Roulin and Bize 2007, Schielzeth 2021). We believe that *M. brevipennis* is a polyphenic species over than a polymorphic one, once in polymorphism, morphs are usually not separated in time. Another point is that in polymorphic species, morphs are discrete and most “easier” to tell apart, while in polyphenic species the degree of variation is, usually, continuous. Polymorphism in Mantodea is

highly reported for neotropical species, (Agudelo et al. 2019, Rivera and Svenson 2020), but small and continuous variations as we see in *M. brevipennis* are rare.

Greenish females of *M. brevipennis* preferred green habitats over brown habitats, a morpho-specific choice stronger than observed in brownish females. In polymorphic grasshoppers, there is also a stronger morpho-specific habitat preference in green morphs over the others (Heinze et al. 2022). Actually, many studies with polymorphic species have shown that morpho-specific choice usually occurs in one morpho only (Stevens and Ruxton 2019), but there is still no evidence of why these differences happen.

Both females and males of *M. brevipennis* did not differ in their backgrounds under the visual systems of hymenopterans and dipterans. O'Hanlon et al. (2014) studying the orchid mantis *Hymenopus coronatus* reported that they were inconspicuous from the flowers they resemble in the vision of hymenopterans too. *M. brevipennis* and *H. coronatus* are aiming to be concealed from their preys' eyes, demonstrating how these animals had evolved camouflage to optimize their prey capture (Pembury Smith and Ruxton 2020).

Although animals could use the perception of their color to achieve camouflage by actively choosing the best available background (Eacock 2019), we do not believe that *M. brevipennis* uses this way, as mantis are more likely to be color blind (Van Der Koi et al. 2021). It is more likely that mantises are using some other cues in the environment to make their decision, or even being under some other genetic and behavioral triggers (see Heinze et al 2022). However, it is possible that background matching was achieved by predation on worse-matched individuals, selecting for better crypsis (Went et al. 2005).

For birds, both avian predators could indeed see them against some specific backgrounds and may play a role in selecting phenotypes. Despite most insectivorous birds prey on insects during flight or foraging on the ground (Ferrari et al. 2022, Pinheiro et al. 2003), some of them inspect the vegetation looking for small arthropods (Gonçalves 2011). While we found all our

individuals on *B. laevifolia* leaves, females of *M. brevipennis* were conspicuous to birds only on this same plant. Females are unable to escape from a predator by flying due to their brachypterous wings, thus once their camouflage fails, they are likely to be eaten. On other hand, males were cryptic against *B. laevifolia* but not against other plants in the environment. They do have fully developed wings to escape, males usually fly just small distances (pers. Observ.), which could be enough to escape from a conspecific or some cursorial predators (e.g., jumping spiders), but from not an avian predator. This means that the main predator that drove the background choice and/or prevalence of them is possible the birds.

In this study, we described how *M. brevipennis* is a highly phenotypic variable and how it is synchronized with Cerrado's dynamics. In a scenario of increasing climatic changes, many different outcomes could fall over plastic species. Populations may go under divergent evolutionary paths, favoring some strategies over others or even extinguishing a part of their variety (Cosentino et al. 2017). If the color is related to abiotic factors, species could become darker to protect against dissection or radiation (Parksh et al. 2009) or could even evolve phenotypes that do not match the environment anymore. If it is regulated by daylight hours, it is most likely that animals will be negatively affected by a mismatch in their seasonal color and the color of the main background, leading to a declined survivor (Stevens 2016). Regardless of the outcome, changes in the environment will heavily impact *M. brevipennis* dynamics, so studying this species could help us not only to better understand the role of phenotypic plasticity in seasonal environments but also how breaks in this synchronism could affect biodiversity.

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Conclusões Gerais

Através do estudo de diversos traços morfológicos, comportamentais e da história de vida de *Metaphotina brevipennis*, nós demonstramos a plasticidade dessa espécie em lidar com um ambiente altamente sazonal e complexo. A variação na fenologia das populações, tanto na presença de adultos quanto na de ootecas demonstra a capacidade dessa espécie de louva-a-deus a se adaptar as condições do ambiente. A forma como a cor predominante da população se alterou ao longo das estações é outro sinal da sua sincronia e adaptabilidade ao Cerrado. Seu comportamento de preferência morfo-específica por um substrato e sua capacidade de camuflar-se sob a visão das suas presas e alguns dos seus predadores, demonstra como a coloração é uma estratégia importante nessa espécie, com potencial para regular sua dinâmica populacional.

A alta plasticidade estratégias demonstradas aqui, aliada a larga ocorrência dessa espécie por todo o Cerrado demonstra que em um cenário de mudanças climáticas, onde os ambientes áridos tendem a se expandir, essa espécie pode se beneficiar, expandindo ainda mais a sua área de ocorrência. Entretanto, estudos para avaliar os possíveis impactos negativos de tal mudança ainda são necessários para estabelecer sob quais trade-offs *M. brevipennis* estaria sujeita.

Essa tese, até onde os autores tem conhecimento, é a primeira feita no Brasil a abranger diversos aspectos da história natural e da biologia de uma espécie de louva-a-deus, com observações naturais e experimentação em laboratório. Nós esperamos que as informações providas aqui auxiliem demais pesquisadores a avançarem no conhecimento desta e de muitas

outras espécies de louva-a-deus no Brasil, que tem a maior diversidade do grupo dentro da América do Sul, mas cujo conhecimento é ainda bastante críptico, assim como os animais que compõe essa carismática e intrigante ordem.