UNIVERSIDADE FEDERAL
DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

TESE DE DOUTORADO

ARANHAS SOB IMPACTO DE PASTEJO: UMA ABORDAGEM EM MULTI-ESCALAS

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Linha de Pesquisa: Biodiversidade

Porto Alegre

Janeiro/2022

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DO RIO GRANDE DO SUL

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, da Universidade Federal do Rio Grande do Sul como requisito para obtenção do grau de Doutor em Biologia Animal.

Aprovada em _26_ de 2022.

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Silva, Guilherme Oyarzabal da

Aranhas sob impacto de pastejo: Uma abordagem em multi-escalas. Guilherme Oyarzabal da Silva. – Porto Alegre: IBIO/UFRGS, 2022, [128 pp.].

Tese de Doutorado – Universidade Federal do Rio Grande do Sul. Instituto de Biociências, Programa de Pós-Graduação em Biologia Animal. Porto Alegre, RS - BR, 2022.

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DEDICATÓRIA

Aos que sabem que educação e conhecimento salvam vidas

Aos que lutam por uma ciência livre

Aos que tentam exercer alteridade e empatia

Para aqueles que sabem que o chão não combina com a gente

"Irmão,

Você não percebeu que você é o único representante

do seu sonho na face da terra...

Se isso não fizer você correr, chapa

Eu não sei o que vai".

- Levanta e Anda (part. Rael da Rima). Emicida.

AGRADECIMENTOS

Espero não cometer nenhuma injustiça a agradecer todos que, de alguma forma, estiveram presentes nesta jornada.

Obrigado Lana Resende. Por todo amor, a fé e o café destes anos. Pelo colo, pelo abraço apertado, pelo puxão de orelha, pela compreensão. Pelo sorriso, pelas fotos de boa sorte. Por estar presente mesmo tão longe. Passarinho anilhado continua voando.

Obrigado minha mãe, Angelita e meu pai, Salvador, por terem me dado vida e seus exemplos. Amo vocês.

Obrigado minha mana, Mariucha. Sem você, eu não seria metade do ser humano e do homem que sou hoje. Sem você, eu não seria professor. Sem você, eu não acreditaria na educação. Sem você, eu não acreditaria num mundo sem injustiça, onde a gente ainda pode lutar por uma vida melhor.

Obrigado, vó Zoel e vô Vitor, por trabalharem tanto para me dar a educação que tenho hoje. Não estaria aqui se não fossem vocês.

Obrigado aos meus amigos mais chegados, por nossas amizades 10-15-20 anos. Clarissa Dreon, Claudia Gomes, Débora Aguiar, Fernando Cardoso, Germano Rosa, Letícia Nieto, Paula Ramos, em ordem alfabética para evitar prioridades! Vocês têm me acompanhado por tanto tempo que essa conquista também é de vocês. Muito obrigado pela mão amiga, pelas risadas e por toda a confusão.

Obrigado ao meu orientador, Murilo Guimarães, pelas conversas sobre ciência, sobre o futuro e os ensinamentos sobre ecologia. Pelos devaneios sobre o que fazer nesse mundo e sobre sonhos e vontades que temos.

Obrigado minha terapeuta, Audrey Blackwall, por todo o suporte emocional durante todo esse período.

Obrigado Andressa Gigante, por todo o apoio durante os campos e as conversas de coração aberto.

Obrigado Maria João Ramos Pereira e todos os colegas do BimaLab por todas as nossas conversas, risadas, comilanças e acolhimento que me deram durante estes anos de doutorado.

Obrigado Eillen Hebets por ter me recebido tão bem nos EUA. Obrigado por ter me acolhido na sua casa, no seu laboratório, entre seus colegas, família e amigos.

Obrigado Brandi Pessman, Laura Segura, Pallabi Kundu, Kenna Lehmann, Noori Choi, Dan Schoenberg e Seth Griger por todo o apoio pessoal, científico e logístico durante todo o tempo que estive nos EUA. Obrigado por me fazerem sentir parte de um laboratório, pela paixão compartilhada pelos aracnídeos e por serem pessoas reais, com seus medos, sonhos e lutas.

Obrigado Aaron Swartz e Alexandra Elbakyan pela ousadia de querer tornar o conhecimento científico público e gratuito.

Obrigado aos meus professores, mestres e doutores da escola, do colégio, da universidade. Vocês formaram os degraus da escada que me fez subir até aqui.

Obrigado Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa de Doutorado.

Obrigado Neotropical Grassland pela concessão do Student Grant que tornou viável minhas pesquisas de campo no Brasil.

Obrigado a Fulbright Brasil pela concessão do Doctoral Dissertation Research Abroad (DDRA) que me permitiu ir aos EUA e realizar um capítulo completo desta tese.

Obrigado ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal do Rio Grande do Sul (UFRGS) e a University of Nebraska – Lincoln pelas estruturas físicas e pessoal para realização do meu projeto.

Obrigado a todas, todos e todes! Vocês fazem parte desta conquista.

SUMÁRIO

RESUMO

Ecossistemas campestres representam a maior parte da área agrícola do mundo. Das atividades antrópicas comuns em campos, a pecuária tem como objetivo a produção, principalmente, de carne, leite e couro. Como efeito do pastejo, campos acabam tendo a sua biomassa vegetal acima do solo removida, o que pode contribuir positivamente para a diversidade vegetal e animal. Entretanto, quando em alta intensidade, a pressão de pastejo degrada o ambiente, homogeneizando o habitat e promovendo a perda de diversidade em diferentes níveis tróficos. Plantas e artrópodes figuram como os principais elementos bióticos em ecossistemas campestres, tendo papel fundamental na engenharia destes ambientes. De forma particular, o pastejo afeta plantas através de danos físicos e diminuição na riqueza de espécies. Ao mesmo tempo, artrópodes sofrem perdas importantes em sua abundância e na sua riqueza de táxons. Desta forma, impacto intenso do pastejo afeta de forma ampla a saúde ambiental de ecossistemas campestres. Considerando o pastejo como eixo central desta tese e aranhas como um organismo modelo, eu busquei investigar: (i) através de uma extensa revisão bibliográfica, como a pressão direta e indireta de pastadores afeta a abundância, a riqueza e a funcionalidade das aranhas; (ii) através de um estudo populacional, como diferentes níveis de pastejo afetam a abundância de aranhas e; (iii) através de um estudo com individuos, como o pastejo afeta a interação de aranhas e plantas. Concluo que aranhas são um componente essencial na saúde de ecossistemas campestres e sua variabilidade intrínseca é chave para entender a relação de impactos antrópicos. Isto se torna mais evidente devido a relação direta da exclusão de aranhas no ambiente e a remoção da vegetação causada pelo pastejo. A presença de aranhas, a manutenção de suas populações e, por consequência, seus serviços ecossistêmicos, estão à mercê de que o impacto antrópico exista ou não nos ambientes campestres. Em suma, apesar da relevância ecossistêmica de artrópodes o grupo é vastamente desprezado em termos de conservação e manutenção das populações. Alternativas sustentáveis para a produção de comida assim como a restauração dos ecossistemas campestres é urgente. A nossa frente temos um eminente colapso ambiental e a conservação de artrópodes, aranhas e ecossistemas campestres é essência para evitá-lo.

PALAVRAS-CHAVE: Araneae, diversidade, impacto antropogênico, pastejo, revisão sistemática.

ABSTRACT

Grassland ecosystems represent most of the world's agricultural area. From the anthropic activities common in grasslands, livestock raising has the objective to produce, mainly, meat, milk, and leather. As a result of the grazing impact, grasslands end up having their aboveground vegetal biomass removed, which can contribute positively to plant and animal diversity. However, when at high intensity, grazing pressure degrades the environment, causing habitat homogenization since it promotes losses in diversity in different trophic levels. Plants and arthropods are the main biotic components in grassland ecosystems, playing fundamental roles in the engineering of these environments. On the one hand grazing affects plants through physical damage and a decrease in species richness. On the other hand, due to grazing arthropods suffer important losses in their abundance and in their taxa richness. In this way, the intense impact of grazing has a broadly affect in the environmental health of grassland ecosystems. Considering grazing impact as the central axis of this thesis and using spiders as a model organism, I investigated: (i) through an extensive literature review, how the direct and indirect grazing pressure affects the abundance, richness and functional diversity of spiders; (ii) through a population study, how different levels of grazing affect the abundance of spiders and; (iii) through study of individuals, how grazing affects the interaction of spiders and plants. I conclude that spiders are an essential component on grassland ecosystems health and their intrinsic variability is key to understanding the relationship of anthropic impacts. This becomes more evident due to the direct relationship between the exclusion of spiders in the environment and the vegetal removal caused by grazing. The presence of spiders, the maintenance of their populations and, consequently, their ecosystem services, are at the mercy of whether the anthropic impact exists or not in grasssland environments. Finally, despite the ecosystem relevance of arthropods, the group is largely neglected in terms of conservation and maintenance of their populations. Sustainable alternatives for food production as well as the restoration of grassland ecosystems are urgent. Before us we have an imminent environmental collapse, and the conservation of arthropods, spiders and grassland ecosystems is essential to avoid it.

KEY WORDS: Anthropogenic impact, araneae, diversity, grazing, systematic review.

INTRODUÇÃO GERAL

Ecossistemas campestres (pradarias, savanas e pastagens) cobrem cerca de 40% da superfície do nosso planeta e são amplamente encontrados em todos os continentes (Ojima et al., 2013; Zhang et al., 2020). Estes ecossistemas representam quase 70% da área agrícola do mundo (O'Mara, 2012), sendo vastamente utilizados para criação de rebanhos (gado, ovelhas, porcos, etc) e no cultivo das mais diversas plantas alimentícias (Jiang et al., 2019; Ojima et al., 2013). Dessa forma, extensas áreas campestres ao redor do mundo têm sido convertidas, ao longo dos séculos 20 e 21 (Crist et al., 2017; O'Mara, 2012), em terras agrícolas para a produção de alimento (Egan et al., 2018; Starks et al., 2019; Whitehead et al., 2018).

Particularmente, a pecuária consiste na criação de animais domesticados de pequeno (aves), médio (caprinos, ovinos e suínos) e grande (bovinos) portes que, em ecossistemas campestres, tem como objetivo final a produção de carne, lã, leite, ovos e couro (FAO, 2019; O'Mara, 2012). Os efeitos da pecuária têm sido estudados desde o início do século 20 (Middleton, 1905) e autores geralmente concordam que a remoção moderada de biomassa vegetal acima do solo pode contribuir positivamente para a diversidade vegetal e animal, já que proporciona oportunidades de colonização e forrageio para as espécies (Fedrigo et al., 2018; Milchunas et al., 1988; Tälle et al., 2016; Valliere et al., 2019; Wang and Tang, 2019; Zettlemoyer et al., 2019). No entanto, em altas intensidades, a pecuária pode acabar por degradar ecossistemas campestres já que provoca mudanças na química e na compactação do solo, além da homogeneização do habitat, que por fim leva a perda de biodiversidade em diferentes níveis tróficos (He et al., 2019; Kehoe et al., 2020; Oñatibia et al., 2018; Torma et al., 2019; Wang and Tang, 2019; Wilson and Fox, 2020).

Sob alta intensidade, a pecuária afeta a diversidade de plantas, influenciando a cobertura vegetal e reduzindo a riqueza de espécies (Wang and Tang, 2019). Além disso, o pastejo acaba por induzir lesões mecânicas e estresse nos indivíduos (Rasulov et al., 2019; Tóth et al., 2018), afetando de forma geral a comunicação química (Kirstine and Galbally, 2012; Kirstine et al., 2002, 1998). Já os efeitos da pecuária em animais também dependem da intensidade da atividade, ora aumentando as oportunidades de forrageio (Gordon et al., 2017b; McGregor et al., 2014; Schuette et al., 2013) ora induzindo perda de estrutura ambiental e indisponibilidade de presas (Filazzola et al., 2020; Reinhard et al., 2019) por meio da exclusão pela caça ou cercamento dos campos (Gordon et al., 2017a; Letnic et al., 2009).

Os artrópodes figuram entre os principais elementos faunístico em ecossistemas campestres (Barnett and Facey, 2016), tendo papel fundamental na engenharia de ecossistemas, por meio da polinização, ciclagem de nutrientes e predação (herbivoria e carnivoria) (Barnett and Facey, 2016; Kehoe et al., 2020). Tal grupo representa peça fundamental para a economia e saúde humanas, atuando de forma primária e secundária na produção de alimentos, como vetores de doenças, pestes e no controle de pragas agrícolas (Chakravarthy et al., 2016). No entanto, a discussão em torno dos efeitos do pastejo sobre artrópodes ainda permanece aberta, pois não existe um padrão claro na literatura que aponte efeitos positivos ou negativos. Por exemplo, a riqueza e abundância de espécies de artrópodes mesopredadores é fortemente reduzida em detrimento do pastejo (Helden et al., 2020; Prather and Kaspari, 2019; Reinhard et al., 2019; Zhao et al., 2018). Isto se torna ainda mais evidente em aranhas mesopredadores onde o pastejo leve e moderado tende a aumentar a diversidade de aranhas (Ferreira et al., 2020; Oyarzabal and Guimarães, 2021; Szmatona-Túri et al., 2018; Wang and Tang, 2019) ao passo que o pastejo intenso afeta negativamente a diversidade do grupo (Hashemi et al., 2019; Oyarzabal and Guimarães, 2021; Szmatona-Túri et al., 2018; Wang and Tang, 2019). Entretanto, o efeito do pastejo ainda é assunto em discussão já que, por vezes, não é possível encontrar relação clara com a diversidade de aranhas (Pétillon et al., 2018; Silva and Ott, 2017).

Aranhas são um grupo extremamente rico, com mais de 49.000 espécies descritas em 129 famílias (World Spider Catalog, 2021). Possuem diferentes histórias de vida, formas de corpo, hábitos e estratégias de caça e reprodução (Cardoso et al., 2011; Muvengwi et al., 2018). Estão alocadas em oito guildas funcionais, com enorme variação nos modos de caça (Cardoso et al., 2011), sendo mesopredadores de extrema importância nas redes tróficas (Dennis et al., 2015; Michalko et al., 2019; Rodriguez-Artigas et al., 2016), com capacidade de remover até 800 milhões de toneladas de presas por ano (Nyffeler and Birkhofer, 2017). A interação de aranhas com o pastejo é inevitável, e é de se esperar que o pastejo exerça pressões diretas e indiretas de modo diferenciado sobre estes organismos, levando a importantes alterações na dinâmica das comunidades e populações. Assim, considerando o pastejo em áreas campestres como eixo central, esta tese busca investigar como aranhas respondem à pressão direta e indireta da ação de pastadores. Neste sentido, esta pesquisa de dividiu em três ramos principais: (i) uma extensa revisão bibliográfica buscando, por todo o mundo, evidências dos efeitos do pastejo sobre a riqueza, abundância e diversidade de guildas funcionais de aranhas; (ii) em seguida demonstro o efeitos de diferentes níveis de pastejo em campos sobre a abundância das aranhas orbiculares *Argiope argentata* (Fabricius, 1775) e *Alpaida quadrilorata* (Simon, 1897); e por fim, (iii) exploro a interação de aranhas e plantas, com enfoque sobre a escolha de habitat baseada em pistas ambientais.

Os ramos principais serão apresentados em três diferentes capítulos, redigidos em inglês, e em formato de artigo científico. O Capítulo I já está publicado na revista *Ecological Entomology*. O Capítulo II será submetido a revista *Agriculture, Ecology and Enviroment*. E o Capítulo III para o *The Journal of Arachnology*. Ao final deste documento, apresento a conclusão geral deste trabalho.

CAPÍTULO I

FRIEND AND FOE? THE EFFECTS OF GRASSLAND MANAGEMENT ON GLOBAL PATTERNS OF SPIDER DIVERSITY

Publicado na revista *Ecological Entomology*

Submetido em: 23 de janeiro de 2021

Aceito em: 17 de junho de 2021

Publicado em: 30 de junho de 2021

Abstract

1. Grassland ecosystems have been used worldwide for food production through pastoral and cropping activities. In these ecosystems, spiders constitute important mesopredators, which are affected by grassland management in opposite ways. Historically, the spider taxonomic diversity has been the main focus in studies of grazing impacts in grassland ecosystems, while the intrinsic variability of traits within spiders have been neglected, which may have led to mistaken conclusions. Our objective is to reanalyze the effects of grazing on spider taxonomic and functional guilds on worldwide grasslands.

2. We conducted a systematic review of the literature from the last 10 years, to assess the influence of grazing on the taxonomic and functional guild diversity of spiders worldwide. Using Generalised Linear Mixed Models, we assessed the effects of grazing pressure and type of herd on abundance, richness of spider species, and guilds.

3. In the taxonomic perspective, we found no evidence of grazing impact on the abundance and richness of spiders. However, in the functional guild perspective, high grazing pressure reduced the diversity of web building spiders and enhanced diversity of ground dwelling spiders. Moreover, pastures containing more than one grazing species enhanced the diversity of ambush spiders.

4. Overall, the functional guild diversity of spiders in grassland ecosystems seems to be more influenced by grazing intensity. Our results suggest that grazing intensity can change the guild composition of the araneofauna in grasslands, with guilds responding differently to grazing.

Key words. Anthropogenic impact, araneae, diversity, grazing, spider guilds, systematic review.

Introduction

Grassland ecosystems cover about 40% of the surface of our planet, and are extensively found throughout continents (Ojima et al., 2013; Zhang et al., 2020). Grasslands are worldwide used for pastoral and cropping purposes (Ojima et al., 2013; Jiang et al., 2019), representing almost 70% of the agricultural area of the world (O’Mara, 2012). Throughout the last century, extensive grassland areas within many countries around the world have been converted into crops for food production (O'Mara, 2012; Crist et al., 2017) and pastures (Egan et al., 2018; Whitehead et al., 2018; Starks et al., 2019).

Livestock production, one of the main activities in grasslands, is used to produce meat, milk and leather (O'Mara, 2012; FAO, 2019), constituting a common management technique that promotes above-ground biomass removal (Tälle et al., 2016). The effects of livestock on grasslands have been studied since the beginning of the 20th century (Middleton, 1905) and authors generally agree that moderate removal of above-ground biomass may positively contribute to plant and animal diversity in grasslands (Tälle et al., 2016; Fedrigo et al., 2018; Valliere et al., 2019). However, under high intensities, such management technique may degrade ecosystems through changes in soil chemistry, soil compaction and habitat homogenization, leading to loss of biodiversity (Oñatibia et al., 2018; He et al., 2019; Torma et al., 2019; Kehoe et al., 2020; Wilson & Fox, 2020).

As a main faunal component, arthropods play a pivotal role in grasslands by ecosystem engineering, pollination, nutrient cycling, predation and competition (Barnett & Facey, 2016; Kehoe et al., 2020). The human economy is extremely dependent on arthropods due to their importance as main or secondary agents in food production, as well as vectors and controllers of pests and diseases (Chakravarthy et al., 2016). Among arthropods, spiders are mesopredators (Michalko et al., 2019) of great importance along trophic chains (Dennis et al., 2015; Rodriguez-Artigas et al., 2016), representing an abundant and rich group with more than 48,000 described species in 128 families (World Spider Catalog, 2020). Spiders can consume up to 800 million metric tons of fresh weight mass per year (Nyffeler & Birkhofer, 2017), consisting on vertebrates (Shine & Tamayo, 2016; Nyffeler & Vetter, 2018), invertebrates, including other spiders (Wise, 2006; Michalko et al., 2019), and even nectar (Nyffeler et al., 2016).

The effects of grazing on spiders are usually in accordance with the general trend found in other taxa, where low to moderate grazing regimes may support higher spider taxonomic and guild diversity (Vona-Túri et al., 2017; Lyons et al., 2018a; Szmatona-Túri et al., 2018; Ferreira et al., 2020), whereas heavy grazing (e.g. high density of grazers) is related to negative impacts on spider diversity (Polchaninova et al., 2016; Hashemi et al., 2019; Torma et al., 2019). Yet, several authors were unable to link intense grazing to negative effects on spiders, showing no relationship between grazing and spider taxonomic and guild diversities (Silva & Ott, 2017; Pétillon et al., 2018).

Different authors suggest that treating spiders as a single group may mask effects and trends due to the diversity of shapes and habits among species (Cardoso et al., 2011; Szmatona-Túri et al., 2017; Muvengwi et al., 2018). Spiders are classified in eight different functional guilds, with variable life histories, according to their hunting strategies, such as active hunters and web weavers (Cardoso et al., 2011). Grazing may affect spiders in different ways and ignoring the striking variability within the group may lead to mistaken conclusions (Birkhofer et al., 2015). Hence, assessing the effects of grazing on spiders from a functional guild perspective may be an alternative to the classical taxonomic approach, allowing us to further advance our comprehension on the effects of grazing in grasslands (Birkhofer et al., 2015).

Here we performed a systematic review on the effects of grazing on global patterns of spiders from grassland ecosystems. Our approach is achieved in two steps, where first we treat spiders as a single group, in a taxonomic perspective, looking at effects on species´ abundance and richness. Secondly, we reinterpret the literature data, accommodating species in guilds, and explore the effects of grazing from a functional guild perspective to contrast with the taxonomic perspective (Birkhofer et al., 2015). We hypothesized that the number of individuals (herein ‘species abundance’), the number of species (herein ‘species richness’) and the functional guild diversity, given by the number of individuals in guilds (herein ‘guild abundance’) and species in guilds (herein ‘guild richness’) differ according to grassland management. We predict that high-intensity grazing will have negative effect on species abundance, species richness, guild abundance and guild richness. Low and moderate grazing will have a positive effect on species abundance, spider richness, guild abundance and guild richness.

Methods

Systematic search

We performed a systematic search in three different databases, Scopus, Portal Periódicos Capes (a website provided by the Brazilian Government that includes Web of Science, Pubmed, ScienceDirect and Scielo, besides scientific journals) and Google Scholar. The PECO was designated as: Population – Spiders, Exposure – managed grasslands, Comparison – different types of grazing management and, Outcome – species abundance and species richness. We tested different combinations of the words “araneae”, “spider”, “livestock”, “grazing”, “cattle”, “sheep”, “goat”, “horse” to make the best Boolean terms and access our target studies. At last, we choose the combination of the Boolean terms “araneae” AND (“grazing” OR “cattle” OR “sheep” OR “goat” OR “horse”) since these were those that returned more studies. Due to the great number of papers produced on our topic, the search strategy was delimited to the last decade, from January 2009 until May 2019, avoiding gray literature and without writing language restriction. We built a flowchart with the number of studies found in each database and the number of studies used in the systematic review (Supplementary Fig. 1).

We checked titles and abstracts of all studies, and if one or both were partially or completely consistent with our PECO, the paper was downloaded for posterior full analysis. From each paper, we extracted data related to grazing effects on species abundance and richness, as well as number of spider families and genera. We recorded studies that did not match with our proposed PECO and stored the file in a specific exclusion folder. Spider species were allocated in guilds by us, following Cardoso et al. (2011), who divided all species in eight different guilds, as follows: Ambush hunters, Ground hunters, Orb weavers, Other hunters, Sense webs, Sheet webs, Space webs and Specialists. We used only data on adult individuals.

Besides the data related to spiders, we also extracted from each paper: year of publication, country, field site coordinates, altitude, vegetation type, sampling time period, and season. These information are detailed in Supplementary Table 1. We synthesized the outcomes, methodologies and conclusions of all articles (Supplementary Table 2) and assessed the methodological quality of each study through 13 questions (Supplementary Table 3), adapting the checklist available at the Agency of Healthcare Research and Quality (AHRQ, 2020).

Data analysis

We used Generalized Linear Mixed Models (GLMM) with Negative Binomial error to assess the effects of random and fixed terms in the following response variables: i) species abundance, ii) species richness, iii) guild abundance and, iv) guild richness. The random effect was applied to the GLMM intercepts.

We used six variables as fixed terms in the analysis. Three of them were used to evaluate grazing effect: 1) Number of livestock types (three levels: one ruminant grazing herd, more than one ruminant grazing herd with/without mowing, or ungrazed), 2) Grazing pressure (given by Animal units per hectare (AU/ha)) and 3) the quadratic effect of Grazing pressure. The grazing pressure (AU/ha) was calculated using the original stock density of each study. According to the literature, one animal unit (1 AU) equals the metabolic rate of a 454-kg cow (1 AU = one cow) and can be compared, for example, to five sheep individuals, 50 rabbits, 1.1 horses or 4.4 blesbok (Ndang'ang'a et al., 2002; Blüthgen et al., 2012; Boakye et al., 2013; Eurostat Statistics, 2013; Jansen et al., 2013; Clendenin, 2016; Committee, 2017). The other three variables were used to control for sampling effects within the studies: 4) Sampling method (three levels: active sampling, passive sampling, or both methods used), 5) Continent (five levels: Africa, Asia, Europe, North America, South America, America divided due to longitudinal range) and 6) Altitude. As our main interest is the biological effect of grazing, we emphasize these effects in our results. The effects of sampling variables were not discussed but were presented in the supplementary material (Supplementary Tables 4 and 5). The numeric variables were standardized to have zero mean and one standard deviation. The studies were accounted for as random effects.

For each response variable, we built models using all the fixed and random terms. After that, we compared these models using the Akaike Information criterion (AIC) using the 'lme4' R package (Bates & Mächler, 2015). Models with Delta AIC ≤ 2 were considered the best models in our analysis (Arnold, 2010). We used species richness as an offset for species abundance response and species abundance as offset for species richness response. The presence/absence of each guild was the offset for guild abundance and guild richness responses.

The explained variance was presented through R^2 marginal (R^2m, proportion of variance explained by the fixed terms) and R^2 conditional (R^2c, proportion of variance explained by the fixed and random terms) (Nakagawa & Schielzeth, 2013), using the delta estimative from 'MuMIn' R package (Bartoń, 2019).

To plot the predicted effects we used ‘ggeffects’ R package (Lüdecke, 2018). All analyses were performed in software R (Team, 2018) and the R script can be found in Supplementary Material 1.

Results

Systematic review

The search on Scopus retrieved 1,580 papers, Portal Periódicos Capes retrieved 1,711 papers and Google Scholar retrieved 8,690 papers. The higher number of documents in Google Scholar was due to the presence of gray literature. After removing duplicated papers and those beyond the scope of our review, we selected 79 articles for the descriptive systematic review and 67 for the statistical analysis (References in Supplementary Material 2). Twelve studies were excluded from the statistical analysis because they used repeated data (García et al., 2009; Rosa García et al., 2010, 2011), focused on only one spider guild (Zakkak et al., 2014), sampled on ski trails (Negro et al., 2013), or road verges (Vona-Túri et al., 2017), included only two species (Bowser et al., 2017) or focused only on mowing regimes (Noordijk et al., 2010; Košulič & Hula, 2012; Braschler & Baur, 2016; Buri et al., 2016; Tölgyesi et al., 2018) (Supplementary Fig. 1).

We retrieved papers from 26 countries, mostly from Western Europe (19 countries). Most studies (n = 60, 76%) came from Europe, followed by South America (n = 8, 10%), Africa (n = 5, 6%), North America (n = 4, 5%) and Asia (n = 2, 3%). Following the AHRQ checklist for methodological analysis, it was impossible to be certain if sampling and analyses were performed by the authors in 69% of the studies, due to the lack of active voice in the writing. Furthermore, in most studies, sampling was not randomized in any way (60%), authors did not address bias in analysis or sampling (84%) and missing data (87%) were not reported. In addition, 69% of the studies reported tested hypotheses, the period of sampling (97%), eventual data exclusions (51%) and appropriate statistical analysis to assess their data (93%). Twenty-six studies (33%) reported negative effects of grazing on spider diversity, while 18 studies (23%) reported positive effects and 14 studies (18%) reported neutral effects. The remaining 21 studies (26%) were inconclusive or did not assess the relationship between management techniques and spider diversity (Supplementary Table 3).

Taxonomic diversity: species abundance and species richness

The best-fitted model for both abundance and richness of species included all fixed terms (Supplementary Table 4). However, neither the number of livestock types nor grazing pressure precluded species abundance and species richness (Table 1; For other variables see Supplementary Table 5). For species abundance the fixed effects explained 23% of data variance (R^2m) while the fixed/random effect explained 83% (R^2c) of the variance (Supplementary Table 6). For species richness, the fixed effects explained 22% of data variance (R^2m) while the fixed/random effect explained 87% (R^2c) of the variance (Supplementary Table 6).

Functional guild diversity: abundance and richness

The effect of the fixed terms on abundance and richness of guilds varied among the eight guilds (Supplementary Table 4). The abundance and richness within the Ambush hunters was both benefited from mixed ruminants ($\beta_{Mixed} = 1.515$, $p = 0.005$, $\beta_{Mixed} = 0.714$, $p = 0.015$, respectively), whereas the abundance of Other hunters increased in the presence of only one ruminant type ($\beta_{Grazed} = 2.134$, $p = 0.002$) (Fig. 1; Table 1; For other variables see Supplementary Table 5).

Grazing pressure reduced the abundance of Orb weavers ($\beta P_{ressure}^2 = -0.042$, $p = 0.017$), Sense webs ($\beta_{Pressure}^2 = -2.164$, $p = <2e-16$), and Specialists ($\beta Pressure = -1.767$, $p = 0.005$). Richness was also influenced by grazing pressure, both positively, in Ground hunters ($\beta_{Pressure}^2 = 0.119$, $p = 0.035$), Other hunters ($\beta_{Pressure}^2 = 0.126$, $p = 0.001$) and Space webs ($\beta_{Pressure}^2 = 0.205$, $p = 0.0201$), and negatively, in Sheet webs ($\beta_{Pressure} = -0.261$, $p = 0.027$) (Fig. 1; Table 1; For other variables see Supplementary Table 5). The fixed terms used to control sampling effects also influenced the abundance and richness of guilds, which we show in Supplementary Table 4.

The proportion of variance explained by the fixed terms was more important in the following guilds and response variables, Orb weavers' richness (47% R²m, 52% R²c), Sense webs' abundance (94% R²m, 99% R²m) and richness (91% R²m, 91% R²c) as well as Specialists' richness (78% R²m, 79% R²c). In all other models and guilds, we found a difference of, at least, 40% between R²m and R²c (Supplementary Table 6).

