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AMPLITUDE DE NICHO TRÓFICO EM *Tidarren haemorrhoidale* (ARANEAE, THERIDIIDAE): DETERMINANTES COMPORTAMENTAIS E IMPLICAÇÕES NUTRICIONAIS SOBRE PARÂMETROS DE HISTÓRIA DE VIDA

RENAN DE BRITO PITILIN

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Tese apresentada à Universidade Federal de Uberlândia, como parte das exigências à defesa de Doutorado do Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais.

Orientador

Prof. Dr. Marcelo de Oliveira Gonzaga

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“A tarefa não é tanto ver aquilo que ninguém viu, mas pensar o que ninguém ainda pensou sobre aquilo que todo mundo vê.”

Arthur Schopenhauer

ÍNDICE

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INTRODUÇÃO GERAL

Uma das hipóteses ecológicas mais antigas, proposta por Darwin (1859), sugere que a luta pela sobrevivência pode ser mais forte entre espécies filogeneticmente próximas. O princípio da exclusão competitiva preve que espécies ecologicamente semelhantes vivendo em simpatria podem potencialmente levar o competidor menos eficiente à exclusão se o recurso for limitante (Thomas & Rand 1971). A teoria de nicho prevê que espécies coexistentes limitarão os efeitos da competição interespecífica por meio da partição de recursos compartilhados, que também podem selecionar diferenças fenotípicas (Chesson 2000). Os mecanismos mais prováveis que permitem a coexistência dessas espécies são segregações em diferentes locais no espaço (horizontal), em alturas diferentes (vertical) ou ainda indivíduos ocorrendo em épocas diferentes (temporal). Mesmo quando estes se sobrepõem, no entanto, pode haver ainda uma diferença no nicho trófico determinada por variações morfológicas ou comportamentais entre as espécies (Navarro *et al*. 2013). Pequenas variações no microhabitat, por exemplo, podem ser cruciais para o estabelecimento e manutenção local de espécies potencialmente competidoras. É o caso de trutas do ártico, onde diferenças na distribuição vertical das espécies podem ser determinadas por uma variação de dois graus na temperatura da água (Langeland *et al*. 1991). Já as aranhas construtoras de teias orbiculares (Tetragnathidae) minimizam a potencial sobreposição em seus nichos espaciais, variando características de suas teias que levam a diferenças substanciais em seus nichos tróficos (Nasir *et al.* 2007).

A utilização de tipos específicos de presas pode ter evoluído devido a demandas conflitantes relacionadas à sobrevivência, crescimento e reprodução, ou uma resposta imediata devido a condições ambientais específicas; e.g. a dominância de certa espécie de presa ou competição interespecífica (Pekár & Haddad 2011). Utilizando a predação como exemplo, é possível que as espécies sejam estenófagas, pois possuem adaptações especializadas em capturar um ou alguns poucos tipos de presas e dessa forma são necessariamente ineficientes ou incapazes de capturar e consumir presas alternativas. Em espécies de peixes *Gasterosteus* spp. (Gasterosteidae) foi demonstrado que formas morfologicamente diferentes variam em suas habilidades para explorar recursos. Quando o morfotipo adaptado ao ambiente bentônico foi exposto experimentalmente às presas do ambiente litorâneo sua eficiência de captura caiu drasticamente tendo um efeito imediato no ganho de peso (Schluter 1995). Em outro cenário podemos encontrar predadores estenófagos, com comportamente de forrageamento generalista, uma vez que possuem adaptações versáteis que lhes permitem capturar e processar uma variedade maior de itens alimentares em ambientes com diversas presas (Sherry 1990). Por exemplo, herbívoros generalistas podem atuar como especialistas em comunidades locais, explorando uma faixa estreita de plantas que são abundantes em determinada área (Fox & Morrow 1981).

Em algumas espécies, a dieta de cada indivíduo pode ser mais restrita que a dieta da população em que estão inseridos (West 1986; Araujo & Gonzaga 2007; Pitilin *et al*. 2012). Os tentilhões da ilha de Cocos (*Pinaroloxias inornata* Gould, 1943), por exemplo, se alimentam como especialistas apresentando comportamentos individuais específicos de forrageamento, enquanto a população como um todo é extremamente generalista e explora uma grande variedade de recursos alimentares (Werner & Sherry 1987). Essa variação de nível individual é conhecida como "especialização individual" e sua ocorrência é comum em diversos grupos taxonômicos (Bolnick *et al*. 2003). A habilidade com que cada indivíduo explora os recursos disponíveis geralmente é limitada por sua incapacidade ou ineficiência em executar vários comportamentos distintos para obtenção de alimento, muitas vezes necessários para diversificação da dieta. Essas limitações ocorrem em vários aspectos do forrageamento, incluindo o reconhecimento, interceptação e imobilização das presas. Além disso, também podem haver restrições individuais acerca da digestão de muitos tipos diferentes de itens alimentares (Bolnick *et al*. 2003).

Em aranhas o forrageamento se inicia com a seleção de um local específico para construção de teia, espreita ou procura ativa. Após o estabelecimento, sua permanência depende do fornecimento de uma quantidade de presas suficiente para suprir seus requerimentos energéticos. As estratégias de forrageamento, considerando todo o grupo taxonômico, são bastante variadas, incluindo perseguição ativa, captura por emboscada, construção de teias ou malhas de captura, atração de presas através da utilização de substâncias que mimetizam feromônios das presas e até mesmo um mimetismo agressivo (Uetz 1992). Além disso, mesmo dentro de cada espécie podem existir diversas rotinas comportamentais envolvidas e variações essenciais para o sucesso de captura de cada tipo e/ou tamanho de presa incluído na dieta. (Robinson & Robinson 1976; Viera 1995; Japyassú & Viera 2002). A espécie *Argiope argentata* (Fabricius, 1775) (Araneidae), por exemplo, consegue discriminar lepidópteros de outros insetos de tamanhos similares, usando diferentes tipos de ataques que envolvem sequências distintas de picadas e enrolamento da presa (Robinson & Robinson 1976). Já *Neospintharus trigonum* (Hentz, 1850) (Theridiidae) é um forrageador versátil podendo se comportar como predador de outras aranhas hospedeiras ou como cleptoparasita utilizando, em cada situação, diferentes sequências de captura (Cangialosi 1997).

Alguns estudos com artrópodes sugerem que a experiência com um tipo de presa pode aumentar a eficiência de forrageamento em eventos subsequentes com o mesmo tipo (Heiling & Herberstein 1999; Morse 2000; Punzo 2005). Na vespa *Pepsis mildei* (Stål,

1857) (Pompilidae), por exemplo, o tempo necessário para que o indivíduo oriente seu corpo em direção ao hospedeiro, faça a aproximação e complete a sequência de captura, diminui durante sucessivas capturas (Punzo 2005). Apesar de algumas famílias de aranhas serem conhecidas por possuírem comportamentos de caça estereotipados, algumas espécies podem aprender durante os eventos de forrageamento (Foelix 2010). Aranhas do gênero *Portia* (Salticidae) são predadores versáteis capazes de aprender um variado repertório de táticas predatórias, específicos para diferentes circunstâncias ou diferentes tipos de presas (Jackson & Pollard 1996). Já a espécie *Larinioides sclopetarius* (Clerck, 1757) (Araneidae) usa experiências anteriores em relação aos locais da teia que foram mais eficazes na interceptação de insetos para ajustar a arquitetura de modo mais eficiente (Heiling & Herberstein 1999).

O padrão de respostas comportamentais e fisiológicas do predador a diferentes tipos de presas pode fornecer uma base para hipóteses acerca da seleção de presas e amplitude de nichos tróficos (Toft & Wise 1999). Embora exista certa plasticidade comportamental no aprendizado de estratégies de captura, é pouco provável que um predador especializado passe a atacar indiscriminadamente diferentes tipos de presas, mesmo quando suas taxas de ingestão de energia caem abaixo dos níveis necessários para evitar inanição (McNamara & Houston 1990). Isso ocorre porque essas espécies podem possuir adaptações fisiológicas que restringem a dieta, fazendo com que obtenham pouco ou nenhum benefício energético ou nutricional das presas alternativas disponíveis (Pekár *et al*. 2009). Assim, a especialização da dieta pode estar relacionada à alta eficiência na utilização e absorção de nutrientes. Por outro lado, no entanto, uma dieta generalista pode conter uma gama maior de recursos, sendo possível para espécies eurífagas obter um balanço nutricional mais equilibrado (Pekár *et al*. 2010; Terraube *et al*. 2011).

Greenstone (1979) sugeriu pela primeira vez que os predadores podem selecionar itens alimentares de acordo com o conteúdo de nutrientes. Para cada espécie, a qualidade da dieta deve combinar todos os aspectos do valor nutricional da presa, incluindo a energia adquirida, os nutrientes essenciais e até mesmo as toxinas (Toft & Wise 1999a). Alguns estudos em aranhas que exploraram as implicações de uma dieta composta por um espectro mais amplo de presas indicaram que elas podem ter um efeito positivo (Uetz et *al*. 1992; Toft & Wise 1999a; Toft & Wise 1999b; Oelbermann & Scheu 2002). Na espécie construtora de teia orbicular *Zygiella x-notata* (Clerck, 1757) (Araneidae), por exemplo, a qualidade dos nutrientes das presas possui um efeito significativo no tempo de duração de cada instar, no peso, na fecundidade e nas taxas de sobrevivência (Mayntz *et al*. 2003). Além disso, algumas espécies de aranhas podem regular a ingestão de macronutrientes específicos em sua dieta através de adaptações fisiológicas e comportamentais (Jensen *et al*. 2011).

Apesar da diversidade de trabalhos com espécies de aranhas da família Theridiidae, não existem estudos sobre determinação de amplitude de dieta, comportamentos de forrageamento e qualidade nutricional dos itens consumidos no gênero *Tidarren*. A inovação proposta nessa tese foi explorar em uma única espécie, *Tidarren haemorrhoidale* (Bertkau, 1880), os diferentes aspectos ligados à alimentação: a possível segregação de nichos tróficos envolvendo outra espécie simpátrica de Theridiidae, a possibilidade de especialização individual dentro da população, rotinas comportamentais utilizadas para captura de presas diferentes, o papel das experiências prévias para eficiência de forrageamento e de como diferentes dietas afetam a fecundidade e a sobrevivência dos indivíduos. Essas abordagens foram distribuídas nos três capítulos a seguir incluindo um conjunto de experimentos realizados em campo e em condições controladas de laboratório.

Esse estudo fornece conhecimento sobre vários aspectos da história natural da espécie, além de proporcionar uma visão integrativa sobre diversas linhas de pesquisa em ecologia de aranhas.

Referências

Araújo, M.S., & Gonzaga, M.O. (2007) Individual specialization in the hunting-wasp *Trypoxylon* (*Trypargilum*) *albonigrum* (Hymenoptera: Cabronidae). *Behavioral Ecology and Sociobiology*, **61**, 1855–1863. https://doi.org/10.1007/s00265-007-0425-z

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, **161**, 1–28. https://doi.org/10.1086/343878

Cangialosi, K. (1997) Foraging versatility and the influence of host availability in *Argyrodes trigonum* (Araneae, Theridiidae). *Journal of Arachnology*, **25**, 182–193.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology, Evolution, and Systematics*, **31**, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection* (eds J. Murray). London.

Foelix, R. (2011) Biology of spiders (3rd ed). Oxford University Press, Oxford.

Fox, L.R. & Morrow, P.A. (1981) Specialization: species property or local phenomenon? *Science*, **211**, 887–893. https://doi.org/10.1126/science.211.4485.887

Greenstone, M.H. (1979) Spider feeding behaviour optimises dietary essential amino acid composition. *Nature*, **282**, 501–503. https://doi.org/10.1038/282501a0

Harwood, J.D., Sunderland, K.D. & Symondson, W.O.C. (2003) Web location by linyphiid spiders: prey-specific aggregation and foraging strategies. *Journal of Animal Ecology*, **72**, 745–756.

https://doi.org/10.1046/j.1365-2656.2003.00746.x

Heiling, A.M. & Herberstein, M.E. (1999) The role of experience in web-building spiders (Araneidae). *Animal Cognition*, **2**, 171–177.

https://doi.org/10.1007/s100710050037

Jackson, R.R. & Pollard, S.D. (1996) Predatory behavior of jumping spiders. *Annual Review of Entomology*, **1**, 287–308.

https://doi.org/10.1146/annurev.en.41.010196.001443

Japyassú, H.F. & Viera, C. (2002) Predatory plasticity in *Nephilengys cruentata* (Araneae: Tetragnathidae): relevance for phylogeny reconstruction. *Behaviour*, **139**, 529–544.

https://doi.org/10.1163/15685390260135998

Jensen, K., Mayntz, D., Toft, S., Raubenheimer, D. & Simpson, S.J. (2011) Nutrient regulation in a predator, the wolf spider Pardosa prativaga. *Animal Behavior*, **81**, 993–999.

https://doi.org/10.1016/j.anbehav.2011.01.035

Langeland, A., L'Abe´e-Lund, J.H., Jonsson, B. & Jonsson, N. (1991) Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta. Journal of Animal Ecology*, **60**, 895–912.

https://doi.org/10.2307/5420

Mayntz, D., Toft, S. & Vollrath, F. (2003) Effects of prey quality and availability on the life history of a trap-building predator. *Oikos*, **101**, 631–638.

https://doi.org/10.1034/j.1600-0706.2003.12408.x

McNamara, J.M. & Houston, A.I. (1990) The starvation-predation trade-off and some behavioral and ecological consequences. *Behavioral Mechanisms of Food Selection* (eds . R.N. Hughes), pp. 39–59. Springer, Germany.

https://doi.org/10.1007/978-3-642-75118-9_3

Morse, D.H. (2000) The effect of experience on the hunting success of newly emerged spiderlings. *Animal Behavior*, **60**, 827–835.

https://doi.org/10.1006/anbe.2000.1546

Navarro, J., Votier, S.C., Aguzzi, J., Chiessa, J.J., Forero, M.G. & Phillips, R.A. (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *PLoS ONE*, **8**, e622897.

https://doi.org/10.1371/journal.pone.0062897

Oelbermann, K. & Scheu, S. (2002) Effects of prey type and mixed diets on survival, growth and development of a generalist predator, *Pardosa lugubris*. *Basic and Applied Ecology*, **3**, 285–291.

https://doi.org/10.1078/1439-1791-00094

Pekár, S. & Haddad, C.R. (2011) Trophic strategy of ant-eating *Mexcala elegans* (Araneae: Salticidae): looking for evidence of evolution of prey-specialization. *Journal of Arachnology*, **39**, 133–138.

https://doi.org/10.1636/Hi10-56.1

Pekár, S., Mayntz, D., Riberio, T. & Herberstein, M.E. (2010) Specialist ant-eating spiders selectively feed on different body parts to balance nutrient intake. *Animal Behaviour*, **79**, 1301–1306.

https://doi.org/10.1016/j.anbehav.2010.03.002

Pekár, S. & Toft, S. (2009) "Can ant-eating Zodarion spiders (Araneae: Zodariidae) develop on a diet optimal for euryphagous arthropod predators?" *Physiological Entomology*, **34**, 195–201.

https://doi.org/10.1111/j.1365-3032.2009.00672.x

Pitilin, R.B., Araújo, M.S. & Buschini, M.L.T. (2012) Individual Specialization in the Hunting-wasp *Trypoxylon* (*Trypargilum*) *agamemnon* Richards (Hymenoptera: Crabronidae) *Zoological Studies*, **51**, 655–662.

Punzo, F. (2005) Experience affects hunting behavior of the wasp, *Pepsis mildei* Stål (Hymenoptera: Pompilidae). *Journal of the New York Entomological Society*, **113**, 222–229.

https://doi.org/10.1664/0028-7199(2005)113[0222:EAHBOT]2.0.CO;2

Robinson, M.H. & Robinson, B. (1976) Discrimination between prey types: an innate component of the predatory behavior of araneid spiders. *Zeitschrift für Tierpsychologie*, **41**, 266–276.

https://doi.org/10.1111/j.1439-0310.1976.tb00482.x

Sherry, T.W. (1990) When are birds dietary specialized? Distinguishing ecological from evolutionary approaches. *Studies in Avian Biology*, **13**, 337–352.