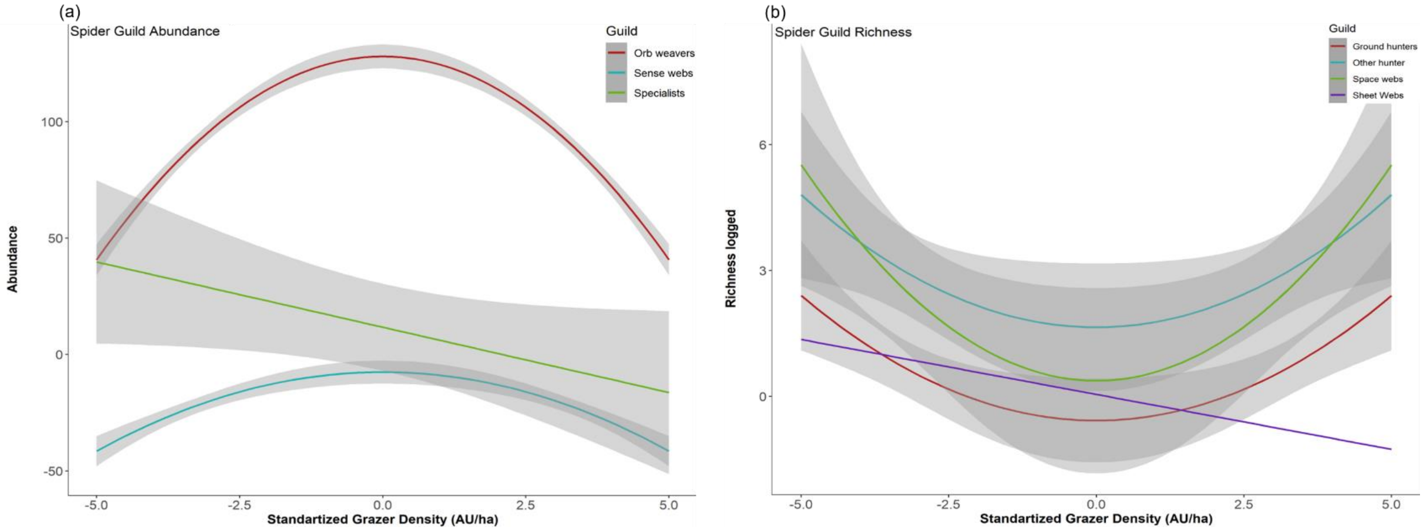

Figure 1 - Standardized effects of Grazer Density (AU ha−1) on (a) abundance and (b) richness of spider guilds. Values of spider guild richness were richness log transformed.

Discussion

At least, 8,000 theses, dissertations and published papers were produced between 2009 and 2019 about the effects of grazing on spider diversity. A quick search in Google Scholar, using only "spider" as subject from 2009 to 2019, returned 233,000 studies, showing that the main theme of our research covered, at least, 3% of the scientific production on spiders during this period. Interestingly, the biggest beef producers - United States, Brazil, China and India - were all underrepresented in our study (Hocquette et al., 2018; Smith et al., 2018; FAO, 2019), suggesting a potential lack of knowledge on the effects of grazing on spiders in these countries. In contrast, the European Union, which is considered the third largest beef producer of the world, containing the fifth largest cattle stock (Hocquette et al., 2018; Smith et al., 2018; FAO, 2019), was well represented in our research.

The difficulty in identifying if authors were responsible for data gathering and analysis, besides the lack of any kind of sampling randomization and bias control (Szmatona-Túri et al., 2018; Řezáč & Heneberg, 2019; Torma et al., 2019), were the main problems we found when synthesizing the results. Additionally, most studies were short-term or presented limited spatial range, which may hamper the perception of the effects of herbivores on arthropod assemblages (Foster et al., 2014). Applying randomization methods for sampling and addressing possible bias in data constitute important steps to enhance study quality.

Although we retrieved 26 studies reporting negative effects of grazing and 18 studies reporting positive effects, the overall observed effect of grazing on the taxonomic diversity of spiders was negligible. Similar effects were also observed for abundance and richness of ants (Barton et al., 2019), bugs, crickets and springtails (Cecil et al., 2019), and other arthropods (Ford et al., 2013). These results suggest the use of additional metrics may be necessary to assess biodiversity, since the taxonomic identity of total abundance and richness may not provide a good overview (McGill et al., 2006; Villéger et al., 2010). As demonstrated for other arthropod groups (Cagnolo et al., 2002; Woodcock et al., 2005; Moranz et al., 2013; Gobbi et al., 2015), and here for spiders, functional guild traits may be used as an alternative to evaluate changes caused by grazing (Birkhofer et al., 2015).

Grazing reduced the abundance and richness of guilds of web building spiders (Orb weavers, Sense webs and Sheet webs) as well as Specialists (species with particular niches that barely overlap resources) (Cardoso et al., 2011). Specifically, the negative quadratic effect of grazing pressure on Orb Weavers (e.g. Araneidae) and Sense webs (e.g. Mygalomorph), suggest that the tridimensional vegetal structure maintained by intermediate levels of grazing can benefit web building spiders, as previously advocated (Sasaki et al., 2009; Nogueira & Pinto-da-Rocha, 2016; Gao & Carmel, 2019; Hu et al., 2019; Wang & Tang, 2019; Ferreira et al., 2020).

On the other hand, the richness of active hunter species (guilds of Ground hunters and Other hunters) as well as Space webs was positively affected by grazing pressure. According to the results, richness increased under low and high grazing impacts, while it was reduced under intermediate impacts. This result may be explained by a new hypothesis. Considering that guilds of Active hunters and Space webs are composed of ground-dwelling abundant species, ranging from small to large body sizes (Höfer & Ott, 2009; Cardoso et al., 2011; World Spider Catalog, 2020), our results could be explained by changes in species composition due to different grazing pressures, thus maintaining high species richness. Low grazing pressure may benefit small-body size species within these guilds, while high impacts of grazing would benefit large species (Kaspari & Weiser, 1999), suggesting species turnover (Samu et al., 2018; Pitta et al., 2019; Rocha-Ortega et al., 2019).

Besides grazing pressure, the presence of one ruminant herd was positive for the abundance of Other hunters while more than one ruminant herd was positive for Ambush hunters' abundance and richness. We are aware that addressing ruminant herds as one or mixed herd categories is certainly an oversimplification of the actual impact that different types of ruminants can cause on grassland ecosystems (Liu et al., 2015). However, grazing by one or more herds may enhance the multifunctionality and multidiversity in grassland ecosystems, thus causing an effect comparable to intermediate impacts (McGregor, 2010; Clement et al., 2018; Wang et al., 2019). Such trend can be observed in the diversity of plant communities (Ross et al., 2016; Pakeman et al., 2019), flies (Clement et al., 2018), butterflies (Fraser et al., 2014), rodents (Evans et al., 2015; Li et al., 2019b) and birds (Fraser et al., 2014; Evans et al., 2015). This effect may have been observed only on Ambush hunters and Other hunters because, even though these guilds are known to hunt on the surface of flowers and leaves, with a higher dominance of families like Thomisidae and Salticidae than other families, they are also capable of adopting hunting strategies on the ground and other substrates, thus not relying only in one type of vegetation structure (Gomes et al., 2018; Joseph et al., 2018; Lyons et al., 2018b, 2018c; da Silva Bomfim et al., 2021).

The low to moderate proportion of variance explained by the fixed terms within models (Nakagawa & Schielzeth, 2013) suggests that at least four sources of heterogeneity precluding taxonomic and functional guild diversity of spiders may have been left out. First, although all of our data was published in the last decade, the samples for those studies were obtained in the last three decades, and environmental variations are disregarded here. Secondly, information about each species is generally scarce for most spiders because they are only known for its taxonomic description (World Spider Catalog, 2020), and basic information on phenology and demography is unknow (Wiśniewski et al., 2018; Rix et al., 2019). Third, ruminant species present different grazing patterns of vegetational removal, trampling and energy intakes (Mendonça et al., 2019; Scasta et al., 2019) and the interaction with spiders may lead to different outcomes. And lastly, grassland type (native, semi-natural or cultivated) (Horváth et al., 2019; Smith DiCarlo & DeBano, 2019) and management can alter soil chemistry, soil erosion and plant biomass (Mosier et al., 1991; Liu et al., 2017; Li et al., 2019a). All this, in turn, may influence spider diversity through changes in food sources, shelter and mortality (Pekár, 2012; Gerlach et al., 2013; Hashemi et al., 2019; Řezáč & Heneberg, 2019; Torma et al., 2019). Finally, a proper measure of mowing managements, similar to Animal Units per hectare (Kumhála et al., 2007), as well as a proper investigation of the effects of wild grazers (Pryke et al., 2016), would provide a better understanding of the diversity of spiders in grassland ecosystems.

In conclusion, our work is another step forward to realize the ecosystem services that spiders provide and treating them as a homogeneous group might obfuscate the effects of grazing management. We found that, although taxonomic diversity does not respond to grazing pressure and type of herd, such management have the potential to threat spiders. Thus, taxonomy only (abundance and richness of species) should not be the major proxy to understand spider diversity in grassland ecosystems managed by grazing. We suggest considering the intrinsic variability of traits and habits within Araneae, and thus, the functional guild diversity may be a good alternative to understand the relationship between grazing and spiders. In this way, considering a scenario of limited resources to study the araneofauna altogether, we encourage focusing on species with high dependence on vegetal structures to build webs, such as the Orb weavers, Sheet webs and Sense webs, or spiders with high mobility that forage on the ground, and thus with low dependence on vegetal structure, such as the Ground hunters and Other hunters.

Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

Acknowledgments

We are grateful to all authors and the data provided by them for the accomplish of this work. We also are grateful for CAPES and the scholarship granted to the first author (process #88882.439370/2019-01). The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

All authors contributed to the study conception and design. All author performed the screening and analyzed of the data, as well as the writing and revision of the text, tables and images. Finally, all authors read and approved the final manuscript.

Conflicts of interest statement:

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supporting materials:

Supplementary Material 1 – R script.

```
#Friend and foe? The effects of grassland management on global patterns of spider diversity
#Guilherme Oyarzabal da Silva & Murilo Guimarães

#To go to specific group of analysis you can search:
#Abund_Analy        #Richn_Analy
#Ambus_Analy        #Groun_Analy
#Orbwe_analy        #Other_Analy
#Sense_Analy        #Sheet_Analy
#Space_Analy        #Speci_Analy

#Packages
library(lme4)
library(AICcmodavg)
library(MuMIn)
library(ggplot2)
library(ggeffects)

#Overdispersion Function
overdisp_fun <- function(model){
  rdf <- df.residual(model)
  rp <- residuals(model,type="pearson")
  Pearson.chisq <- sum(rp^2)
  prat <- Pearson.chisq/rdf
  pval <- pchisq(Pearson.chisq, df=rdf, lower.tail=FALSE)
  c(chisq=Pearson.chisq,ratio=prat,rdf=rdf,p=pval)
}

#DATA
data <- read.table("Spiders_2.0.csv", head=T, as.is=T, sep=";")
```

```
#Local dos dados
refe <- as.factor(data[,2]) #Study reference
cont <- as.factor(data[,4]) #Study place
alti <- as.numeric(data[,5]) #Altitud
graz <- as.factor(data[,6]) #Grass cut, none, one grazer, mixed grazed or mowed
samp <- as.factor(data[,7]) #Sampling method, passive, active or both
auha <- as.numeric(data[,8]) #Animal units per hectare
abun <- as.numeric(data[,9]) #Spider abundance
fami <- as.numeric(data[,10]) #Spider family richness
gene <- as.numeric(data[,11]) #Spider genus richness
spec <- as.numeric(data[,12]) #Spider species richness
ambP <- as.numeric(data[,13]) #Ambush hunter presence
ambA <- as.numeric(data[,14]) #Ambush hunter abundance
ambR <- as.numeric(data[,15]) #Ambush hunter richness
groP <- as.numeric(data[,16]) #Ground hunter presence
groA <- as.numeric(data[,17]) #Ground hunter abundance
groR <- as.numeric(data[,18]) #Ground hunter richness
orbP <- as.numeric(data[,19]) #Orb weavers presence
orbA <- as.numeric(data[,20]) #Orb weavers abundance
orbR <- as.numeric(data[,21]) #Orb weavers richness
othP <- as.numeric(data[,22]) #Other hunters presence
othA <- as.numeric(data[,23]) #Other hunters abundance
othR <- as.numeric(data[,24]) #Other hunters richness
senP <- as.numeric(data[,25]) #Sense webs presence
senA <- as.numeric(data[,26]) #Sense webs abundance
senR <- as.numeric(data[,27]) #Sense webs richness
sheP <- as.numeric(data[,28]) #Sheet webs presence
sheA <- as.numeric(data[,29]) #Sheet webs abundance
sheR <- as.numeric(data[,30]) #Sheet webs richeness
spaP <- as.numeric(data[,31]) #Space webs presence
spaA <- as.numeric(data[,32]) #Space webs abundance
spaR <- as.numeric(data[,33]) #Space webs richness
speP <- as.numeric(data[,34]) #Specialist presence
speA <- as.numeric(data[,35]) #Specialist abundance
speR <- as.numeric(data[,36]) #Specialist richness

#Standart
#Altitud
meanalti <- mean(alti, na.rm = TRUE)
sdalti <- sd(alti, na.rm = TRUE)
alti.ST <- (alti - meanalti)/sdalti
#AU/ha
meanauha <- mean(auha, na.rm = TRUE)
sdauha <- sd(auha, na.rm = TRUE)
auha.ST <- (auha - meanauha)/sdauha

###########################Abund_Analy############################
#Spider Abundance: Abundance data coming for each species.
mAbu0 <- glmer.nb(abun~1+(1|refe), data=data)#null
mAbu1 <- glmer.nb(abun~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(log(spec))+(1|refe),data=data)
#
mAbu2 <- glmer.nb(abun~cont+offset(log(spec))+(1|refe),data=data)
mAbu3 <- glmer.nb(abun~graz+offset(log(spec))+(1|refe),data=data)

#New model addition
cand.setAbun <- list(mAbu0,mAbu1,mAbu2,mAbu3)
#
namesAbun <-c("mAbu0_null","mAbu1_comp+off(spec)+refe",
        "mAbu2_cont+off(spec)+refe",
        "mAbu3_graz+off(spec)+refe")
#Last AIC
aicAbun <-aictab(cand.setAbun, modnames=namesAbun)
#                          K    AICc Delta_AICc AICcWt Cum.Wt       LL
#mAbu1_comp+off(spec)+refe 13 1332.95       0.00      1      1  -651.11
#mAbu2_cont+off(spec)+refe  6 2065.32     732.37      0      1 -1026.36
#mAbu3_graz+off(spec)+refe  5 2075.09     742.14      0      1 -1032.33
#mAbu0_null                 3 2280.22     947.27      0      1 -1137.03
```

```
################################################
summary(mAbu1)
#                  Estimate Std. Error z value Pr(>|z|)
#contAfrica         3.319613   0.675580   4.914 8.94e-07 ***
#contAsia          -0.637804   1.053279  -0.606    0.545
#contEurope        -0.324016   0.700825  -0.462    0.644
#contSouth_America -1.933473   0.868398  -2.226    0.026 *
#alti.ST           -0.147861   0.159240  -0.929    0.353
#grazMixed          0.029956   0.208154   0.144    0.886
#grazUngrazed      -0.142820   0.150621  -0.948    0.343
#sampActPas        -0.697744   0.732865  -0.952    0.341
#sampPassive       -0.005192   0.479637  -0.011    0.991
#auha.ST           -0.236999   0.219472  -1.080    0.280
#I(auha.ST^2)       0.016368   0.067914   0.241    0.810

qqnorm(resid(mAbu1))
qqline(resid(mAbu1))

overdisp_fun(mAbu1)
#59.8247146  0.7669835 78.0000000  0.9372492

r.squaredGLMM(mAbu1, mAbu0)
#               R2m       R2c
#delta     0.2315094 0.8313947
#lognormal 0.2342506 0.8412387
#trigamma  0.2284184 0.8202941

###########################Richn_Analy##############################
#Spider Richness: Richness data coming for each study.
mRic0 <- glmer.nb(spec~1+(1|refe), data=data)#null
mRic1 <- glmer.nb(spec~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(log(abun))+(1|refe),data=data)
#
mRic2 <- glmer.nb(spec~cont+offset(log(abun))+(1|refe),data=data)
mRic3 <- glmer.nb(spec~graz+offset(log(abun))+(1|refe),data=data)
#
cand.setRicn <- list(mRic0,mRic1,mRic2,mRic3)
#
namesRicn <-c("mRic0_null","mRic1_comp+off(abun)+refe",
              "mRic2_cont+off(abun)+refe",
              "mRic3_graz+off(abun)+refe")
#Last AIC
aicRicn <-aictab(cand.setRicn, modnames=namesRicn)
#                           K    AICc Delta_AICc AICcWt Cum.Wt      LL
#mRic1_comp+off(abun)+refe 13  844.46       0.00      1      1 -406.87
#mRic0_null                 3 1276.72     432.26      0      1 -635.28
#mRic2_cont+off(abun)+refe  6 1328.80     484.34      0      1 -658.10
#mRic3_graz+off(abun)+refe  5 1337.98     493.52      0      1 -663.78

#Best Model
summary(mRic1)
#                  Estimate Std. Error z value Pr(>|z|)
#(Intercept)       -3.15804    0.70592  -4.474 7.69e-06 ***
#contAsia           0.45630    1.08195   0.422   0.6732
#contEurope         0.29635    0.71926   0.412   0.6803
#contSouth_America  1.81930    0.89110   2.042   0.0412 *
#alti.ST            0.12699    0.15886   0.799   0.4241
#grazMixed         -0.09060    0.18703  -0.484   0.6281
#grazUngrazed       0.13806    0.13329   1.036   0.3003
#sampActPas         0.57532    0.73227   0.786   0.4321
#sampPassive       -0.08884    0.48084  -0.185   0.8534
#auha.ST            0.22258    0.20134   1.105   0.2689
#I(auha.ST^2)      -0.02106    0.06071  -0.347   0.7287

qqnorm(resid(mRic1))
qqline(resid(mRic1)) #OK

overdisp_fun(mRic1)
#chisq       ratio         rdf           p
#85.6502805  1.0980805 78.0000000  0.2589627
```

```
r.squaredGLMM(mRic1,mRic0)
#             R2m       R2c
#delta     0.2201549 0.8725099
#lognormal 0.2216073 0.8782659
#trigamma  0.2185617 0.8661956

###########################Ambus_Analy############################
#Ambush hunters Abundance
mAmbA0 <- glmer.nb(ambA~1+(1|refe), data=data)#null
mAmbA1 <- glmer.nb(ambA~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(ambP)+(1|refe), data=data)
#
mAmbA2 <- glmer.nb(ambA~cont+graz+offset(ambP)+(1|refe), data=data)
mAmbA3 <- glmer.nb(ambA~cont+offset(ambP)+(1|refe), data=data)
#
cand.setAmbA <- list(mAmbA0,mAmbA1,mAmbA2,mAmbA3)
#
namesAmbA <-c("mAmbA0_null","mAmbA1_comp+off(ambP)+refe",
            "mAmbA2_cont+graz+off(ambP)+refe",
            "mAmbA3_cont+off(ambP)+refe")
#Final AIC
aicAmbA <-aictab(cand.setAmbA, modnames=namesAmbA)
#                              K    AICc Delta_AICc AICcWt Cum.Wt      LL
#mAmbA1_comp+off(ambP)+refe      14  736.21       0.00      1      1 -351.60
#mAmbA3_cont+off(ambP)+refe       7 1129.28     393.07      0      1 -557.26
#mAmbA2_cont+graz+off(ambP)+refe  9 1130.66     394.45      0      1 -555.71
#mAmbA0_null                      3 1171.79     435.58      0      1 -582.81

summary(mAmbA1)
#                 Estimate Std. Error z value Pr(>|z|)
#(Intercept)       -2.00424    1.76223  -1.137  0.25540
#contAsia           0.03897    2.17904   0.018  0.98573
#contEurope         1.83538    1.50835   1.217  0.22368
#contNorth_America  4.95384    2.04164   2.426  0.01525 *
#contSouth_America -1.01001    1.88867  -0.535  0.59281
#alti.ST           -0.09862    0.32339  -0.305  0.76041
#grazMixed          1.51532    0.54604   2.775  0.00552 **
#grazUngrazed       0.44040    0.36980   1.191  0.23368
#sampActPas         2.76836    1.85791   1.490  0.13621
#sampPassive        1.27967    1.15496   1.108  0.26787
#auha.ST            0.05876    0.43260   0.136  0.89195
#I(auha.ST^2)      -0.04979    0.05877  -0.847  0.39686

qqnorm(resid(mAmbA1))
qqline(resid(mAmbA1)) #OK

overdisp_fun(mAmbA1)
#chisq        ratio         rdf          p
#48.4295762  0.5697597 85.0000000  0.9995168

r.squaredGLMM(mAmbA1, mAmbA0)#OK
#             R2m       R2c
#delta     0.2835644 0.8976253
#lognormal 0.2902082 0.9186562
#trigamma  0.2730903 0.8644696

########################################################
#Ambush hunters Richness
mAmbR0 <- glmer.nb(ambR~1+(1|refe), data=data)#null
mAmbR1 <- glmer.nb(ambR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(ambP)+(1|refe), nb.control = glmerControl(optimizer
= "bobyqa"), data=data)
#
mAmbR2 <- glmer.nb(ambR~graz+offset(ambP)+(1|refe),data=data)
#
cand.setAmbR <- list(mAmbR0,mAmbR1,mAmbR2)
#
namesAmbR <-c("mAmbR0_null","mAmbR1_comp+off(ambP)+refe",
            "mAmbR2_graz+off(ambP)+refe")
#Final AIC
```

```
aicAmbR <-aictab(cand.setAmbR, modnames=namesAmbR)
#                          K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mAmbR1_comp+off(ambP)+refe 13 373.03       0.00      1      1 -171.32
#mAmbR2_graz+off(ambP)+refe  5 559.88     186.84      0      1 -274.74
#mAmbR0_null                3 621.40     248.36      0      1 -307.62

summary(mAmbR1)
#                    Estimate Std. Error z value Pr(>|z|)
#(Intercept)         -0.77716    0.77376  -1.004   0.3152
#contAsia           -17.59833 5252.79982  -0.003   0.9973
#contEurope           0.60018    0.65077   0.922   0.3564
#contSouth_America   -0.61135    0.93909  -0.651   0.5150
#alti.ST             -0.06352    0.16331  -0.389   0.6973
#grazMixed            0.71421    0.29382   2.431   0.0151 *
#grazUngrazed         0.14326    0.22752   0.630   0.5289
#sampActPas           0.76470    0.67937   1.126   0.2603
#sampPassive          0.04782    0.46972   0.102   0.9189
#auha.ST             -0.12159    0.25786  -0.472   0.6372
#I(auha.ST^2)         0.05113    0.07616   0.671   0.5020

qqnorm(resid(mAmbR1))
qqline(resid(mAmbR1)) #OK

overdisp_fun(mAmbR1)
#chisq        ratio        rdf          p
#49.4039033  0.5881417 84.0000000  0.9990557

r.squaredGLMM(mAmbR2, mAmbR0)#OK
#              R2m       R2c
#delta     0.10331333 0.6160611
#lognormal 0.11005994 0.6562914
#trigamma  0.09501237 0.5665621

############################Groun_Analy##############################
#Ground hunters Abundance
mGroA0 <- glmer.nb(groA~1+(1|refe), data=data)#null
mGroA1 <- glmer.nb(groA~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(groP)+(1|refe), data=data)
#
mGroA2 <- glmer.nb(groA~cont+samp+offset(groP)+(1|refe), data=data)

cand.setGroA <- list(mGroA0,mGroA1,mGroA2)
#
namesGroA <-c("mGroA0_null","mGroA1_comp+off(groP)+refe",
             "mGroA2_cont+graz+off(groP)+refe")
#Final AIC
aicGroA <-aictab(cand.setGroA, modnames=namesGroA)
#                           K    AICc Delta_AICc AICcWt Cum.Wt      LL
#mGroA1_comp+off(groP)+refe      14 1139.37       0.00      1      1 -553.18
#mGroA2_cont+graz+off(groP)+refe  9 1710.01     570.64      0      1 -845.39
#mGroA0_null                      3 1756.34     616.97      0      1 -875.09

summary(mGroA1)
#                  Estimate Std. Error z value Pr(>|z|)
#(Intercept)       -3.19968    1.63226  -1.960 0.049963 *
#contAsia           1.97201    1.96384   1.004 0.315301
#contEurope         1.60172    1.35375   1.183 0.236741
#contNorth_America  2.20643    1.87458   1.177 0.239186
#contSouth_America  0.17298    1.62559   0.106 0.915258
#alti.ST            0.30134    0.27883   1.081 0.279819
#grazMixed          0.15371    0.33388   0.460 0.645250
#grazUngrazed      -0.02115    0.23526  -0.090 0.928376
#sampActPas         6.35737    1.68322   3.777 0.000159 ***
#sampPassive        6.02188    1.07944   5.579 2.42e-08 ***
#auha.ST           -0.08528    0.32327  -0.264 0.791939
#I(auha.ST^2)       0.00345    0.05142   0.067 0.946496

qqnorm(resid(mGroA1))
qqline(resid(mGroA1)) #OK
```

```
overdisp_fun(mGroA1)
#chisq        ratio         rdf           p
#48.9868025  0.5763153 85.0000000  0.9993975

r.squaredGLMM(mGroA1, mGroA0)#OK
#            R2m       R2c
#delta     0.6041088 0.9626130
#lognormal 0.6071894 0.9675219
#trigamma  0.6000131 0.9560868

############################################################
#Ground hunters Richness
mGroR0 <- glmer.nb(groR~1+(1|refe), data=data)#null
mGroR1 <- glmer.nb(groR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(groP)+(1|refe), data=data)
#
mGroR2 <- glmer.nb(groR~cont+alti.ST+samp+auha.ST+I(auha.ST^2)+offset(groP)+(1|refe), data=data)
mGroR3 <- glmer.nb(groR~samp+auha.ST+I(auha.ST^2)+offset(groP)+(1|refe), data=data)
#
cand.setGroR <- list(mGroR0,mGroR1,mGroR2,mGroR3)
#
namesGroR <-c("mGroR0_null","mGroR1_comp+off(groP)+refe",
            "mGroR2_cont+alti+samp+auha+auha^2+off(groP)+refe",
            "mGroR3_samp+auha+auha^2+off(groP)+refe")
#Final AIC
aicGroR <-aictab(cand.setGroR, modnames=namesGroR)
#                                          K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mGroR3_samp+auha+auha^2+off(groP)+refe            7 540.81       0.00   0.75   0.75 -262.78
#mGroR2_cont+alti+samp+auha+auha^2+off(groP)+refe 11 543.65       2.84   0.18   0.93 -259.27
#mGroR1_comp+off(groP)+refe                      13 545.64       4.84   0.07   1.00 -257.63
#mGroR0_null                                   3 899.73     358.92   0.00   1.00 -446.79

summary(mGroR3)
#             Estimate Std. Error z value Pr(>|z|)
#(Intercept)   -1.41993    0.50039  -2.838  0.00454 **
#sampActPas    3.35125    0.82317   4.071 4.68e-05 ***
#sampPassive   2.72226    0.51862   5.249 1.53e-07 ***
#auha.ST      -0.27738    0.11301  -2.454  0.01411 *
#I(auha.ST^2)  0.11915    0.05666   2.103  0.03546 *

qqnorm(resid(mGroR3))
qqline(resid(mGroR3)) #OK

overdisp_fun(mGroR3)
#chisq        ratio         rdf           p
#38.8484402  0.4316493 90.0000000  0.9999995

r.squaredGLMM(mGroR3, mGroR0)#OK
#            R2m       R2c
#delta     0.5269485 0.9542791
#lognormal 0.5280353 0.9562472
#trigamma  0.5257612 0.9521289

#############################Orbwe_Analy###############################
#Orb weavers Abundance
mOrbA0 <- glmer.nb(orbA~1+(1|refe), data=data)#null
mOrbA1 <- glmer.nb(orbA~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(orbP)+(1|refe), data=data)
#
mOrbA2 <- glmer.nb(orbA~alti.ST+samp+auha.ST+I(auha.ST^2)+offset(orbP)+(1|refe), data=data)
mOrbA3 <- glmer.nb(orbA~samp+alti.ST+I(auha.ST^2)+offset(orbP)+(1|refe), data=data)

cand.setOrbA <- list(mOrbA0,mOrbA1,mOrbA2,mOrbA3)
#
namesOrbA <-c("mOrbA0_null","mOrbA1_comp+off(orbP)+refe",
            "mOrbA2_alti+samp+auha+auha^2+off(orbP)+refe",
            "mOrbA3_alti+samp+auha^2+off(orbP)+refe")

#Final AIC
aicOrbA <-aictab(cand.setOrbA, modnames=namesOrbA)
#                                      K    AICc Delta_AICc AICcWt Cum.Wt      LL
```

```
#mOrbA3_alti+samp+auha^2+off(orbP)+refe       7  863.40       0.00   0.75   0.75  -424.09
#mOrbA2_alti+samp+auha+auha^2+off(orbP)+refe  8  865.58       2.17   0.25   1.00  -423.99
#mOrbA0_null                              3 1288.14     424.74   0.00   1.00  -640.99
#mOrbA1_comp+off(orbP)+refe                 14 2938.85    2075.45   0.00   1.00 -1452.92

summary(mOrbA3)
#            Estimate Std. Error z value Pr(>|z|)
#(Intercept)   4.10157    0.76609   5.354 8.61e-08 ***
#sampActPas   -1.13190    1.50925  -0.750  0.45327
#sampPassive  -2.68509    0.83790  -3.205  0.00135 **
#alti.ST      -0.69740    0.26756  -2.607  0.00915 **
#I(auha.ST^2) -0.04287    0.01812  -2.366  0.01799 *

qqnorm(resid(mOrbA3))
qqline(resid(mOrbA3)) #OK

overdisp_fun(mOrbA3)
#chisq        ratio         rdf          p
#50.4192179  0.5480350 92.0000000  0.9998723

r.squaredGLMM(mOrbA3, mOrbA0)#OK
#            R2m       R2c
#delta     0.3276809 0.8752772
#lognormal 0.3375836 0.9017286
#trigamma  0.3118802 0.8330715

##########################################################
#Orb weavers Richness
mOrbR0 <- glmer.nb(orbR~1+(1|refe), data=data)#null
mOrbR1 <- glmer.nb(orbR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(orbP)+(1|refe), data=data)
#
mOrbR2 <- glmer.nb(orbR~graz+samp+offset(orbP)+(1|refe), data=data)
mOrbR3 <- glmer.nb(orbR~alti.ST+samp+I(auha.ST^2)+offset(orbP)+(1|refe), data=data)
#
cand.setOrbR <- list(mOrbR0,mOrbR1,mOrbR2)
#
namesOrbR <-c("mOrbR0_null","mOrbR1_comp+off(orbP)+refe",
            "mOrbR2_graz+samp+refe")
#Final AIC
aicOrbR <-aictab(cand.setOrbR, modnames=namesOrbR)
#                         K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mOrbR1_comp+off(orbP)+refe 13 341.65       0.00      1      1 -155.63
#mOrbR2_graz+samp+refe       7 535.90     194.25      0      1 -260.57
#mOrbR0_null                 3 597.84     256.20      0      1 -295.84

summary(mOrbR1)
#                  Estimate Std. Error z value Pr(>|z|)
#(Intercept)        0.49576    0.45684   1.085   0.2778
#contAsia           0.50963    0.58417   0.872   0.3830
#contEurope         0.19094    0.46038   0.415   0.6783
#contSouth_America -0.46453    0.57535  -0.807   0.4194
#alti.ST           -0.22282    0.15986  -1.394   0.1634
#grazMixed          0.43486    0.25472   1.707   0.0878 .
#grazUngrazed       0.05429    0.19661   0.276   0.7825
#sampActPas         0.06691    0.37399   0.179   0.8580
#sampPassive       -1.22406    0.24317  -5.034 4.81e-07 ***
#auha.ST           -0.21381    0.26555  -0.805   0.4207
#I(auha.ST^2)       0.07234    0.07258   0.997   0.3189

qqnorm(resid(mOrbR1))
qqline(resid(mOrbR1)) #OK

overdisp_fun(mOrbR1)
#chisq        ratio         rdf          p
#64.1359884  0.7635237 84.0000000  0.9474697

r.squaredGLMM(mOrbR1,mOrbR0)#OK
#            R2m       R2c
#delta     0.4713740 0.5296369
```

```
#lognormal 0.5194058 0.5836056
#trigamma  0.4118587 0.4627654

###########################Other_Analy#############################
#Other hunters Abundance
mOthA0 <- glmer.nb(othA~1+(1|refe), data=data)#null
mOthA1 <- glmer.nb(othA~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(othP)+(1|refe), data=data)
#
mOthA2 <- glmer.nb(othA~cont+offset(othP)+(1|refe), data=data)
mOthA3 <- glmer.nb(othA~graz+alti.ST+samp+auha.ST+I(auha.ST^2)+offset(othP)+(1|refe), data=data)
mOthA4 <- glmer.nb(othA~alti.ST+graz+samp+offset(othP)+(1|refe), data=data)
#
cand.setOthA <- list(mOthA0,mOthA1,mOthA2,mOthA3,mOthA4)
#
namesOthA <-c("mOthA0_null","mOthA1_comp+off(othP)+refe",
            "mOthA2_cont+off(othP)+refe+cont",
            "mOthA3_alti+graz+samp+auha+auha^2+refe",
            "mOthA4_alti+graz+samp+refe")
#Final AIC
aicOthA <-aictab(cand.setOthA, modnames=namesOthA)
#                                    K    AICc Delta_AICc AICcWt Cum.Wt      LL
#mOthA3_alti+graz+samp+auha+auha^2+refe 10 1110.65       0.00   0.81   0.81 -544.08
#mOthA1_comp+off(othP)+refe             14 1113.61       2.96   0.19   1.00 -540.31
#mOthA2_cont+off(othP)+refe+cont         7 1714.14     603.49   0.00   1.00 -849.69
#mOthA4_alti+graz+samp+refe              8 1720.46     609.81   0.00   1.00 -851.74
#mOthA0_null                             3 1733.29     622.64   0.00   1.00 -863.57

summary(mOthA3)
#             Estimate Std. Error z value Pr(>|z|)
#(Intercept)   2.134135   0.711948   2.998  0.00272 **
#grazMixed     0.474408   0.345917   1.371  0.17023
#grazUngrazed -0.352004   0.237366  -1.483  0.13808
#alti.ST      -0.518980   0.217289  -2.388  0.01692 *
#sampActPas    1.146899   1.331171   0.862  0.38892
#sampPassive   1.608539   0.745826   2.157  0.03103 *
#auha.ST      -0.375670   0.321526  -1.168  0.24265
#I(auha.ST^2)  0.004837   0.045781   0.106  0.91585

qqnorm(resid(mOthA3))
qqline(resid(mOthA3)) #OK

overdisp_fun(mOthA3)
#chisq        ratio         rdf          p
#56.1752182  0.6311822 89.0000000  0.9974408

r.squaredGLMM(mOthA3, mOthA0)#OK
#            R2m       R2c
#delta     0.2593926 0.8937551
#lognormal 0.2637585 0.9087981
#trigamma  0.2534688 0.8733442

#########################################################
#Other hunters Richness
mOthR0 <- glmer.nb(othR~1+(1|refe), data=data)#null
mOthR1 <- glmer.nb(othR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(othP)+(1|refe), data=data)
#
mOthR2 <- glmer.nb(othR~auha.ST+I(auha.ST^2)+offset(othP)+(1|refe)+(1|cont), data=data)
#
cand.setOthR <- list(mOthR0,mOthR1,mOthR2)
#
namesOthR <-c("mOthR0_null","mOthR1_comp+off(othP)+refe",
            "mOthR2_auha+auha^2+off(othP)+refe+cont")
#First AIC
aicOthR <-aictab(cand.setOthR, modnames=namesOthR)
#                                    K    AICc Delta_AICc AICcWt Cum.Wt      LL
#mOthR2_auha+auha^2+off(othP)+refe+cont  6 619.43       0.00   0.97   0.97 -303.25
#mOthR1_comp+off(othP)+refe             13 626.56       7.13   0.03   1.00 -298.09
#mOthR0_null                             3 985.57     366.14   0.00   1.00 -489.71
```

```
summary(mOthR2)
#              Estimate Std. Error z value Pr(>|z|)
#(Intercept)   0.73069    0.44523   1.641  0.10077
#auha.ST      -0.42204    0.14377  -2.936  0.00333 **
#I(auha.ST^2)  0.12625    0.04021   3.140  0.00169 **

qqnorm(resid(mOthR2))
qqline(resid(mOthR5)) #OK

overdisp_fun(mOthR2)
#chisq        ratio         rdf           p
#66.6486405  0.7324026 91.0000000  0.9741983

r.squaredGLMM(mOthR2, mOthR0)#OK
#              R2m       R2c
#delta     0.01720803 0.9483025
#lognormal 0.01723355 0.9497089
#trigamma  0.01718105 0.9468160

#########################Sense_Analy###########################
#Sense webs Abundance
mSenA0 <- glmer.nb(senA~1+(1|refe), data=data)#null
mSenA1 <- glmer.nb(senA~cont+alti.ST+graz+samp+auha.ST+offset(senP)+(1|refe), data=data)
#
mSenA2 <- glmer.nb(senA~graz+alti.ST+auha.ST+offset(senP)+(1|refe), data=data)
mSenA3 <- glmer.nb(senA~graz+offset(senP)+(1|refe), data=data)
mSenA4 <- glmer.nb(senA~I(auha.ST^2)+offset(senP)+(1|refe), data=data)

cand.setSenA <- list(mSenA0,mSenA1,mSenA2,mSenA3,mSenA4)
#
namesSenA <-c("mSenA0_null","mSenA1_comp(+cont)+off(senP)+refe",
              "mSenA2_graz+alti+auha+refe",
              "mSenA3_agraz+refe",
              "mSenA4_auha^2+refe")
#AIC
aicSenA <-aictab(cand.setSenA, modnames=namesSenA)
#                                     K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mSenA4_auha^2+refe                4 133.99       0.00   0.92   0.92  -62.78
#mSenA2_graz+alti+auha+refe         7 139.04       5.05   0.07   1.00  -61.91
#mSenA1_comp(+cont)+off(senP)+refe 13 147.42      13.44   0.00   1.00  -58.57
#mSenA3_agraz+refe                 5 221.75      87.76   0.00   1.00 -105.68
#mSenA0_null                       3 240.34     106.35   0.00   1.00 -117.09
#

summary(mSenA4)
#               Estimate Std. Error z value Pr(>|z|)
#(Intercept)   -4.118779   0.005239  -786.2   <2e-16 ***
#I(auha.ST^2) -2.164410   0.005273  -410.5   <2e-16 ***

qqnorm(resid(mSenA4))
qqline(resid(mSenA4))

overdisp_fun(mSenA4)
#chisq      ratio        rdf          p
#12.8341264  0.1350961 95.0000000  1.0000000

r.squaredGLMM(mSenA4,mSenA0)#OK
#              R2m       R2c
#delta     0.9449591 0.9984265
#lognormal 0.9451927 0.9986734
#trigamma  0.9446285 0.9980772

##########################################################
#Sense web Richness
mSenR0 <- glmer.nb(senR~1+(1|refe), data=data)#null
mSenR1  <-  glmer.nb(senR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(senP)+(1|refe),  nb.control  =  glmerControl(optimizer  =
"bobyqa"), data=data)
#
mSenR2 <- glmer.nb(senR~alti.ST+graz+offset(senP)+(1|refe), data=data)
```

```
#
cand.setSenR <- list(mSenR0,mSenR1,mSenR2)
#
namesSenR <-c("mSenR0_null","mSenR1_comp+off(senP)+refe",
            "mSenR2_graz+alti+off(senP)+refe")
#Final AIC
aicSenR <-aictab(cand.setSenR, modnames=namesSenR)
#                              K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mSenR1_comp+off(senP)+refe      13 104.50       0.00      1      1 -37.06
#mSenR2_graz+alti+off(senP)+refe  6 166.23      61.74      0      1 -76.84
#mSenR0_null                      3 192.68      88.18      0      1 -93.26

summary(mSenR1)
#                Estimate Std. Error z value Pr(>|z|)
#(Intercept)      -21.7229 12875.3709  -0.002   0.9987
#contAsia         -0.4507 33491.8184   0.000   1.0000
#contEurope       -0.6340     0.6921  -0.916   0.3597
#contSouth_America 0.1286     0.8908   0.144   0.8852
#alti.ST           0.4198     0.2204   1.904   0.0569 .
#grazMixed         0.6378     0.5413   1.178   0.2387
#grazUngrazed      0.7624     0.7745   0.984   0.3250
#sampActPas        0.2326 28245.2512   0.000   1.0000
#sampPassive       19.8855 12875.3709   0.002   0.9988
#auha.ST          -2.6430     3.2406  -0.816   0.4147
#I(auha.ST^2)     -4.5782    10.0234  -0.457   0.6478

qqnorm(resid(mSenR1))
qqline(resid(mSenR1)) #OK

overdisp_fun(mSenR1)
#chisq        ratio         rdf          p
#35.1441433  0.4183827 84.0000000  0.9999995

r.squaredGLMM(mSenR1)#OK
#            R2m       R2c
#delta     0.9174450 0.9174450
#lognormal 0.9831200 0.9831200
#trigamma  0.4356127 0.4356127

###########################Sheet_Analy#############################
#Sheet webs Abundance
mSheA0 <- glmer.nb(sheA~1+(1|refe), data=data)#null
mSheA1 <- glmer.nb(sheA~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(sheP)+(1|refe), data=data)
#
mSheA2 <- glmer.nb(sheA~alti.ST+offset(sheP)+(1|refe), data=data)
mSheA3 <- glmer.nb(sheA~alti.ST+auha.ST+I(auha.ST^2)+offset(sheP)+(1|refe), data=data)
#
cand.setSheA <- list(mSheA0,mSheA1,mSheA2,mSheA3)
#
namesSheA <-c("mSheA0_null","mSheA1_comp+off(sheP)+refe",
            "mSheA2_alti+off(sheP)+refe",
            "mSheA3_alti+auha+auha^2+refe")
#Final AIC
aicSheA <-aictab(cand.setSheA, modnames=namesSheA)
#                           K    AICc Delta_AICc AICcWt Cum.Wt      LL
#mSheA3_alti+auha+auha^2+refe  6  982.00       0.00   0.98   0.98 -484.54
#mSheA1_comp+off(sheP)+refe   14  989.66       7.66   0.02   1.00 -478.33
#mSheA2_alti+off(sheP)+refe    4 1437.00     455.00   0.00   1.00 -714.37
#mSheA0_null                   3 1461.52     479.52   0.00   1.00 -727.68

summary(mSheA3)
#             Estimate Std. Error z value Pr(>|z|)
#(Intercept)   2.79744    0.33831   8.269  < 2e-16 ***
#alti.ST      -0.81155    0.30393  -2.670  0.00758 **
#auha.ST      -0.18804    0.38132  -0.493  0.62191
#I(auha.ST^2) -0.07795    0.11769  -0.662  0.50777

qqnorm(resid(mSheA3))
qqline(resid(mSheA3)) #OK
```

```
overdisp_fun(mSheA3)
#chisq        ratio         rdf          p
#48.1759588  0.5180211 93.0000000  0.9999672

r.squaredGLMM(mSheA3, mSheA0)#OK
#            R2m       R2c
#delta     0.2734223 0.9241506
#lognormal 0.2773020 0.9372636
#trigamma  0.2677456 0.9049637

#########################################################
#Sheet web Richness
mSheR0 <- glmer.nb(sheR~1+(1|refe), data=data)#null
mSheR1 <- glmer.nb(sheR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(sheP)+(1|refe), data=data)
#
mSheR2 <- glmer.nb(sheR~cont+auha.ST+offset(sheP)+(1|refe), data=data)
mSheR3 <- glmer.nb(sheR~cont+offset(sheP)+(1|refe), data=data)
mSheR4 <- glmer.nb(sheR~auha.ST+offset(sheP)+(1|refe), data=data)
#
cand.setSheR <- list(mSheR0,mSheR1,mSheR2,mSheR3,mSheR4)
#
namesSheR <-c("mSheR0_null","mSheR1_comp+off(sheP)+refe",
            "mSheR2_cont+auha+off(sheP)+refe",
            "mSheR3_cont+off(sheP)+refe",
            "mSheR4_auha+off(sheP)+refe")
#Final AIC
aicSheR <-aictab(cand.setSheR, modnames=namesSheR)
#                               K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mSheR2_cont+auha+off(sheP)+refe  7 484.37       0.00   0.97   0.97 -234.56
#mSheR4_auha+off(sheP)+refe       4 491.44       7.07   0.03   1.00 -241.50
#mSheR1_comp+off(sheP)+refe      13 497.22      12.85   0.00   1.00 -233.42
#mSheR3_cont+off(sheP)+refe       7 769.88     285.51   0.00   1.00 -377.56
#mSheR0_null                      3 787.71     303.34   0.00   1.00 -390.78
#
summary(mSheR2)
#                  Estimate Std. Error z value Pr(>|z|)
#(Intercept)        -0.8082     0.4930  -1.639  0.10112
#contAsia            0.9691     0.9976   0.971  0.33136
#contEurope          1.8542     0.5063   3.662  0.00025 ***
#contSouth_America   0.2222     0.7458   0.298  0.76574
#auha.ST            -0.2619     0.1189  -2.204  0.02753 *

qqnorm(resid(mSheR2))
qqline(resid(mSheR2)) #OK

overdisp_fun(mSheR2)
#chisq        ratio         rdf          p
#37.5424158  0.4171380 90.0000000  0.9999998

r.squaredGLMM(mSheR2, mSheR0)#OK
#            R2m       R2c
#delta     0.3405559 0.8785781
#lognormal 0.3432658 0.8855692
#trigamma  0.3375040 0.8707048

###########################Space_Analy#############################
#Space webs Abundance
mSpaA0 <- glmer.nb(spaA~1+(1|refe), data=data)#null
mSpaA1 <- glmer.nb(spaA~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(spaP)+(1|refe), data=data)
#
mSpaA2 <- glmer.nb(spaA~cont+graz+offset(spaP)+(1|refe), data=data)
mSpaA3 <- glmer.nb(spaA~graz+offset(spaP)+(1|refe), data=data)

cand.setSpaA <- list(mSpaA0,mSpaA1,mSpaA2,mSpaA3)
#
namesSpaA <-c("mSpaA0_null","mSpaA1_comp+off(spaP)+refe",
            "mSpaA2_cont+graz+refe",
            "mSpaA3_graz+refe")
```

```
#Final AIC
aicSpaA <-aictab(cand.setSpaA, modnames=namesSpaA)
#                          K    AICc Delta_AICc AICcWt Cum.Wt      LL
#mSpaA1_comp+off(spaP)+refe 14  769.89       0.00      1      1 -368.45
#mSpaA3_graz+refe            5 1089.49     319.60      0      1 -539.54
#mSpaA2_cont+graz+refe       9 1095.02     325.13      0      1 -537.89
#mSpaA0_null                3 1136.00     366.11      0      1 -564.92

summary(mSpaA1)
#                  Estimate Std. Error z value Pr(>|z|)
#(Intercept)        0.41600    1.30441   0.319   0.7498
#contAsia           1.62915    1.65314   0.986   0.3244
#contEurope         1.18940    1.27411   0.934   0.3506
#contNorth_America  2.84730    1.72229   1.653   0.0983 .
#contSouth_America  0.46468    1.48458   0.313   0.7543
#alti.ST           -0.28928    0.28732  -1.007   0.3140
#grazMixed          0.60830    0.55226   1.101   0.2707
#grazUngrazed       0.65347    0.34745   1.881   0.0600 .
#sampActPas        -1.02061    1.49097  -0.684   0.4936
#sampPassive       -0.33232    0.86322  -0.385   0.7003
#auha.ST            0.04034    0.44584   0.090   0.9279
#I(auha.ST^2)      -0.02141    0.06621  -0.323   0.7464

qqnorm(resid(mSpaA1))
qqline(resid(mSpaA1)) #OK

overdisp_fun(mSpaA1)
#chisq        ratio         rdf           p
#60.5570047  0.7124353 85.0000000  0.9793134

r.squaredGLMM(mSpaA1, mSpaA0)#OK
#             R2m       R2c
#delta     0.1426848 0.7769448
#lognormal 0.1519584 0.8274413
#trigamma  0.1277512 0.6956287
#########################################################
#Space webs Richness
mSpaR0 <- glmer.nb(spaR~1+(1|refe), data=data)#null
mSpaR1 <- glmer.nb(spaR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(spaP)+(1|refe), data=data)
#
mSpaR2 <- glmer.nb(spaR~graz+auha.ST+I(auha.ST^2)+offset(spaP)+(1|refe), data=data)
mSpaR3 <- glmer.nb(spaR~graz+I(auha.ST^2)+offset(spaP)+(1|refe), data=data)
#
cand.setSpaR <- list(mSpaR0,mSpaR1,mSpaR2,mSpaR3)
#
namesSpaR <-c("mSpaR0_null","mSpaR1_comp+off(sheP)+refe",
           "mSpaR2_graz+auha+auha^2+refe",
           "mSpaR3_graz+auha^2+refe")
#Final AIC
aicSpaR <-aictab(cand.setSpaR, modnames=namesSpaR)
#                            K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mSpaR2_graz+auha+auha^2+refe  7 347.26       0.00   0.58   0.58 -166.00
#mSpaR3_graz+auha^2+refe       6 347.90       0.65   0.42   1.00 -167.49
#mSpaR1_comp+off(sheP)+refe   13 358.90      11.64   0.00   1.00 -164.26
#mSpaR0_null                   3 613.48     266.22   0.00   1.00 -303.66

summary(mSpaR2)
#             Estimate Std. Error z value Pr(>|z|)
#(Intercept)  -0.35769    0.19400  -1.844   0.0652 .
#grazMixed     0.60284    0.31429   1.918   0.0551 .
#grazUngrazed -0.09442    0.22791  -0.414   0.6786
#auha.ST      -0.61326    0.34558  -1.774   0.0760 .
#I(auha.ST^2)  0.20575    0.08852   2.324   0.0201 *

qqnorm(resid(mSpaR2))
qqline(resid(mSpaR2)) #OK

overdisp_fun(mSpaR2)
#chisq        ratio         rdf           p
```

```
#39.6011116  0.4400124 90.0000000  0.9999992

r.squaredGLMM(mSpaR2, mSpaR0)#OK
#             R2m       R2c
#delta     0.07854078 0.6368629
#lognormal 0.08313047 0.6740793
#trigamma  0.07290892 0.5911959

###########################Speci_Analy#############################
#Specialist hunters Abundance
mSpeA0 <- glmer.nb(speA~1+(1|refe), data=data)#null
mSpeA1 <- glmer.nb(speA~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(speP)+(1|refe), data=data)
#
mSpeA2 <- glmer.nb(speA~cont+alti.ST+samp+auha.ST+offset(speP)+(1|refe), data=data)
mSpeA3 <- glmer.nb(speA~alti.ST+samp+auha.ST+offset(speP)+(1|refe), data=data)
#
cand.setSpeA <- list(mSpeA0,mSpeA1,mSpeA2,mSpeA3)#
#
namesSpeA <-c("mSpeA0_null","mSpeA1_comp+off(speP)+refe",
            "mSpeA2_cont+alti+samp+auha+off(speP)+refe",
            "mSpeA3_alti+samp+auha+off(speP)+refe")
#Final AIC
aicSpeA <-aictab(cand.setSpeA, modnames=namesSpeA)
#                                    K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mSpeA3_alti+samp+auha+off(speP)+refe       7 334.50       0.00   0.94   0.94 -159.63
#mSpeA2_cont+alti+samp+auha+off(speP)+refe 11 340.11       5.61   0.06   1.00 -157.54
#mSpeA1_comp+off(speP)+refe               14 345.43      10.93   0.00   1.00 -156.21
#mSpeA0_null                               3 578.07     243.57   0.00   1.00 -285.96

summary(mSpeA3)
#             Estimate Std. Error z value Pr(>|z|)
#(Intercept)   -4.5865     1.4596  -3.142  0.00168 **
#alti.ST       0.8215     0.2998   2.740  0.00614 **
#sampActPas    4.3797     1.9754   2.217  0.02661 *
#sampPassive   3.6841     1.4566   2.529  0.01143 *
#auha.ST      -1.7670     0.6361  -2.778  0.00547 **

qqnorm(resid(mSpeA3))
qqline(resid(mSpeA3)) #OK

overdisp_fun(mSpeA3)
#chisq        ratio         rdf          p
#46.6169842  0.5067063 92.0000000  0.9999785

r.squaredGLMM(mSpeA3,mSpeA0)#OK
#             R2m       R2c
#delta     0.6223926 0.8785704
#lognormal 0.6506085 0.9184000
#trigamma  0.5630024 0.7947350

#########################################################
#Specialist Richness
mSpeR0 <- glmer.nb(speR~1+(1|refe), data=data)#null
mSpeR1 <- glmer.nb(speR~cont+alti.ST+graz+samp+auha.ST+I(auha.ST^2)+offset(speP)+(1|refe), data=data)
#
mSpeR2 <- glmer.nb(speR~cont+graz+samp+offset(speP)+(1|refe), data=data)
mSpeR3 <- glmer.nb(speR~cont+samp+offset(speP)+(1|refe), data=data)
#
cand.setSpeR <- list(mSpeR0,mSpeR1,mSpeR2,mSpeR3)
#
namesSpeR <-c("mSpeR0_null","mSpeR1_comp+off(sheP)+refe",
            "mSpeR2_cont+graz+samp+off(sheP)+refe",
            "mSpeR3_cont+samp+off(sheP)+refe")
#Final AIC
aicSpeR <-aictab(cand.setSpeR, modnames=namesSpeR)
#                                    K   AICc Delta_AICc AICcWt Cum.Wt      LL
#mSpeR1_comp+off(sheP)+refe          13 186.99       0.00      1      1  -78.30
#mSpeR3_cont+samp+off(sheP)+refe       9 281.82      94.83      0      1 -131.30
#mSpeR2_cont+graz+samp+off(sheP)+refe 11 283.36      96.37      0      1 -129.77
```

```
#mSpeR0_null                    3 325.99     139.00      0      1 -159.92

summary(mSpeR1)
#                  Estimate Std. Error z value Pr(>|z|)
#(Intercept)       -3.0301     1.0095  -3.002  0.00269 **
#contAsia          -14.7200     9.2723  -1.587  0.11239
#contEurope        -0.3350     0.5583  -0.600  0.54853
#contSouth_America -0.5260     0.8998  -0.584  0.55885
#alti.ST            0.2213     0.1657   1.335  0.18181
#grazMixed          0.6135     0.3381   1.815  0.06959 .
#grazUngrazed       0.3371     0.3779   0.892  0.37227
#sampActPas         2.8376     1.0474   2.709  0.00674 **
#sampPassive        2.0907     0.9268   2.256  0.02408 *
#auha.ST           -0.3159     0.5554  -0.569  0.56947
#I(auha.ST^2)       0.1150     0.3030   0.380  0.70426

qqnorm(resid(mSpeR1))
qqline(resid(mSpeR1))

overdisp_fun(mSpeR1)
#chisq        ratio         rdf           p
#38.5026700  0.4583651 84.0000000  0.9999951

r.squaredGLMM(mSpeR1, mSpeR0)#OK
#             R2m       R2c
#delta     0.7827421 0.7986469
#lognormal 0.8656029 0.8831914
#trigamma  0.5848772 0.5967615

######################
################################Graphs###############################
theme_set(theme_bw())

theme_set(theme_bw() + theme(panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
                         legend.position = 'none', axis.text = element_text(size=13), axis.title = element_text(size=13, face="bold"),
                         axis.text.x = element_text(size=13),axis.title.y = element_text(margin = margin(r=20)),
                         plot.margin = unit(c(1,3,1,1),"lines")))

###################################
#Abund
#Orb Abu3, I(auha.ST^2) -0.04287    0.01812  -2.366  0.01799 *
#Sen Abu4, I(auha.ST^2) -2.164410   0.005273 -410.5  <2e-16 ***
#Spe Abu3, auha.ST      -1.7670     0.6361  -2.778  0.00547 **
pred1 <- ggpredict(model = mOrbA3,
                 terms = "auha.ST [-5:5]",
                 ci.lvl = 0.95,
                 type = "re",
                 typical = "mean",
                 condition = NULL,
                 back.transform = TRUE,
                 na.rm = F)
pred2 <- ggpredict(model = mSenA4,
                 terms = "auha.ST [-5:5]",
                 ci.lvl = 0.95,
                 type = "re",
                 typical = "mean",
                 condition = NULL,
                 back.transform = TRUE,
                 na.rm = F)
pred3 <- ggpredict(model = mSpeA3,
                 terms = "auha.ST [-5:5]",
                 ci.lvl = 0.95,
                 type = "re",
                 typical = "mean",
                 condition = NULL,
                 back.transform = TRUE,
                 na.rm = F)
tiff(file="Fig_DensityAbundanceGuild.tiff", width = 10, height = 8, units="in",res=300)
```

```
ggplot() +
  geom_smooth(data=pred1, aes(x = x, y = predicted), color="#B22222",method = lm, formula = y ~ I(x^2)) +
  geom_smooth(data=pred2, aes(x = x, y = log(predicted)), color='#22B2B2',method = lm, formula = y ~ I(x^2))+
  geom_smooth(data=pred3, aes(x = x, y = predicted), color='#6AB222',method = lm)+
  xlab("Standartized Grazer Density (AU/ha)") +
  ylab("Abundance") +
  ggtitle("Spider Guild Abundance")+
  theme(
    legend.position = c(.99, .93),
    legend.justification = c("right"),
    legend.box.just = "right",
    legend.margin = margin(6, 6, 6, 6))+
  scale_color_identity(name = "Guild",
                       breaks = c("firebrick","blue4"),
                       labels = c("Orb weavers", "Sense Webs"),
                       guide = "legend")
dev.off()
##################################
#Richness
#Gro Riq3, I(auha.ST^2)  0.11915    0.05666   2.103  0.03546 *
#Oth Riq2, I(auha.ST^2)  0.12625    0.04021   3.140  0.00169 **
#Spa Riq2, I(auha.ST^2)  0.20575    0.08852   2.324  0.0201 *
#She Riq2, auha.ST      -0.2619     0.1189  -2.204  0.02753 *
pred4 <- ggpredict(model = mGroR3,
                   terms = "auha.ST [-5:5]",
                   ci.lvl = 0.95,
                   type = "re",
                   typical = "mean",
                   condition = NULL,
                   back.transform = TRUE,
                   na.rm = F)
pred5 <- ggpredict(model = mOthR2,
                   terms = "auha.ST [-5:5]",
                   ci.lvl = 0.95,
                   type = "re",
                   typical = "mean",
                   condition = NULL,
                   back.transform = TRUE,
                   na.rm = F)
pred6 <- ggpredict(model = mSpaR2,
                   terms = "auha.ST [-5:5]",
                   ci.lvl = 0.95,
                   type = "re",
                   typical = "mean",
                   condition = NULL,
                   back.transform = TRUE,
                   na.rm = F)
pred7 <- ggpredict(model = mSheR2,
                   terms = "auha.ST [-5:5]",
                   ci.lvl = 0.95,
                   type = "re",
                   typical = "mean",
                   condition = NULL,
                   back.transform = TRUE,
                   na.rm = F)
tiff(file="Fig_DensityRichnessGuild.tiff", width = 10, height = 8, units="in",res=300)

ggplot() +
geom_smooth(data=pred4, aes(x = x, y = log(predicted)), color='#B22222', method = lm, formula = y ~ I(x^2))+
  geom_smooth(data=pred5, aes(x = x, y = log(predicted)), color='#22B2B2', method = lm, formula = y ~ I(x^2))+
  geom_smooth(data=pred6, aes(x = x, y = log(predicted)), color='#6AB222', method = lm,formula = y ~ I(x^2))+
  geom_smooth(data=pred7, aes(x = x, y = log(predicted)), color='#6A22B2', method = lm)+
  xlab("Standartized Grazer Density (AU/ha)") +
  ylab("Richness logged") +
  ggtitle("Spider Guild Richness")

dev.off()
# End
```

Supplementary Material 2 – Appendices of Data Source, with the reference of all studies used for this manuscript.

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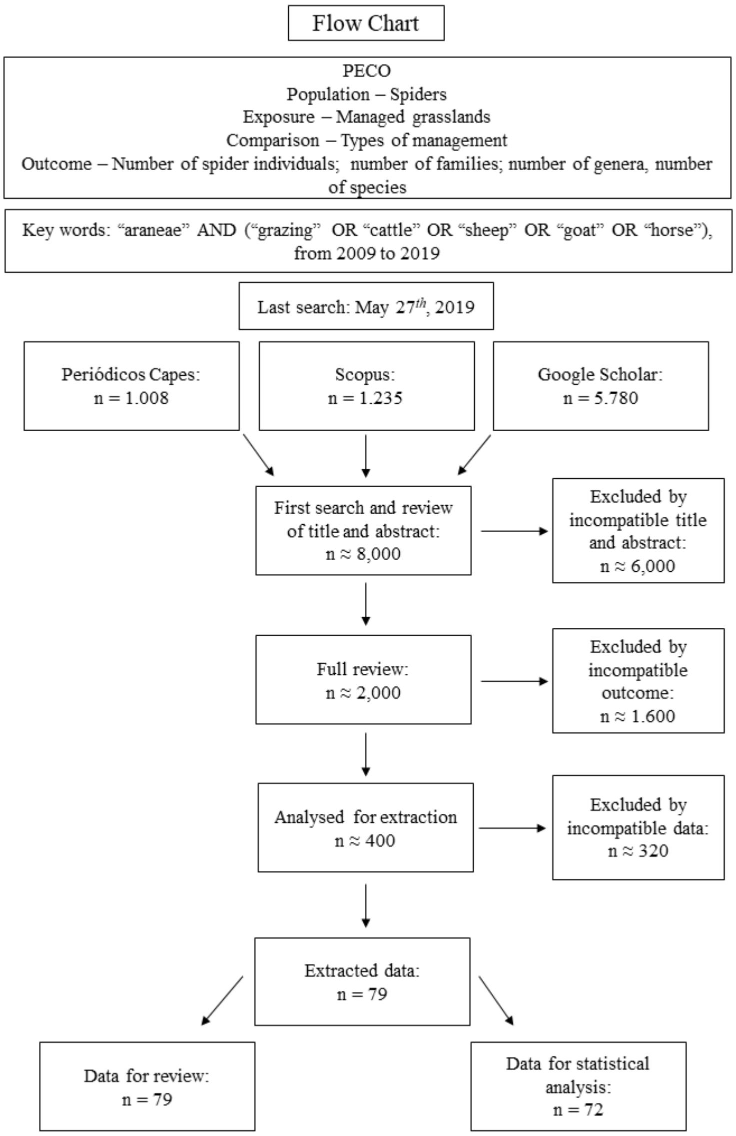
Supplementary Fig. 1 - Flow chart of systematic review research. The chart contains the number of papers found in each database and the number of papers designated to the systematic review and the statistical analysis.