Schluter, D. (1995) Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology*, **76**, 82–90.

https://doi.org/10.2307/1940633

Terraube, J., Arroyo, B., Madders, M. & Mougeot, F. (2011) Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos*, **120**, 234–244.

https://doi.org/10.1111/j.1600-0706.2010.18554.x

Toft S. & Wise, D.H. (1999a) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia*, **119**, 191–197.

https://doi.org/10.1007/s004420050776

Toft S. & Wise, D.H. (1999b) Behavioral and ecophysiological responses of a generalist predator to single- and mixedspecies diets of different quality. *Oecologia*, **119**, 198–207.

https://doi.org/10.1007/s004420050777

Uetz, G.W. (1992) Foraging strategies of spiders. *Trends in Ecology & Evolution*, **7**, 155–159.

https://doi.org/10.1016/0169-5347(92)90209-T

Uetz, G., Bischoff, J. & Raver, J. (1992) Survivorship of wolf spiders (Lycosidae) reared on different diets. *Journal of Arachnology*, **20**, 207–211.

Viera, C. (1995) Discriminacion por *Metepeira seditiosa* (Keyserling) (Araneae, Araneidae) en condiciones experimentales sobre dos presas frecuentes en el medio. *Journal of Arachnology*, **23**, 17–24.

Werner, T.K. & Sherry, T.W. (1987) Behavioral feeding specialization in *Pinaroloxias inornata*, the “Darwin’s Finch” of Cocos Island, Costa Rica. *Proceedings of the National Academy of Sciences*, **84**, 5506–5510.

https://doi.org/10.1073/pnas.84.15.5506

West, L. (1986). Interindividual variation in prey selection by the snail *Nucella* (= *Thais*) *emarginata*. *Ecology*, **67**, 798–809.

https://doi.org/10.2307/1937702

Zaret, T.M. & Rand, A.S. (1971) Competition in Tropical Stream Fishes: Support for the Competitive Exclusion Principle. *Ecology*, **52**, 336–342.

https://doi.org/10.2307/1934593

Capítulo 1

Trophic niche segregation and individual specialization in two sympatric species of cobweb spiders (Araneae: Theridiidae)

Abstract

Niche segregation has been largely linked to competition in ecological literature, and may play a crucial role in explaining patterns of coexistence between and within species. This study evaluated the trophic niche breadth of two species of sympatric cobweb spiders (Theridiidae) that occur in areas of *Eucalyptus* monoculture, the characteristics of their webs, the spatial distribution and the possible occurrence of individual specialization. We observed that although *Tidarren haemorrhoidale* and *Nihonhimea tesselata* construct their webs in the same environment, they captured different prey. These species had distinct web architectures and attached their webs to distinct positions in the trees. These differences are problaby determinant factors promoting the capture of different types of insects. Individual specialization did not occur in both studied species. In addition, we observed that individual diet is not influenced by spatial position of the webs, once there is no correlation between distance between webs and diet similarity.

Keywords: interspecific competition, niche differentiation, co-occurrence, spatial distribution

Introduction

Phylogenetically closely related species often present similar ecological niches (Webb *et al.* 2002; Wiens & Graham 2005; Burns & Strauss 2011). When in sympathy, individuals of these species may compete for the exploitation of similar resources. This competition may potentially lead to the local exclusion of those species less efficient in obtaining the resources under contest (Violle *et al.* 2011). In this scenario, there is a pressure for the differentiation of trophic niches through the narrowing of the niche occupied by each species (Traba *et al.* 2015; Tarjuelo *et al.* 2017). Therefore, natural selection favors individuals of each species that preferentially use resources outside the overlapping range. Alternatively, the increasing of the niche width when a closelly related species occurs in sympatry is also possible (e.g. Mazzoni *et al.* 2012). In this case, the addition of other items to the diet of each population (food plasticity) could minimize the dependence on shared items (see Cunha *et al.* 1951). The increasing in trophic niche width of the species could occur with each individual exploring sub-optimal resources at a frequency higher than that observed in an allopatric condition.

Interspecific competition (and its effects) can be minimized in a number of ways. Two or more species that explore similar resources may, for example, present different patterns of horizontal or vertical spatial distribution in the environment (Herberstein 1998; Purcell *et al.* 2012; Cardoso *et al.* 2018). By avoiding spatial overllaping they can have access to resources unavailable to the potential competitor. Another possibility to avoid competition is the variation in the strategies used for foraging. Nasir *et al.* (2017), for example, showed that variations in the characteristics of the webs of several sympatric spider species of the family Tetragnathidae determine trophic niche partition, allowing their coexistence. Likewise, several species of *Anelosimus* (Araneae, Theridiidae) coexist in an area of southeastern Brazil, probably baecause they present distinct social systems (number of individuals by colonies and complexity of social interactions) that determine variations in foraging strategies. In species with complex social structures, more individuals participate in activities of web construction and repair, and in the events of immobilization and consumption of food items, capturing a greater variety of prey types and sizes (Guevara *et al.* 2011).

Finally, competition (intra and interspecific) has effects on the occurrence of individual specialization (Araújo *et al.* 2011). Intraspecific competition tends to promote interindividual variation in diet. Several studies have demonstrated the existence of positive correlations between population density, used as a proxy of the intensity of intraspecific competition, and the levels of individual especialization (e.g. Frederich *et al.* 2010). Other studies showed that new resources are added to the trophic niche of a population by increasing interindividual variation under conditions of resource scarcity (Svanbäck *et al.* 2011). In addition, under these conditions, intra-population diversification in the use of microhabitats may occur, with consequent interindividual diversification in the use of resources (Kobler *et al.* 2009). Interspecific competition may have an opposite effect, reducing the intensity of individual specialization in the population. There are studies showing that fish populations sharing sites with several other closely related species present less interindividual variation in diet than populations of the same species occurring in sites with few other competing species (Knudsen *et al.* 2007). Experimental studies with contradictory results, however, suggest that the pattern still needs confirmation (see Bolnick *et al.* 2010; Araújo *et al.* 2011).

The co-occurrence of abundant populations of two or more spider specie from the family Theridiidae is very common and has been reported in environments with very distinct abiotic characteristics and vegetation types (e.g. Sørensen 2004; Gonzalez *et al.* 2016; Rodrigues *et al.* 2016). It is possible that environments with a high degree of disturbance of anthropogenic origin and structural simplification, such as monoculture areas of *Eucalyptus*, present greater potential for competition between these species, since the prey diversity is limited by the usually adverse conditions found in the understory vegetation (Oliveira *et al.* 1995; Marinho *et al.* 1997; Majer & Recher 1999). Thus, it would be expected that in these environments the synoptic occurrence of theridiid species depended on (1) the horizontal and/or vertical spatial segregation and/or (2) differentiation of diet as a consequence of distinct foraging behaviors characteristics and/or variation in prey capture strategies. In addition, interspecific competition could limit the occurrence of individual specialization.

In this study we investigated spatial distribution and diet patterns (considering the trophic niche amplitude of the populations and individuals) of two sympatric species of Theridiidae, *Tidarren haemorrhoidale* (Bertkau, 1880) and *Nihonhimea tesselata* (Yoshida, 2016), in an area covered by *Eucalyptus* silviculture in southeastern Brazil and we test whether there is individual especialization in both species. The determination of these patterns can clarify how populations of phylogenetically closely related species can present high densities, in sympatry, even in altered environments. We hypothesized that these species are segregated in space and/or present a reduced overlapping in their diets.

Material and Methods

Study area

The study was developed in an *Eucalyptus* plantation at Fazenda Nova Monte Carmelo (18º45'11 "S, 47º51'28" W), Estrela do Sul, MG, Brazil. The areas covered by *Eucalyptus* in the FNMC are interspersed by fragments of Cerrado vegetation, but our research was restricted to regions within the monoculture at a very advanced age. All the webs were located during the day among the rows of *Eucalyptus* trees in an area of 41,600 m^2. The webs were marked individually and the prey collections were made always in the morning. Every other day all the webs were inspected. Twenty expeditions were made lasted approximately two months and were carried out from June to July 2016.

Species

Tidarren haemorrhoidale has a wide geographic distribution, occurring from the USA to Argentina. Their webs are composed of an irregular structure of threads connected to the vegetation at many points and support a shelter, formed by a dry rolled leaf (Fig. 1A e B, Benjamin & Zschokke 2003; Eberhard *et al*. 2008). The web has no viscid or gumfooted threads. Webs spun by *N. tesselata* were previously described by Benjamin & Zchokke (2003) and included in the Coleosoma-type category (see also Jörger & Eberhard 2007). Webs in this category have a horizontal sheet at the base of the web, do not have sticky elements (yarn or shoes) and have an irregular yarn structure on the sheet characterized as KN (Knock-down trap) (Fig. 1C e D, Benjamin & Zchokke 2003). The genus *Nihonhimea* was described by Yoshida (2016) and it is currently composed of three species, removed from *Parasteatoda*. It closely related to *Tidarren* considering the phylogeny presented by Eberhard *et al.* (2008).

Diet

Diet determination for the two populations was made through the collection of insects found in the webs. We were able to mark in the area 120 *N. tesselata* webs and 60 *T. haemorrhoidale* webs. In all the expeditions prey were collected. Only prey items being manipulated or consumed by the spiders were collected. All the prey were removed and transported to the laboratory, where they were identified at the taxonomic level of order.

The order formicidae was differentiated from the other hymenoptera because its foraging behavior is different, involving active walking through the trunk.

Characterization of webs

As the webs present a complex three-dimensional structure, their volumes were evaluated considering the limits of the geometric figure that was closest to the shape of the web. We use a tape measure for web measurements. For *N. tesselata* the volume was calculated from the volume formula of a cone with elliptical base and for *T. haemorrhoidale* of a trapezoidal prism.

Statistical analyzes

We estimated the trophic niche overlapping using the Pianka index (1973) with Lawlor's third randomization algorithm (1980) (RA3). The RA3 randomizes the number of individuals captured by the same predator among prey species, which is an efficient approach to detect possible patterns of niche overlapping (Winemiller & Pianka 1990; Gotelli *et al.* 2015). We used this algorithm to produce a null distribution with a total of 5,000 Monte Carlo simulations ($\alpha < 0.05$) (Gotelli *et al.* 2015). The analysis reveals whether the average niche overlap, calculated among all species pairs, is superior or inferior than would be expected if species used resource categories independently of each other. We performed the data analysis in the software R, version 3.5.1 (R Development Core Team 2018), using the "EcoSimR" package (Gotelli *et al.* 2015).

To quantify individual specialization in *N. tesselata* and *T. haemorrhoidale* an adaptation of Schoener's (1968) proportional similarity index was used. The PS index measures the overlapping between the individual diet, i's, and the population's diet (see Bolnick *et al.* 2002):

$$PS_i = 1 - 0.5\sum_j \left| p_{ij} - q_j \right|$$

Where *PS*i represents the overlapping between the individual niche i's and the population niche; p_{ij} represents the proportion of prey of category j in the individual diet of i's; and q_j is the proportion of resource category j in the population niche, calculated using the formula:

$$q_j = \frac{\sum_i n_{ij}}{\sum_i \sum_j n_{ij}}$$

Where n_{ij} represents the number of items in the individual i's diet that is included in category j. The value of *PS*i will be equal to 1 for individuals who consume prey in the same proportion as the population as a whole. After determining the *PS*i values for each individual, it is possible to quantify the occurrence of individual specialization in the population by calculating *IS* (see Bolnick *et al.* 2002). IndSpec 1.0 software (Bolnick *et al.* 2002) was used to test whether the *IS* measure is significantly different from a null model. We used 10,000 replications in Monte Carlo bootstrap simulations to obtain the value of *P*. For this, the program IndSpec 1.0 generates matrices in which for each individual i is assigned the observed number of food items, but each item is positioned in categories of resources with probabilities determined from the use of population resources (q'_{is}). For each resampled population, PS_i and *IS* values are calculated. The program then reports the proportion of individuals (i's) with PS_i values lower than the PS_i observed and the proportion of populations with resampled *IS'*s lower than the observed *IS*. These values are used as estimates of the probability of observing the actual indexes of diet overlapping when the individuals are generalists, presenting a probability of using resources equal to those of the population.

Spatial distribution

A map of the horizontal position of all the webs of the two species found in an area of 160 x 260m (41,600m^2) in the *Eucalyptus* understory was done. The distance of three meters between each tree was used as a reference to map the distance from one web to all other. For each web was also recorded the height from the soil and the distance from the trunk of the *Eucalyptus* where the web was fixed. ANOVA tests were used to determine if there were any differences between the species in the volume and position of the webs ($\alpha < 0.05$).

In order to determine if the spatial distribution of the *N. tesselata* and *T. haemorrhoidale* webs influences the selection of food items consumed, a Mantel test was performed using the "ecodist" package (Goslee & Urban 2007), correlating the distance matrix between the webs with the matrix of overlapping diets. The data of the first matrix constitute the linear distances between all pairs of sampled webs (Euclidean distances) and the second matrix involves the determination of the diet overlap between pairs of webs (Bray-Curtis dissimilarities). Analysis was performed using the software R version 3.5.1 (R Development Core Team 2018).

Results

Diet of the species

We collected 484 prey items captured and consumed by both species. 117 individuals of *Nihonhimea tesselata* captured 392 insects, included into eight orders, with

Psocoptera being the most abundant (38.7%), followed by Hemiptera (18.1%) and Hymenoptera (only ants) (16.8%). In relation to *Tidarren haemorrhoidale*, 39 individuals captured 92 insects, included into six orders, with Hymenoptera (only ants) being the most abundant (69.5%), followed by Hemiptera (11.9%) and Coleoptera (8.6%) (Fig. 2). Although both spider species shared some types of prey, there was separation of food niches between them (Pianka's index = 0.45, $P = 0.121$), i.e. there was no niche overlap.

Individual specialization

The observed value of *IS* for *N. tesselata* was 0.57 and for *T. haemorrhoidale* was 0.69. The bootstrap tests showed that in both cases these values were not different ($P > 0.05$) from the expected based on the null model. Therefore, there is no difference between the diets of individuals and the diet of population (Fig. 3).

Spatial distribution

Horizontal spatial distribution of the webs of both species suggest a random distribution in the environment and no spatial segregation (Fig. 4A). However, we found differences in the position of webs considering their distances from trunk of the trees ($F_{38,1} = 94.67$; $P < 0,05$) (Fig. 4B). There was also a difference between the volume of the webs between species ($F_{38.1} = 11.18$; $P < 0.05$), but not in the height of their webs from the ground ($F_{38,1} = 0.03$, $P = 0.85$) (Fig. 4C).

There is no significant correlation between spatial distance matrices and diet overlapping among individuals for both species, *N. tesselata* ($r = 0.055$, $P = 0.23$) and *T. haemorrhoidale* ($r = 0.046$, $P = 0.41$), indicating that the pattern of prey capture is not a consequence of the spatial distribution of the resources.

Discussion

We investigated the existence of resource partitioning among two sympatric spider species of the family Theridiidae and tested the occurrence of individual specialization for each of them based on the prey taxa captured by individuals within the population. *Nihonhimea tesselata* and *T. haemorrhoidale* segregate their niches by exploiting distinct taxonomic groups of prey. These differences in diet may be a consequence of variation in prey interception promoted by differences in web positioning, size and web architecture patterns. Although we showed that individuals do not use all the resources consumed by population, individual specialization was not observed in both species. In addition, we found no correlation between the matrices of spatial distance of the webs and diet similarity among individuals, indicating that diet is not determined by spatial distribution of potencial prey items.

Nihonhimea tesselata captured mainly Psocoptera and winged insects, and the sum of these categories represented 83% of all prey items collected in their webs. These spiders establish their webs in positions far from the trunks, attached to thin branches of the trees. Their webs act as traps for flying insects and jumpers that reach the top mesh, fall on the sheet, and are attacked by the spider (Eberhard 1972; Barrentes & Weng 2006). Spiders from other closely related genera, such as *Achaearanea cinnabarina* (Levi, 1963), however, uses both sheets and anchor gumfooted threads attached to the ground and nearby vegetation to capture their prey. These hunting tatics allows the interception of both, flying and cursorial insects (Japyassú & Jotta 2005). Variation within Theridiidae is high, including prey interception based on the construction of web structures completely covered by viscid silk (such as in *Helvibis longicauda* Keyserling, 1891 and *Chrysso intervales* Gonzaga, Leiner & Santos, 2006 – see Gonzaga *et al*. 2006) and others in which prey interception is based on a few points of viscid glue positioned in the attachement points of threads to the vegetation (gumfooted threads). This seems to be the case of *T. haemorrhoidale*. Thus, segregation of the trophic niches between these sympatric species may be detemined by different foraging strategies (web position and structure), minimizing interspecific competition.