Supplementary Tables – Podem ser encontradas no material suplementar do artigo publicado em: Oyarzabal & Guimaraes 2021 - Friend and foe? The effects of grassland management on global patterns of spider diversity. **Ecological Entomology**, 46(5), Pag. 1195-1204. https://doi.org/10.1111/een.13065

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CAPÍTULO II

TRIALS BY GRAZING: SMALL MESOPREDATORS AND LIVESTOCK HERDING

Em preparação para *Agrculture, Ecology and Envrioment*

Abstract

Mesopredators are carnivorous that usually have a more generalist diet than a top predator. Despite that, these animals are also widely affected by anthropogenic impact. For instance, livestock grazing can exclude these predators due the direct human conflict or indirectly by changes in environmental traits. In a more particular context, the effects of livestock grazing on mesopredator spiders have been extensively studied globally. Authors usually agree that spider diversity follow a trend of intermediate impact, where a certain degree of grazing can enhance this group diversity. However, the intensive removal of plant biomass can also directly exclude some spider groups, hence lowering the animal diversity on those grazed environments. In this way, here we investigate if the abundance of orb-weaver spiders is directly affected by different levels of grazing. We predict that high grazing, due the removal of vegetation structure, will have a negative impact on orb-weavers. To do this, we evaluated the abundance of two orb-weaver spider species, *Argiope argentata* and *Alpaida quadrilorata* in three different grazing treatments, low, moderate, and high grazing. We also evaluated how vegetation density affect the abundance of this species. Our results corroborate past finds where intermediate impact can enhance the diversity of spiders. At the same time, high grazing impact negatively those same spider species. Since high grazing remove more vegetation structure and, since these spiders have a biological need of structure to build webs, the removal of vegetation ends up excluding these species. Moreover, livestock grazing seems to act as an apex predator for spiders, controlling, suppressing, and excluding spider populations. In this way, regarding the maintenance of spiders' populations, high grazing seems not to be the best solution for environment management unless it is limited to a moderate pressure.

Keywords: Araneae; Grasslands; N-mixture modeling; Pasture; Population Ecology.

Introduction

Mesopredators are midranking carnivorous that vary in many shapes and sizes, playing an important role in regulating, mainly, herbivores (Gagnon et al., 2019; Michalko et al., 2019; Prugh et al., 2009). Mesopredators usually occur sympatrically and have similar needs of food and energy intakes, as well as broader diets than apex predators (Lesmeister et al., 2015; Prugh et al., 2009; Ripple et al., 2013). Although generalist in relation to their food consumption, mesopredators are also largely affected by anthropogenic impacts like crops and pastures, since these activities may threat them directly, through human conflict and environment degradation or indirectly, through declines in prey population (Newsome et al., 2017; Wang et al., 2015).

Livestock grazing particularly affect mammalian mesopredators, such as foxes, small cats, and coyotes, in two ways: on the one hand, they are usually excluded from pastures and grasslands through fencing and hunting, since they can prey on sheep and cattle (Gordon et al., 2017a; Letnic et al., 2009). On the other hand, when they are not excluded, the low grass height caused by the livestock grazing can enhance their hunt capacity, since their preys would have less shelter to hide (Gordon et al., 2017b; McGregor et al., 2014; Schuette et al., 2013). Arthropod mesopredators in turn, when under severe grazing impact, suffer losses on species richness and abundance (Helden et al., 2020; Prather and Kaspari, 2019; Reinhard et al., 2019; Zhao et al., 2018). Similarly to mammalian mesopredators, such losses may stem from direct modifications on habitat heterogeneity (Prather and Kaspari, 2019; Wang and Tang, 2019), and indirect, through changes on prey availability (Filazzola et al., 2020; Reinhard et al., 2019).

Despite the importance that mesopredators play in grassland ecosystems, the understanding of their roles and influences depends directly on in situ studies. When it comes to mammalian mesopredators, logistical difficulties can prevent the study from being carried out, since manipulating large grassland areas with these animals, and therefore large home ranges, becomes an impediment (Meadows et al., 2017; Schuette et al., 2013). On the other hand, arthropods mesopredators, with their small body sizes, short home ranges, short life spam and huge biomass (Fernández-Tizón et al., 2020; Meadows et al., 2017), are easier to study and manipulate, while maintaining a similar, but smaller, ecosystem role as mammalians mesopredators (Meadows et al., 2017).

Among arthropods mesopredators, spiders have been one of the main focuses in studies of grazing impacts (Filazzola et al., 2020). Despite some authors being unable to find evidence for changes in spider diversity due to grazing impact (Muvengwi et al., 2018; Samu et al., 2018; Silva and Ott, 2017), results usually follow a trend of intermediate disturbance (Oyarzabal and Guimarães, 2021; Wang and Tang, 2019). Ungrazing, low and moderate grazing usually enhance spider diversity (Ferreira et al., 2020a; Oyarzabal and Guimarães, 2021; Szmatona-Túri et al., 2018), while heavy grazing negatively affects spider diversity (Hashemi et al., 2019; Oyarzabal and Guimarães, 2021; Szmatona-Túri et al., 2018). Moreover, evidence suggests orb-weaver spiders populations respond directly to the vegetation structure removal caused by grazing (Neilly et al., 2020; Nogueira and Pinto-da-Rocha, 2016).

The removal of above ground plant biomass provoked by grazing (da Silva Bomfim et al., 2021; Ferreira et al., 2020b; Pett and Bailey, 2019; Tälle et al., 2016), directly affect the primary biological need that orb-weavers have: the tridimensional vegetal structure to build webs (Nogueira and Pinto-da-Rocha, 2016). Without structure, these species cannot find preys (Fischer et al., 2021; Helden et al., 2020; Torma et al., 2019) and mates (Cory and Schneider, 2018; Weiss and Schneider, 2021) as well as avoid predation (Blackledge and Wenzel, 1999; da Silva Bomfim et al., 2021; Narimanov et al., 2021). Moreover, orb-weavers have an immeasurable role in controlling, mainly, the population of herbivore insect pests in agroecosystems (Hlivko and Rypstra, 2003; Zhong et al., 2017). Hence, without these environmental aspects, these species turn out to be excluded from grasslands (Oyarzabal and Guimarães, 2021). Considering these specific needs, orb-weaver spiders could be an amazing proxy to study grazing impact in grasslands. Follow this, our objective is to assess the effects of grazing pressure on abundance of orb-weaver spiders in grasslands ecosystems. We hypothesized that the abundance of mesopredator orb-weaver spiders on grasslands is directly affected by the levels of grazing impact. We predict high grazing impact, through the removal of vegetation structure, will negatively influence the abundance of orb-weavers, while low and moderate grazing, will positively affect the abundance of orb-weavers.

Methods

Subject, study site and sampling design

We choose two orb-weaver spider species, from the Araneidae family, which are very abundant in grasslands (Nogueira and Pinto-da-Rocha, 2016; Rodrigues et al., 2009). The first species is *Argiope argentata* (Fabricius, 1775), that have a broad range distribution, from Canada to Argentina (Agnarsson et al., 2016; World Spider Catalog, 2015) and the second species is *Alpaida quadrilorata* (Simon, 1897), that are distributed in Argentina, Brazil, Paraguay and Uruguay (Vasconcellos-Neto et al., 2017; World Spider Catalog, 2015) (Fig. 1).

Figure 2 - Orb-weaver spider species from the Araneidae family. Photos A and B represent *Argiope argentata* and photos C and D represent *Alpaida quadrilorata*.

Our study took place in the Pampa grasslands, southern South America. The climate is subtropical with hot and dry summers and humid and cold winters. Temperatures surpass 40°C in summer and vary from 4°C to 28°C in winter. Between 1,200 and 1,600 mm of rainfall occur through the year (Kottek et al., 2006). The samplings occurred at *Estação Experimental Agronômica da Universidade Federal do Rio Grande do Sul (UFRGS)* located in Eldorado do Sul municipality, Rio Grande do Sul, Brazil (30º06’08’’S; 51º40’56’’W). Since 1987, an experiment called *Nativão* is conducted to assess the effects of different intensities of cattle grazing in an area that covers about 52 hectares (Nabinger et al., 2009). In the year

2000, the area was subdivided in 14 plots with different cattle grazing treatments that vary in a fixed and daily levels of grass forage supply for cattle, expressed in kg of vegetal dry matter [DM]/100 kg of live weight [LW] (% LW). In this way, these areas are defined by a percentage of vegetal dry matter remaining, meaning the less matter that remains, the greater the grazing pressure (Nabinger et al., 2009).

Six plots were selected for sampling: two plots (3.05 ha and 3.14 ha) with high grazing impact (4% LW, around 0.86 Animal Units (AU)/ha/year); two plots (2.73 ha and 3.67 ha) of moderate impact (8% LW, around 0.59 AU/ha/year); and two plots (5.27 ha and 5.42 ha) of low grazing impact (16% LW, around 0.45 AU/ha/year) (Nabinger et al., 2009). Considering the known home range and movement capacity of one of our focus species (Craig et al., 2001), we superimposed a grid on the top of each of the six plots with cell size 5x5m, using the QGIS software (QGIS.org, 2020). From the total of cells per plot, a subgroup of 50 cells was randomly sorted for all surveys (50 cells per plot, 300 in total). Then, on each campaign 16 cells were surveyed from the 50 pre-selected cells of each plot (96 in total per campaign). Lastly, the order that the plots were surveyed was always randomized in each campaign.

Seven monthly campaigns occurred from October 2017 to April 2018 and six monthly campaigns from October 2018 to April 2019, through austral spring and summer, when spiders are more active (Rodrigues et al., 2015). Each campaign was composed by two days (surveys) and species were surveyed in the field from dawn to mid-day (06:00 am to 12:30 pm) and from afternoon to dusk (03:00 pm to 09:00 pm). Cells were surveyed until exhaustion, counting adults and juveniles of *A. argentata* and *A. quadrilorata* species. In a paper spreadsheet, we registered how many individuals of each species we found in the cells. Two to three trained observers were deployed on each campaign (a total of eight people through the experiment).

Data analysis

Environmental variables were registered through the campaigns and surveys to be used as detection and abundance predictor variables. To estimate detection probability, we included air temperature (degrees Celsius) and time (expressed as minutes after midnight). Air temperature was measured three times during each survey (beginning, mid and end). Time was measured on the beginning of each cell survey. To estimate occupancy probability, we considered the following spatial variables: grazing treatment (three levels: high grazing, moderate grazing, and low grazing), vegetation density, and the quadratic effect of vegetation density. Although vegetation density is directly correlated to the grazing treatments, during our field work, we perceived that there was a variation on vegetation height even inside the same treatments. Therefore, vegetation density was obtained taking four photos of the vegetation on each cell. Four photos one time in 2018 (corresponding to year one) and four photos one time in 2019 (corresponding to year two). A 1x1 m white cardboard was used as a background to measure vegetation density on every photo. Then, we used ImageJ software (Schneider et al., 2012) to convert images to black and white scale, hence, the black pixels were counted as a measure of vegetation density in contrast with the white cardboard background (Ford et al., 2017). The arithmetic mean of black pixels between the four photos was considered as a proxy of vegetation density for each cell and in each year. The numeric variables (temperature, time, and vegetation density) were standardized to have zero mean and one standard deviation.

We fitted a single-season N-Mixture model (Royle, 2004) for each sampling year, using the count of spiders per cell as our response variable, to estimate abundance (N) and detection (p) probabilities of *A. argentata* and *A. quadrilorata* separately (MacKenzie et al., 2002). We built three sets of five models to evaluate how abundance and detection variables behave in different scenarios: (i) a set that include all variables influencing the detection parameter (Grazing, Vegetation, Vegetation^2, Temperature and Time) while the abundance parameter was influenced by different combinations of spatial variables (Grazing, Vegetation, Vegetation2 together and each one alone); (ii) a set that include only spatial variables on detection (Grazing, Vegetation, Vegetation2) and the abundance variables changing (Grazing, Vegetation, Vegetation2 together and each one alone); and (iii) a set that include only temporal variables on detection (Temperature and Time) and the abundance variables changing (Grazing, Vegetation, Vegetation2 together and each one alone) (Table S1). We compared all models using Akaike's Information Criterion (AIC) and models with Delta AIC ≤2 were considered those better supported (Arnold, 2010) (Table S1). Moreover, those best models were model-averaged to provide estimated effects of variables on parameters (Table S2). All analysis were performed using ‘unmarked’ package (Chandler et al., 2021) in the software R (Team, 2021). The R script can be found in Supplementary data. The effects of temporal variables were not discussed but were presented in the supplementary material (Tables S1).

Results

A total of 889 individuals of *A. argentata* (25 in high, 278 in moderate and 586 in low grazing) were found in 324 cells in year one and 883 individuals (83 in high, 510 in moderate and 290 in low grazing) were found in 289 cells in year two. For *A. quadrilorata*, a total of 430 individuals (one in high, 266 in moderate and 163 in low grazing) were found in 198 cells in year one and 348 individuals (three in high, 263 in moderate and 82 in low grazing) were found in 178 cells in year two.

Argiope argentata abundance and detection

In year one, *A. argentata* abundance estimates increased under low ($\beta_{LGrazY1}$ = 5.224, p = 1.99e-16) and moderate grazing impact ($\beta_{MGrazY1}$ = 4.872, p = 3.56e-20), while it decreases with the quadratic effect of vegetation density (β_{Veg2Y1} = -0.150, p = 3.63e-02) (Fig. 2). In year two, we found the same increase in *A. argentata* abundance estimates regarding moderate grazing impact ($\beta_{MGrazY2}$ = 0.921, p = 2.86e-03) as well as vegetation density (β_{VegY2} = 0.609, p = 1.35e-04). Interestingly though, high grazing ($\beta_{HGrazY2}$ = 3.112, p = 2.50e-20) also had a positive impact on *A. argentata* abundance estimates, while the quadratic effect of vegetation density (β_{Veg2Y1} = -0.370, p = 4.81e-04) still maintained its negative effect (Fig. 2).

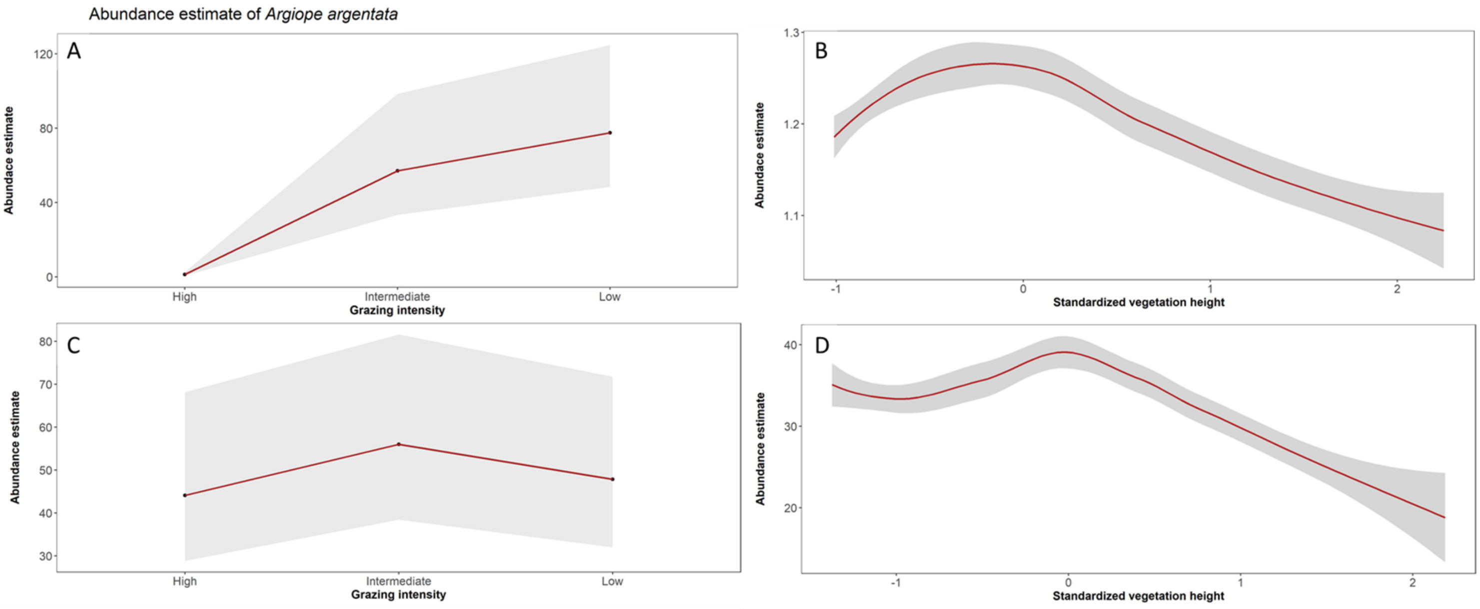


Figure 3 - Abundance estimate of *Argiope argentata* in year one and year two of sampling. Graphs A and B represent year one and graphs C and D represent year two. Red lines indicate the abundance estimate. Grey shadows indicate the standard deviations.

For the *A. argentata* detection probability, low grazing had a negative effect in year one but not in year two ($\beta_{LGrazY1}$ = -2.433, p = 3.77e-04; $\beta_{LGrazY2}$ = 0.491, p = 0.176) while moderate grazing had a negative effect on year one and a positive effect I year two ($\beta_{MGrazY1}$ = -2.392, p = 9.44e-05; $\beta_{MGrazY2}$ = 1.072, p = 4.19e-04). High grazing though, only had a significant negative effect in year two ($\beta_{HGrazY2}$ = -1.024, p = 0.068; $\beta_{HGrazY2}$ = -3.95, p = 1.90e-35), following the same pattern that vegetation density (β_{VegY2} = 0.088, p = 0.744; β_{VegY2} = 0.586, p = 2.97e-04) (Fig. S1). Lastly, temperature had a positive effect in detection in year two (β_{TempY1} = -0.035, p = 0.371; β_{TempY2} = 0.279, p = 2.97e-08) while time had a significant negative effect in year two (β_{TimeY1} = 0.104; p = 0.0930; β_{TimeY2} = -0.202; p = 2.88e-06) (Fig. S1).

Alpaida quadrilorata abundance and detection

In year one, *A. quadrilorata* abundance estimates had had a not significant mild decreased with only vegetation (β_{VegY1} = -0.040, p = 0.882), while had also a not significant mild increased with the quadratic effect of vegetation (β_{Veg2Y1} = 0.005, p = 0.948) (Fig. 3). In year two however, *A. quadrilorata* abundance estimates increased with low ($\beta_{LGrazY2}$ = 2.575, p = 2.82e-04) and moderate grazing impact ($\beta_{MGrazY2}$ = 4.025, p = 2.58e-09) as well as vegetation density ($\beta_{VegY2 =}$ 0.429, p = 2.79e-02). However, high grazing impact ($\beta_{HGrazY2}$ = -0.215, p = 0.791) and the quadratic effect of vegetation density (β_{Veg2Y2} = -0.106, p = 0.450) had no significant effect in *A. quadrilorata* abundance (Fig. 3).

The detection probability of *A. quadrilorata* increased in both years with low ($\beta_{LGrazY1}$ = 4.190, p = 6.08e-05; $\beta_{LGrazY2}$ = 2.779, p = 4.06 4.86e-05) and moderate grazing impact ($\beta_{MGrazY2}$ = 5.553, p = 4.39e-08; $\beta_{MGrazY2}$ = 4.3, p = 5.32e-12), as well vegetation density (β_{VegY1} = 0.46, p = 2.65e-04; β_{VegY2} = 0.336, p = 0.028) and temperature (β_{TempY1} = 0.341, p = 1.95e-08; β_{TempY2} = 0.213, p = 0.004) (Fig. S2). High grazing impact though, had a negative effect on detection in both years ($\beta_{HGrazY1}$ = -8.966, p = 2.51e-17; $\beta_{HGrazY2}$ = -7.615, p = 1.72e-25). Lastly, time had its effect changed from one year to another (β_{TimeY1} = 0.244; p = 0.008; β_{TimeY2} = -0.159; p = 0.011) (Fig. S2).

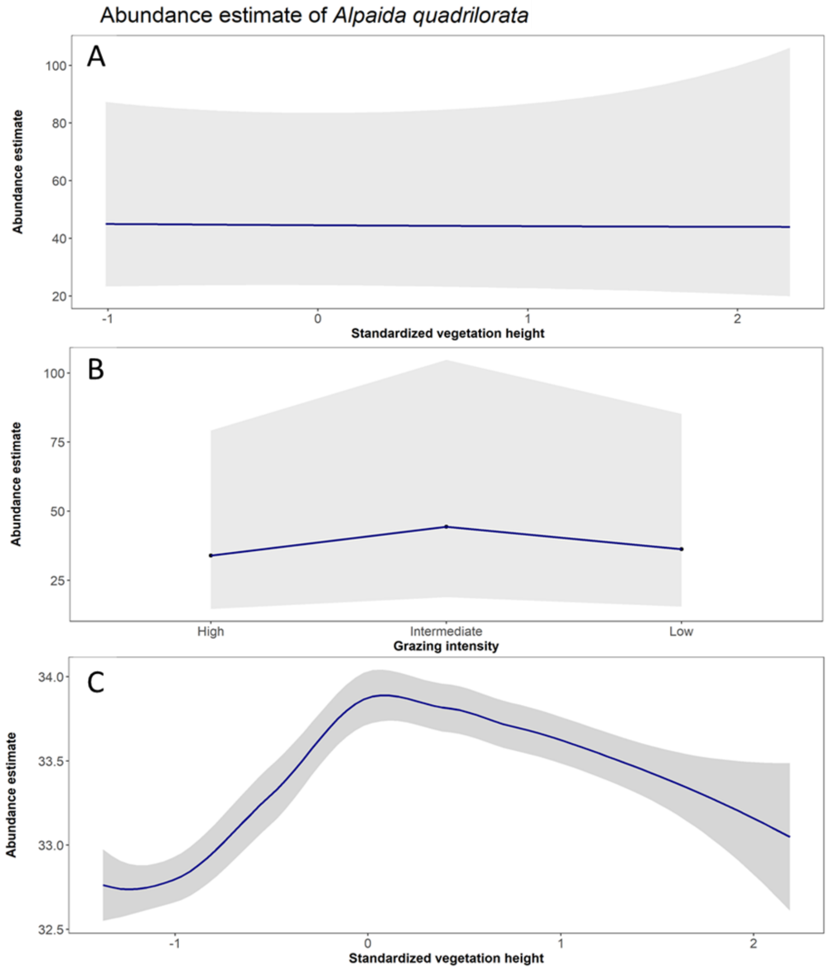


Figure 4 - Abundance estimate of *Alpaida quadrilorata* in year one and year two of sampling. Graphs A represent year one and graphs B and C represent year two. Blue lines indicate the abundance estimate. Grey shadows indicate the standard deviations.

Discussion

Following the results, we can support our hypothesis of the levels of grazing impact affecting the abundance of mesopredators. However, we cannot fully support our predictions since we found a contradictory result where high cattle grazing negatively affected the *A. argentata* in year one and positively affected the same species in year two. Despite this, the abundance of both species of orb-weavers was enhanced by vegetation density. Along with the negative quadratic effect of grazing pressure that we found, our result corroborates past findings where orb-weaver spiders seems to be beneficiated by intermediate levels of grazing (Ferreira et al., 2020a; Hu et al., 2019; Oyarzabal and Guimarães, 2021; Wang and Tang, 2019). Moreover, although grazing may not be the best solution for all kinds of grassland management (Helden et al., 2020), moderate grazing using limited animal load, up to 0.6 AU/ha/year (Clendenin, 2016;

Committee, 2017; Jansen et al., 2013), has the potential to maintain and preserve mesopredators that are intrinsically linked to vegetation structure (Helden et al., 2020; Oyarzabal and Guimarães, 2021).

Interestingly though, our results point to a similar effect of livestock grazing on spiders as apex predators have on mesopredators, where populations of mesopredators can be controlled, suppressed, and excluded by apex predators (Newsome et al., 2017). Here, with livestock and spiders, we see the same pattern, where intense grazing suppresses the vegetation, modifying the landscape and hence excluding orb-weaver spiders and possibly other mesopredators like foxes and small cats (Bruggisser et al., 2012; Filazzola et al., 2020; Gordon et al., 2017a, 2017b; Kehoe et al., 2020; Simons et al., 2014; Wilson and Fox, 2020). In this way, although grazing management seems to be important to restore and conserve biodiversity in grassland ecosystems, high livestock grazing may not guarantee the persistence of small mesopredators (Helden et al., 2020). Moreover, given that the presence and abundance of arthropod mesopredators may enable other species to occur (Helden et al., 2020), the absence of spiders could induce cascading events resulting in the rise of pest herbivores (Aguilera et al., 2021; Yadav and Kumar, 2021), the starvation of vertebrates mesopredators (e.g., birds and reptiles) (Goosey et al., 2019; Goulson, 2019), and therefore, endangering grassland ecosystems (Lark, 2020).

At the same time, since apex predators are important to control mesopredator distribution, one could argue that, in the same way, livestock grazing would be maintaining spiders and other arthropod mesopredator populations under control, avoiding a mesopredator release or, in other words, a dramatic increase in mesopredators abundance (Newsome et al., 2017; Prugh et al., 2009). However, in most cases, livestocks are not composed by native herbivores (Pitt et al., 2019), hence, its top-down affect can be interpreted as an exotic apex predator that effects the presence of native mesopredator and prey species (Ehlman et al., 2019; Murphy et al., 2019; Tadey and Farji-Brener, 2007). Furthermore, even where livestock (cattle and sheep) is comprised by native species (Europe, Asia, and Africa) (Pitt et al., 2019), its populations outnumber any other animal species (USDA, 2021), suggesting that livestock super-dominance could be also impacting other native species in terms of food web, nutrient cycling, and local extinction (Pivello et al., 2018; Vitule et al., 2021). Hence, despite being managed, the overpopulation of livestock (more than 0.6 AU/ha/year) seems to not be the best alternative to conserve grassland environments (Orihuela, 2021).

As advocated by other authors (Barton et al., 2020; Meadows et al., 2017) and corroborated by our results, the use of arthropod mesopredators seems promising as a proxy to formulate ecological hypotheses and to study management, anthropogenic impacts, and conservation. Besides the study of grazing impact, arthropods in general are amazing candidates to study climate change in more fine scales (Høye, 2020). Variation in temperature and rainfall have been affecting the group in terms of survival, reproduction, body size, clutch size, behavior, and physiology (Høye, 2020; Supriya et al., 2019; Walsh et al., 2019), as was also observed in chordates such as anurans (González-del-Pliego et al., 2020), reptiles (Diele-Viegas et al., 2020), birds (Bateman et al., 2020) and mammals (Mitchell et al., 2018). The conservation and protection of charismatic animal species (e.g., mammals), who may function as umbrella species for the environment (Schlagloth et al., 2018; Wang et al., 2021), is undoubtfully important. However, given the importance of arthropods in food webs, both as predators and prey, and in the ecosystem functioning, their disappearance induced by anthropogenic actions may lead to unpredictable ecosystem dynamics, jeopardizing landscape conservation in much worse ways than one might think (Blubaugh et al., 2017; Goulson, 2019; Samways et al., 2020).

In conclusion, the conservation of arthropods, especially of pollinating insects, has been the subject of debate for the past 15 years, since beekeepers began to see declines in hive populations (Hamzelou, 2007). Despite the awareness of the social and economic relevance of arthropods (Goulson, 2019; Torma et al., 2019), their diversity is still in danger (Goulson, 2019; Hallmann et al., 2017; Samways et al., 2020) and we still lack studies targeting this problem (Branco and Cardoso, 2020; Lark, 2020; Oyarzabal and Guimarães, 2021). Arthropod diversity losses can lead to unfeasible maintenance of communities. So, it is of utmost importance to further study the group, not just in an environmental perspective, but also in a social and economic perspectives. In this way, considering their particular traits as animals with small life spam, huge biomass and rapid response to environmental changes (Fernández-Tizón et al., 2020; Meadows et al., 2017), we encourage the study of arthropods mesopredators and other arthropods as a proxy for anthropogenic impact. Lastly, sustainable alternatives, as well as restoration actions, are necessary to prevent the collapse of grassland and other ecosystems around the world. To do this, collaboration and communication between scientists, governments and the public are the only way to perform effective conservation efforts (Gibson et al., 2021). We don’t have much time, so we must act now (IPCC, 2021).

Acknowledgements

We are grateful for CAPES and the scholarship granted to the first author (process #88882.439370/2019-01). We are also grateful for Neotropical Grassland Conservancy and the Student Grant granted to the first author. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

All authors contributed to the study conception and design. All authors performed the screening and analysis of the data, as well as the writing and revision of the text, tables, and images. Finally, all authors read and approved the final manuscript.

Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article.