In the studied *Eucalyptus* environment, the webs of *T. haemorrhoidale* have characteristics quite different from *N. tesselata*. *Tidarren haemorrhoidale* presents webs composed of a tangle of non-viscid silk threads connected to the vegetation at several points and located very close to the tree trunks. The position and architecture of these webs facilitates the perception of insects that walk on the trunks, and these insects, mainly ants, represented more than 70% of its diet. A similar result was found for *T. haemorrhoidale* in cacao plantations in Mexico (Moreno-Mendonza *et al.* 2012) where the ants were captured in a higher frequency. In cotton plantations, however, this species builds its webs in a lower position, between herbaceous plants. In this situation individuals capture mainly aphids that are abundant in this agroecosystem (Nyffeler *et al.* 1988).

Competition may lead to differentiation of trophic niches between populations, favoring individuals outside the overlapping spectrum or individuals who are located in microhabitats not occupied by the other competitor. Spiders sharing the same environment usually construct their webs at distinct microhabitats and/or present different foraging strategies to minimize this problem. Nasir *et al.* (2007), for example, found that orbicular spider species (Tetragnathidae) construct their webs with variation in architecture characteristics that are in accordance to their habitats, geographic location or the presence of other species of the same genus, maximizing foraging success. Similarly, spiders constructing irregular webs can present a great plasticity in web architecture and in the occupation of microhabitats (Eberhard *et al.* 2008). In the case studied here, however, the irregular distribution of threads on webs of both theridiids present substantial differences (a sheet in *N. tesselata* and gumfooted lines in *T. haemorrhoidale*) and fine scale alterations (web construction plasticity) to reduce competiton were probably unnecessary.

Experimental and comparative studies have confirmed that intra and interspecific competition may limit the population to certain resources influencing the width of the population niche (Araújo *et al.* 2011). According to Araújo *et al.* (2011), individual specialization is less pronounced in species-rich communities, where interspecific competition must be stronger. Considering this afirmation, it would be expected that individual specialization would occur in our system, since individuals within sympatric species using different prey and not competing with each other could specialize, reducing intraspecific competition. However, we did not find individual specialization in both studied species. A similar result was found by Michalko & Pekár (2014) studying three species of the family Philodromidae. In this case individual specialization was absent considering prey types, but they verified that the smaller species can specialize in prey of different sizes. According to the authors it is probably motivated by competitive interference with the other larger species.

Individual specialization may be a consequence of some characteristics, such as: intraspecific morphological variation (determining the consumption of large prey items by some individuals and small by others), physiological restrictions of some individuals to digest some resources available, or cognitive limitations (specific behavioral routines are necessary to capture distinct prey items and each individual is unable to efficiently perform all the variations). This last possibility seems to be likely in spiders, once insects from different orders usually have very distinct behaviors when intercepted (see Souza *et al.*

2007). One possibility to explain the lack of individual specialization observed in our study is that individuals in these spiders may have the skills to capture and consume different types of prey using relatively stable (stereotyped) behavior routines. Many theridiids are known to be generalist predators (Nyffeler 1988) and exhibiting attack behaviors based on involving the prey with sticky silk masses before the initial bite (Nentwing 1987). Investigation of behavioral foraging sequences will be conducted in a further study (see chapter 2).

Differently from the results found in this work, Pêgo (2014) observed individual specialization in *T. haemorrhoidale* studied in a population located in Atlantic Forest, in the Serra do Japi. In this locality there are a greater habitat heterogeneity and diversity of insects compared to an agroecossystem composed exclusively of *Eucalyptus*. Although it has not been tested, it is possible that habitat heterogeneity may favor individual specialization in *T. haemorrhoidale*. There is some evidence in the literature that this process may occur (see Bolnick *et al.* 2003). One example was observed by Angerbjorn *et al.* (1994) where individual variation among arctic foxes can probably be caused by habitat heterogeneity and territoriality. Another possibility is that in environments with anthropogenic disturbances and a highly simplified structure, such as *Eucalyptus* agroecosystems, *T. haemorrhoidale* and *N. tesselata* are competing with other theridiids and orbicular spiders also abundant in that place, since the prey diversity may be limited. In this scenario interspecific competition may have a negative effect on individual specialization, depending on the preferences of the competing species and the value of the resources (Bolnick *et al.* 2010; Araújo *et al*. 2011).

In this work we could conclude that although *T. haemorrhoidale* and *N. tesselata* construct their webs in the same environment they capture different prey and segregate their niches, allowing coexistence at the same habitat and microhabitats. These species have differences in the position of the webs and different characteristics in web architecture, problebly determining factors to explain the interception of different types of insects. Individual specialization did not occur in both studied species, with individual niches being similar to population niche. Finally, diet of individuals of both species seems to be independent of the spatial distribution of the webs because we observed that individuals with nearby webs do not present greater overlapping in their diets.

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References

Angerbjorn, A., Hersteinsson, P., Liden, K. & Nelson, E. (1994) Dietary variation in arctic foxes (*Alopex lagopus*) an analysis of stable isotopes. *Oecologia*, **99**, 226–232. https://doi.org/10.1007/BF00627734

Araújo, M.S., Bolnick, D.I. & Layman, C.A. (2011) The ecological causes of individual specialization. *Ecology Letters*, **14**, 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Barrantes, G. & Weng, J.L. (2006) The prey attack behavior of *Achaearanea tesselata* (Araneae, Theridiidae). *Journal of Arachnology*, **34**, 456–466.

https://doi.org/10.1636/S05-73.1

Benjamin, S.P. & Zschokke, S. (2003) Webs of theridiid spiders: construction, structure and evolution. *Biological Journal of the Linnean Society*, **78**, 293–305.

https://doi.org/10.1046/j.1095-8312.2003.00110.x

Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L., Lau, O.L. & Paull, J. (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society of London Ser. B: Biol. Sci.*, **277**, 1789–1797.

https://doi.org/10.1098/rspb.2010.0018

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003) The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist*, **161**, 1–28.

https://doi.org/10.1086/343878

Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanbäck, R. (2002) Measuring individual-level resource specialization. *Ecology*, **83**, 2936–2941.

https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

Burns, J.H. & Strauss, S.Y. (2011) More closely related species are more ecologically similar in an experimental test. *Proceedings of National Academy of Sciences*, **108**, 5302–5307.

https://doi.org/10.1073/pnas.1013003108

Cardoso, J.C.F., Michalko, R. & Gonzaga, M.O. (2018) Specific parasites indirectly influence niche occupation of non-hosts community members. *Oecologia*, **188**, 343–353.

https://doi.org/10.1007/s00442-018-4163-x

Castanheira, P., Pérez-González, A. & Baptista, R. (2016) Spider diversity (Arachnida: Araneae) in Atlantic Forest areas at Pedra Branca State Park, Rio de Janeiro, Brazil. *Biodiversity Data Journal*, **4**, e7055.

https://doi.org/10.3897/BDJ.4.e7055

Cunha, A.B., Dobzhansky, T. & Sokoloff, A. (1951) On food preferences of sympatric species of *Drosophila*. *Evolution*, **2**, 97–101.

https://doi.org/10.1111/j.1558-5646.1951.tb02766.x

Eberhard, W.G. (1972) Observations on the biology of *Achaearanea tesselata* (Araneae: Theridiidae). *Psyche*, **79**, 209–212.

https://doi.org/10.1155/1972/43487

Eberhard, W.G., Agnarsson, I. & Levi, H.W. (2008) Web forms and the phylogeny of theridiid spiders (Araneae: Theridiidae): chaos from order. *Systematics and Biodiversity*, **6**, 415–475.

https://doi.org/10.1017/S1477200008002855

Enders, F. (1974) Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. *Ecology*, **55**, 317–328.

https://doi.org/10.2307/1935219

Frederich, B., Lehanse, O., Vandewalle, P. & Lepoint, G. (2010) Trophic niche width, shift, and specialisation of *Dascyllus aruanus* in Toliara Lagoon, Madagascar. *Copeia*, **2**, 218–226.

https://doi.org/10.1643/CE-09-031

Gonzaga, M.O., Leiner, N.O. & Santos, A.J. (2006) On the stick cobwebs of two theridiidae spiders (Araneae: Theridiidae). *Journal of Natural History*, **40**, 293–306.

https://doi.org/10.1080/00222930600703433

Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19.

https://doi.org/10.18637/jss.v022.i07

Gotelli, N. J., Hart, E.M. & Ellison, A.M. (2015) EcoSimR: Null model analysis for ecological data.

Guevara, J., Gonzaga, M.O., Vasconcellos-Neto, J. & Avilés, L. (2011) Sociality and resource use: insights from a community of social spiders in Brazil. *Behavioral Ecology*, **22**, 630–638.

https://doi.org/10.1093/beheco/arr022

Herberstein, M.E. (1998) Web placement in sympatric linyphiid spiders (Arachnida, Araneae): individual foraging decisions reveal inter–specific competition. *Acta Oecologica*, **19**, 67–71.

https://doi.org/10.1016/S1146-609X(98)80009-X

Japyassú, H.F. & Jotta, E.G. (2005) Forrageamento em *Achaearanea cinnabarina* levi 1963 (Araneae, Theridiidae) e evolução da caça em aranhas de teia irregular. *Biota Neotropica*, **5**, (n1a).

https://doi.org/10.1590/S1676-06032005000200005

Jörger, K.M. & Eberhard, W.G. (2007) Web construction and modification by *Achaearanea tesselata* (Araneae, Theridiidae). *Journal of Arachnology*, **34**, 511–523.

https://doi.org/10.1636/S05-30.1

Knudsen, R., Amundsen, P.A., Primicerio, R., Klemetsen, A. & Sorensen, P. (2007) Contrasting niche-based variation in trophic morphology within Arctic charr populations. *Evolutionary Ecology Research*, **9**, 1005–1021.

Kobler, A., Klefoth, T., Mehner, T. & Arlinghaus, R. (2009) Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia*, **161**, 837–847.

https://doi.org/10.1007/s00442-009-1415-9

Majer, J.D. & Recher, H.F. (1999) Are eucalypts Brazil's friend or foe? An entomological viewpoint. *Anais da Sociedade Entomológica do Brasil*, **28**, 185–200.

https://doi.org/10.1590/S0301-80591999000200001

Marinho, C.G.S., Soares, S.M. & Della Lucia, T.M.C. (1997) Diversidade de invertebrados edáficos em áreas de eucalipto e mata secundária. *Acta Biologica Leopoldensia*, **19**, 157–164.

Mazzoni, R., Marques, P.S., Rezende, C.F. & Iglesias–Rios, R. (2012) Niche enlargement as a consequence of co-existence: a case study. *Brazilian Journal of Biology*, **72**, 267–274.

https://doi.org/10.1590/S1519-69842012000200006

Michalko, R. & Pekár, S. (2014) Is different degree of individual specialization in three spider species caused by distinct selection pressures? *Basic and Applied Ecology*, **15**, 496–506.

https://doi.org/10.1016/j.baae.2014.08.003

Michalko, R. & Pekár, S. (2015) Niche partitioning and niche filtering jointly mediate the coexistence of three closely related spider species (Araneae, Philodromidae). *Ecological Entomology*, **40**, 22–33.

https://doi.org/10.1111/een.12149

Moreno-Mendoza, S. D., Ibarra-Núñez, G., Chamé-Vázquez, E.R. & Valle-Mora, F.J. (2012) Gama de presas capturadas por cuatro especies de arañas tejedoras (Arachnida: Araneae) en un agroecosistema de cacao en chiapas, México. *Tropical and Subtropical Agroecosystems*, **15**, 457–469.

Nasir, D.M., Goh, T.G., Bakri, A., Rahim, F., Mohamed, Z. & Yusoff, N.R. (2017) Web characteristics determine niche partitioning for orb-web spiders (Araneae, Tetragnathidae) in Malaysia. *Oriental Insects*, **51**, 262–275.

https://doi.org/10.1080/00305316.2017.1282385

Nentwig, W. (1987) The prey of spiders. *Ecophysiology of Spiders* (eds W. Nentwig), pp. 251. Springer-Verlag, Berlin.

https://doi.org/10.1007/978-3-642-71552-5

Nyffeler, M., Dean, D.A. & Sterling, W.L. (1988) Prey records of the web-building spiders *dictyna segregata* (Dictynidae), *Theridion australe* (Theridiidae), *Tidarren haemorrhoidale* (theridiidae), and *Frontinella pyramitela* (Linyphiidae) in a cotton agroecosystem. *The Southwestern Naturalist*, **33**, 215–218.

https://doi.org/10.2307/3671897

Nyffeler, M. & Georg, B. (1988) Prey analysis of the spider *Achaearanea riparia* (Blackw.) (Araneae, Theridiidae), a generalist predator in winter wheat fields. *Journal of Applied Entomology*, **106**, 425–431

https://doi.org/10.1111/j.1439-0418.1988.tb00615.x

Oliveira, M.A., Della Lucia, T.M.C., Araújo, M.S. & Cruz, A.P. (1995) A fauna de formigas em povoamentos de eucalipto e em mata nativa no estado do Amapá. *Acta Amazonica*, **25**, 117–126.

https://doi.org/10.1590/1809-43921995252126

Pêgo, P.T. (2014) Especialização individual em *Tidarren haemorrhoidale* (Bertkau, 1880) (Araneae, Theridiidae). Dissertação (Mestrado em Ecologia e Conservação de Recursos Naturais) - Universidade Federal de Uberlândia). Uberlândia, MG. Brasil.

Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, **4**, 53–74.

https://doi.org/10.1146/annurev.es.04.110173.000413

Purcell, J., Vasconcellos-Neto, J., Gonzaga, M.O., Fletcher, J.A. & Avilés, L. (2012) Spatio-temporal differentiation and sociality in spiders. *PLoS ONE*, **7**, e34592.

https://doi.org/10.1371/journal.pone.0034592

R Development Core Team, R. (2018) R: A language and environment for statistical computing.

Rodrigues, E.N.L., Rodrigues, P.E.S. & Mendonça Jr., M.S. (2016) Spider species composition in the tree-shrub strata of riparian forests and its microhabitats in Southern Brazil. *Zoologia*, **33**, e20150102.

https://doi.org/10.1590/S1984-4689zool-20150102

Schoener, T.W. (1968) The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, **49**, 704–726.

https://doi.org/10.2307/1935534

Sørensen, L.L. (2004) Composition and diversity of the spider fauna in the canopy of a montane forest in Tanzania. *Biodiversity and Conservation*, **13**, 437–452.

https://doi.org/10.1023/B:BIOC.0000006510.49496.1e

Souza, A.L.T., Gonzaga, M.O. & Vasconcellos-Neto, J. (2007) Prey capture behaviour in the social spider *Anelosimus eximius* (Araneae: Theridiidae): responses to prey size and type. *Ethology*, **113**, 856–861.

https://doi.org/10.1111/j.1439-0310.2007.01384.x

Souza, H.S.S., Messas, Y.F., Gonzaga, M.O. & Vasconcellos-Neto, J. (2015) Substrate selection and spatial segregation by two congeneric species of *Eustala* (Araneae: Araneidae) in southeastern Brazil. *Journal of Arachnology*, **43**, 59–66.

https://doi.org/10.1636/J14-23.1

Svanbäck, R., Rydberg, C., Leonardsson, K. & Englund, G. (2011) Diet specialization in a fluctuating population of *Saduria entomon*: a consequence of resource or forager densities? *Oikos*, **120**, 848–854.

https://doi.org/10.1111/j.1600-0706.2010.18945.x

Tarjuelo, R., Morales, M.B., Arroyo, B., Mañosa, S., Bota, G., Casas, F. & Traba, J. (2017) Intraspecific and interspecific competition induces density-dependent habitat niche shifts in an endangered steppe bird. *Ecology and Evolution*, **7**, 9720–9730.

https://doi.org/10.1002/ece3.3444

Traba, J., Morales, M.B., Carmona, C.P. & Delgado, M.P. (2015) Resource partitioning and niche segregation in a steppe bird assemblage. *Community Ecology*, **16**, 178–188.

https://doi.org/10.1556/168.2015.16.2.5

Uetz, G. (1977) Coexistence in a guild of wandering spiders. *Journal of Animmal Ecology*, **46**, 531–541.

https://doi.org/10.2307/3828

Violle, C., Nemergut, D.R., Pu, Z. & Jiang, L. (2011) Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, **14**, 782–787.

https://doi.org/10.1111/j.1461-0248.2011.01644.x

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.

https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Yoshida, H. (2016). *Parasteatoda*, *Campanicola*, *Cryptachaea* and two new genera (Araneae: Theridiidae) from Japan. *Bulletin of the Yamagata Prefectural Museum*, **34**, 13–30.