Supporting materials:

Supplementary Material 1 – R script.

```
#Ocuppancy modeling of Argiope argentata and Alpaida quadrilorata

library("unmarked")
library("ggplot2")
library("AICcmodavg")

###########Argiope argentata############
##########Alpaida quadrilorata###########
#################Data################
###############Year One##############
datay1 <- read.table("N-ocupancyAa-Aq-year1.csv", head=T, as.is=T, sep=";") #Data for occupancy
#
datay1 [,2] <- as.factor(unlist(datay1 [,2]))#Grazing year one
datay1 [,3] <- as.numeric(unlist(datay1 [,3]))#Vegetation height Year one
datay1 [,18:24] <- as.numeric(unlist(datay1 [,18:24]))#Temperature year one
datay1 [,25:31] <- as.numeric(unlist(datay1 [,25:31]))#Hour year one
#
#set number of detections, sites, year, and repetitions
dAay1 <- as.matrix(datay1 [4:10])  #Argiope argentata detec year one
```

```
dAqy1 <- as.matrix(datay1 [11:17]) #Alpaida quadrilorata detec year one
#
temp1 <- as.matrix(datay1 [,18:24]) #temperature for year one
dim(temp1[rowSums(is.na(temp1)) != ncol(temp1),]) #Matrix with, at least, one visit per line = 288 sites.
#
hour1 <- as.matrix(datay1 [,25:31]) #hour for year one
dim(hour1[rowSums(is.na(hour1)) != ncol(hour1),]) #Matrix with, at least, one visit per line = 288 sites.
#
vege1 <- as.matrix(datay1 [,3]) #vegetation for year one
#
graz1 <- as.factor(datay1 [,"grazing"]) #Treatments year one
#
#Standartization
#Also, force imputing of missing values
#
#Temperature for detection of A. argentata and A. quadrilorata, year one
meantemp1 <- mean(temp1, na.rm = TRUE)
sdtemp1 <- sd(temp1, na.rm = TRUE)
TEMP1.ST <- (temp1 - meantemp1)/sdtemp1
#
#Time for detection of A. argentata and A. quadrilorata, year one
meanhour1 <- mean(hour1, na.rm = TRUE)
sdhour1 <- sd(hour1, na.rm = TRUE)
HOUR1.ST <- (hour1 - meanhour1)/sdhour1
#
#Vegetation for year one
meanvege1 <- mean(vege1, na.rm = TRUE)
sdvege1 <- sd(vege1, na.rm = TRUE)
VEGE1.ST <- (vege1 - meanvege1)/sdvege1
#
###########Argiope argentata#############
##############Occupancy##################
############UNMARK MODEL 01##############
#
#Unmark components for A. argentata year one
unmarkAay1 = unmarkedFramePCount(y = dAay1,
                              siteCovs = data.frame(graz1=graz1, VEGE1.ST=VEGE1.ST),
                              obsCovs = list(TEMP1.ST=TEMP1.ST, HOUR1.ST=HOUR1.ST))
#
summary(unmarkAay1)
#
# Assembling models. Argiope argentata, year one
#p = probability of detection
#psi = probability of occupancy
#Models structure -> ~detec ~occ
#Aa - A. argentata
#y1 - Year one
#mxx - Model number
#
#Model Zero, Null model
#
Aay1m00 <- pcount(~1 ~1, data = unmarkAay1, K = 250, mixture = "NB") ###########
#Models 01 to 05 with all variables on detection. Occupancy variables changing.
Aay1m01 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST  ~graz1+VEGE1.ST+I(VEGE1.ST^2), data = unmarkAay1, K = 250, mixture = "NB")
Aay1m02 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~graz1, data = unmarkAay1, K = 250, mixture = "NB")
Aay1m03 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~VEGE1.ST, data = unmarkAay1, K = 250, mixture = "NB")
Aay1m04 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~I(VEGE1.ST^2), data = unmarkAay1, K = 250, mixture = "NB")
Aay1m05 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~1, data = unmarkAay1, K = 250, mixture = "NB")
#Models 06 to 10 with only spacial variables on detection.Occupancy variables changing.
Aay1m06 <- pcount(~graz1+VEGE1.ST ~graz1+VEGE1.ST+I(VEGE1.ST^2), data = unmarkAay1, K = 250, mixture = "NB")
Aay1m07 <- pcount(~graz1+VEGE1.ST ~graz1, data = unmarkAay1, K = 250, mixture = "NB")
Aay1m08 <- pcount(~graz1+VEGE1.ST ~VEGE1.ST, data = unmarkAay1, K = 250, mixture = "NB")
Aay1m09 <- pcount(~graz1+VEGE1.ST ~I(VEGE1.ST^2), data = unmarkAay1, K = 250, mixture = "NB")
Aay1m10 <- pcount(~graz1+VEGE1.ST ~1, data = unmarkAay1, K = 250, mixture = "NB")
#Models 11 to 15 with only temporal variables on detection.Occupancy variables changing.
Aay1m11 <- pcount(~TEMP1.ST+HOUR1.ST ~graz1+VEGE1.ST+I(VEGE1.ST^2), data = unmarkAay1, K = 250, mixture = "NB")
Aay1m12 <- pcount(~TEMP1.ST+HOUR1.ST ~graz1, data = unmarkAay1, K = 250, mixture = "NB")
Aay1m13 <- pcount(~TEMP1.ST+HOUR1.ST ~VEGE1.ST, data = unmarkAay1, K = 250, mixture = "NB")
```

```
Aay1m14 <- pcount(~TEMP1.ST+HOUR1.ST ~I(VEGE1.ST^2), data = unmarkAay1, K = 250, mixture = "NB")
Aay1m15 <- pcount(~TEMP1.ST+HOUR1.ST ~1, data = unmarkAay1, K = 250, mixture = "NB")
#
##### Modelos
mod.unmarkAay1 <- fitList('Aay1m00 p(.) psi(.)'= Aay1m00,
                  'Aay1m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)'= Aay1m01,
                  'Aay1m02 p(Graz+Vege+Temp+Hour) psi(Graz)'= Aay1m02,
                  'Aay1m03 p(Graz+Vege+Temp+Hour) psi(Vege)'= Aay1m03,
                  'Aay1m04 p(Graz+Vege+Temp+Hour) psi(Vege2)'= Aay1m04,
                  'Aay1m05 p(Graz+Vege+Temp+Hour) psi(.)'= Aay1m05,
                  'Aay1m06 p(Graz+Vege) psi(Graz+Vege+Vege2) '= Aay1m06,
                  'Aay1m07 p(Graz+Vege) psi(Graz) '= Aay1m07,
                  'Aay1m08 p(Graz+Vege) psi(Vege)' = Aay1m08,
                  'Aay1m09 p(Graz+Vege) psi(Vege2)' = Aay1m09,
                  'Aay1m10 p(Graz+Vege) psi(.) '= Aay1m10,
                  'Aay1m11 p(Temp+Hour) psi(Graz+Vege+Vege2) '= Aay1m11,
                  'Aay1m12 p(Temp+Hour) psi (Graz)' = Aay1m12,
                  'Aay1m13 p(Temp+Hour) psi (Vege)' = Aay1m13,
                  'Aay1m14 p(Temp+Hour) psi (Vege2)' = Aay1m14,
                  'Aay1m15 p(Temp+Hour) psi (.)' = Aay1m15)
#
modselAay1 <- modSel(mod.unmarkAay1)
modselAay1
#                                                   nPars     AIC  delta   AICwt cumltvWt
#Aay1m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)    12 1847.63   0.00 2.1e-01     0.21
#Aay1m06 p(Graz+Vege) psi(Graz+Vege+Vege2)            10 1847.81   0.18 1.9e-01     0.39
#Aay1m11 p(Temp+Hour) psi(Graz+Vege+Vege2)             9 1847.82   0.19 1.9e-01     0.58
#Aay1m02 p(Graz+Vege+Temp+Hour) psi(Graz)             10 1848.31   0.68 1.5e-01     0.73
#Aay1m07 p(Graz+Vege) psi(Graz)                        8 1848.62   0.99 1.2e-01     0.85
#Aay1m12 p(Temp+Hour) psi (Graz)                       7 1849.34   1.71 8.7e-02     0.94
#Aay1m09 p(Graz+Vege) psi(Vege2)                       7 1851.91   4.28 2.4e-02     0.96
#Aay1m04 p(Graz+Vege+Temp+Hour) psi(Vege2)             9 1852.07   4.44 2.2e-02     0.98
#Aay1m10 p(Graz+Vege) psi(.)                           6 1854.72   7.09 5.9e-03     0.99
#Aay1m05 p(Graz+Vege+Temp+Hour) psi(.)                 8 1854.80   7.18 5.7e-03     1.00
#Aay1m08 p(Graz+Vege) psi(Vege)                        7 1856.58   8.95 2.3e-03     1.00
#Aay1m03 p(Graz+Vege+Temp+Hour) psi(Vege)              9 1856.67   9.04 2.2e-03     1.00
#Aay1m13 p(Temp+Hour) psi (Vege)                       6 2022.22 174.59 2.5e-39     1.00
#Aay1m00 p(.) psi(.)                                   3 2073.71 226.08 1.7e-50     1.00
#Aay1m15 p(Temp+Hour) psi (.)                          5 2074.02 226.39 1.4e-50     1.00
#Aay1m14 p(Temp+Hour) psi (Vege2)                      6 2075.76 228.13 5.9e-51     1.00
#
summary(Aay1m01) #AIC 0.00
#             Estimate     SE      z  P(>|z|)
#(Intercept)     -0.793 0.4941 -1.605 1.08e-01
#graz1Low         5.224 0.6353  8.223 1.99e-16
#graz1Med         4.872 0.5295  9.201 3.56e-20
#VEGE1.ST         0.074 0.2867  0.258 7.96e-01
#I(VEGE1.ST^2)   -0.150 0.0716 -2.093 3.63e-02

#Detection (logit-scale):
#            Estimate     SE      z  P(>|z|)
#(Intercept)  -1.0241 0.5616 -1.823 6.82e-02
#graz1Low     -2.4333 0.6843 -3.556 3.77e-04
#graz1Med     -2.3920 0.6126 -3.905 9.44e-05
#VEGE1.ST      0.0888 0.2717  0.327 7.44e-01
#TEMP1.ST     -0.0358 0.0400 -0.894 3.71e-01
#HOUR1.ST      0.1048 0.0624  1.680 9.30e-02
#
Aay1m01Psi1 <- linearComb(Aay1m01, c(1,0,0,0,0), type = 'state') ##
backTransform(Aay1m01Psi1)
#High grazing
#Estimate    SE LinComb
#   0.452 0.224  -0.793
#
Aay1m01Psi2 <- linearComb(Aay1m01, c(1,1,0,0,0), type = 'state') ##
backTransform(Aay1m01Psi2)
#Intermediate grazing
#Estimate    SE LinComb
#      84  23.9    4.43
```

```
#
Aay1m01Psi3 <- linearComb(Aay1m01, c(1,0,1,0,0), type = 'state') ##
backTransform(Aay1m01Psi3)
#Low grazing
#Estimate   SE LinComb
#    59.1 18.9    4.08
#
Aay1m01Psi4 <- linearComb(Aay1m01, c(1,0,0,1,0), type = 'state') ##
backTransform(Aay1m01Psi4)
#Vegetation
#Estimate    SE LinComb
#   0.487 0.334  -0.719
#
Aay1m01Psi5 <- linearComb(Aay1m01, c(1,0,0,0,1), type = 'state') ##
backTransform(Aay1m01Psi5)
#Vegetation2
#Estimate    SE LinComb
#   0.389 0.185  -0.943
#
summary(Aay1m06) #AIC 0.18
#              Estimate     SE      z  P(>|z|)
#(Intercept)    -0.7575 0.5025 -1.507 1.32e-01
#graz1Low        5.1857 0.6409  8.091 5.91e-16
#graz1Med        4.8265 0.5363  8.999 2.27e-19
#VEGE1.ST        0.0745 0.2853  0.261 7.94e-01
#I(VEGE1.ST^2)  -0.1524 0.0718 -2.122 3.39e-02

#Detection (logit-scale):
#            Estimate    SE      z  P(>|z|)
#(Intercept)  -1.0673 0.568 -1.879 0.060196
#graz1Low     -2.3704 0.689 -3.442 0.000577
#graz1Med     -2.3365 0.615 -3.797 0.000146
#VEGE1.ST      0.0894 0.270  0.331 0.740713
#
summary(Aay1m11) #AIC 0.19
#              Estimate     SE     z  P(>|z|)
#(Intercept)      1.307 0.3355  3.90 9.79e-05
#graz1Low         3.033 0.3106  9.77 1.58e-22
#graz1Med         2.730 0.2796  9.76 1.65e-22
#VEGE1.ST         0.181 0.1333  1.36 1.74e-01
#I(VEGE1.ST^2)   -0.162 0.0725 -2.24 2.51e-02

#Detection (logit-scale):
#            Estimate     SE       z  P(>|z|)
#(Intercept)  -3.3627 0.1855 -18.131 1.81e-73
#TEMP1.ST     -0.0366 0.0398  -0.921 3.57e-01
#HOUR1.ST      0.0968 0.0618   1.568 1.17e-01
#
# Weighted average of the models with Delta AIC less than two
#Argiope argentata year one
Aay1m01 #delta AIC 0.00
Aay1m06 #delta AIC 0.18
Aay1m11 #delta AIC 0.19
Aay1m02 #delta AIC 0.68
Aay1m07 #delta AIC 0.99
Aay1m12 #delta AIC 1.71

fmListAay1 <- fitList(Best=Aay1m01, Second=Aay1m06, Third=Aay1m11, Fourth = Aay1m02,
                      Fifth = Aay1m07, Sixth = Aay1m12)

coef(fmListAay1)
#Abund    lam(Int) lam(graz1Low) lam(graz1Med) lam(VEGE1.ST) lam(I(VEGE1.ST^2))
#Best   -0.7931364      5.223895      4.871894    0.07399973         -0.1498284
#Second -0.7574912      5.185704      4.826475    0.07445973         -0.1523503
#Third   1.3070422      3.033042      2.729602    0.18143119         -0.1622750
#Fourth -1.0173006      5.289920      5.056525            NA                 NA
#Fifth  -0.9829004      5.250178      5.008987            NA                 NA
#Sixth   0.9988663      3.237329      2.960696            NA                 NA
#
```

```
#p          p(Int) p(graz1Low) p(graz1Med) p(VEGE1.ST) p(TEMP1.ST) p(HOUR1.ST) alpha(alpha)
#Best      1.024062   -2.433265   -2.392013  0.08881667 -0.03576772  0.10483892    1.0341038
#Second   -1.067322   -2.370435   -2.336514  0.08935396          NA          NA    1.0228528
#Third    -3.362710          NA          NA          NA -0.03661267  0.09684407    0.9779446
#Fourth   -1.092001   -2.245696   -2.347483 -0.05429326 -0.03827837  0.10466371    1.0141743
#Fifth    -1.140182   -2.176053   -2.286217 -0.05645760          NA          NA    1.0039029
#Sixth    -3.349617          NA          NA          NA -0.03873912  0.09760914    0.9459204
#
SE(fmListAay1)
#Abund   lam(Int) lam(graz1Low) lam(graz1Med) lam(VEGE1.ST) lam(I(VEGE1.ST^2))
#Best   0.4941224     0.6353097     0.5295216     0.2867349         0.07157220
#Second 0.5025430     0.6409105     0.5363195     0.2853037         0.07180884
#Third  0.3355151     0.3105822     0.2796330     0.1333318         0.07245057
#Fourth 0.4017452     0.4549204     0.4963344            NA                 NA
#Fifth  0.4116688     0.4640419     0.5034911            NA                 NA
#Sixth  0.2928857     0.2374323     0.2445147            NA                 NA
#
#p         p(Int) p(graz1Low) p(graz1Med) p(VEGE1.ST) p(TEMP1.ST) p(HOUR1.ST) alpha(alpha)
#Best   0.5616233  0.6843123   0.6126094  0.27174036  0.03998789  0.06241355    0.1933846
#Second 0.5679195  0.6886051   0.6153323  0.27002557          NA          NA    0.1917676
#Third  0.1854655         NA          NA          NA  0.03975778  0.06177694    0.1908883
#Fourth 0.5168222  0.5738792   0.5957364  0.08117497  0.03995333  0.06244793    0.1923430
#Fifth  0.5238314  0.5802688   0.5992242  0.08151234          NA          NA    0.1909713
#Sixth  0.1886735         NA          NA          NA  0.03977863  0.06187357    0.1879100
#
Aay1m01P1 <- linearComb(Aay1m01, c(1,0,0,0,0,0), type = 'det') ##
backTransform(Aay1m01P1)
#High grazing detection estimate
#Estimate    SE LinComb
#   0.264 0.109   -1.02
#
Aay1m01P2 <- linearComb(Aay1m01, c(1,1,0,0,0,0), type = 'det') ##
backTransform(Aay1m01P2)
#Moderate grazing detection estimate
#Estimate   SE LinComb
#  0.0318 0.01   -3.42
#
Aay1m01P3 <- linearComb(Aay1m01, c(1,0,1,0,0,0), type = 'det') ##
backTransform(Aay1m01P3)
#Low grazing detection estimate
#Estimate    SE LinComb
#  0.0318  0.01   -3.42
#
Aay1m01P4 <- linearComb(Aay1m01, c(1,0,0,1,0,0), type = 'det') ##
backTransform(Aay1m01P4)
#Vegetation detection estimate
#Estimate    SE LinComb
#  0.282  0.141  -0.935
#
Aay1m01P5 <- linearComb(Aay1m01, c(1,0,0,0,1,0), type = 'det') ##
backTransform(Aay1m01P5)
#Temperature detection estimate
#Estimate     SE LinComb
#   0.257  0.108   -1.06
#
Aay1m01P6 <- linearComb(Aay1m01, c(1,0,0,0,0,1), type = 'det') ##
backTransform(Aay1m01P6)
#Hour detection estimate
#Estimate    SE LinComb
#   0.285 0.116  -0.919
#
#########Alpaida quadrilorata###########
#########################################
##########UNMARK MODEL 01##############
#
#Unmark components for A. quadrilorata year one
unmarkAqy1 = unmarkedFramePCount(y = dAqy1,
                          siteCovs = data.frame(graz1=graz1, VEGE1.ST=VEGE1.ST),
                          obsCovs = list(TEMP1.ST=TEMP1.ST, HOUR1.ST=HOUR1.ST))
```

```
#
summary(unmarkAqy1)
#
# Assembling models. Argiope argentata, year one
#p = probability of detection
#psi = probability of occupancy
#Models structure -> ~detec ~occ
#Aq - A. quadrilorata
#y1 - Year one
#mxx - Model number
#
#Model Zero, Null model
Aqy1m00 <- pcount(~1 ~1, data = unmarkAqy1, K = 250, mixture = "NB") ############
#Models 01 to 05 with all variables on detection. Occupancy variables changing.
Aqy1m01 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~graz1+VEGE1.ST+I(VEGE1.ST^2), data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m02 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~graz1, data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m03 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~VEGE1.ST, data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m04 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~I(VEGE1.ST^2), data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m05 <- pcount(~graz1+VEGE1.ST+TEMP1.ST+HOUR1.ST ~1, data = unmarkAqy1, K = 250, mixture = "NB")
#Models 06 to 10 with only spacial variables on detection.Occupancy variables changing.
Aqy1m06 <- pcount(~graz1+VEGE1.ST ~graz1+VEGE1.ST+I(VEGE1.ST^2), data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m07 <- pcount(~graz1+VEGE1.ST ~graz1, data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m08 <- pcount(~graz1+VEGE1.ST ~VEGE1.ST, data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m09 <- pcount(~graz1+VEGE1.ST ~I(VEGE1.ST^2), data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m10 <- pcount(~graz1+VEGE1.ST ~1, data = unmarkAqy1, K = 250, mixture = "NB")
#Models 11 to 15 with only temporal variables on detection.Occupancy variables changing.
Aqy1m11 <- pcount(~TEMP1.ST+HOUR1.ST ~graz1+VEGE1.ST+I(VEGE1.ST^2), data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m12 <- pcount(~TEMP1.ST+HOUR1.ST ~graz1, data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m13 <- pcount(~TEMP1.ST+HOUR1.ST ~VEGE1.ST, data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m14 <- pcount(~TEMP1.ST+HOUR1.ST ~I(VEGE1.ST^2), data = unmarkAqy1, K = 250, mixture = "NB")
Aqy1m15 <- pcount(~TEMP1.ST+HOUR1.ST ~1, data = unmarkAqy1, K = 250, mixture = "NB")
#
##### Modelos
mod.unmarkAqy1 <- fitList('Aqy1m00 p(.) psi(.)'= Aqy1m00,
                    'Aqy1m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)'= Aqy1m01,
                    'Aqy1m02 p(Graz+Vege+Temp+Hour) psi(Graz)'= Aqy1m02,
                    'Aqy1m03 p(Graz+Vege+Temp+Hour) psi(Vege)'= Aqy1m03,
                    'Aqy1m04 p(Graz+Vege+Temp+Hour) psi(Vege2)'= Aqy1m04,
                    'Aqy1m05 p(Graz+Vege+Temp+Hour) psi(.)'= Aqy1m05,
                    'Aqy1m06 p(Graz+Vege) psi(Graz+Vege+Vege2) '= Aqy1m06,
                    'Aqy1m07 p(Graz+Vege) psi(Graz) '= Aqy1m07,
                    'Aqy1m08 p(Graz+Vege) psi(Vege)' = Aqy1m08,
                    'Aqy1m09 p(Graz+Vege) psi(Vege2)' = Aqy1m09,
                    'Aqy1m10 p(Graz+Vege) psi(.) '= Aqy1m10,
                    'Aqy1m11 p(Temp+Hour) psi(Graz+Vege+Vege2) '= Aqy1m11,
                    'Aqy1m12 p(Temp+Hour) psi (Graz)' = Aqy1m12,
                    'Aqy1m13 p(Temp+Hour) psi (Vege)' = Aqy1m13,
                    'Aqy1m14 p(Temp+Hour) psi (Vege2)' = Aqy1m14,
                    'Aqy1m15 p(Temp+Hour) psi (.)' = Aqy1m15)
#
modselAqy1 <- modSel(mod.unmarkAqy1)
modselAqy1
#                                           nPars     AIC  delta   AICwt cumltvWt
#Aqy1m05 p(Graz+Vege+Temp+Hour) psi(.)                8 1111.66   0.00 4.5e-01     0.45
#Aqy1m03 p(Graz+Vege+Temp+Hour) psi(Vege)              9 1113.64   1.98 1.7e-01     0.62
#Aqy1m04 p(Graz+Vege+Temp+Hour) psi(Vege2)             9 1113.66   2.00 1.7e-01     0.78
#Aqy1m11 p(Temp+Hour) psi(Graz+Vege+Vege2)             9 1114.01   2.34 1.4e-01     0.92
#Aqy1m02 p(Graz+Vege+Temp+Hour) psi(Graz)             10 1115.45   3.79 6.7e-02     0.99
#Aqy1m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)    12 1119.35   7.69 9.6e-03     1.00
#Aqy1m12 p(Temp+Hour) psi (Graz)                      7 1122.81  11.14 1.7e-03     1.00
#Aqy1m10 p(Graz+Vege) psi(.)                          6 1142.96  31.30 7.2e-08     1.00
#Aqy1m09 p(Graz+Vege) psi(Vege2)                      7 1144.92  33.25 2.7e-08     1.00
#Aqy1m08 p(Graz+Vege) psi(Vege)                       7 1144.96  33.30 2.6e-08     1.00
#Aqy1m07 p(Graz+Vege) psi(Graz)                       8 1146.73  35.06 1.1e-08     1.00
#Aqy1m06 p(Graz+Vege) psi(Graz+Vege+Vege2)           10 1150.59  38.93 1.6e-09     1.00
#Aqy1m13 p(Temp+Hour) psi (Vege)                      6 1279.26 167.60 1.8e-37     1.00
#Aqy1m15 p(Temp+Hour) psi (.)                         5 1301.94 190.27 2.2e-42     1.00
#Aqy1m14 p(Temp+Hour) psi (Vege2)                     6 1303.68 192.02 9.0e-43     1.00
```

```
#Aqy1m00 p(.) psi(.)                       3 1341.69 230.02 5.1e-51     1.00
#
summary(Aqy1m05) #AIC 0.00
#Abundance (log-scale):
#             Estimate    SE  z  P(>|z|)
#(Intercept)       3.8 0.317 12 5.34e-33

#Detection (logit-scale):
#            Estimate     SE     z  P(>|z|)
#(Intercept)   -8.966 1.0589 -8.47 2.51e-17
#graz1Low       4.190 1.0449  4.01 6.08e-05
#graz1Med       5.553 1.0144  5.47 4.39e-08
#VEGE1.ST       0.460 0.1263  3.65 2.65e-04
#TEMP1.ST       0.341 0.0608  5.62 1.95e-08
#HOUR1.ST       0.244 0.0927  2.63 8.46e-03
#
summary(Aqy1m03) #AIC 1.98
#            Estimate    SE      z  P(>|z|)
#(Intercept)   3.7992 0.313 12.119 8.38e-34
#VEGE1.ST     -0.0407 0.275 -0.148 8.82e-01

#Detection (logit-scale):
#            Estimate     SE     z  P(>|z|)
#(Intercept)   -8.967 1.0582 -8.47 2.36e-17
#graz1Low       4.188 1.0450  4.01 6.12e-05
#graz1Med       5.553 1.0143  5.47 4.39e-08
#VEGE1.ST       0.501 0.3062  1.64 1.01e-01
#TEMP1.ST       0.342 0.0609  5.61 1.97e-08
#HOUR1.ST       0.244 0.0927  2.63 8.45e-03
#
summary(Aqy1m04) #AIC 2.00
#Abundance (log-scale):
#              Estimate     SE       z  P(>|z|)
#(Intercept)    3.79016 0.3375 11.2316 2.85e-29
#I(VEGE1.ST^2)  0.00549 0.0839  0.0654 9.48e-01

#Detection (logit-scale):
#            Estimate     SE     z  P(>|z|)
#(Intercept)   -8.971 1.0613 -8.45 2.84e-17
#graz1Low       4.200 1.0558  3.98 6.96e-05
#graz1Med       5.562 1.0239  5.43 5.55e-08
#VEGE1.ST       0.453 0.1750  2.59 9.72e-03
#TEMP1.ST       0.341 0.0608  5.61 1.98e-08
#HOUR1.ST       0.244 0.0927  2.63 8.54e-03
#
# Weighted average of the models with Delta AIC less than two
#Alpaida quadrilorata year one
Aqy1m05 #delta AIC 0.00
Aqy1m03 #delta AIC 1.98
Aqy1m04 #delta AIC 2.00

fmListAqy1 <- fitList(Best=Aqy1m05, Second=Aqy1m03, Third=Aqy1m04)
coef(fmListAqy1)
#Abund      lam(Int)
#Best       3.797233
#Second     3.799170
#Third      3.790160
#
#P          p(Int) p(graz1Low) p(graz1Med) p(VEGE1.ST) p(TEMP1.ST) p(HOUR1.ST) alpha(alpha) lam(VEGE1.ST) lam(I(VEGE1.ST^2))
#Best    -8.966441    4.189671    5.553343   0.4604977   0.3414105   0.2440004    0.5202334            NA                 NA
#Second  -8.967459    4.188230    5.552801   0.5014927   0.3418223   0.2441320    0.5212971   -0.04071537                 NA
#Third   -8.970904    4.199519    5.562382   0.4525586   0.3413186   0.2438170    0.5210460            NA        0.005485676
#
SE(fmListAqy1)
#Abund      lam(Int)
#Best      0.3173308
#Second    0.3134899
#Third     0.3374563
#
```

```
#P          p(Int) p(graz1Low) p(graz1Med) p(VEGE1.ST) p(TEMP1.ST) p(HOUR1.ST)   alpha(alpha) lam(VEGE1.ST) lam(I(VEGE1.ST^2))
#Best       1.058948    1.044924    1.014397   0.1262605  0.06078412  0.09266858      0.2161830            NA                NA
#Second     1.058156    1.044962    1.014329   0.3061790  0.06088507  0.09270518      0.2161898     0.2752155                NA
#Third      1.061256    1.055792    1.023887   0.1750217  0.06079792  0.09270520      0.2166784            NA        0.08388844
#
#
###########Argiope argentata############
##########Alpaida quadrilorata###########
#################Data####################
##############Year Two#################
datay2 <- read.table("N-ocupancyAa-Aq-year2.csv", head=T, as.is=T, sep=";")
#
datay2 [,2] <- as.factor(unlist(datay2 [,2]))#Grazing year two
datay2 [,3] <- as.numeric(unlist(datay2 [,3]))#Vegetation height Year two
datay2 [,16:21] <- as.numeric(unlist(datay2 [,16:21]))#Temperature year two
datay2 [,22:27] <- as.numeric(unlist(datay2 [,22:27]))#Hour year two
#
#set number of detections, sites, year, and repetitions
dAay2 <- as.matrix(datay2 [4:9])  #Argiope argentata detec year two
dAqy2 <- as.matrix(datay2 [10:15]) #Alpaida quadrilorata detec year two
#
temp2 <- as.matrix(datay2 [,16:21]) #temperature for year two
dim(temp2[rowSums(is.na(temp2)) != ncol(temp2),]) #Matrix with, at least, one visit per line = 288 sites.
#
hour2 <- as.matrix(datay2 [,22:27]) #hour for year two
dim(hour2[rowSums(is.na(hour2)) != ncol(hour2),]) #Matrix with, at least, one visit per line = 288 sites.
#
vege2 <- as.matrix(datay2 [,3]) #vegetation for year two
#
graz2 <- as.factor(datay2 [,"grazing"]) #Treatments year two
#
#Standartization
#Also, force imputing of missing values
#
#Temperature for detection of A. argentata and A. quadrilorata, year one
meantemp2 <- mean(temp2, na.rm = TRUE)
sdtemp2 <- sd(temp2, na.rm = TRUE)
TEMP2.ST <- (temp2 - meantemp2)/sdtemp2
#
#Time for detection of A. argentata and A. quadrilorata, year one
meanhour2 <- mean(hour2, na.rm = TRUE)
sdhour2 <- sd(hour2, na.rm = TRUE)
HOUR2.ST <- (hour2 - meanhour2)/sdhour2
#
#Vegetation for year one
meanvege2 <- mean(vege2, na.rm = TRUE)
sdvege2 <- sd(vege2, na.rm = TRUE)
VEGE2.ST <- (vege2 - meanvege2)/sdvege2
#
#
###########Argiope argentata############
#####################################
##########UNMARK MODEL 02#######
#
#Unmark components for A. argentata year two
unmarkAay2 = unmarkedFramePCount(y = dAay2,
                            siteCovs = data.frame(graz2=graz2, VEGE2.ST=VEGE2.ST),
                            obsCovs = list(TEMP2.ST=TEMP2.ST, HOUR2.ST=HOUR2.ST))
#
summary(unmarkAay2)
#
# Assembling models. Argiope argentata, year one
#p = probability of detection
#psi = probability of occupancy
#Models structure -> ~detec ~occ
#Aa - A. argentata
#y2 - Year two
#mxx - Model number
#
```

```
#Model Zero, Null model
Aay2m00 <- pcount(~1 ~1, data = unmarkAay2, K = 250, mixture = "NB") ###########
#Models 01 to 05 with all variables on detection. Occupancy variables changing.
Aay2m01 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~graz2+VEGE2.ST+I(VEGE2.ST^2), data = unmarkAay2, K = 250,
mixture = "NB")
Aay2m02 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~graz2, data = unmarkAay2, K = 250, mixture = "NB")
Aay2m03 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~VEGE2.ST, data = unmarkAay2, K = 250, mixture = "NB")
Aay2m04 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~I(VEGE2.ST^2), data = unmarkAay2, K = 250, mixture = "NB")
Aay2m05 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~1, data = unmarkAay2, K = 250, mixture = "NB")
#Models 06 to 10 with only spacial variables on detection.Occupancy variables changing.
Aay2m06 <- pcount(~graz2+VEGE2.ST ~graz2+VEGE2.ST+I(VEGE2.ST^2), data = unmarkAay2, K = 250, mixture = "NB")
Aay2m07 <- pcount(~graz2+VEGE2.ST ~graz2, data = unmarkAay2, K = 250, mixture = "NB")
Aay2m08 <- pcount(~graz2+VEGE2.ST ~VEGE2.ST, data = unmarkAay2, K = 250, mixture = "NB")
Aay2m09 <- pcount(~graz2+VEGE2.ST ~I(VEGE2.ST^2), data = unmarkAay2, K = 250, mixture = "NB")
Aay2m10 <- pcount(~graz2+VEGE2.ST ~1, data = unmarkAay2, K = 250, mixture = "NB")
#Models 11 to 15 with only temporal variables on detection.Occupancy variables changing.
Aay2m11 <- pcount(~TEMP2.ST+HOUR2.ST ~graz2+VEGE2.ST+I(VEGE2.ST^2), data = unmarkAay2, K = 250, mixture = "NB")
Aay2m12 <- pcount(~TEMP2.ST+HOUR2.ST ~graz2, data = unmarkAay2, K = 250, mixture = "NB")
Aay2m13 <- pcount(~TEMP2.ST+HOUR2.ST ~VEGE2.ST, data = unmarkAay2, K = 250, mixture = "NB")
Aay2m14 <- pcount(~TEMP2.ST+HOUR2.ST ~I(VEGE2.ST^2), data = unmarkAay2, K = 250, mixture = "NB")
Aay2m15 <- pcount(~TEMP2.ST+HOUR2.ST ~1, data = unmarkAay2, K = 250, mixture = "NB")
#
##### Modelos
mod.unmarkAay2 <- fitList('Aay2m00 p(.) psi(.)'= Aay2m00,
                 'Aay2m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)'= Aay2m01,
                 'Aay2m02 p(Graz+Vege+Temp+Hour) psi(Graz)'= Aay2m02,
                 'Aay2m03 p(Graz+Vege+Temp+Hour) psi(Vege)'= Aay2m03,
                 'Aay2m04 p(Graz+Vege+Temp+Hour) psi(Vege2)'= Aay2m04,
                 'Aay2m05 p(Graz+Vege+Temp+Hour) psi(.)'= Aay2m05,
                 'Aay2m06 p(Graz+Vege) psi(Graz+Vege+Vege2) '= Aay2m06,
                 'Aay2m07 p(Graz+Vege) psi(Graz) '= Aay2m07,
                 'Aay2m08 p(Graz+Vege) psi(Vege)' = Aay2m08,
                 'Aay2m09 p(Graz+Vege) psi(Vege2)' = Aay2m09,
                 'Aay2m10 p(Graz+Vege) psi(.) '= Aay2m10,
                 'Aay2m11 p(Temp+Hour) psi(Graz+Vege+Vege2) '= Aay2m11,
                 'Aay2m12 p(Temp+Hour) psi (Graz)' = Aay2m12,
                 'Aay2m13 p(Temp+Hour) psi (Vege)' = Aay2m13,
                 'Aay2m14 p(Temp+Hour) psi (Vege2)' = Aay2m14,
                 'Aay2m15 p(Temp+Hour) psi (.)' = Aay2m15)
#
modselAay2 <- modSel(mod.unmarkAay2)
modselAay2
#                                            nPars     AIC  delta   AICwt cumltvWt
#Aay2m04 p(Graz+Vege+Temp+Hour) psi(Vege2)              9 1842.33   0.00 6.0e-01     0.60
#Aay2m11 p(Temp+Hour) psi(Graz+Vege+Vege2)              9 1843.56   1.23 3.3e-01     0.93
#Aay2m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)    12 1846.97   4.64 5.9e-02     0.99
#Aay2m05 p(Graz+Vege+Temp+Hour) psi(.)                  8 1851.38   9.05 6.5e-03     1.00
#Aay2m03 p(Graz+Vege+Temp+Hour) psi(Vege)               9 1853.38  11.05 2.4e-03     1.00
#Aay2m02 p(Graz+Vege+Temp+Hour) psi(Graz)              10 1854.97  12.63 1.1e-03     1.00
#Aay2m12 p(Temp+Hour) psi (Graz)                        7 1855.88  13.55 6.9e-04     1.00
#Aay2m09 p(Graz+Vege) psi(Vege2)                        7 1883.31  40.98 7.6e-10     1.00
#Aay2m06 p(Graz+Vege) psi(Graz+Vege+Vege2)             10 1888.18  45.85 6.7e-11     1.00
#Aay2m10 p(Graz+Vege) psi(.)                            6 1890.70  48.36 1.9e-11     1.00
#Aay2m08 p(Graz+Vege) psi(Vege)                         7 1892.68  50.35 7.0e-12     1.00
#Aay2m07 p(Graz+Vege) psi(Graz)                         8 1894.16  51.82 3.4e-12     1.00
#Aay2m13 p(Temp+Hour) psi (Vege)                        6 1913.61  71.28 2.0e-16     1.00
#Aay2m14 p(Temp+Hour) psi (Vege2)                       6 1943.62 101.29 6.1e-23     1.00
#Aay2m15 p(Temp+Hour) psi (.)                           5 1956.07 113.74 1.2e-25     1.00
#Aay2m00 p(.) psi(.)                                    3 1980.37 138.04 6.4e-31     1.00
#
summary(Aay2m04) #AIC 0.00
#            Estimate     SE      z  P(>|z|)
#(Intercept)     4.021 0.1933 20.80 3.94e-96
#I(VEGE2.ST^2)   -0.333 0.0986 -3.38 7.30e-04

#Detection (logit-scale):
#           Estimate     SE      z  P(>|z|)
#(Intercept)   -3.959 0.3186 -12.43 1.90e-35
#graz2Low       0.491 0.3628   1.35 1.76e-01
```

```
#graz2Med      1.072 0.3038   3.53 4.19e-04
#VEGE2.ST      0.586 0.1619   3.62 2.97e-04
#TEMP2.ST      0.279 0.0504   5.54 2.97e-08
#HOUR2.ST     -0.202 0.0432  -4.68 2.88e-06
#
summary(Aay2m11) #AIC 1.23
#Abundance (log-scale):
#             Estimate    SE     z  P(>|z|)
#(Intercept)     3.112 0.337  9.24 2.50e-20
#graz2Low        0.391 0.357  1.09 2.74e-01
#graz2Med        0.921 0.309  2.98 2.86e-03
#VEGE2.ST        0.609 0.160  3.82 1.35e-04
#I(VEGE2.ST^2)  -0.370 0.106 -3.49 4.81e-04

#Detection (logit-scale):
#           Estimate     SE      z  P(>|z|)
#(Intercept)   -2.916 0.1842 -15.83 1.98e-56
#TEMP2.ST       0.282 0.0507   5.56 2.74e-08
#HOUR2.ST      -0.198 0.0430  -4.62 3.88e-06
#
# Weighted average of the models with Delta AIC less than two
#Argiope argentata year two
Aay2m04 #delta AIC 0.00
Aay2m11 #delta AIC 1.23

fmListAay2 <- fitList(Best=Aay2m04, Second=Aay2m11)
coef(fmListAay2)
#Abund    lam(Int) lam(I(VEGE2.ST^2))
#Best     4.021348         -0.3331457
#Second   3.111959         -0.3702350
#
#p                  p(Int)  p(graz2Low)  p(graz2Med)  p(VEGE2.ST)  p(TEMP2.ST)  p(HOUR2.ST)  alpha(alpha)  lam(graz2Low)  lam(graz2Med)
lam(VEGE2.ST)
#Best     -3.958884   0.4906826    1.071666   0.5856943   0.2792207  -0.2022442    0.4713903           NA           NA           NA
#Second    -2.915583          NA          NA          NA   0.2817510  -0.1984651    0.4764212    0.3913121    0.9211095     0.609224
#
SE(fmListAay2)
#Abund     lam(Int) lam(I(VEGE2.ST^2))
#Best     0.1932916         0.09862238
#Second   0.3368465         0.10605180
#
#p                  p(Int)  p(graz2Low)  p(graz2Med)  p(VEGE2.ST)  p(TEMP2.ST)  p(HOUR2.ST)  alpha(alpha)  lam(graz2Low)  lam(graz2Med)
lam(VEGE2.ST)
#Best      0.3186074   0.3627629   0.3037941   0.1618984  0.05037357  0.04321883    0.1602543           NA           NA           NA
#Second    0.1841974          NA          NA          NA  0.05069707  0.04298146    0.1605108    0.3574307    0.3088779    0.1596243
#
#########Alpaida quadrilorata###############
###########################################
##########UNMARK MODEL 02###########
#
#Unmark components for A. quadrilorata year two
unmarkAqy2 = unmarkedFramePCount(y = dAqy2,
                              siteCovs = data.frame(graz2=graz2, VEGE2.ST=VEGE2.ST),
                              obsCovs = list(TEMP2.ST=TEMP2.ST, HOUR2.ST=HOUR2.ST))
#
summary(unmarkAqy2)
#
# Assembling models. Argiope argentata, year one
#p = probability of detection
#psi = probability of occupancy
#Models structure -> ~detec ~occ
#Aq - A. quadrilorata
#y2 - Year two
#mxx - Model number
#
#Model Zero, Null model
Aqy2m00 <- pcount(~1 ~1, data = unmarkAqy2, K = 250, mixture = "NB") ############
#Models 01 to 05 with all variables on detection. Occupancy variables changing.
```

```
Aqy2m01 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~graz2+VEGE2.ST+I(VEGE2.ST^2), data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m02 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~graz2, data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m03 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~VEGE2.ST, data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m04 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~I(VEGE2.ST^2), data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m05 <- pcount(~graz2+VEGE2.ST+TEMP2.ST+HOUR2.ST ~1, data = unmarkAqy2, K = 250, mixture = "NB")
#Models 06 to 10 with only spacial variables on detection.Occupancy variables changing.
Aqy2m06 <- pcount(~graz2+VEGE2.ST ~graz2+VEGE2.ST+I(VEGE2.ST^2), data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m07 <- pcount(~graz2+VEGE2.ST ~graz2, data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m08 <- pcount(~graz2+VEGE2.ST ~VEGE2.ST, data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m09 <- pcount(~graz2+VEGE2.ST ~I(VEGE2.ST^2), data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m10 <- pcount(~graz2+VEGE2.ST ~1, data = unmarkAqy2, K = 250, mixture = "NB")
#Models 11 to 15 with only temporal variables on detection.Occupancy variables changing.
Aqy2m11 <- pcount(~TEMP2.ST+HOUR2.ST ~graz2+VEGE2.ST+I(VEGE2.ST^2), data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m12 <- pcount(~TEMP2.ST+HOUR2.ST ~graz2, data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m13 <- pcount(~TEMP2.ST+HOUR2.ST ~VEGE2.ST, data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m14 <- pcount(~TEMP2.ST+HOUR2.ST ~I(VEGE2.ST^2), data = unmarkAqy2, K = 250, mixture = "NB")
Aqy2m15 <- pcount(~TEMP2.ST+HOUR2.ST ~1, data = unmarkAqy2, K = 250, mixture = "NB")
#
##### Modelos
mod.unmarkAqy2 <- fitList('Aqy2m00 p(.) psi(.)'= Aqy2m00,
                 'Aqy2m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)'= Aqy2m01,
                 'Aqy2m02 p(Graz+Vege+Temp+Hour) psi(Graz)'= Aqy2m02,
                 'Aqy2m03 p(Graz+Vege+Temp+Hour) psi(Vege)'= Aqy2m03,
                 'Aqy2m04 p(Graz+Vege+Temp+Hour) psi(Vege2)'= Aqy2m04,
                 'Aqy2m05 p(Graz+Vege+Temp+Hour) psi(.)'= Aqy2m05,
                 'Aqy2m06 p(Graz+Vege) psi(Graz+Vege+Vege2) '= Aqy2m06,
                 'Aqy2m07 p(Graz+Vege) psi(Graz) '= Aqy2m07,
                 'Aqy2m08 p(Graz+Vege) psi(Vege)' = Aqy2m08,
                 'Aqy2m09 p(Graz+Vege) psi(Vege2)' = Aqy2m09,
                 'Aqy2m10 p(Graz+Vege) psi(.) '= Aqy2m10,
                 'Aqy2m11 p(Temp+Hour) psi(Graz+Vege+Vege2) '= Aqy2m11,
                 'Aqy2m12 p(Temp+Hour) psi (Graz)' = Aqy2m12,
                 'Aqy2m13 p(Temp+Hour) psi (Vege)' = Aqy2m13,
                 'Aqy2m14 p(Temp+Hour) psi (Vege2)' = Aqy2m14,
                 'Aqy2m15 p(Temp+Hour) psi (.)' = Aqy2m15)
#
modselAqy2 <- modSel(mod.unmarkAqy2)
modselAqy2
#                                                  nPars     AIC  delta   AICwt cumltvWt
#Aqy2m05 p(Graz+Vege+Temp+Hour) psi(.)                 8  921.59   0.00 3.4e-01     0.34
#Aqy2m11 p(Temp+Hour) psi(Graz+Vege+Vege2)             9  922.69   1.10 1.9e-01     0.53
#Aqy2m04 p(Graz+Vege+Temp+Hour) psi(Vege2)             9  923.01   1.42 1.6e-01     0.69
#Aqy2m03 p(Graz+Vege+Temp+Hour) psi(Vege)              9  923.54   1.95 1.3e-01     0.82
#Aqy2m12 p(Temp+Hour) psi (Graz)                       7  924.28   2.69 8.8e-02     0.91
#Aqy2m02 p(Graz+Vege+Temp+Hour) psi(Graz)             10  925.00   3.41 6.1e-02     0.97
#Aqy2m01 p(Graz+Vege+Temp+Hour) psi(Graz+Vege+Vege2)    12  927.75   6.17 1.5e-02     0.98
#Aqy2m10 p(Graz+Vege) psi(.)                           6  929.30   7.71 7.1e-03     0.99
#Aqy2m09 p(Graz+Vege) psi(Vege2)                       7  930.77   9.18 3.4e-03     1.00
#Aqy2m08 p(Graz+Vege) psi(Vege)                        7  931.26   9.67 2.7e-03     1.00
#Aqy2m07 p(Graz+Vege) psi(Graz)                        8  932.35  10.76 1.5e-03     1.00
#Aqy2m06 p(Graz+Vege) psi(Graz+Vege+Vege2)            10  935.28  13.69 3.6e-04     1.00
#Aqy2m13 p(Temp+Hour) psi (Vege)                       6 1064.46 142.87 3.2e-32     1.00
#Aqy2m14 p(Temp+Hour) psi (Vege2)                      6 1073.78 152.19 3.0e-34     1.00
#Aqy2m00 p(.) psi(.)                                   3 1086.21 164.62 6.0e-37     1.00
#Aqy2m15 p(Temp+Hour) psi (.)                          5 1088.39 166.80 2.0e-37     1.00
#
summary(Aqy2m05) #AIC 0.00
#Abundance (log-scale):
#          Estimate    SE    z  P(>|z|)
#(Intercept)    3.78 0.387 9.77 1.52e-22

#Detection (logit-scale):
#            Estimate     SE      z  P(>|z|)
#(Intercept)   -7.615 0.7298 -10.43 1.72e-25
#graz2Low       2.779 0.6841   4.06 4.86e-05
#graz2Med       4.300 0.6235   6.90 5.32e-12
#VEGE2.ST       0.336 0.1535   2.19 2.85e-02
#TEMP2.ST       0.213 0.0752   2.83 4.58e-03
```

```
#HOUR2.ST      -0.159 0.0629  -2.52 1.16e-02
#
summary(Aqy2m11) #AIC 1.10
#Abundance (log-scale):
#              Estimate    SE      z  P(>|z|)
#(Intercept)     -0.215 0.810 -0.265 7.91e-01
#graz2Low         2.575 0.709  3.631 2.82e-04
#graz2Med         4.025 0.676  5.956 2.58e-09
#VEGE2.ST         0.429 0.195  2.199 2.79e-02
#I(VEGE2.ST^2)   -0.106 0.140 -0.756 4.50e-01

#Detection (logit-scale):
#            Estimate     SE     z  P(>|z|)
#(Intercept)   -3.329 0.4844 -6.87 6.33e-12
#TEMP2.ST       0.217 0.0757  2.86 4.20e-03
#HOUR2.ST      -0.156 0.0631 -2.48 1.31e-02
#
summary(Aqy2m04) #AIC 1.42
#              Estimate    SE      z  P(>|z|)
#(Intercept)      3.823 0.424  9.010 2.06e-19
#I(VEGE2.ST^2)   -0.105 0.139 -0.757 4.49e-01

#Detection (logit-scale):
#            Estimate     SE     z  P(>|z|)
#(Intercept)   -7.430 0.7845 -9.47 2.77e-21
#graz2Low       2.610 0.7158  3.65 2.66e-04
#graz2Med       4.089 0.6794  6.02 1.76e-09
#VEGE2.ST       0.435 0.2014  2.16 3.08e-02
#TEMP2.ST       0.216 0.0752  2.87 4.15e-03
#HOUR2.ST      -0.157 0.0630 -2.50 1.25e-02
#
summary(Aqy2m03) #AIC 1.95
#            Estimate    SE     z  P(>|z|)
#(Intercept)    3.746 0.497 7.537 4.82e-14
#VEGE2.ST       0.132 0.562 0.235 8.14e-01

#Detection (logit-scale):
#            Estimate     SE      z  P(>|z|)
#(Intercept)   -7.580 0.7778 -9.746 1.92e-22
#graz2Low       2.786 0.6849  4.068 4.74e-05
#graz2Med       4.305 0.6241  6.897 5.32e-12
#VEGE2.ST       0.201 0.5951  0.337 7.36e-01
#TEMP2.ST       0.213 0.0752  2.834 4.60e-03
#HOUR2.ST      -0.159 0.0629 -2.526 1.15e-02
#
# Weighted average of the models with Delta AIC less than two
#Alpaida quadrilorata year two
Aqy2m05 #delta AIC 0.00
Aqy2m11 #delta AIC 1.10
Aqy2m04 #delta AIC 1.42
Aqy2m03 #delta AIC 1.95
#
fmListAqy2 <- fitList(Best=Aqy2m05, Second=Aqy2m11, Third=Aqy2m04, Fourth=Aqy2m03)
coef(fmListAqy2)
#Abund       lam(Int)
#Best        3.785106
#Second     -0.214922
#Third       3.823404
#Fouth       3.745540
#
#P                  p(Int) p(graz2Low) p(graz2Med) p(VEGE2.ST) p(TEMP2.ST) p(HOUR2.ST)   alpha(alpha) lam(graz2Low) lam(graz2Med)
lam(VEGE2.ST) lam(I(VEGE2.ST^2))
#Best       -7.615281    2.778750    4.299831   0.3363206   0.2133149  -0.1587157     0.7970526           NA           NA           NA                NA
#Second      -3.328928          NA          NA          NA   0.2168006  -0.1564292     0.7970526           NA           NA           NA                NA
#Third      -7.429742    2.609869    4.088989   0.4349336   0.2155736  -0.1573958     0.8233940     2.575077     4.025433     0.4293943        -
0.1056852
#Fourth     -7.579795    2.786296    4.304581   0.2007187   0.2131480  -0.1590109     0.7955008           NA           NA    0.1321340                NA
#
SE(fmListAqy2)
```

```
#Abund       lam(Int)
#Best       0.4056662
#Second      0.8100674
#Third       0.4243532
#Fourth      0.4969698
#
#P               p(Int) p(graz2Low) p(graz2Med) p(VEGE2.ST) p(TEMP2.ST) p(HOUR2.ST)    alpha(alpha) lam(graz2Low) lam(graz2Med)
lam(VEGE2.ST) lam(I(VEGE2.ST^2))
#Best     0.7297977   0.6840601   0.6234582   0.1535187  0.07524431  0.06289132     0.2807041          NA          NA          NA              NA
#Second     0.4844254            NA            NA            NA  0.07573994  0.06307764       0.2849530        0.70914      0.6758447       0.1952884
0.1398084
#Third      0.7844644    0.7158337    0.6794122    0.2013908  0.07520307  0.06298918       0.2837284             NA             NA             NA
0.1385679
#Fourth     0.7777562    0.6848966    0.6241383    0.5950815  0.07521242  0.06293725       0.2807057             NA             NA      0.5623248
NA
```