Figures

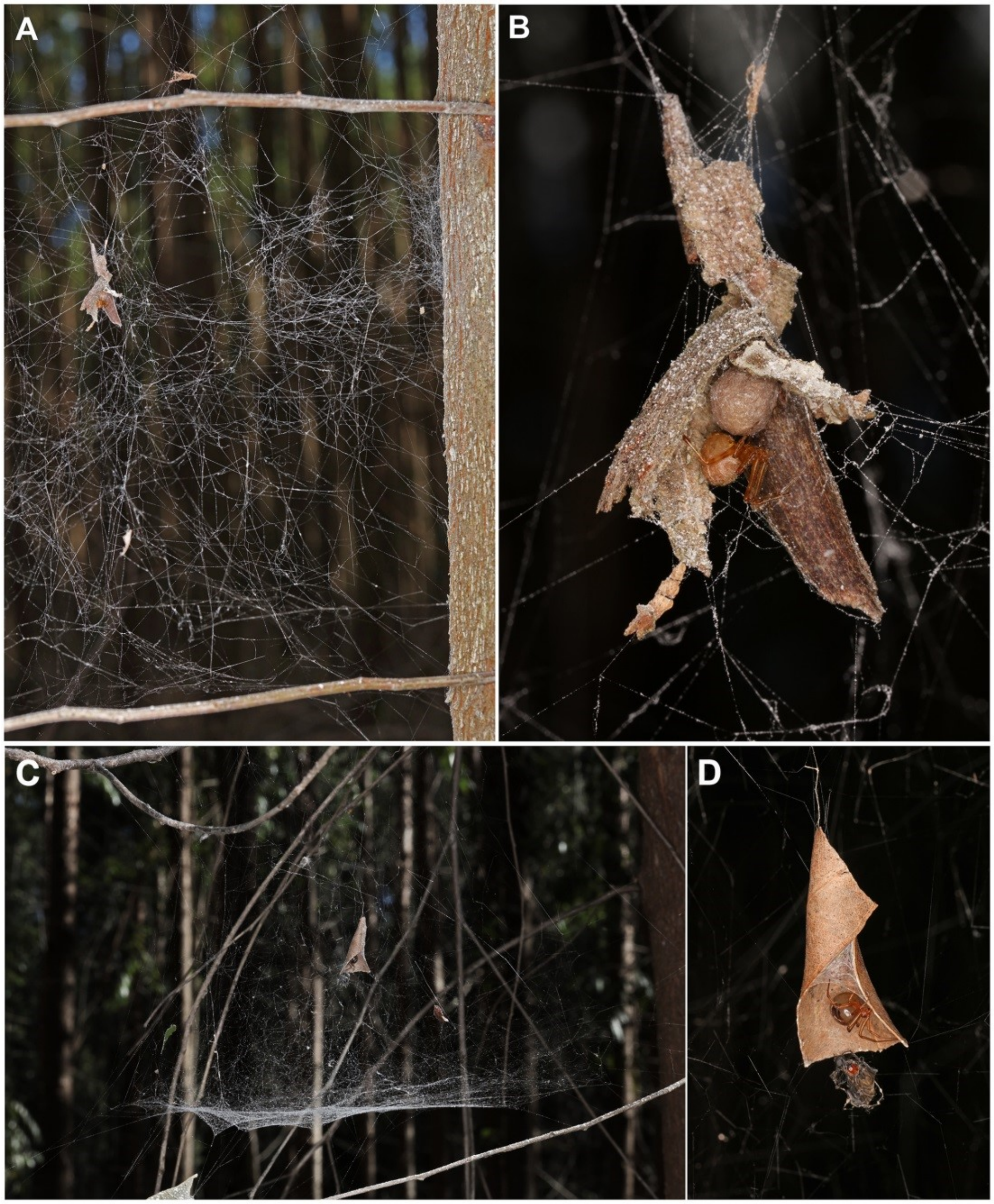

Fig. 1. Webs of the two species studied. A and B. *Tidarren haemorrhoidale*; C and D. *Nihonhimea tesselata*.

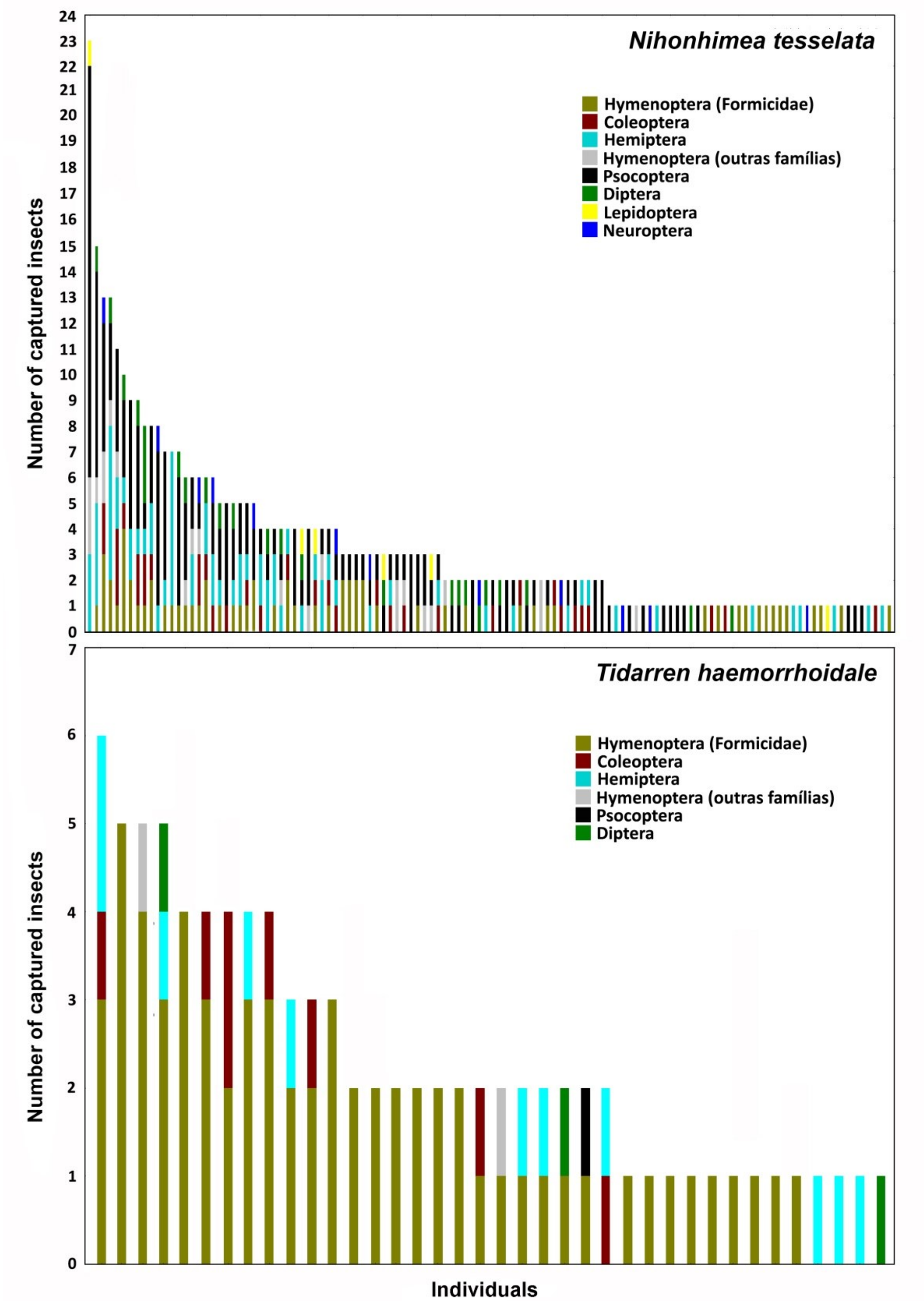

Fig. 2. Preys captured by *Nihonhimea tesselata* and *Tidarren haemorrhoidale*. Each bar represents the diet of an individual.

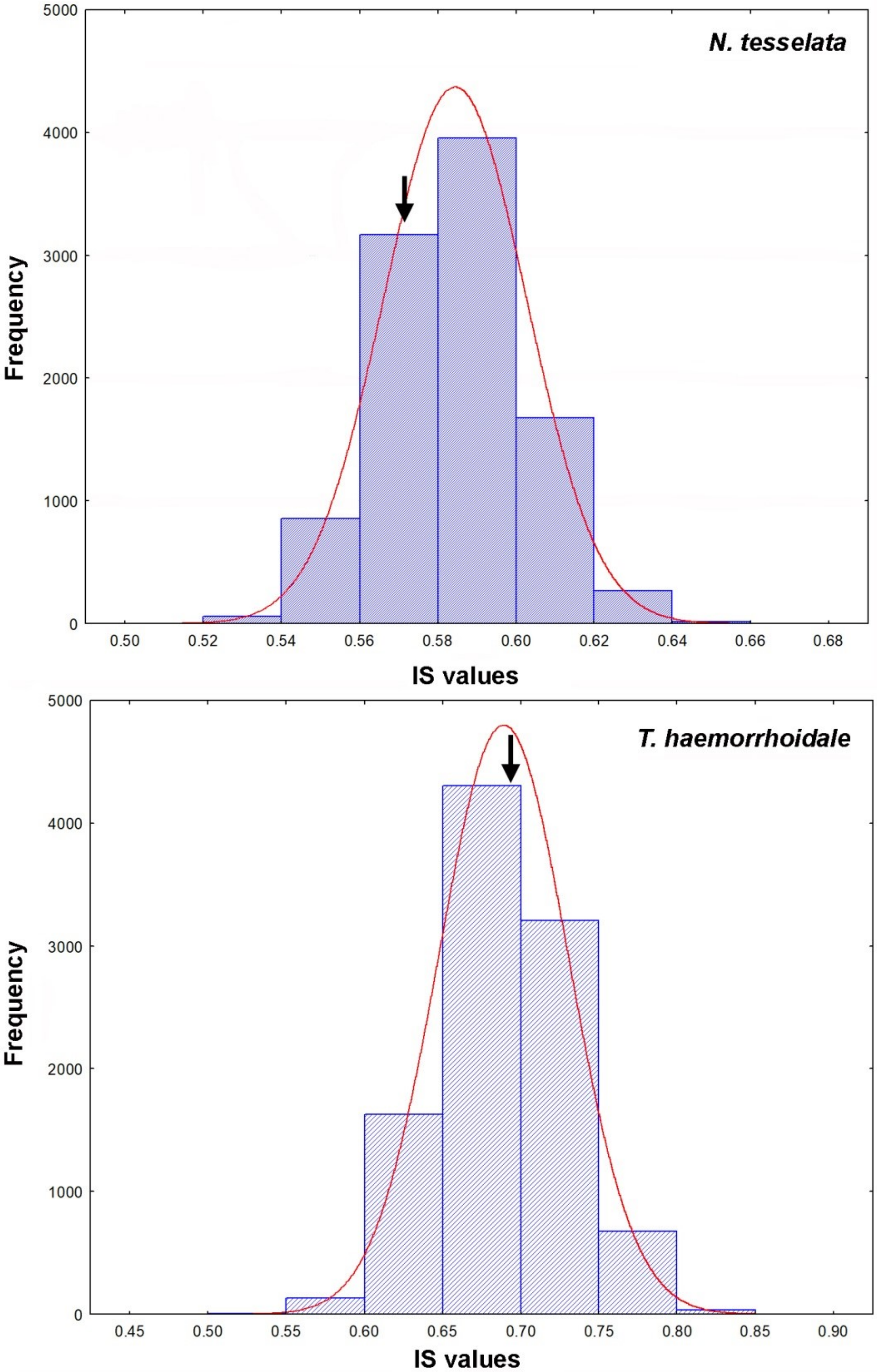

Fig. 3. Monte Carlo Bootstrap with IS values for the 10000 simulations and the observed value indicated by an arrow for *Nihonhimea tesselata* (A) and *Tidarren haemorrhoidale* (B).

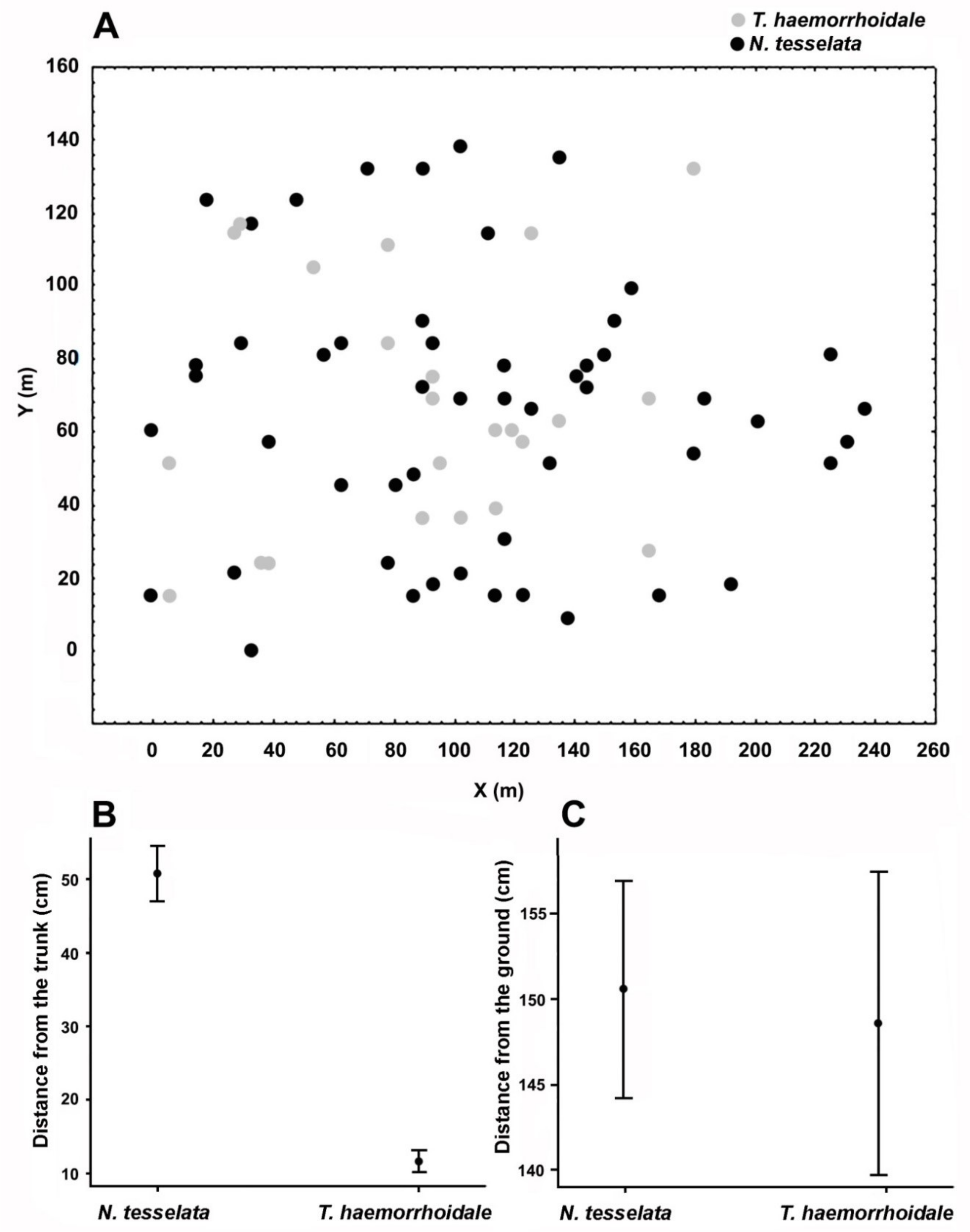

Fig. 4. Vertical and horizontal spatial distribution of the webs of the two species. A. Map of the horizontal distribution of the webs; B and C. Comparison between heights used to fix the webs and distance of *Eucalyptus* trunks with standard deviation.

Capítulo 2

A importância de experiências prévias na eficiência de captura de presas por *Tidarren haemorrhoidale* (Bertkau, 1880) (Araneae, Theridiidae)

Resumo

Os repertórios de forrageamento podem ter uma base inata ou serem aprendidos, seja por tentativa e erro ou observando outros indivíduos. Embora as aranhas sejam mais conhecidas por seu comportamento estereotipado, muitos experimentos demonstraram sua capacidade de aprender e sua plasticidade comportamental. Nesse estudo analisamos o desempenho de *Tidarren haemorrhoidale* (Theridiidae) capturando dois tipos de presas, uma mais abundante em sua dieta (formigas) e outra pouco frequente (besouros) e avaliamos se havia uma redução no tempo de captura com o aumento da experiência em eventos consecutivos. As aranhas foram acondicionadas individualmente em recipientes que simulam seu ambiente natural e divididas em dois grupos. No primeiro foram ofertadas formigas em cinco eventos de alimentação e posteriormente besouros por mais cinco eventos. No segundo grupo a ordem de oferta das presas foi invertida. Pudemos observar que os tempos de forrageamento foram maiores em formigas independente do grupo, possivelmente devido ao sistema defensivo desses insetos que exigia maior tempo em alguns pontos específicos da sequência de comportamentos envolvidos na captura. A experiência não foi um fator determinante pra essa espécie uma vez que os tempos foram variáveis ao longo do experimento. É possível que a estereotipia comportamental observada restrinja-se aos tipos de presa utilizados. A dieta pouco diversificada encontrada no ambiente natural pode ser ao menos em parte, um reflexo da inadequação desse tipo específico de sequência para outros tipos de presas disponíveis.

Palavras–chave: aprendizado, forrageamento, estereotipia, rotinas comportamentais

Introdução

A obtenção de alimento está entre os principais desafios cotidianos de qualquer espécie animal. Sem a energia e os nutrientes obtidos durante o forrageamento, outras atividades, como a reprodução e fuga de predadores, ficam comprometidas (Kamil & Clements 1990). O forrageamento, entretanto, também envolve riscos e investimentos. Quando um animal encontra um item alimentar, ele necessariamente gasta algum tempo (que pode variar de acordo com o tipo de presa) no reconhecimento, interceptação e manipulação (que, em alguns casos, envolve subjugar presas), para que possa consumi-lo (Pyke 1984). Assim, o tempo dispendido para encontrar cada item e o tempo e energia gastos para manipulação, além do potencial risco de injúria durante as capturas, podem constituir variáveis importantes na definição da dieta de um predador (Hughes 1979). Em casos onde a captura de cada tipo de presa demanda comportamentos específicos, é possível que experiências prévias promovam um ajuste de rotinas que maximizem a eficiência de captura (diminuindo o tempo para subjugar a presa e o risco de fuga). Esse aprendizado e aumento de eficiência podem ser muito importantes para aumentar o sucesso do forrageamento (Johnson 1991; Punzo 2005; Reid *et al*. 2010).

De maneira geral, o forrageamento pode ser interpretado como sendo o resultado de um processo de avaliação em que o animal seleciona constantemente entre potenciais fontes de alimento fazendo suas escolhas com base em características inatas e/ou aprendidas (Lewis 1986; Edwards & Jackson 1994; Gumbert 2000). Borboletas e abelhas, por exemplo, podem exibir constância na seleção floral, especializando-se no consumo de determinadas plantas (Lewis 1986; Riffell *et al*. 2008; Amaya-Marquez 2009). Lewis (1986) estudando as borboletas *Pieris rapae* (Linnaeus, 1758) (Pieridae), por exemplo, constatou que a eficiência dos indivíduos em extrair o néctar das flores aumentava com o tempo, seguindo uma curva de aprendizado. Além disso, os indivíduos mostravam consistência ao longo do dia sobre o tipo de flor explorada. Já as formigas *Messor pergandei* (Mayr, 1886) e *Pogonomyrmex rugosus* (Emery, 1895) são capazes de aprender um conjunto de comportamentos específicos que melhoram a eficiência de forrageamento de sementes, reduzindo o tempo de busca após sucessivas tentativas (Johnson 1991).

O aprendizado vem sendo estudado em vários níveis de complexidade em diversos grupos de invertebrados, como abelhas (Gumbert 2000), vespas parasitóides (Vet *et al*. 1995), baratas (Durier & Rivault 2000) e insetos fitófagos (Papaj & Prokopy 1989). Embora artrópodes predadores, como as aranhas, sejam conhecidos por possuírem comportamentos de caça estereotipados (pré-programados), muitos experimentos demonstraram a capacidade de algumas espécies de aprender e investigaram a plasticidade comportamental durante o forrageamento (Foelix 2010). *Phidippus princeps* (Peckham & Peckham, 1883) (Salticidae), por exemplo, é capaz de aprender a encontrar grilos escondidos em labirintos através de pistas com cores específicas associadas à presa (Jakob *et al*. 2008). Em indivíduos imaturos de *Misumena vatia* (Clerck, 1757) (Thomisidae), o tempo de orientação e captura de moscas da fruta diminuiu rapidamente nas primeiras duas ou três tentativas, permanecendo baixo e relativamente constante (Morse 2000). Já a espécie *Larinioides sclopetarius* (Clerck, 1757) (Araneidae), pode ajustar a arquitetura das suas teias de acordo com eventos de capturas em regiões específicas, usando a experiência para construir desenhos mais eficazes (Heiling & Herberstein 1999).

A eficiência de captura e as rotinas comportamentais desempenhadas durante a atividade de forrageamento em aranhas dependem de diversos fatores como, por exemplo, o tipo e do tamanho da presa, das experiências anteriores, da fase de desenvolvimento do indivíduo e até mesmo da fome. (Japyassú & Caires 2008). *Theridion evexum* (Keyserling,

1884) (Theridiidae), por exemplo, apresenta variações comportamentais importantes frente a duas presas diferentes: formigas do gênero *Atta* (Formicidae) e larvas do besouro *Tenebrio molitor* (Linnaeus, 1758) (Tenebrionidae). Apesar do comportamento de captura nessa espécie ser bastante estereotipado, as sequências de picada, enrolamento e transporte diante dessas presas foram distintas, constituindo respostas eficientes para sua imobilização (Garcia & Japyassú 2008).

Apesar de alguns casos bem estudados (e.g. Sandoval 1994; Japyassú & Caires 2008), relativamente pouco se sabe sobre o aprendizado em aranhas construtoras de teia. A maior parte dos trabalhos sobre a variação em rotinas comportamentais, aprendizado e suas consequências em relação à eficiência de captura de presas tem foco em aranhas cursoriais da família Salticidae (Edwards & Jackson 1993; Jackson *et al*. 2002; Jakob *et al*. 2007). Esse trabalho teve como objetivo avaliar como *Tidarren haemorrhoidale* (Bertkau, 1880) se comporta capturando formigas (tipo de presa mais abundantes da sua dieta) e besouros (presas pouco frequentes) comparando os tempos de captura e também analisar o tempo gasto após sucessivos eventos de alimentação. Nossa primeira hipótese é que exista diferença entre os tempos de captura entre as presas analisadas e a segunda é que haja redução no tempo de captura com o aumento da experiência adquirida com eventos consecutivos de captura do mesmo tipo de presa. É possível que exista uma limitação cognitiva que restrinja o desempenho eficiente de muitas variações comportamentais. Nossa expectativa é que diferenças nas rotinas de captura, geralmente necessárias para captura de distintos tipos de presas, e a possível existência de uma limitação cognitiva restringindo o desempenho eficiente de muitas variações comportamentais determinem um menor tempo de manipulação para formigas.

Material e métodos

Área de estudo

O estudo foi desenvolvido no Laboratório de Aracnologia da Universidade Federal de Uberlândia de Junho a Julho de 2017. Para realização dos experimentos, aranhas fêmeas adultas de *T. haemorrhoidale* foram coletadas previamente em um plantio de *Eucalyptus* na Fazenda Nova Monte Carmelo (18º45´11"S, 47º51'28"W), Estrela do Sul, MG, Brasil, e transportadas para o laboratório. As aranhas foram acondicionadas em potes de plástico transparentes com 18 cm de profundidade e 18 cm de diâmetro, que possuíam galhos de eucalipto fixados em seu interior para servirem de pontos de fixação para as teias.

Captura e manipulação das presas

Foram coletadas 30 aranhas adultas e acondicionadas individualmente nos potes e deixadas durante dois dias para possibilitar a construção das teias. As aranhas foram divididas aleatoriamente em dois grupos com 15 indivíduos em cada grupo. Para determinar se existe aprendizado com aumento da experiência, foram realizados 10 eventos de alimentação em cada grupo. Para o primeiro grupo foram fornecidos besouros adultos (*Ulomoides dermestoides* Fairmaire, 1893) durante cinco eventos de alimentação consecutivos, com intervalos de dois dias entre eles. Posteriormente esse grupo recebeu formigas da casta dos soldados (*Camponotus blandus* Smith, 1858) por mais cinco eventos de alimentação, com os mesmos intervalos. Para o segundo grupo, foi o inverso. Foram fornecidas formigas durante cinco eventos de alimentação consecutivos, com intervalos de dois dias entre eles e, posteriormente, esse grupo recebeu besouros por mais cinco eventos de alimentação. Os comportamentos de captura foram registrados com uma câmera Canon EOS 5Ds, e os tempos para captura da presa foram registrados usando as gravações. O tempo de captura foi definido como o intervalo entre o momento que a aranha apresentava alguma resposta motora à introdução da presa até momento que ela se afastava da presa após a picada inicial.

Análises estatísticas

Usamos modelos lineares generalizados mistos (MLGM) com distribuição de Poisson para testar as duas hipóteses do trabalho. Foi testado se o tempo para imobilização da presa era maior com as formigas em relação aos besouros. A variável resposta foi o tempo de captura em segundos (da percepção até o fim da primeira picada), a variável preditora o tipo de presa e as variáveis aleatórias a identidade do indivíduo e a ordem de oferta. Testamos também os efeitos da experiência prévia na manipulação das presas usando um MLGM, sendo a variável resposta o tempo de captura, a variável preditora a ordem de oferta e a variável aleatória a identidade do indivíduo. Para cada grupo foram realizados testes no período inicial (primeiros cinco eventos de captura) e no período após a troca do tipo de presa (cinco eventos finais). Foram realizados testes de comparações planejadas para examinar as diferenças entre as ordens de oferta da presa (primeira pra segunda, da segunda pra terceira e assim sucessivamente) e analisar se ocorre diminuição dos tempos em sucessivos eventos de captura. Foram adotados os seguintes critérios para retirada de alguns valores das análises: 1) quando um indivíduo excedeu o tempo de captura de 1800 segundos e 2) quando um indivíduo morreu antes do término dos experimentos. Analisamos as premissas dos modelos usando gráficos dos resíduos e testes de superdispersão. Realizamos todas as análises de dados no software R, versão 3.5.1 (R Development Core Team 2018), usando os pacotes “lme4” (Bates *et al.* 2015), “car” (Fox & Weisberg 2011) e “ggplot2” (Wickham 2009).

Resultados

As sequências comportamentais observadas durante a captura dos dois tipos de presas foram semelhantes (Figs. 1–3). Quando as formigas eram introduzidas nas teias, as aranhas se orientavam rapidamente em direção às presas lançando fios pegajosos a partir de uma distância que não permitia o contato com o inseto. Os movimentos evasivos das formigas faziam com que ficassem cada vez mais envoltas pelos fios e substâncias viscosas, possibilitando a aproximação das aranhas para a picada após a redução dos movimentos. Nesse momento, a aranha geralmente evitava a região próxima à cabeça da presa e picava a ponta do tarso ou articulações várias vezes. Somente quando a presa permanecia imóvel ou apenas com poucos movimentos esporádicos, a aranha picava a região da cabeça (antenas ou olhos). De forma semelhante quando um besouro era introduzido à aranha, o predador se orientava rapidamente em direção à presa e lançava fios pegajosos ainda sem aproximar-se. Como besouros têm uma menor mobilidade quando interceptados pela teia e cessavam seus movimentos em pouco tempo, as aranhas conseguiam enrolar o inseto e picar a região da cabeça e tórax em um curto intervalo desde a detecção. Em ambas as presas, as sequências de enrolamento, picada e afastamento eram repetidas várias vezes até que ficassem completamente imóveis e assim fossem transportadas para região do abrigo onde eram consumidas.

O tempo de captura dos besouros foi menor que o de formigas, independente de que presa foi inicialmente ofertada ($\chi^2 = 4605,9$; gl = 1; $P < 0,001$) (Fig. 4). O tempo médio de captura dos besouros foi de 484,8±313,2 segundos com o menor tempo sendo 73 e o maior 1577 segundos (Fig. 5). Já para as formigas o tempo médio de captura foi de 684,5±322,8 segundos com o menor tempo sendo 134 e o maior 1728 segundos (Fig. 6). Não foi observada a redução dos tempos de captura com a adição de eventos de captura (aumento de experiência com o tipo de presa) em nenhum dos grupos (Figs. 5 e 6, Tab. 1).

Discussão

Esse estudo mostrou que aranhas da espécie *T. haemorrhoidale* podem capturar presas raramente incluídas em sua dieta seguindo basicamente as mesmas rotinas comportamentais observadas durante a captura de formigas, item mais frequente em sua alimentação. O tempo de captura dos besouros foi menor, independente do tipo de presa que é inicialmente ofertada. Isso possivelmente ocorreu porque formigas comportam-se de forma muito distinta quando são interceptadas pela teia, movimentando-se muito mais e inibindo uma pronta aproximação do predador. A aproximação para a picada ocorre apenas após a presa estar completamente envolta por fios pegajosos e com movimentos reduzidos. A cautela e hesitação para aproximação podem reduzir os riscos de injúria durante a captura de um tipo de presa potencialmente perigosa (veja Pekár 2004; Líznarová & Pekár 2013, sobre riscos de captura de formigas). Da mesma forma, em *Zodarion* sp. (Zodariidae), outra espécie de aranha com hábitos essencialmente mirmecofágicos, o tempo de manipulação aumenta em espécies de formigas mais agressivas (Pekár 2005). Já os besouros, se movem muito pouco e não representam riscos, facilitando a aproximação para a picada. Como não possuem mandíbulas que ofereçam risco, as picadas nessas presas ocorriam diretamente entre o tórax e a cabeça, possibilitando uma imobilização muito mais rápida (veja Pollard 1990).

Os tempos de captura para ambas as espécies de presas não foram diminuindo após sucessivos eventos de alimentação. É possível que a utilização de aranhas adultas para o experimento tenha influenciado esse resultado, uma vez que todos os indivíduos já haviam tido experiências prévias de captura em campo. Isso explicaria a ausência de variação temporal na eficiência, ao menos para formigas. Uma outra possibilidade, seria a existência de sequências comportamentais estereotipadas e pouco variáveis para distintos tipos de presas. Realmente observamos que as rotinas comportamentais durante o forrageamento para captura de besouros e formigas são muito similares. As diferenças estão restritas ao início do processo de imobilização, quando pode haver uma picada diretamente na cabeça ou tórax de besouros, mas geralmente há uma primeira picada nas pernas de formigas. Em *Achaearanea cinnabarina* (Levi, 1963) à medida a presa vai sendo imobilizada, a estereotipia nas rotinas comportamentais desempenhadas para distintas presas também aumenta. Isso indica que a variabilidade das respostas iniciais da presa tem grande influência na plasticidade comportamental das aranhas durante o forrageamento (Japyassú & Jota 2005).