Table S1 – AIC tables ranking the models for abundance estimates for *Argiope argentata* and *Alpaida quadrilorata*. p = Variables influencing species presence; abu = Variables influencing species abundance; Graz = Grazing effect with three levels, low, moderate, and high; Vege = Mean of vegetation height; Vege2 = Quadratic mean of vegetation height; Temp = Temperature; Hour = Time when the cell of sampled.

Argiope argentata					
Year one model	**AIC**	**Delta**	**Year two models**	**AIC**	**Delta**
p(Graz+Vege+Temp+Hour) abu(Graz+Vege+Vege2)	1847.6	0	p(Graz+Vege+Temp+Hour) abu(Vege2)	1842.3	0
p(Graz+Vege) abu(Graz+Vege+Vege2)	1847.8	0.18	p(Temp+Hour) abu(Graz+Vege+Vege2)	1843.5	1.23
p(Temp+Hour) abu(Graz+Vege+Vege2)	1847.8	0.19	p(Graz+Vege+Temp+Hour) abu(Graz+Vege+Vege2)	1846.9	4.64
p(Graz+Vege+Temp+Hour) abu(Graz)	1848.3	0.68	p(Graz+Vege+Temp+Hour) abu(.)	1851.3	9.05
p(Graz+Vege) abu(Graz)	1848.6	0.99	p(Graz+Vege+Temp+Hour) abu(Vege)	1853.3	11.05
p(Temp+Hour) abu (Graz)	1849.3	1.71	p(Graz+Vege+Temp+Hour) abu(Graz)	1854.9	12.63
p(Graz+Vege) abu(Vege2)	1851.9	4.28	p(Temp+Hour) abu (Graz)	1855.8	13.55
p(Graz+Vege+Temp+Hour) abu(Vege2)	1852.0	4.44	p(Graz+Vege) abu(Vege2)	1883.3	40.98
p(Graz+Vege) abu(.)	1854.7	7.09	p(Graz+Vege) abu(Graz+Vege+Vege2)	1888.1	45.85
p(Graz+Vege+Temp+Hour) abu(.)	1854.8	7.18	p(Graz+Vege) abu(.)	1890.7	48.36
p(Graz+Vege) abu(Vege)	1856.5	8.95	p(Graz+Vege) abu(Vege)	1892.6	50.35
p(Graz+Vege+Temp+Hour) abu(Vege)	1856.6	9.04	p(Graz+Vege) abu(Graz)	1894.1	51.82
p(Temp+Hour) abu (Vege)	2022.2	174.5	p(Temp+Hour) abu (Vege)	19136	71.28
p(.) abu(.)	2073.7	226.8	p(Temp+Hour) abu (Vege2)	1943.6	101.2
p(Temp+Hour) abu (.)	2074	226.3	p(Temp+Hour) abu (.)	1956.0	113.7
p(Temp+Hour) abu (Vege2)	2075.7	228.1	p(.) abu(.)	1980.3	138.0
Alpaida quadrilorata					
Year one models			**Year two models**		
p(Graz+Vege+Temp+Hour) abu(.)	1111.6	0	p(Graz+Vege+Temp+Hour) abu(.)	921.59	0
p(Graz+Vege+Temp+Hour) abu(Vege)	1113.6	1.98	p(Temp+Hour) abu(Graz+Vege+Vege2)	922.69	1.1
p(Graz+Vege+Temp+Hour) abu(Vege2)	1113.6	2	p(Graz+Vege+Temp+Hour) abu(Vege2)	923.01	1.42
p(Temp+Hour) abu(Graz+Vege+Vege2)	1114.0	2.34	p(Graz+Vege+Temp+Hour) abu(Vege)	923.54	1.95
p(Graz+Vege+Temp+Hour) abu(Graz)	1115.4	3.79	p(Temp+Hour) abu (Graz)	924.28	2.69
p(Graz+Vege+Temp+Hour) abu(Graz+Vege+Vege2)	1119.3	7.69	p(Graz+Vege+Temp+Hour) abu(Graz)	925	3.41
p(Temp+Hour) abu (Graz)	1122.8	11.14	p(Graz+Vege+Temp+Hour) abu(Graz+Vege+Vege2)	927.75	6.17
p(Graz+Vege) abu(.)	1142.9	31.3	p(Graz+Vege) abu(.)	929.3	7.71
p(Graz+Vege) abu(Vege2)	1144.9	33.25	p(Graz+Vege) abu(Vege2)	930.77	9.18
p(Graz+Vege) abu(Vege)	1144.9	33.3	p(Graz+Vege) abu(Vege)	931.26	9.67
p(Graz+Vege) abu(Graz)	1146.7	35.06	p(Graz+Vege) abu(Graz)	932.35	10.76

p(Graz+Vege) abu(Graz+Vege+Vege2)	1150.5	38.93	p(Graz+Vege) abu(Graz+Vege+Vege2)	935.28	13.69
p(Temp+Hour) abu (Vege)	1279.2	167.6	p(Temp+Hour) abu (Vege)	1064.4	142.8
p(Temp+Hour) abu (.)	1301.9	190.2	p(Temp+Hour) abu (Vege2)	1073.7	152.1
p(Temp+Hour) abu (Vege2)	1303.6	192.0	p(.) abu(.)	1086.2	164.6
p(.) abu(.)	1341.6	230.0	p(Temp+Hour) abu (.)	1088.3	166.8

Table S2 – Model-averaged for models if AIC <2. Abundance estimates for *Argiope argentata* and *Alpaida quadrilorata*. p = Variables influencing species presence; abu = Variables influencing species abundance; , SE = Standard error; Graz = Grazing effect with three levels, low, moderate, and high; Vege = Mean of vegetation height; Vege2 = Quadratic mean of vegetation height; Temp = Temperature; Hour = Time when the cell of sampled.

Argiope argentata						
Year one Abundance						
	Graz high	Graz Low	Graz Moderate	Veg	Veg 2	
Best model	-0.793, SE = 0.494	5.223, SE = 0.635	4.871, SE = 0.529	0.074, SE = 0.286	-0.149, SE = 0.071	
Second model	-0.757, SE = 0.502	5.185, SE = 0.6	4.826, SE = 0.536	0.074, SE = 0.285	-0.152, SE = 0.071	
Third model	1.307, SE = 0.335	3.033, SE = 0.31	2.729, SE = 0.279	0.181, SE = 0.133	-0.162, SE = 0.072	
Fourth model	-1.017, SE = 0.401	5.289, SE = 0.454	5.056, SE = 0.496334	NA	NA	
Fifth model	-0.982, SE = 0.411	5.25, SE = 0.464	5.008, SE = 0.503	NA	NA	
Sixth model	0.998, SE = 0.292	3.237, SE = 0.237	2.96, SE = 0.244	NA	NA	
Year one Detection						
	Graz high	Graz Low	Graz Moderate	Veg	Temp	Hour
Best model	1.024, SE = 0.561	-2.433, SE = 0.684	-2.392, SE = 0.612	0.088, SE = 0.271	-0.035, SE = 0.039	0.104, SE = 0.062
Second model	-1.067, SE = 0.567	-2.37, SE = 0.688	-2.336, SE = 0.615	0.089, SE = 0.27	NA	NA
Third model	-3.362, SE = 0.185	NA	NA	NA	-0.036, SE = 0.039	0.096, SE = 0.061
Fourth model	-1.092, SE = 0.516	-2.245, SE = 0.573	-2.347, SE = 0.595	-0.054, SE = 0.081	-0.038, SE = 0.039	0.104, SE = 0.062
Fifth model	-1.140, SE = 0.523	-2.176, SE = 0.58	-2.286, SE = 0.599	-0.056, SE = 0.081	NA	NA
Sixth model	-3.349, SE = 0.188	NA	NA	NA	-0.038, SE = 0.039	0.097, SE = 0.061
Year two Abundance						
	Vege	Vege 2				
Best model	4.021, SE = 0.193	-0.333, SE = 0.098				
Second model	3.111, SE = 0.336	-0.37, SE = 0.106				
Year one Detection						
	Graz high	Graz Low	Graz Moderate	Vege	Temp	Hour
Best model	-3.958, SE = 0.318	0.49, SE = 0.362	1.071, SE = 0.303	0.585, SE = 0.161	0.279, SE = 0.05	-0.202, SE = 0.043
Second model	-2.915, SE = 0.184	NA	NA	NA	0.281, SE = 0.05	-0.198, SE = 0.042
Alpaida quadrilorata						
Year one Abundance						
	Intercept					
Best model	3.797, SE = 0.31					

Second model	3.799, SE = 0.31					
Third model	3.790, SE = 0.33					
			Year one Detection			
	Graz high	Graz Low	Graz Moderate	Vege	Temp	Hour
Best model	-8.966, SE = 1.058	4.189, SE = 1.044	5.553, SE = 1.014	0.460, SE = 0.126	0.341, SE = 0.06	0.244, SE = 0.092
Second model	-8.967, SE = 1.058	4.188, SE = 1.044	5.552, SE = 1.014	0.501, SE = 0.306	0.341, SE = 0.06	0.244, SE = 0.092
Third model	-8.97, SE = 1.061	4.19, SE = 1.055	5.562, SE = 1.023	0.452, SE = 0.175	0.452, SE = 0.06	0.341, SE = 0.092
			Year two Abundance			
	Veg					
Best model	3.785, SE = 0.405					
Second model	-0.214, SE = 0.81					
Third model	3.823, SE = 0.424					
Fourth model	3.745, SE = 0.496					
			Year two Detection			
	Graz high	Graz Low	Graz Moderate	Vege	Temp	Hour
Best model	-7.615, SE = 0.729	2.778, SE = 0.684	4.299, SE = 0.623	0.336, SE = 0.153	0.213, SE = 0.075	-0.158, SE = 0.062
Second model	-3.328, SE = 0.484	NA	NA	NA	0.216, SE = 0.075	-0.156, SE = 0.063
Third model	-7.429, SE = 0.784	2.609, SE = 0.715	4.088, SE = 0.679	0.434, SE = 0.201	0.215, SE = 0.075	-0.157, SE = 0.062
Fourth model	-7.57, SE = 0.777	2.786, SE = 0.684	4.304, SE = 0.624	0.2, SE = 0.595	0.213, SE = 0.75	-0.159, SE = 0.062

Figure S1: Detection estimate of *Argiope argentata* in year one and year two of sampling. Graphs A to D represent year one and graphs E to H represent year two. Red lines indicate the detection estimate. Grey shadows indicate the standard deviations.