É possível que a estereotipia comportamental observada nos experimentos restrinja-se aos tipos de presa utilizados e que existam comportamentos muito distintos envolvidos na captura de outros tipos com estratégias evasivas diferentes, como a alta frequência de batimento de asas. Em seu ambiente natural, *T. haemorrhoidale* mostra-se capaz de capturar insetos de outras ordens, como Hemiptera, Coleoptera e Diptera (veja capítulo 1). Assim, seria interessante determinar se a estabilidade na execução da mesma sequência de comportamentos de captura é observada também para essas outras potenciais presas. Dessa forma, a ocorrência de aprendizado e aumento progressivo na eficiência de captura em *T. haemorrhoidale* não pode ser negada com base apenas na comparação dos tempos de captura para dois tipos de presas. Em contraste com outras famílias, as aranhas da família Theridiidae mostram um pequeno conjunto de táticas de ataque (Japyassú & Caires 2008). As espécies *Achaearanea digitus* (Buckup & Marques, 2006) e *Theridion evexum*

(Keyserling, 1884), por exemplo, possuem mais de 40% do repertório predatório estereotipado. Se o comportamento for semelhante também durante a captura de outras presas em *T. haemorroidale*, é possível que a dieta pouco diversificada seja, ao menos em parte, um reflexo da variação na eficiência desse tipo específico de sequência para os tipos de presas disponíveis.

Segundo Heiling & Herberstein (1999) o comportamento de construção de teias nas aranhas é inato, contudo esses predadores podem aprender através de encontros com presas a construírem teias mais seletivas e, assim, forragear de forma mais eficiente (Sandoval 1994). Edwards & Jackson (1994) demonstraram que os comportamentos predatórios de imaturos e adultos de *Phidippus regius* (L.Koch, 1846) eram semelhantes, indicando que a estratégia predatória condicional é pré-programada nesta espécie (ou seja, diferentes respostas a diferentes presas não dependem da experiência anterior com essas presas). Estudos futuros comparando os tempos de captura entre adultos e imaturos de *T. haemorrhoidale* poderiam explicar se o aprendizado é adquirido com a experiência ou se as rotinas de manipulação de presas são inatas para essa espécie.

Nesse trabalho concluimos que os tempos de forrageamento foram maiores em formigas, pois esses insetos possuem um sistema defensivo que exige rotinas mais demoradas entre aproximação, enrolamento e picada para que sejam completamente dominados. A experiência não foi um fator determinante uma vez que os indivíduos conseguiram manipular as presas de forma eficiente desde a primeira captura, apresentando tempos variáveis nos eventos subsequentes. As rotinas comportamentais aparentemente não envolvem categorias comportamentais muito distintas, dessa forma o tempo necessário para captura depende do comportamento da presa interceptada e/ou seu potencial risco de injúria para o predador. Além disso, experiências prévias com besouros e formigas podem ter ajudado na manipulação das presas, resultando na similaridade entre os tempos e comportamentos desempenhados desde o início até o término dos experimentos. Estudos futuros que analisem a relação entre experiência e aprendizado em diferentes estágios de desenvolvimento podem aumentar a compreensão do tema em *T. haemorrhoidale* e outras aranhas da família Theridiidae.

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Referências

Amaya-Marquez, M. (2009) Floral constancy in bees: a revision of theories and a comparison with other pollinators. *Revista Colombiana de Entomologia*, **35**, 206–216.

Durier, V. & Rivault, C. (2000) Learning and foraging efficiency in German cockroaches, *Blattella germanica* (L.) (Insecta: Dictyoptera). *Animal Cognition*, **3**, 139–145.
https://doi.org/10.1007/s100710000065

Edwards, G.B. & Jackson, R.R. (1993) Use of prey-specific predatory behaviour by North American jumping spiders (Araneae, Salticidae) of the genus *Phidippus*. *Journal of Zoology*, **229**, 709–716.
https://doi.org/10.1111/j.1469-7998.1993.tb02666.x

Edwards, G.B. & R.R. Jackson. (1994) The role of experience in the development of predatory behavior in *Phidippus regius*, a jumping spider (Araneae, Salticidae) from Florida. *New Zealand Journal of Zoology*, **21**, 269–277.

https://doi.org/10.1080/03014223.1994.9517994

Foelix, R. (2011) *Biology of spiders* (3rd ed). Oxford University Press, Oxford.

Garcia, C.R.M. & Japyassú, H.F. (2005) Estereotipia e plasticidade na sequência predatória de *Theridion evexum* Keyserling 1884 (Araneae: Theridiidae). *Biota Neotropica*, **5**, 27–43.

https://doi.org/10.1590/S1676-06032005000200003

Gumbert, A. (2000) Colour choices by bumblebees (*Bombus terrestris*): innate preferences and generalization after learning. *Behavioural Ecology and Sociobiology*, **48**, 36–43.

https://doi.org/10.1007/s002650000213

Heiling, A.M. & Herberstein, M.E. (1999) The role of experience in web-building spiders (Araneidae). *Animal Cognition*, **2**, 171–177.

https://doi.org/10.1007/s100710050037

Hughes, R.N. (1979) Optimal diets under the energy maximization premise: the effects of recognition time and learning. *The American Naturalist*, **113**, 209–221.

https://doi.org/10.1086/283380

Jackson, R.R., Pollard, S.D., Li, D.Q. & Fijn, N. (2002) Interpopulation variation in the risk-related decisions of *Portia labiata*, an araneophagic jumping spider (Areneae, Salticidae), during predator sequences with spitting spiders. *Animal Cognition*, **5**, 215–223.

https://doi.org/10.1007/s10071-002-0150-y

Jakob, E.M., Skow, C.D., Haberman, M.P. & Plourde, A. (2007) Jumping spiders associate food with color cues in a T-maze. *Journal of Arachnology*, **35**, 487–492.

https://doi.org/10.1636/JOA-ST06-61.1

Japyassú, H.F. & Caires, R.A. (2008) Hunting Tactics in a Cobweb Spider (Araneae–Theridiidae) and the Evolution of Behavioral Plasticity. *Journal of Insect Behavior*, **21**, 258–284.

https://doi.org/10.1007/s10905-008-9124-5

Japyassú, H.F. & Jotta, E.G. (2005) Forrageamento em *Achaearanea cinnabarina* levi 1963 (Araneae, Theridiidae) e evolução da caça em aranhas de teia irregular. *Biota Neotropica*, **5**, 53–67.

https://doi.org/10.1590/S1676-06032005000200005

Johnson, R.A. (1991) Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. *Ecology*, **72**, 1408–1419.

https://doi.org/10.2307/1941112

Kamil, A.C. & Clements, K.C. (1990) Learning, memory, and foraging behavior. *Contemporary issues in comparative psychology* (eds D.A. Dewsbury), pp. 7–30. Sunderland (MA), Sinauer Associates.

https://doi.org/10.1037/11525-001

Lewis, A.C. (1986) Memory constraints and flower choice in *Pieris_rapae*. *Science*, **232**, 863–865.

https://doi.org/10.1126/science.232.4752.863

Líznarová, E. & Pekár, S. (2013) Dangerous prey is associated with a type 4 functional response in spiders. *Animal Behaviour*, **85**, 1183–1190.

https://doi.org/10.1016/j.anbehav.2013.03.004

Morse, D.H. (2000) The effect of experience on the hunting success of newly emerged spiderlings. *Animal Behavior*, **60**, 827–835.

https://doi.org/10.1006/anbe.2000.1546

Papaj, D.R. & Prokopy, R.J. (1989) Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology*, **34**, 315–350.

https://doi.org/10.1146/annurev.en.34.010189.001531

Pekár, S. (2004) Predatory behavior of two European ant-eating spiders (Araneae, Zodariidae). *Journal of Arachnology*, **32**, 31–41.

https://doi.org/10.1636/S02-15

Pekár, S. (2005) Predatory characteristics of ant-eating *Zodarion* spiders (Araneae: Zodariidae): potential biological control agents. *Biological Control*, **34**, 196–203.

https://doi.org/10.1016/j.biocontrol.2005.05.008

Pollard, S.D. (1990) The feeding strategy of a New Zealand crab spider *Diaea* sp. indet. (Araneae, Thomisidae): post-capture decision rules. *Journal of Zoology*, **222**, 601–615.

https://doi.org/10.1111/j.1469-7998.1990.tb06017.x

Punzo F. (2005) Experience affects hunting behavior of the wasp, *Pepsis mildei* Stål (Hymenoptera: Pompilidae). *Journal of the New York Entomological Society*, **113**, 222–229.

https://doi.org/10.1664/0028-7199(2005)113[0222:EAHBOT]2.0.CO;2

Pyke, G. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15**, 523–75.

https://doi.org/10.1146/annurev.es.15.110184.002515

R Development Core Team, R. (2018) R: A language and environment for statistical computing.

Reid, A.L., Seebacher, F. & Ward, A.J.W. (2010) Learning to hunt: the role of experience in predator success. *Behaviour*, **147**, 223–233.

https://doi.org/10.1163/000579509X12512871386137

Riffell, J.A., Alarcon, R., Abrell, L., Davidowitz, G., Bronstein, J.L. & Hildebrand, J.G. (2008) Behavioral consequences of innate preferences and olfactory learning in hawkmoth-flower interactions. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 3404–3409.

https://doi.org/10.1073/pnas.0709811105

Sandoval, C.P. (1994) Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology*, **8**, 701–707.

https://doi.org/10.2307/2390229

Vet, L.E.M., Lewis, W.J. & Cardé, R.T. (1995) Parasitoid foraging and learning. *Chemical Ecology of Insects 2* (eds R.T. Cardé & W.J. Bell) pp. 65–101. New York, Chapman & Hall.

https://doi.org/10.1007/978-1-4615-1765-8_3

Figuras

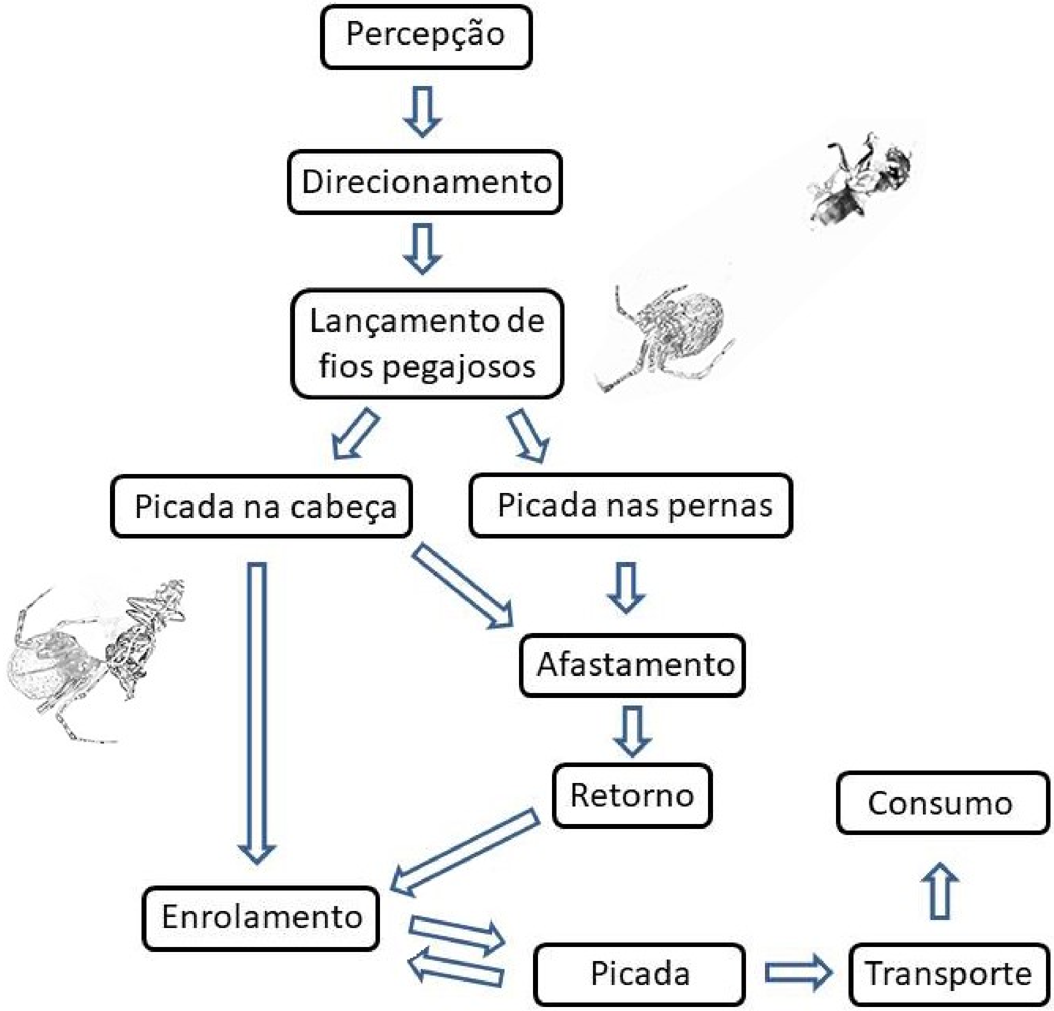

Fig. 1. Etograma qualitativo apresentando as sequências comportamentais observadas durante a captura de presas por *Tidarren haemorrhoidale*.

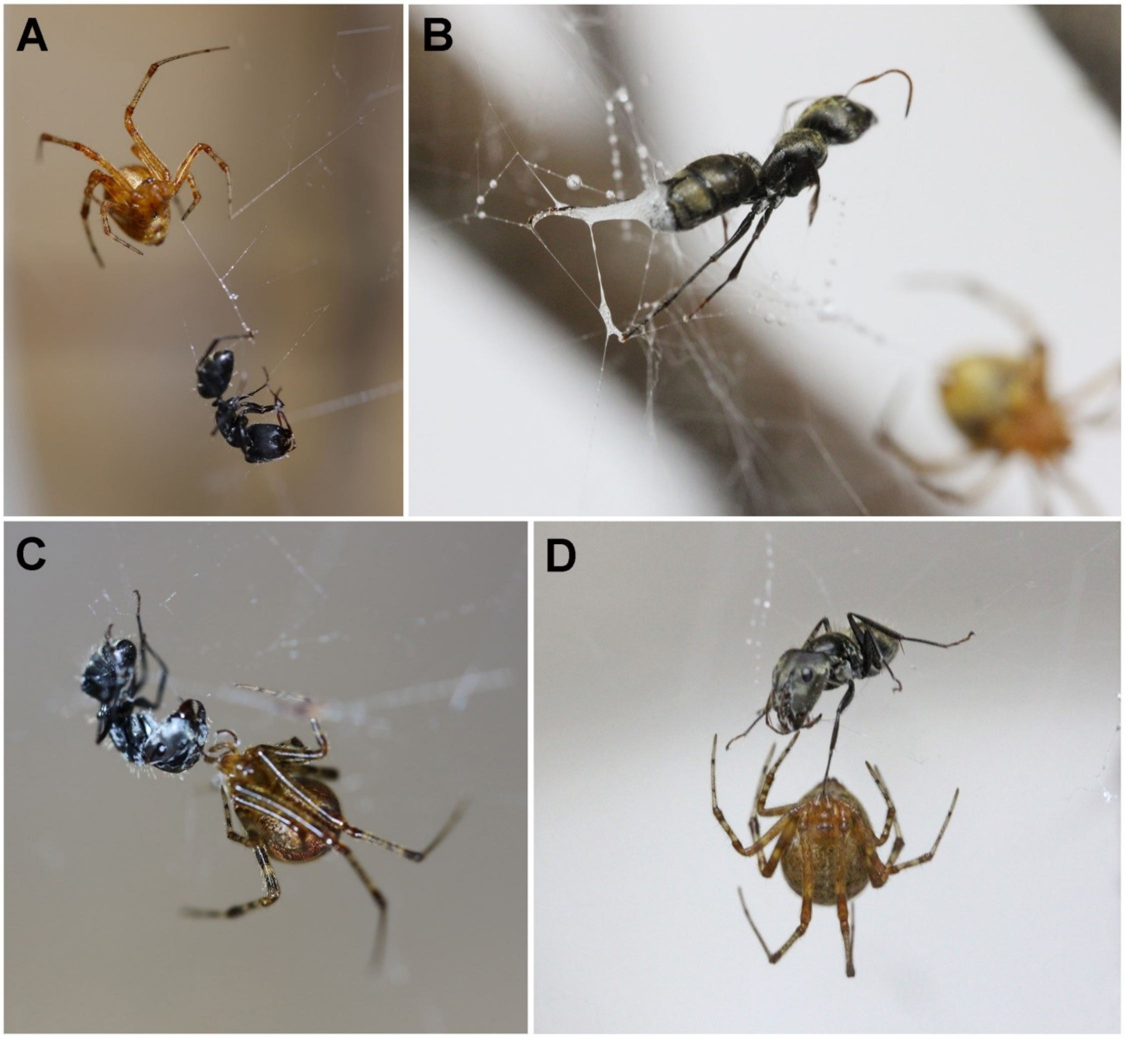

Fig. 2. Comportamentos envolvidos no início do processo de captura de formigas por *T. haemorrhoidale*. As fotos A e B mostram o lançamento de fios pegajosos e as fotos C e D os locais de picada.