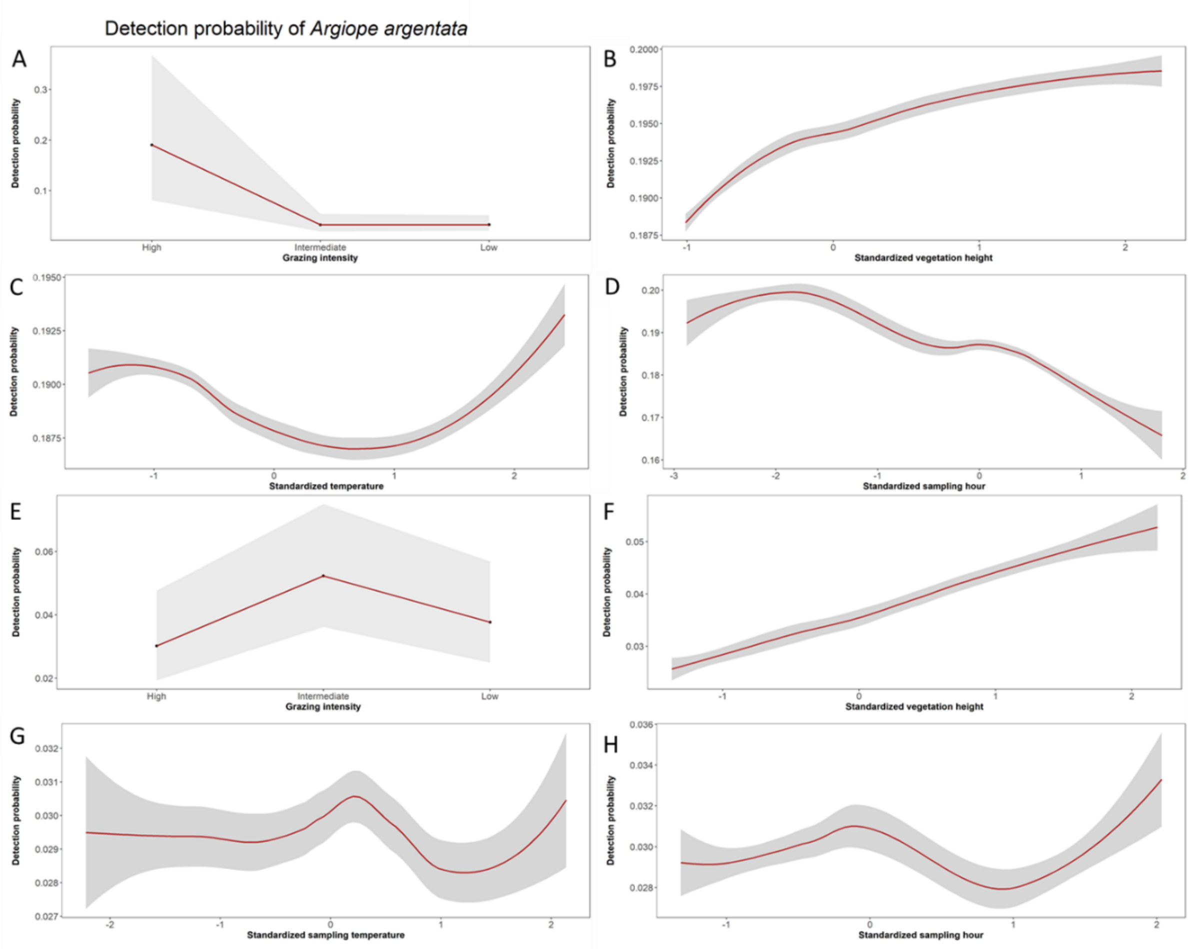
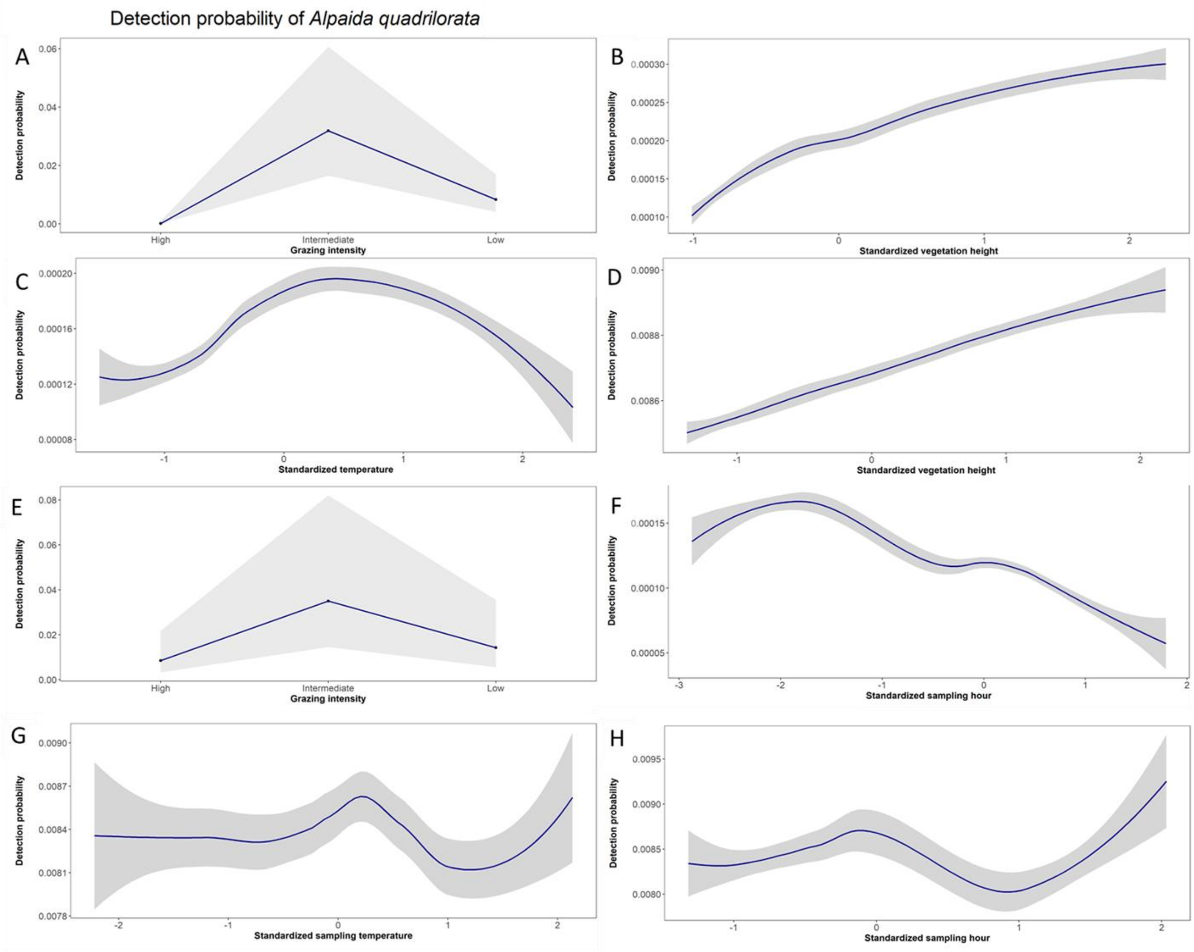


Figure S2: Detection estimate of *Alpaida quadrilorata* in year one and year two of sampling. Graphs A to D represent year one and graphs E to H represent year two. Blue lines indicate the detection estimate. Grey shadows indicate the standard deviations.



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CAPÍTULO III

WHAT DOES PLANTS TELL SPIDERS ABOUT DISTURBANCES IN GRASSLANDS?

Em preparação para *The Journal of Arachnology*

Abstract

Grazing and mowing are management technics largely used in grasslands and can improve plant and animal diversities. However, in high intensities, these techniques can cause mechanical injuries in plants and losses in animal richness and abundance. In response to injuries, plants emit herbivore-induced plant volatiles (HIPVs) that act as recruitment signals for arthropods predators. Among them, spiders have been associated as responder for HIPVs as a pest predator. However, it is unknown if spiders could sense these HIPVs and use them as a proxy for habitat quality. In this way, here we investigate the effects of HIPVs in the habitat choice and their deterrence or recruitment on the orb-weaver spider *Argiope trifasciata*. First, we conducted a field experiment to quantify mowing influence on spider abundance. Then, we performed a choice experiment to evaluate microhabitat choice for cut or uncut grass. Lastly, using an olfactometer we tested the influence of HIPV in the movement and choice pattern of *A. trifasciata*. Our major results corroborate other findings that microhabitat choice in orb-weaver spiders is driven by vegetation structure present in the habitat. However, our results do not provide evidence that these spiders are deterred or recruited by HIPVs, hence, that they use these chemical signals as an indicator of habitat quality. We suggest that environmental perception in our study species should be linked to light and shade incidence, as well as the presence of prey and reproductive mates.

Keywords: Araneae; Behavior; Grass-scent; Methyl salicylate; Orb-weaver; Pastures.

Introduction

Grassland ecosystems are dry environments that cover around 40% of Earth’s land surface and are historically used for livestock and cropping raise (Balasubramanian et al., 2020; Lark, 2020). To enhance the productivity and control agricultural impacts grasslands are usually managed with mowing and grazing (Egan et al., 2018; Szukics et al., 2019; Whitehead et al., 2018). These two techniques can promote a higher environmental heterogeneity that can improve plants and animal diversities (Fedrigo et al., 2018; Tälle et al., 2018, 2016; Valliere et al., 2019). Ironically though, in high intensity managed areas, these techniques cause species homogenization, losses in biodiversity and environment degradation (Klink et al., 2019; Lerman and Contosta, 2019; Torma et al., 2019).

Not only do mowing and grazing affect grassland biodiversity, but they also induce mechanical injuries and stress to local grassland plants (Rasulov et al., 2019; Tóth et al., 2018). In response to this injury, plants emit herbivore-induced plant volatiles (HIPVs), which are chemical cues that humans recognize as the smell of fresh cut grass – i.e., methyl salicylate (MeSA), cis-3-hexenyl acetate (HxAc) and cis-3-hexen-1-ol (HxO) (Díaz-Mula et al., 2017; Fischer et al., 2021; Kirstine et al., 2002; Malidaki and Laska, 2018). Grassland plant species release HIPVs in large quantities when grazed, reaching 180 times higher emissions than the rate observed in undamaged plants (Kirstine and Galbally, 2012; Kirstine et al., 2002, 1998). These HIPVs, in turn, can have a variety of influences in the recruitment of local arthropods, including both pests and pest predators (Garvey et al., 2020; Gasmi et al., 2019).

As the most diverse and abundant animals in grassland (Barnett and Facey, 2016), arthropods are widely affected by mowing (Tälle et al., 2018) and grazing (Oyarzabal and Guimarães, 2021). Whether these effects are positive or negative, however, remain unresolved. For instance, prior research on one group of common grassland arthropod predators – spiders, show contradictory effects regarding mowing and grazing (Kaltsas et al., 2019; Oyarzabal and Guimarães, 2021; Řezáč and Heneberg, 2019). Spider diversity can be negatively impacted by heavy mowing and grazing since the removal of plant biomass through cutting, trampling or herbivory, can cause direct mortality and loss of shelter and food sources (Oyarzabal and Guimarães, 2021; Řezáč and Heneberg, 2019; Torma et al., 2019). At the same time, these management practices may alter the environment and provide more habitat structures, increase microclimate diversity and prey availability, and thereby enhance spider richness and abundance (Oyarzabal and Guimarães, 2021; Valliere et al., 2019).

Little is known about the extent to which grassland management practices influence the ability of movement and/or colonization of spiders (Ferreira et al., 2020). In particular, it is unknown whether structural and/or chemical characteristics of the grassland environment affect the distribution and abundance of these important arthropod predators. Chemical cues are important for spiders in many aspects of their life. Spiders are known to assess and use volatile and non-volatile compounds found in their feces, cuticle and, most notable, webs (Beyer et al., 2021; Fischer, 2019). Additionally, chemical communication in spiders is widely used for mating, acting as aphrodisiac substances for males and females and for offspring recognition to prevent females from feeding on their young (Beyer et al., 2021; Fischer, 2019; Guimarães et al., 2018). However, the spider's ability to perceive environmental cues is less studied, with just a handful of papers associating and testing such trait (Fischer, 2019).

For instance, crab spiders (Thomisidae) seem to be attracted to clove oil and floral scents, such as β-caryophyl-lene and nerolidol while nicotine, mint, and chestnut oil seems to repel wolf spiders, recluse spiders and orb-weavers (Lycosidae, Theridiidae and Araneidae, respectively) (Fischer, 2019; Fischer et al., 2018). Other compounds, such as lemon oil and other phytochemicals do not seem to influence these same spiders (Fischer, 2019; Fischer et al., 2018). Moreover, a blend containing eight HIPV compounds presented a weak deterrent effect on the false black widow (Theridiidae, *Steatoda grossa* (C. L. Koch, 1838)), while the same eight compounds alone did not have any effect on this spider species (Fischer et al., 2021). From those eight HIPVs, Methyl salicylate (MeSA, C8H8O3) is the only one released by grassland plant species that have been suggested to be associated as a lure for predator and hence, with spiders (Rodriguez-Saona et al., 2011; Salamanca et al., 2019). However, its potential to repel or recruit spiders had not been well explored (Rodriguez-Saona et al., 2011; Rowen et al., 2017; Simpson et al., 2013) since studies had showed no effect on the recruitment nor deterrence of synanthropic spiders (Fischer et al., 2021).

Understanding the way grassland management practices alter the physical and chemical microhabitat choice by spiders may help increase our comprehension on the overall impact of grassland management on arthropod communities (Demirtas et al., 2019; Fischer, 2019; Wakai et al., 2019). The potential influence of the chemical environment on spider behavior would also provide new insights into spider perception and its interaction with environmental cues (Fischer, 2019). Following this, here we combine field and laboratory experiments to test the hypothesis that structural and chemical characteristics of the local environment influence the microhabitat choice of the orb-weaver spider *Argiope trifasciata* (Forsskål, 1775). First, we quantified the influence of grassland mowing on the abundance of *A. trifasciata* in the field (Experiment I). Next, we conducted a laboratory choice experiment to test the hypothesis that grass removal influences microhabitat choice in *A. trifasciata* (Experiment II). Finally, we conducted a laboratory olfactometer assay to test the hypothesis that the HIPV Methyl Salicylate influences the movement pattern of *A. trifasciata* (Experiment III).

Methods

Study species

All three experiments were performed with mature and immature males and females of the orb-weaver spider *A. trisfasciata*. The individuals were captured from July to September of 2021, at Nebraska-Lincoln's Reller Prairie Field Station (40°36'41"N, 96°45'31"W, Lincoln, Nebraska, United States of America) and at approximately 20 km west of Lincoln, Nebraska, U.S.A. (40°46'37"N, 96°52'55"W). After capture, all individuals were brought to the laboratory and settled individually in cubic enclosures of 15 cm (height) x 10 cm (width) x 10 cm (depth) that were under a controlled 24–27°C temperature and a 12:12 light:dark conditions. Spiders had water ad libitum and were fed two crickets (*Acheta domesticus* (Linnaeus, 1758)) twice a week by dropping the crickets in their enclosures.

Experiment I – Field grassland cutting and spider abundance

The field experiment was performed at the University of Nebraska-Lincoln's Reller Prairie Field Station from August 27th to September 30th, 2021. To determine the influence of (a) physical (i.e., vegetal structures available for attaching webs) and (b) chemical (i.e., HIPVs associated with recently cut grass) environmental characteristics on web placement, or microhabitat choice of *A. trifasciata*, we manipulated three distinct 8m long x 8m wide grassland field plots in the following manner. In each enclosure, half of plot was designated as the control area, and it was left undisturbed. Grass in the control was abundant and reached 80 cm of height. The other half was designated as the treatment part, where the grass was mowed using the combination of a hand sickle (35 cm Scythe Curved Blade), an electronic grass shear (Sun Joe HJ604C-SJB 2-in-1 Cordless Grass Shear) and a manually operated lawnmower (ALEKO Hand Push Lawn Mower 40 cm height). We reduced grass height to 10 cm, approximately (Figure 1). The treatment area represented a manipulated chemical environment due to the natural HIPVs released when the grass was cut. Half of the treatment area (2m x 2m) received artificial physical structures to provide substrate for web building. Orb-weaver spiders are known to require tridimensional structures to build their webs (Nogueira and Pinto-da-Rocha, 2016). In summary, the control area of each plot (a 4 X 4 m area) included no chemical manipulation (C-) and presence of natural physical structure (P+). The treatment area included chemical manipulation (C+) and presence of physical structure (P+) in half (2m x 2m), and chemical manipulation (C+) but absence of physical structure (P-) in the other half (2m x 2m) (Figure 2). It was impossible to create a C-/P- areas since uncut grass necessarily provides physical structures for web building. The P+ treatment in the C+ areas were created by placing 168 barbecue bamboo skewers, 15 cm distance apart, with 10 cm height (2 m x 2 m area) and 168 barbecue bamboo skewers, 15 cm distance apart, with 15 cm height (Figure 2).

Figure 5 – Aerial photo of Experiment I at Reller Prairie. Enclosure with the grass half side unmowed and half side mowed (4 m x 4 m). Credits photo: Kent Robinson.

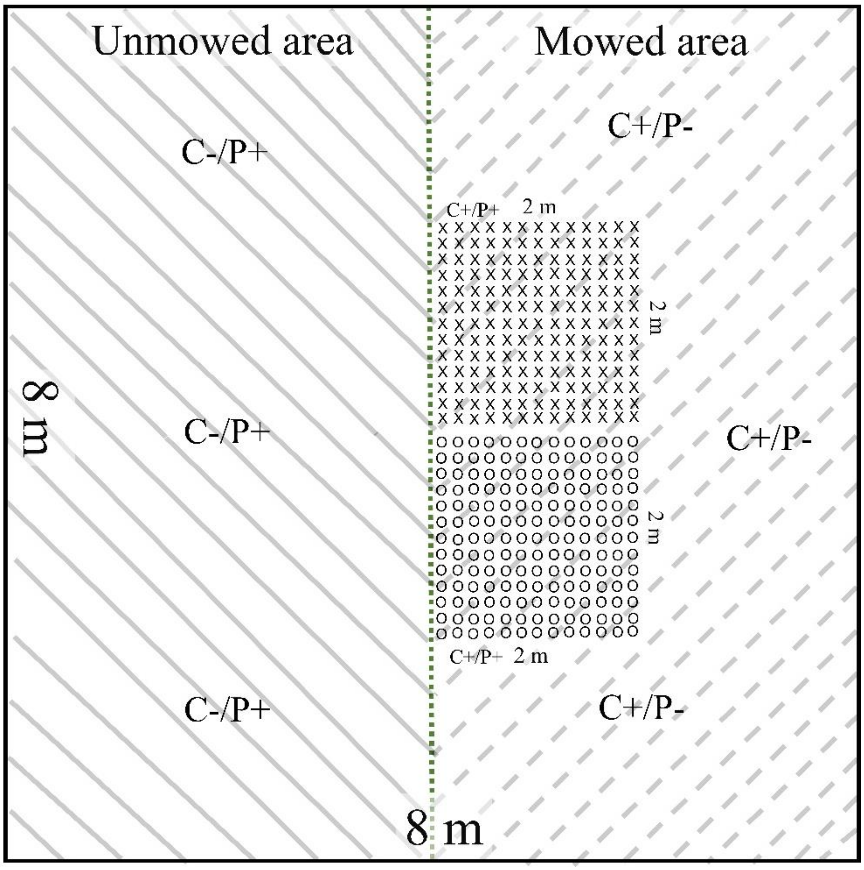

Figure 6 – Experiment I, Reller enclosure with the grass half mowed (4 m x 4 m). Complete lines indicate Unmowed area and dashed lines indicate the Mowed area. C- indicates chemicals HIPV absent; C+ indicates chemical HIPV present; P- indicates physical structures absent; and P+ indicates physical structure present. In the mowed area, we stick to the ground bamboo skewers of 10 cm (X) and 15 cm (O) height. Spiders were released back to the enclosures in the green dotted line.

We randomly chose 45 individuals from the 67 sampled in the field to release back to the enclosures (15 individuals randomly designated for each enclosure). These 45 individuals were marked with the same purple enamel marks and were fed one last time on August 26th. On the day following marking (August 27th), we placed the 15 *A. trifasciata* in each of the three plots. Individuals were released in the exact center of each plot (Figure 2). We surveyed each of the three plots seven times through the boreal summer, from August 27th to September 30th, 2021. We surveyed all plots counting the number of adults (males and females) and juveniles of *A. trifasciata*; either previously marked or unmarked. Surveys occurred from 08:00 am to 10:00 am. On each survey, we recorded the number of individuals found in each enclosure and each section (C-/P+; C+/P+; C+/P-). Two to three trained observers were deployed on each survey (three observers through the experiment).

Since we did not have enough variance in our data for the experiment (see Results), we tested the difference between the abundance of spiders found in the mowed area x the unmowed are using a Student T-test (p level = 0.05).

Experiment II – Laboratory grass cutting and spider microhabitat choice

Simultaneous to the Experiment I (field experiment), we conducted a similar laboratory experiment aiming to answer whether the physical and/or chemical environment influences the choice of web placement in *A. trifasciata*. In the laboratory at the University of Nebraska-Lincoln, we used three distinct plastic tubs measuring 30 cm height x 65 cm width x 40 cm depth. At the bottom of each tub, we placed patched of grass collected from Reller Prairie. Following our field experiment, one-half of each grass patch within the tubs was cut with a hand sickle (35 cm Scythe Curved Blade) and an electronic grass shear (Sun Joe HJ604C-SJB 2-in-1 Cordless Grass Shear) creating C-/C+ treatments. To control for the tridimensional structure in the cut half and uncut half of each box, we placed to the ground eight (four for each half) bamboo skewers with 15 cm height (Figure 3). Each plastic tub had a C+/P+ side and a C-/P+ side. Due to the height of the grass and thus the likelihood of spiders escaping, we increased the height of each plastic tub wall by attaching four plastic laminates that added 25cm to the walls' height (Figure 3). Lastly, petroleum jelly was spread in the entire plastic laminate walls to also prevent spiders to escape.

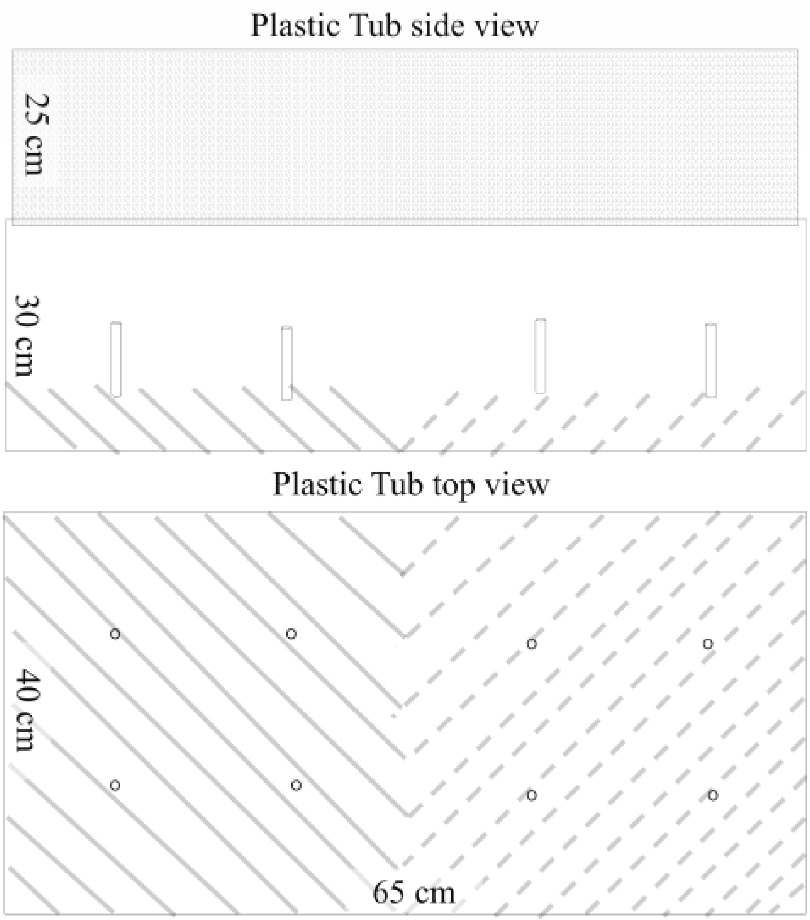

Figure 7 – Experiment II. Plastic tub experiment with half of the tub cut and half uncut. Complete lines indicate Uncut side and dashed lines indicate the Cut side. In both sides we stick to the ground bamboo skewers of 15 cm (O and cilinders) and 15 cm (O). Dotted rectangles indicate the plastic laminate.

The trials started, in no particular time, between 11:00 am and 04:30 pm. At the start of each trial, an individual of *A. trifasciata* (male or female) was released in the center of each tub – i.e., at the intersection of the cut/uncut grass. After release, the lid of the plastic tub was placed above the plastic laminate walls and the plastic tubs were moved to a quiet room under 12:12 light:dark conditions. The first 15 trials were checked daily for three days (72h). Considering that the spider behavior did not change after the first day, the next 19 trials were checked only one time after 24h. With the help of a flashlight, to better visualize the spider silk inside the plastic tubs we checked for a complete orb web presence at the C+/P+ side or the C-/P+ side on each side of the tub. At the end, we have counted how many individuals had built their webs on each side of the tub. Following each trial (e.g., 72 hours for the first 15 trials and 24 hours for the remaining 19 trials), individuals as well as their silk and webs were completely removed from the vegetation with the help of a wood stick and a dry paper towel. Using the same grass patches, we cut the grass again to release new HIPVs. Following this, a new individual of *A. trifasciata* was released inside of the plastic tub. Due to this second cut, the grass in the C+/P+ side, on the second run, was a little bit shorter than the first run. After two trials, grass patches were completely discarded, and new ones were used. At this time, we cleaned the boxes with distilled water, soap, and ethanol 100% before the new patch of grass was placed in the tub. We had a total of 34 trials and from those, four were ran with four individuals that were previously used in this experiment. However, these four individuals did not experience the same grass patch from their previous trial. Hence, 30 individuals of *A. trifasciata* were used in total in this experiment.

The data regarding this experiment also did not have enough variance. Because of that, we tested the difference between the number of complete webs built in the cut part x uncut part using a Student T-test (p level = 0.05).

Experiment III – Olfactometer assay with Methyl salicylate

To test if the results from our field and laboratory experiments were likely due to the effect of HIPVs on *A. trifasciata* movement and choice of web-location, we implemented two olfactometer assays in the laboratory at the University of Nebraska-Lincoln, using one of the main HIPVs components – Methyl salicylate (MeSA, Sigma-Aldrich, Methyl salicylate ReagentPlus®, ≥99%). Since we did not include a control in our first assay, to provide a baseline of *A. trifasciata* behavior in an olfactometer experiment, and since we had a contamination of MeSA smell in the first assay (see Results and Discussion), we used a different olfactometer for the second assay. In this second assay, we performed two trials: one that compared water x water and a second that compared MeSA x water. Besides that, all spider trials were performed through the day, from 8:30am to 6:00pm at room temperature (20°C-22°C) and regular light. Lastly, the individuals used in this experiment never ran the same assay more than once.

First assay: MeSA x distilled water – Here we tested if the HIPV Methyl salicylate can repel or attract spider. The first assay was performed in an olfactometer comprised of three acrylic tube arms of 75 mm diameter, as a Y shape. The “introduction arm” was 61 cm long, and the two shorter “stimulus arms”, were both 48 cm in length. The stimulus arms were connected to the introduction arm by a 3-way “choice chamber”. At the end of the right stimulus arm, 1ml of synthetic MeSA represented the HIPVs stimuli and, at the end of the left arm, 1ml of distilled water provided the control stimuli. An electric fan was affixed to the end of the introduction arm, such that it faced away from the olfactometer and pulled air through both stimulus arms, in direction to the choice chamber, and into the introduction arm (see more details of the olfactometer setup in Stafstrom & Hebets 2019).

On each assay, one individual of *A. trifasciata* (male or female) was released inside the olfactometer through the removable window in the introduction arm (adapted from Stafstrom & Hebets 2019). Then, their movement was monitored for 45 minutes, and we evaluated: (a) first choice – whether the individual, in the first five minutes, moved towards the (i) MeSA side, (ii) water side, or (iii) stayed in introduction arm; and (b) persistency – the time that each individual remained in the (i) MeSA side, (ii) water side, or (iii) in the introduction arm. After each run, the olfactometer was cleanup with paper towels imbibed with ethanol 100%, and rested from 10 min, before the introduction of a new individual.

Second assay: 1 - distilled water x distilled water and 2 - MeSA x distilled water – The second assay (two trials) was performed in an olfactometer comprised by a single 3-way choice acrylic chamber without air flow. Each arm has 17 cm (height) x 17 cm (width) x 23 cm (depth) (Figure 4). Two arms were considered the stimulus arm and the third arm was considered the introduction arm. The chamber had two separated lids, one that covered the introduction arm (16.5 cm x 16.5 cm) and one that covered the rest of the olfactometer (convex hexagon shape, two sides with 23 cm x two sides with 7 cm x two sides with 27.5 cm) (Figure 4). Since the acrylic is difficult for these spiders to grip, the olfactometer had strips of insect screening on the bottom and walls to help spider's locomotion (Stafstrom and Hebets, 2019).

In the first trial, we tested the repellence or attraction of water. At the end of each stimulus arms, we provided 2ml of distilled water as a control stimulus. After that, one individual of *A. trifasciata* was released inside the olfactometer through the removable lid in the introduction arm. Then, their movement was monitored for 35 minutes, and we evaluated: (a) first choice – whether the individual, in the first five minutes, moved towards the (i) water right side, (ii) water left side, or (iii) stayed in introduction arm; and (b) persistency – the time that each individual remained in the (i) water right side, (ii) water left side, or (iii) in the introduction arm. After each run, the cleanup processes were the same as the first assay, cleanup with paper towels imbibed with ethanol 100%, and rested from 10 min, before the introduction of a new individual. All individuals that participated in this trial had also participated in the Experiment II (plastic tub) and in Experiment III first assay.

In the second trial runs, we tested the repellence or attraction of the HIPV Methyl salicylate. At the end of the right stimulus arm 2ml of synthetic MeSA provided the HIPVs stimuli, while in the left stimulus arm, 2ml of distilled water provided the control stimuli. We monitored the spiders in the same way as the second assay first trial, evaluating, in this case: (a) first choice – whether the individual moved towards the (i) MeSA side, (ii) water side, or (iii) stayed in introduction arm; and (b) persistency – the time that each individual remained in each side or introduction arm. After each run, the cleanup process was the same as the previously second assay first trial. All individuals that participated in this trial had also participated in the Experiment II (plastic tub) and in Experiment III first assay. Lastly, only one individual that participated in this trial did not participate in first trial of Experiment III second assay.

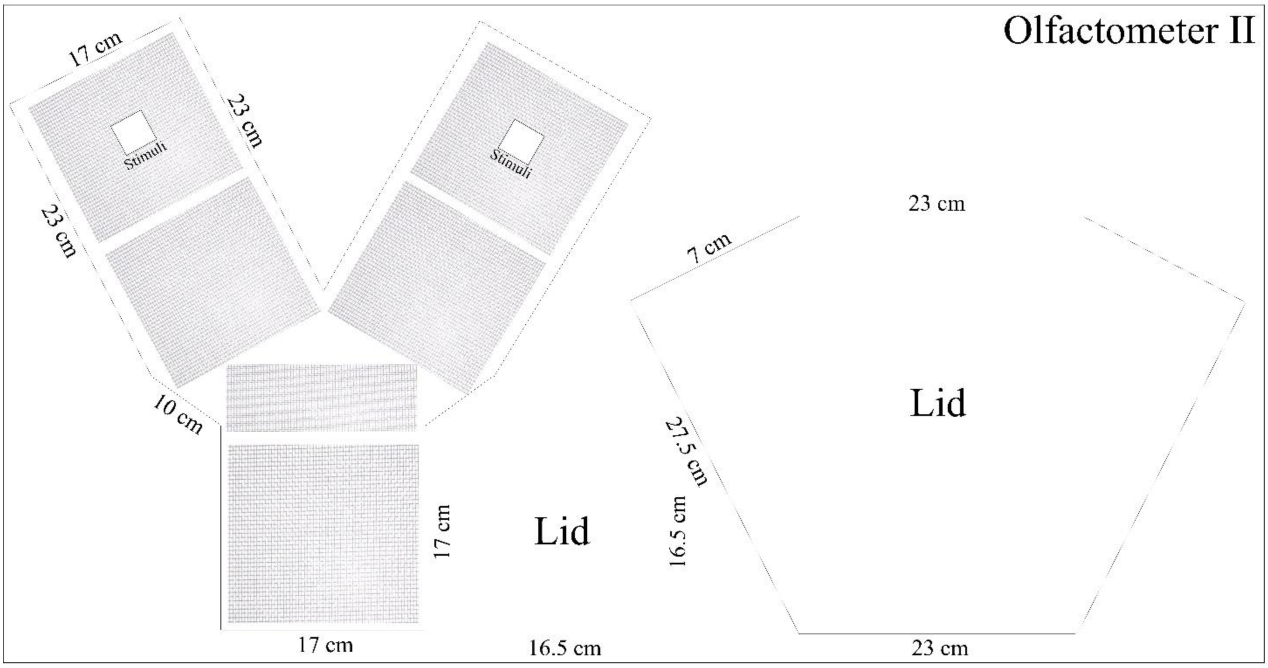

Figure 8 – Olfactometer II used for the second (water x water) and third (MeSA x water) trials.