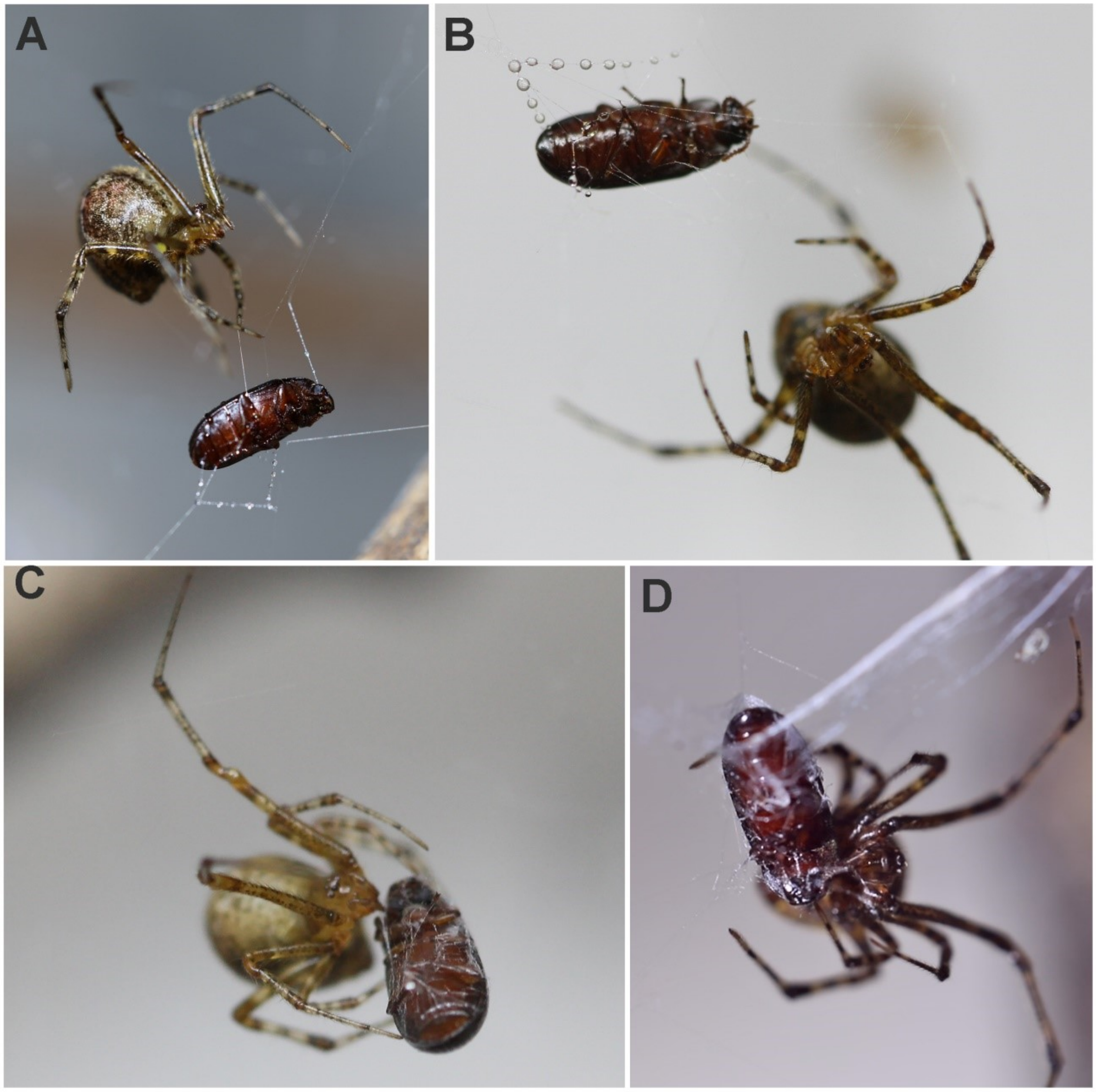

Fig. 3. Comportamentos envolvidos no início do processo de captura de besouros por *T. haemorrhoidale*. As fotos A e B mostram o lançamento de fios pegajosos e as fotos C e D os locais de picada.

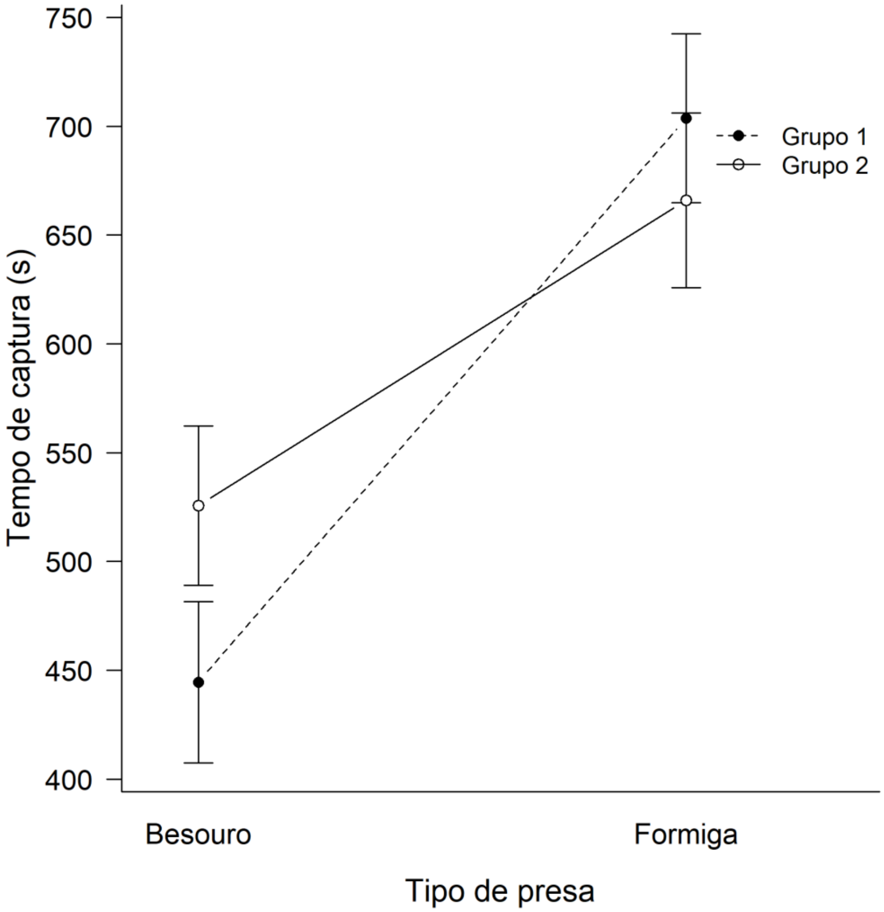

Fig. 4. Tempo de captura de *T. haemorrhoidale* entre os tipos de presa com erro padrão. Grupo 1: inicio com besouros e posteriormente recebiam formigas. Grupo 2: início com formigas, posteriormente recebiam besouros.

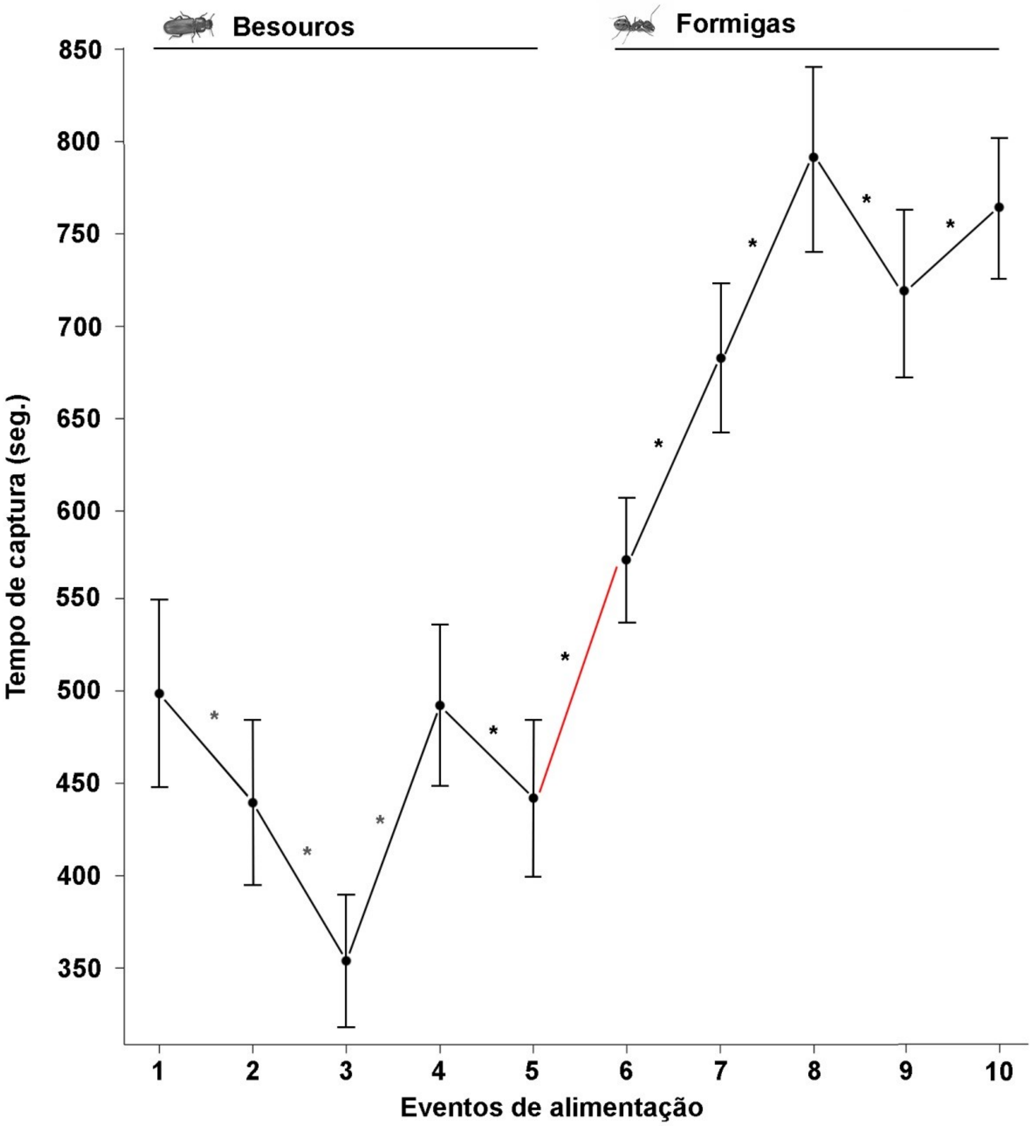

Fig. 5. Tempo de captura de *T. haemorrhoidale* do grupo 1 sendo as cinco primeiras ofertas com besouros e as cinco últimas com formigas. Não houve aprendizado referente à diminuição do tempo após sucessivas capturas. Intervalores apresentam o erro padrão. Valores parciais do modelo depois de descontar a variação atribuída às variáveis aleatórias.

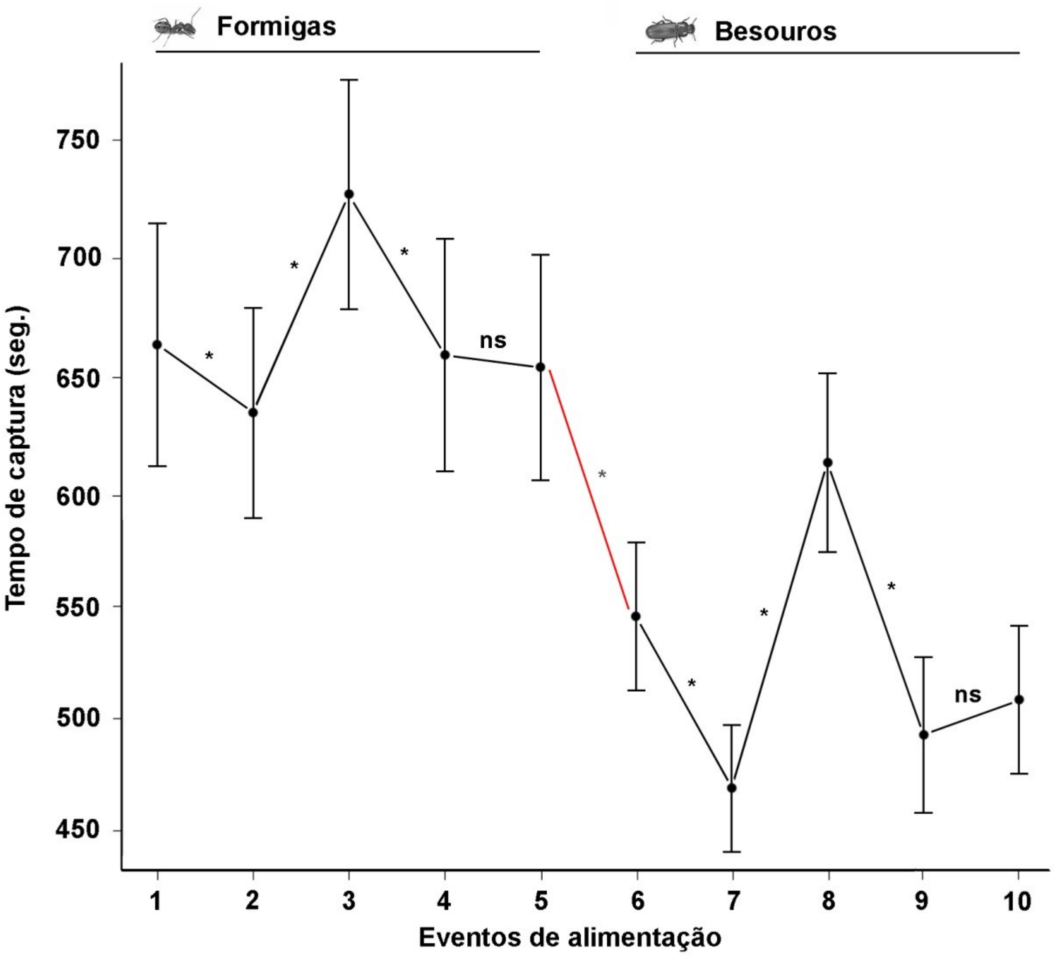

Fig. 6. Tempo de captura de *T. haemorrhoidale* do grupo 2 sendo as cinco primeiras ofertas com formigas e as cinco últimas com besouros. Não houve aprendizado referente à diminuição do tempo após sucessivas capturas. Intervalores apresentam o erro padrão. Valores parciais do modelo depois de descontar a variação atribuída às variáveis aleatórias.

Tabela 1. Resultado do modelo linear generalizado misto realizado para analisar os sucessivos eventos de captura. O tempo de captura foi a variável resposta, a variável preditora foi à ordem de oferta e a variável aleatória a identidade do indivíduo.