For the statistical analysis, we first investigated if individuals were more likely to choose a particular stimulus arm using chi-square. We also performed an Analysis of Variance (ANOVA) and the Tukey Test to evaluate the differences of first choice between each arm (p level = 0.05). Moreover, we used Generalized

Linear Mixed Models (GLMM) with Negative Binomial error to assess the persistence (time expend) of individuals in each arm of the trials. We used the interaction between each assay and each arm as fixed terms and individuals as a random term. The random effect was applied to the GLMM intercepts. After that, we estimated the marginal means (EMM) of the model and performed a Post hoc tests for the pairwise interaction between arms for each experiment (p level = 0.05). All analysis were performed in the software R (Team, 2021) and the GLMM analysis was performed using the 'lme4' package (Bates and Mächler, 2015).

Results

Overall, we captured 84 individuals of *A. trifasciata* (six males and 78 females) during all our research from July to September of 2021.

Experiment II – Laboratory grass cutting and spider microhabitat choice

We didn´t found any of our marked individuals during the field work. Despite that, we found a significantly higher number of individuals of *A. trifasciata* in the unmowed part of the enclosures than in the mowed (t = -6.161, df = 20, p-value = 5.086e-06, lower: -3.441, upper: -1.700). Summing all three enclosures, we had a total of 54 records of *A. trifasciata* in the unmowed part and zero in mowed part (Figure 5). The highest number of individuals found inside one enclosure was six (Table S1).

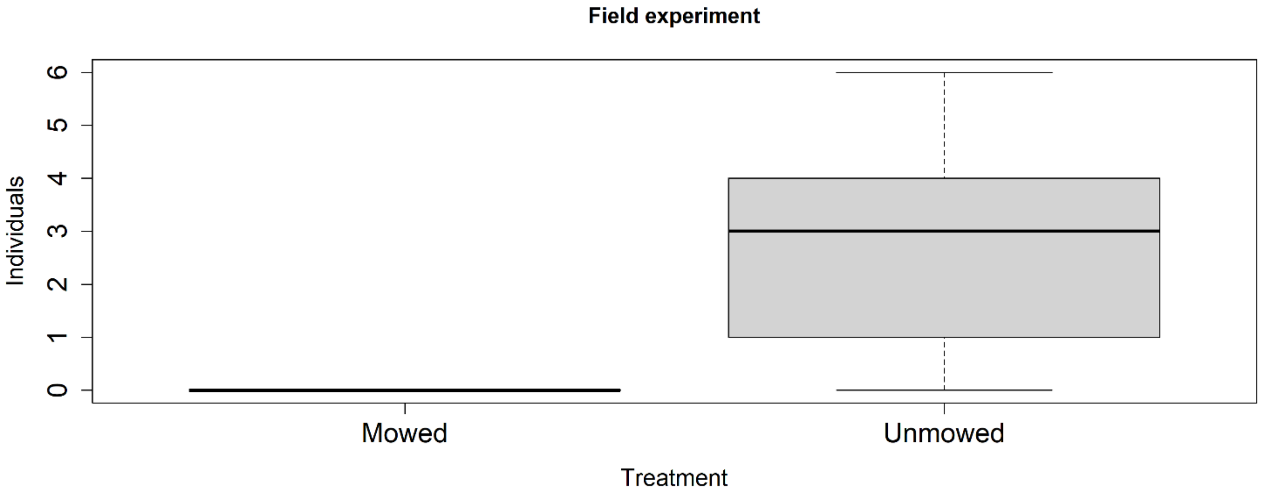

Figure 9 - Plots for raw abundance of *Argiope trisfasciata* on Reller Prairie field experiment.

Experiment II – Laboratory grass cutting and spider microhabitat choice

We ran the Experiment II 23 times with 21 different individuals. In total, individuals build their webs significant more times (p = 4.468e-09) in the unmowed part (N = 20) the mowed part (N = 3). We highlight that both individuals (R17 and R73) that ran this experiment two times, build their webs in the first run in cut part of the box, in their second run built it in the uncut part (see Table S2).

Experiment III – Olfactometer assay with methyl salicylate

The first choice of an arm seems to be independent of the stimulus arm is (53, $\chi2$ = 106, P = 0.427). However, there was a significant difference between arm first choice (F = 22.26, qF = 5.143, p = 0.001), showing that spiders presented preference for the introduction arm (no stimulus) between the MeSA arm (difference in the observed means = -10.666, lower = -15.881, upper = -5.451, p = 0.001) and the water arm (difference in the observed means = -8.666, lower = -13.881, upper = -3.451, p = 0.005) (Figure 5, Tables S3 to S5).

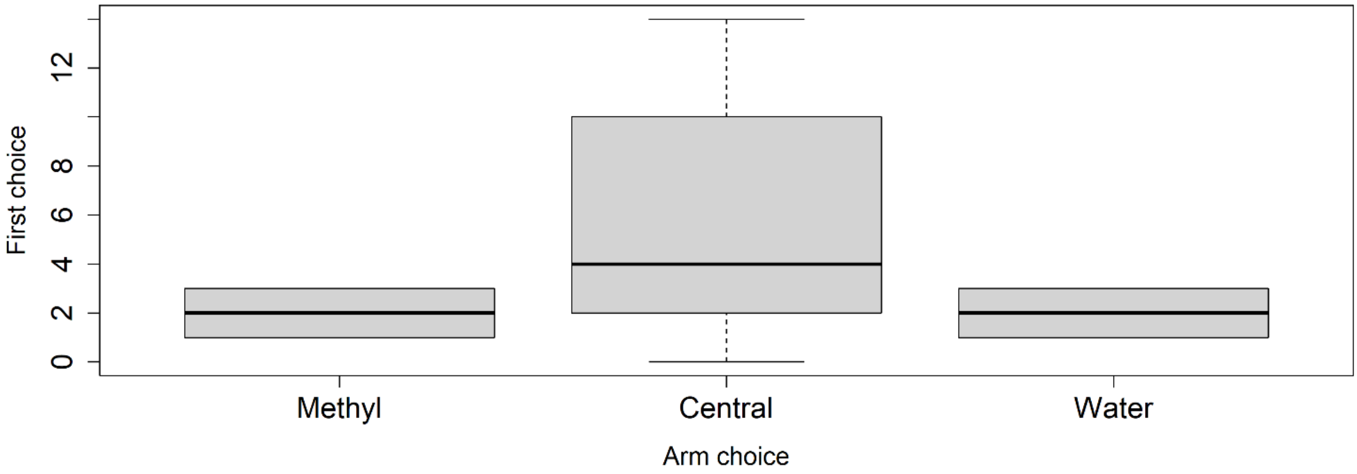

Figure 10 - Box plot for the first choice of *Argiope trisfasciata* on the Experiment III with the olfactometer assay. Methyl: stimulus arm with MeSA; Central: introduction arm without any stimulus; Water: stimulus arm with distilled water.

For spider persistency, in all trials we found that spiders are more likely to stay in the introduction arm ($\beta_{Central}$ = 3.356, p = 2e-16) when compared with the MeSA arm (βMeSA = -1.644, p = 0.008) and the water arm (βWater = -1.718, p = 0.001). Moreover, we found no difference between spiders' persistency in MeSA compared with water (Estimate = 0.0741, p= 0.991) and a persistency preference for the introduction arm when compared with the other two arms (Central – MeSA, Estimate = 1.641, p =0.0241; Central – Water, Estimate = 1.718, p = 0.003) (Tables S3 to S5).

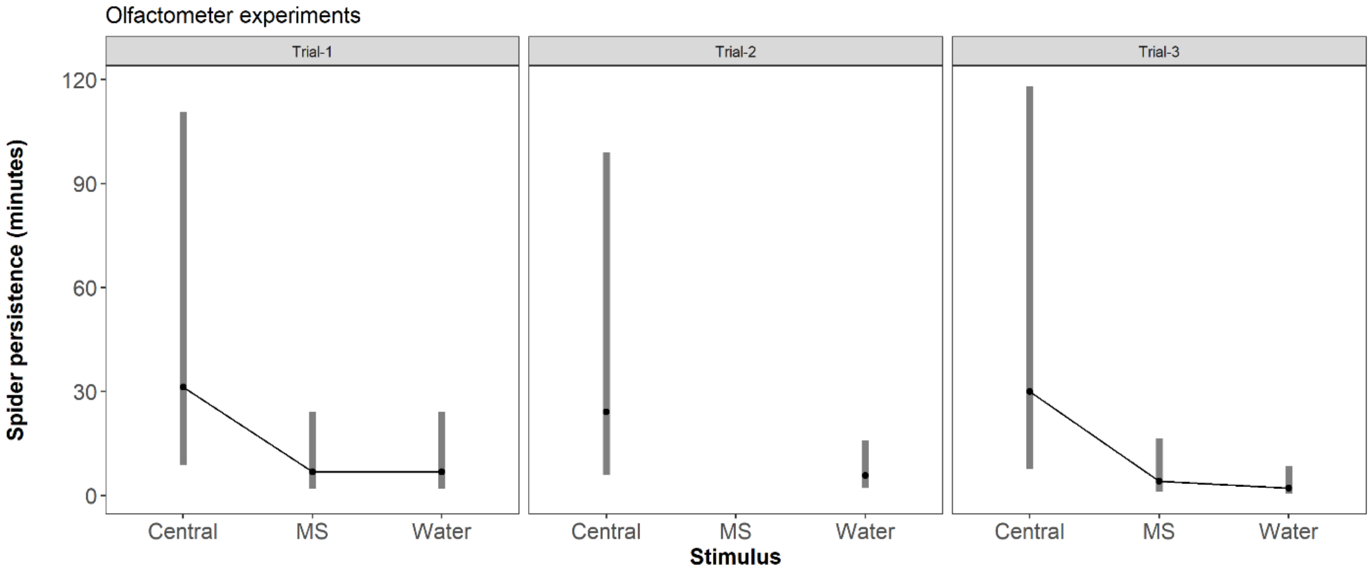

Figure 11 – Persistency (time in minutes) of *Argiope trisfasciata* on each arm of Olfactometer trials experiment. Central: introduction arm without any stimulus; MS: stimulus arm with MeSA; Water: stimulus arm with distilled water.

Discussion

Here we tested the influence of environmental changes, by mechanically removing the vegetation structure and altering herbivore-induced plant volatile concentrations, on the orb-weaver spider, *A. trifasciata*. In general, we support the hypothesis that physical environmental structure influences the microhabitat choice of orb-weaver spiders. However, we were unable to demonstrate that HIPVs influenced the environmental perception of our target species.

In terms of spiders first choice, our three experiments results indicate that site preference will be influenced by the spider perception and their need of habitat structure (Nogueira and Pinto-da-Rocha, 2016; Oyarzabal and Guimarães, 2021). However, despite our evaluation of first choice in the olfactometer experiment, its results cannot be extrapolated and compared to the first choice made in the field or plastic tub experiments, since spider neither had space nor time to assemble their webs. Regarding persistency, we noted that individuals of *A. trifasciata* did not move their webs after they built it, remaining in the same location in the field and tub experiments. Interestingly though, a similar result was found in *Argiope argentata* (Fabricius, 1775), a congeneric species, where the individuals also did not move their webs within a period of three days (Oyarzabal & Guimaraes, unpublished data). This result may suggest that spiders do not reallocate their webs after finding a spot with suitable habitat structure.

In general terms, habitat structure seems to be the main factor for orb-weaver spider´s choice, which may be influenced by several aspects including predator avoidance, prey availability and mating opportunities. Concerning predation, habitats poorly structured do not provide spiders proper spots to avoid enemies (da Silva Bomfim et al., 2021; Narimanov et al., 2021). Particularly for orb-weavers genus *Argiope*, stabilamenta, a singular web structure pattern, are important to avoid predation (Blackledge and Wenzel, 1999; Schoener and Spiller, 1992). Hence, without the proper structure to construct their webs, those species would be more exposed to predators. Regarding prey consumption, prey tend to occur especially in places that are unmowed (Helden et al., 2020; Torma et al., 2019). Therefore, orb-weaver spiders would be adapted to forage in these locations and would search for places that are commonly visited by their prey (Fischer et al., 2021). Finally, in the case of breeding partners, *A. trifasciata* females are responsible to attract males using sex pheromones emitted by their bodies and webs (Cory and Schneider, 2018; Weiss and Schneider, 2021). Without a proper structure to build a web, these females would not be able to attract males and hence, reproduce (Cory and Schneider, 2018).

Ultimately, despite we know primary (habitat structure) and secondary (predator avoidance, prey, and breeding partners availability) factors that would guide *Argiope* habitat choice, we still do not understand how their mental process is and how they analyze if the habitat as suitable or not. Discarding the HIPVs recognition, we would suggest that light and shade incidence would be the judge factor to perceive the presence or absence of habitat structure. So far, authors only have suggested light and shade as factors to caught prey, not to choose habitat (Blamires et al., 2007; da Silva et al., 2021; Herberstein et al., 2000). Hence, light incidence, light position and shade cover should be good alternatives to investigate habitat choice in orb-weaver spiders.

Regarding the olfactometer experiment, our results indicate that regardless of the stimuli provided to *A. trifasciata*, the species preferred to remain in the central arm, the same in which they were released in the beginning of each trial. We believe that staying or even walking around the central arm of the experiments cannot be considered as a choice (Stafstrom and Hebets, 2019). Therefore, our study does not provide support for the role of Methyl Salicylate (MeSA) on the recruitment nor deterrence of orb-weaver spiders. This result corroborates recent finds of MeSA also not causing deterrence in four synanthropic spider species (the cellar spider, *Pholcus phalangioides*, the hobo spider, *Eratigena agrestis*, the false black widow, *Steatoda grossa*, and the western black widow, *Latrodectus Hesperus*) (Fischer et al., 2021). Thus, despite being a HIPV easily recognized by humans, it is unlikely that MeSA can recruit spiders (Fischer et al., 2021). Moreover, the previous mentioned studied also tested the deterrence of a blend of eight different HIPVs (ocimene, (−)-lin-alool, (E)-β-caryophyllene, (E)-4,8-dimethyl-1,3,7-nonatriene (=DMNT), (E)-β-farnesene, (E/Z)-nerolidol, (±)-jasmonic acid and MeSA) (Fischer et al., 2021). Even so, they only found a minor deterrence caused by this mixture for one spider species (the false black widow, *Steatoda grossa*) and not found any deterrence nor attraction effect for the other three species. These results, along with our results, could indicate that, although chemical communication plays a big role in the life of spiders (Beyer et al., 2021; Fischer, 2019; Guimarães et al., 2018), HIPVs seems to not predict habitat choice (Fischer et al., 2021).

In the matter of HIPVs concentration, it is possible that we have used a too great stimulus for our individuals. Recent papers had used stimuli in the microliters (µL) range (Fischer et al., 2021). In this way, the stimuli provided to our spiders were 100 times (Experiment III first assay) and 200 times (Experiment III second assay) stronger than previously tested (Fischer et al., 2021). This certainly explained the smell contamination we had throughout the first olfactometer experiment. Along the same lines, we may have overstimulated our spiders due the high concentration of MeSA (Kralj-Fišer and Gregorič, 2019). Moreover, our sample size did not match similar recent studies (Beyer et al., 2021; Humbel et al., 2021), so it is possible that an N=16 would be too low to test HIPVs for spiders. Furthermore, since it is known that orb-weavers can learn from previous experiences, the behavior that our spiders presented in the follow experiments could be biased from a past learnings (Nogueira and Ades, 2012). However, even with lower concentrations of HIPV than used by us and a higher sample size, MeSA may not play an important role on the recruitment nor deterrence of orb-weaver spiders (Fischer et al., 2021).

In conclusion our results corroborate previous findings extensively reported in the literature that the physical structure of the environment may be the major factor influencing microhabitat selection in orb-weaver spiders (Nogueira and Pinto-da-Rocha, 2016; Oyarzabal and Guimarães, 2021). This would be supported by the relevance of habitat structure for web-building spiders (Nogueira and Pinto-da-Rocha, 2016; Oyarzabal and Guimarães, 2021) in relation to predation (da Silva Bomfim et al., 2021; Narimanov et al., 2021), prey availability (Helden et al., 2020; Torma et al., 2019) and mating opportunities (Cory and Schneider, 2018). However, the way spiders perceive the microhabitat and make the choice to stay on it, remains a mystery. Light and shade positions based on the availability of vegetal structure may be a clue (Blamires et al., 2007; da Silva et al., 2021; Herberstein et al., 2000).

Acknowledgements

We are grateful for CAPES and the scholarship granted to the first author (process #88882.439370/2019-01). We are also grateful for Fulbright Brazil and the Doctoral Dissertation Research Abroad program (DDRA) granted to the first author. We are namely thankful for Kent Robinson photos of the field experiment. We are also thankful for Brandi Pessman and Seth Griger for the help during the fieldwork. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

All authors contributed to the study conception and design. All authors performed the screening and analysis of the data, as well as the writing and revision of the text, tables, and images. Lastly, all authors read and approved the final manuscript.

Supporting materials

Table S1 – Abundance found on each enclosure through the Experiment I at Reller Prairie.

Date, 2021	Enclosure	Survey time	Cut females	Cut males	Uncut female	Uncut males	Total cut	Total uncut
Aug, 27	Enclosure 01	8:15h-8:40h	0	0	5	0	0	5
Aug, 27	Enclosure 02	8:42h-9:05h	0	0	2	0	0	2
Aug, 27	Enclosure 03	9:06h-9:29h	0	0	5	0	0	5
Sep, 03	Enclosure 01	8:24h-8:48h	0	0	5	1	0	6
Sep, 03	Enclosure 02	8:50h-9:13h	0	0	5	0	0	5
Sep, 03	Enclosure 03	9:15h-9:40h	0	0	3	0	0	3
Sep, 07	Enclosure 01	8:08h-8:25h	0	0	3	0	0	3

Sep, 07	Enclosure 02	8:28h-8:45h	0	0	3	0	0	3
Sep, 07	Enclosure 03	8:48h-9:05h	0	0	2	1	0	3
Sep, 17	Enclosure 01	8:01h-8:18h	0	0	1	0	0	1
Sep, 17	Enclosure 02	8:01h-8:18h	0	0	4	0	0	4
Sep, 17	Enclosure 03	8:20h-8:45h	0	0	4	0	0	4
Sep, 23	Enclosure 01	8:08h-8:20h	0	0	0	0	0	0
Sep, 23	Enclosure 02	8:23h-8:38h	0	0	1	0	0	1
Sep, 23	Enclosure 03	8:40h-9:03h	0	0	3	0	0	3
Sep, 24	Enclosure 01	8:10h-8:20h	0	0	0	0	0	0
Sep, 24	Enclosure 02	8:23h-8:40h	0	0	1	0	0	1
Sep, 24	Enclosure 03	8:42h-9:02h	0	0	4	0	0	4
Sep, 30	Enclosure 01	8:05h-8:40h	0	0	0	0	0	0
Sep, 30	Enclosure 02	8:05h-8:20h	0	0	1	0	0	1
Sep, 30	Enclosure 03	8:22h-8:35h	0	0	0	0	0	0

Table S2 – Results from the Expeirment II, plastic tubs

Individual	Box	Start date, 2021	Start time	Day 01	Day 02	Day 03	Final
R001	Box 1	Aug, 11	11:00h	Uncut web	Uncut web	Uncut web	Uncut web
R014	Box 2	Aug, 11	11:00h	Uncut web	Uncut web	Uncut web	Uncut web
R031	Box 3	Aug, 11	11:00h	Uncut web	Uncut web	Uncut web	Uncut web
R025	Box 1	Aug, 18	12:00h	Scaped	Silk uncut	Silk uncut	Silk uncut
R041	Box 2	Aug, 18	12:00h	Uncut web	Uncut web	Uncut web	Uncut web
R046	Box 3	Aug, 18	12:00h	Silk uncut	Silk uncut	Silk uncut	Silk uncut
R059	Box 1	Sep, 08	12:20h	No web	No web	No web	No web
R048	Box 2	Sep, 08	12:20h	Uncut web	Uncut web	Uncut web	Uncut web
R012	Box 3	Sep, 08	12:20h	No web	No web	No web	No web
R070	Box 1	Sep, 14	11:20h	No web	No web	No web	No web
R073	Box 2	Sep, 14	11:20h	Cut web	Cut web	Cut web	Cut web
R017	Box 3	Sep, 14	11:20h	Cut web	Cut web	Cut web	Cut web
R052	Box 1	Sep, 23	11:20h	No web	NA	NA	No web
R070	Box 2	Sep, 23	11:20h	Uncut web	NA	NA	Uncut web
R073	Box 3	Sep, 23	11:20h	Uncut web	NA	NA	Uncut web
R041	Box 1	Sep, 24	11:53h	No web	NA	NA	No web
R071	Box 2	Sep, 24	11:53h	Uncut web	NA	NA	Uncut web
R017	Box 3	Sep, 24	11:53h	Uncut web	NA	NA	Uncut web
R075	Box 1	Sep, 25	16h	Uncut web	NA	NA	Uncut web
R074	Box 2	Sep, 25	16h	Uncut web	NA	NA	Uncut web
R082	Box 1	Sep, 28	16:24h	Scaped	NA	NA	Scaped
R083	Box 2	Sep, 28	16:24h	Uncut web	NA	NA	Uncut web
R084	Box 3	Sep, 28	16:24h	Uncut web	NA	NA	Uncut web
R076	Box 1	Sep, 29	16:30h	Uncut web	NA	NA	Uncut web
R077	Box 2	Sep, 29	16:30h	Uncut web	NA	NA	Uncut web
R078	Box 3	Sep, 29	16:30h	Scaped	NA	NA	Scaped
R079	Box 1	Sep, 30	15:56h	Cut web	NA	NA	Cut web
R080	Box 2	Sep, 30	15:56h	Uncut web	NA	NA	Uncut web

R081	Box 3	Sep, 30	15:56h	Uncut web	NA	NA	Uncut web
R085	Box 1	Aug, 01	15:15h	Scaped	NA	NA	Scaped
R072	Box 2	Aug, 01	15:15h	Uncut web	NA	NA	Uncut web

Table S3 – Data from the Experiment III, first olfactometer assay. Central indicate the central arm; Methyl indicates the Methyl Salicylate stimulus; Water indicates de water stimulus. Minutes indicate where the spider were inside the olfactometer.

Individual	Sex	Date, 2021	Begin hour	00:Minute	15:minute	30:minute	45:minute
R041	Male	Sep, 20	16:17h	Central	Central	Mehtyl	Methyl
R070	Female	Sep, 21	14:37h	Central	Central	Central	Central
R073	Female	Sep, 21	16:00h	Central	Central	Central	Central
R017	Female	Sep, 22	13:27h	Central	Central	Central	Central
R026	Male	Sep, 22	14:37h	Methyl	Methyl	Methyl	Methyl
R052	Female	Sep, 22	15:44h	Water	Central	Central	Central
R072	Female	Sep, 23	12:12h	Water	Water	Water	Water
R071	Female	Sep, 23	13:12h	Central	Central	Central	Central
R074	Female	Sep, 23	14:06h	Central	Central	Central	Central
R075	Female	Sep, 27	09:10h	Methyl	Methyl	Methyl	Methyl
R076	Female	Sep, 28	15:25h	Central	Central	Central	Central
R077	Female	Sep, 28	16:40h	Water	Water	Water	Water
R078	Female	Sep, 29	14:30h	Central	Central	Central	Central
R079	Female	Sep, 29	15:20h	Water	Water	Water	Water
R080	Female	Sep, 29	16:40h	Central	Central	Central	Central
R081	Female	Sep, 30	11:55h	Central	Central	Central	Central
R083	Female	Sep, 30	12:57h	Central	Central	Central	Central
R084	Female	Sep, 30	13:52h	Methyl	Methyl	Central	Central
R085	Female	Aug, 01	11:25h	Central	Central	Central	Central
R082	Female	Aug, 01	12:15h	Central	Central	Central	Central

Table S4 – Data from the Experiment III, second olfactometer assay, first trial. Central indicate the central arm; Water indicates de water stimulus. Minutes indicate where the spider were inside the olfactometer.

Individual	Sex	Date, 2021	Begin hour	00:Minute	10:minute	20:minute	35:minute
R073	Female	Oct, 04	15:08h	Central	Central	Central	Central
R017	Female	Oct, 04	15:48h	Central	Central	Central	Central
R071	Female	Oct, 04	16:27h	Water right	Water right	Water right	Water right
R070	Female	Oct, 05	08:47h	Central	Central	Central	Central
R076	Female	Oct, 05	09:25h	Water right	Water right	Water right	Water right
R074	Female	Oct, 05	10:10h	Water right	Water right	Central	Central
R075	Female	Oct, 05	10:48h	Central	Central	Central	Central
R081	Female	Oct, 05	11:30h	Water left	Water left	Water left	Water left
R084	Female	Oct, 05	12:12h	Central	Central	Central	Central
R085	Female	Oct, 05	12:53h	Central	Central	Central	Central
R072	Female	Oct, 05	13:33h	Central	Central	Central	Central
R082	Female	Oct, 05	14:35h	Central	Central	Central	Central
R080	Female	Oct, 05	15:15h	Water left	Water left	Water left	Water left

R078	Female	Oct, 05	15:55h	Central	Central	Central	Central
R083	Female	Oct, 05	16:33h	Water left	Water left	Water left	Water left
R079	Female	Oct, 05	17:11h	Central	Central	Central	Central

Table 5 – Data from the Experiment III, second olfactometer assay, second trial. Central indicate the central arm; Methyl indicates the Methyl Salicylate stimulus; Water indicates de water stimulus. Minutes indicate where the spider were inside the olfactometer.

Individual	**Sex**	**Date, 2021**	**Begin hour**	**00:Minute**	**10:minute**	**20:minute**	**35:minute**
R077	Female	Oct, 06	08:47h	Central	Central	Central	Central
R017	Female	Oct, 06	09:25h	Central	Central	Central	Central
R071	Female	Oct, 06	10:05h	Central	Central	Central	Central
R070	Female	Oct, 06	10:43h	Central	Central	Central	Central
R073	Female	Oct, 06	11:21h	Central	Central	Central	Central
R084	Female	Oct, 06	12:04h	Central	Central	Central	Central
R081	Female	Oct, 06	12:43h	Central	Central	Central	Central
R074	Female	Oct, 06	13:21h	Central	Central	Central	Central
R076	Female	Oct, 06	14:00h	Water	Water	Water	Water
R072	Female	Oct, 06	14:44h	Central	Central	Central	Central
R075	Female	Oct, 06	15:25h	Methyl	Methyl	Methyl	Methyl
R079	Female	Oct, 07	08:48h	Central	Central	Central	Central
R078	Female	Oct, 07	9:25h	Central	Central	Central	Central
R085	Female	Oct, 07	12:12h	Central	Central	Central	Central
R082	Female	Oct, 07	12:53h	Central	Central	Central	Central
R080	Female	Oct, 07	13:35h	Methyl	Methyl	Methyl	Methyl
R083	Female	Oct, 07	14:12h	Central	Central	Central	Central

References – Capítulo III

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CONCLUSÃO GERAL

Aranhas são um componente essencial na saúde de ecossistemas campestres. Nesta tese pude demonstrar o quanto a araneofauna, de forma geral e ampla, é afetada por efeitos antrópicos de roçado e pastejo. E, usando uma escala mais fina, demonstrei os mesmos efeitos em níveis populacionais e individuais. Considerando estes aspectos gerais, chego a quatro principais conclusões:

1. Como grupo, sempre deve se considerar a variabilidade intrínseca de características e hábitos dentro de Araneae, sua diversidade de funções, hábitos e comportamentos. Contudo, sei que nem sempre temos um cenário de recursos ilimitados em relação à pesquisa e a ciência. Desta forma, sugiro que estudos futuros sobre aranhas e impactos antrópicos em ecossistemas campestres devem forcar em dois grandes grupos de aranhas: (i) aranhas que necessitam da estrutura vegetal para construir teias (teias orbiculares, teias em lençol) e (ii) aranhas que tem pouca necessidade de estrutura vegetal (caçadoras corredoras e caçadoras de espreita). Desta forma, de maneira concisa e rápida se torna possível avaliar o estado de saúde de um ecossistema campestre.
2. De forma geral, para o bioma Pampa, a conservação de aranhas é um forte indicador da qualidade ambiental dos campos. Esta qualidade ambiental pode ser extrapolada em termos de serviços ecossistêmicos providos pelas aranhas, principalmente o controle de pragas agrícolas. Com o controle ambiental e biológico de pragas, há a menor necessidade de uso de defensivos agrícolas, o que pode trazer benefícios em termos de saúde pública e de custo para a manutenção das plantações. Para além disso, a diminuição do impacto antrópico no Pampa não apenas beneficia as populações de aranhas, mas também a diversidade de plantas. Consequentemente, uma maior diversidade de plantas pode prover uma dieta mais distinta e uma maior capacidade nutricional para ruminantes e outros herbívoros de criação. Desta forma, a manutenção das populações de aranhas pode ainda prover uma melhorara na produção e na qualidade de criação de animais pastejadores.

3. Em termos da relação populacional e individual que aranhas orbiculares tem com o impacto antrópico em campos, destaco que a remoção da vegetação feita pelo pastejo exclui diretamente estas aranhas do ambiente. Os rebanhos acabam por funcionar como predadores de topo, sendo superpopulosos ou exóticos, suprimindo as aranhas dos seus habitats naturais. Para além disso, até o momento não conseguimos identificar nenhuma forma de como aranhas poderiam perceber o ambiente impactado e por fim evitá-lo. Desta forma, a presença de aranhas, a manutenção de suas populações e, por consequência, seus serviços ecossistêmicos, estão à mercê de que o impacto antrópico exista ou não nos ambientes campestres. Considerando a vasta transformação de ecossistemas campestres para a produção de comida ao redor do mundo, é seguro dizer que aranhas orbiculares estão ameaçadas em escala global.
4. Por fim, apesar da sabida relevância de artrópodes e, consequentemente, aranhas, o grupo ainda é vastamente desprezado em termos de conservação e manutenção das populações. É inviável a vida humana neste planeta sem artrópodes já que seus serviços ecossistêmicos são transversais a nossa vida. Alternativas sustentáveis na produção de comida assim como a restauração dos ecossistemas campestres é urgente, dado o impacto antrópico negativo causado nas populações de aranhas e outros artrópodes. A nossa frente, por todo o mundo, temos um eminente colapso ambiental em ecossistemas campestres e a conservação de artrópodes e aranhas é essência para evitá-lo.

É urgente que de forma política e científica reduzamos a impacto antrópico em ecossistemas campestres. Seja usando cargas menores de rebanhos, como proposto neste trabalho ou, para além do escopo abordado aqui, a redução do uso de fogo, de agrotóxicos e de monoculturas. A saúde humana é parte da saúde dos ecossistemas. Assim como outras espécies, também dependemos do ambiente em que vivemos. Salvar artrópodes, aranhas e outros organismos é salvar a nós mesmos. Temos pouco tempo restante para evitar um colapso geral da nossa civilização. Precisamos agir agora.

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