Grupos	χ^2	*gl*	*P*
Grupo 1 (eventos 1 – 5)	554,16	4	< 0,001
Grupo 1 (eventos 6 – 10)	551,86	4	< 0,001
Grupo 2 (eventos 1 – 5)	128,23	4	< 0,001
Grupo 2 (eventos 6 – 10)	344,24	4	< 0,001

Capítulo 3

Effect of diet on development, fecundity and survival of *Tidarren haemorrhoidale* (Bertkau, 1880) (Araneae, Theridiidae)

Abstract

The range of trophic niches in spiders vary from very wide, including prey from several insect orders, other arthropods, and even nectar and other plant products, to very narrow, being restricted to specific prey types, such as ants. In all cases, there is some diet restrictions associated with the specific types of webs constructed or other foraging behaviors. In addition, physiological traits and ecological conditions may be involved in diet determination. Previous studies showed that the effects of a mixed diet is beneficial to fecundity, survivorship and growth rate for some species, but not for others. Most of these studies, however, were conducted with cursorial spiders. In this study we evaluated the effects of monotypic diets of beetles, ants, termites and a mixed diet in these parameters for *Tidarren haemorroidale*, a cobweb spider. Adult females were collected in the field, kept in captivity, and divided in four experimental groups, each one submitted to one of these diets for 125 days. Our results indicate that two monotypic diets composed of the main prey types (beetles and ants) previously reported as common items captured by *T. haemorrhoidale* have similar effects on fecundity and weight maintenance compared to a mixed diet. On the other hand, a monotypic diet of termites lead to the production of reduced number of eggs and also affected the weight. Survivorship in all groups was similar. These results indicate that a diversified diet is not required for *T. haemorrhoidale* to achieve its maximum reproductive potential. This characteristic may be important to assure the success of this species in colonization and establishment of large populations even in disturbed habitats, with low prey diversity.

Keywords: specialization of diet, nutritional quality, egg production, favorite prey

Introduction

According to the optimal foraging theory, individuals should use strategies that maximize energy gain during foraging activities, selecting items according to their abundance in the environment and/or nutritional quality. In addition, individuals own ability to detect, obtain, manipulate, and digest these items may also have influence on diet determination (Svanbäck & Bolnick 2005; Jensen *et al.* 2011a). In some cases, nutrient balance in diet may be achieved by the consumption of one or few good quality food types, while in others by mixing prey of imbalanced but complementary composition (Toft 2013). Euryphagous species may have an advantage over oligophagous or stenophagous species in obtaining a balanced diet due to variation in the composition of the several items consumed. On the other hand, highly specialized species can be more efficient at catching and handling their prey. In addition, behavioral and physiological adaptations to restricted diets may minimize possible nutritional constraints associated to the consumption of few food items (Pékar *et al.* 2010; Terraube *et al.* 2011).

The evaluation of the quality of a diet must consider all aspects of the prey nutritional composition (including energy content and essential nutrients), defined as the prey's contribution to the predator's fitness (Toft 1999; Toft & Wise 1999a; Toft & Wise 1999b). It also involves costs associated with capture and digestion, as well as the quantification of indigestible parts of prey and the presence of toxins, which can drastically affect the suitability of an specific item (Oelbermann & Scheu 2002; Wilder 2011). Most of all, however, it is important to consider that different species (and sometimes, individuals) may present distinct nutritional requirements and adaptations to exploit efficiently their preffered prey (e.g. Hooker *et al.* 2017; Pekár *et al.* 2018).

The quality of food items is particularly important for terrestrial predatory arthropods because they are often limited by nutrients and may face prey shortages for long periods (Wise 1993; Wilder & Rypstra 2008). In this group, food limitation and/or the lack of specific nutrition components may interfer in several important life history traits, such as growth rates, survivorship in different instars and reproduction. Diet composition, however, may differently affect even closely related species. Jensen *et al.* (2011a), for example, tested how the nutritional composition of prey affected the body condition and growth of *Pardosa amentata* (Clerk, 1757) (Lycosidae). They found that a protein-poor and lipid-rich diet increased the duration of the instars in this species with annual life cycle. Another cogeneric and sympatric species, *Pardosa prativaga* (L.Koch, 1870), on the other hand, showed behavioral and physiological mechanisms for regulating nutrients acquisition, adjusting capture rate and nutrient extraction in response to prey mass and nutrient composition of offered prey (Jensen et *al*. 2011b). The body composition of individuals of *P. prativaga* was also affected by nutrient composition of prey, but they are adapted to acquiring and maintaining essential components of their diet even in periods of prey shortage or when the availability of suitable items is restricted.

The nutritional status of spiders and the quality of captured prey may be especially important in the reproductive process (Mayntz *et al*. 2003; Wilder & Rypstra 2008; Barry & Wilder 2013) because the egg production in these animals is strongly influenced by their body condition (Fritz & Morse 1985; Head 1995; Mayntz *et al*. 2003). Thus, it is expected that the consumption of high-quality prey items will generally ensure an efficient weight gain in the pre-reproductive period, resulting in a higher fecundity. To corroborate this hypothesis, Wilder & Rypstra (2008) reported that females of *Pardosa milvina* (Hentz, 1844) (Lycosidae) captured in the field and fed with a high quality diet produced eggsacs faster than those who received a low quality diet. Similarly, females of *Zygiella x-notata* (Clerk, 1757) (Araneidae) fed with prey of high nutritional quality, developed faster and produced more eggs in a laboratory experiment (Mayntz *et al.* 2003).

In addition to fecundity, several other life history parameters of spider species, such as survival, growth and the development of spiderlings were previously reported as varying according to diet diversification (Uetz *et al*. 1992; Toft & Wise 1999a; Toft & Wise 1999b; Oelbermann & Scheu 2002). This may occur because the inclusion of several different prey in the diet assures a broader range of nutrients, optimizing the fulfillment of essential nutritional requirements, such as certain amino acids and lipids (Uetz *et al.* 1992).

Spiders of the Theridiidae family are often known to be generalist predators, capturing a wide range of prey that includes mainly insects of the orders Hymenoptera, Hemiptera and Coleoptera (Nyffeler *et al*. 1988; Knoflach & Harten 2006). A few cases of stenophagy were reported for the genera *Asagena*, *Dipoena*, *Euryopis*, *Phycosoma*, *Steatoda*, *Yaginumena* (mirmecophagous species), *Chrsiothes* (termitophagous species), *Cryptachea* and *Phoroncidia* (dipterophagous species) (Pekár *et al.* 2012). However, the impacts of diet diversification on parameters of the spider life history within this group have not been previously investigated. In fact, most previous studies on spider nutrition have been conducted with lycosids (Toft & Wise 1999a; Wilder & Rypstra 2008; Jensen *et al*. 2011a). In this group, it is well stablished that, in some species, a diet of poor nutritional quality can generate trade-offs between development and fecundity, with longer periods at each instar, low egg production or early death.

In this study we compared the effects of one mixed and three different monotypic diets on the weight gain, fecundity and survival of *Tidarren haemorrhoidale* (Bertkau, 1880) (Theridiidae). Considering that ants represent about 70% of the prey items captured by *T. haemorrhoidale* females in the studied population (see chapter 1) and the results indicating individual specialization in beetles or ants reported by Pêgo (2014), we expected that monotypic diets composed of these two prey types would have similar effects than a mixed diet for the species. Termites, on the other hand, are a relatively rare prey and we expect a reduction in weight, fecundity and survival of individuals feeding exclusively on these insects.

Material and Methods

Study species

Tidarren haemorrhoidale build webs composed of a dense non-stick tangle containing a refuge made of a curled dry leaf. It was previously reported feeding mostly on aphids and ants in agricultutural environments (Nyffeler *et al*. 1988; Breene *et al.* 1993; Moreno-Mendoza *et al.* 2012), and mostly on ants and beetles (but also prey included in other nine insect orders) in natural reserve of Atlantic Forest in Southeastern Brazil (Pêgo 2014). Results reported by Pego (2014) suggest that even presenting a populational broad diet range, the diet of individuals of *T. haemorrhoidale* are much more restrict and she suggest that specific sequences of prey capturing behaviors and a cognitive limitation to perform efficiently several of these sequences may induce to individual specialization in this species.

Study site

Spiders were collected in an *Eucalyptus* plantation located in Fazenda Nova Monte Carmelo (18º45′11”S, 47º51’28”W), Estrela do Sul, MG, Brasil. Spiders were maintained in plastic containers (diameter x height = 18x18cm) with *Eucalyptus* branches attached to the walls for web placement and wet cotton to maintain moisture. The study was developed at Laboratório de Aracnologia of Universidade Federal de Uberlândia – MG.

Differential diets

The experiment was conducted between August and December 2017. We initially collected 74 adult females in the field. All spiders were weighted and we excluded the 15 lighter and the 15 heavier spiders. The remaining 44 females were randomly divided in four experimental groups: 1) diet composed exclusively of adult beetles (*Ulomoides dermestoides* Fairmaire, 1893), 2) diet composed of exclusively of termite workers (*Nasutitermes corniger* Motschulsky, 1855), 3) diet composed exclusively of ant soldiers (*Camponotus blandus* Smith, 1858), and 4) mixed diet including all the prey types used in the other groups. The last group received only one type of prey in each feeding event always following the same order. Individuals from all groups received prey every other day. In order to standardize the amount of food available for spiders in each group, we previously fed other females with each prey type, weighting the insect before and after being consumed (Table 1). By conducting this procedure, we were able to determine how much food is extracted from each prey type. The number of prey items (one beetle, one ant or two termites) offered in each feeding event during the experiment was chosen such that the total biomass of food ingested by spiders was equal across the experimental treatments. The experiment was conducted during 125 days, from August 11 to December 14, 2017. All spiders were weekly weighed after the 40th day (September 19) in order to evaluate differences in weight gain among groups. All the eggsacs deposited by females were removed carefully and eggs were counted using a stereomicroscope Leica M205C (Fig. 1).

Prey nutritional content

To determine the nutritiional composition of each prey type we conducted bromatological analysis quantifying moisture content, protein and lipid contents. Nine grams of each prey were sent to the bromatological laboratory LaborNutri to the development of the protocol defined by Compêndio Brasileiro de Alimentação Animal (2013).

Statistical analysis

We tested the effect of diet on weight changes using a general linear mixed model, in which weight was used as response variable, diet as predictor variable, and female identity as a random variable. We conduct an ANOVA to test the effect of diet (predictor variable) on egg production (response variable). To evaluate the effect of diet on female survivorship, we performed a Kaplan-Meier survivorship analysis and compared female survivorship between groups using a log-rank test. All statistical analyses were conducted in the software R, version 3.5.1 (R Development Core Team 2018). We used the following packages: "lme4" (Bates *et al*. 2015), "car" (Fox & Weisberg 2011), "ggplot2" (Wickham 2009), "survival", (Therneau *et al*. 2000), and "coin" (Hothorn *et al.* 2006).

Results

Beetles presented the highest values of both, proteins and lipids. Termites and ants had equivalent amounts of proteins, but ants were poorer in lipids (Table 2). At the beginning of the experiment, spiders in all groups presented similar weights ($F_{3,40} = 0.40$, $P = 0.748$), but, at the end of the experimental period, the weight differed among groups. Diets had distinct impacts on gain/reduction of weight in spiders during the 125 days of experiment ($F_{1,3}$ = 13.82, P < 0.001; Table 3). In the group that received only termites, female weight decreased during the experiment, while it remained constant in the other (Fig. 2).

Egg production depended on diet treatments ($F_{3,37}$ = 3.78, P = 0.018). There was no difference between the "beetle diet" and "mixed diet" groups, and between those groups and "ant diet" group. However, the diet based on termites resulted in a reduced fecundity compared to the "beetle diet" and "mixed diet" groups, but it was not different from "ant diet" group (Fig. 3).

During the experiment, 16 spiders died (six of "ant diet" group, four of "beetle diet" group, four of "mixed diet" group, and two of "termite diet" group). However, spider survivorship was not significantly different between groups (χ^2 = 2.23, df = 3, P = 0.52; Fig. 4).

Discussion

Although spiders are usually classified as generalist predators, there is a wide interspecific variation in breadths of their trophic niches, with several species presenting very restricted diets (Pekár *et al*. 2011; Pékar & Haddad 2011; Pekár & Toft 2014). Even in those species reported as euryphagous, there is also the possibility of individual restrictions, caused, for example, by cognitive limitations to perform very different behavioral routines to capture distinct prey. These limitations may imply in individuals presenting trophic niches much narrower than the populational trophic niche (Pêgo 2014). Thus, although some species may actually benefit from maintaining a varied diet with access to complementary nutritional components (Bilde & Toft 2000; Sisgaard *et al*. 2001; Mayntz *et al*. 2005), many have adaptations for efficient exploitation of the resources contained in one or a few prey taxa (e.g. Pekár *et al.* 2018). Our results indicate that this may be the case for *T. haemorrhoidale*. The mixed diet in fact guaranteed a good body condition and contributed to a large egg production. However, monotypic diets composed of the prey type usually observed being consumed in the field presented similar results.

Narrow trophic niches may be responses to specific ecological conditions, such as the dominance of a certain type of suitable food item in the environment (Líznarová *et al*. 2013) or physiological and/or behavioral trade-offs to capture a particular prey (Zschokke *et al*. 2006; Pekár *et al*., 2008). For *T. haemorrhoidale*, single diets composed only of beetles or ants were efficient in weight maintenance and guaranteed relatively high female fecundity compared to a diet with only termites. Although there are several studies on spiders highlighting the benefits of having a diet composed of a broader spectrum of prey (Toft & Wise 1999a; Oelbermann & Scheu 2002), some species present several adaptations that lead to a very effective exploration of their favorite prey. As an example, the venom of certain stenophagous spiders (specialists in catching ants, termites or other spiders) is more effective for their preferred prey. They have specific toxin compounds that induce the paralysis of these prey in a shorter time (Pékar *et al*. 2018).

Myrmecophagy is the most frequent type of stenophagy observed in spiders, occurring, for example, in species of Zodariidae, Gnaphosidae and Theridiidae (Pekár 2004; Pekár & Haddad 2011; Líznarová *et al*. 2013). Spiders of the genus *Tidarren* have webs especially efficient for catching insects that walk close to the trunk or soil where the silk threads are attached. The webs do not have threads with adhesive droplets throughout their length, as found in some other genera of the family (*e.g. Helvibis* and some *Chrysso* – see Gonzaga *et al*. 2006). This characteristic may restrict the number of flying insects intercepted by the webs. In a previous study (see Chapter 1) conducted at the same study site, we observed that ants are present in all the sampled webs of *T. haemorrhoidale* and almost 70% of the diet of this species in the field is composed of this item. In a natural environment of the Atlantic Forest, the same species captures a greater variety of prey, but the individuals have a diet more restricted than the populational diet, being able to specialize in ants or beetles (Pêgo 2014). This evidence corroborates our hypothesis that *T. haemorrhoidale* can be considered as olygophagous species, obtaining all nutrients from a limited prey range.

Many studies have demonstrated the importance of prey quality on spider's body condition, juveniles development, and female fecundity (Mayntz & Toft 2001; Mayntz *et al*. 2003; Wilder & Rypstra 2008). In our experiment, the nutritional composition (based on the amount of lipids and proteins) varied markedly among the prey categories. However, both the beetle and ant-based diet proved to be efficient for *T. haemorrhoidale,* satisfying its essential needs and assuring the weight maintenance, egg production and survivorship similar to those obtained for individuals in the group with a mixed diet. According to Wilder (2011) the performance of spiders fed with combination of prey may be greater, equal or smaller than spiders fed single diets. For some species a mixed diet can guarantee the complementation of the nutritional requirements of the species. For example, this can occur when one type of consumed prey is richer in lipids and the other in proteins. In other cases, the species may specialize in a prey item that contains all the essential nutrients needed for survival, growth or reproduction and will achive a better condition feeding on this preferred prey. Toft & Wise (1999a), for example, observed in *Schizocosa* sp. (Lycosidae) that a mixed diet composed of the Collembola (*Tomocerus bidentatus* Folsom, 1913) and fruit flies (*Drosophila melanogaster* Meigen, 1830) produces positive effects in relation to growth, but the development and survival rate were similar to those fed with the diet composed exclusively of *T. bidentatus*.

Although the similarity between the nutritional composition of ants and termites regarding the proportions of lipids and proteins, the termite-based diet proved to be inefficient to promote weight maintenance and resulted in a lower egg production in *T. haemorrhoidale*. This result may be due to one or more of the following reasons: 1) termites may present a sub-optimal composition of nutrients (Mayntz & Toft 2001), 2) may include harmful chemicals (Paradise & Stamp 1990), 3) the spiders may be inefficiet in extract or metabolize nutrients from this prey type (Zschokke *et al*. 2006; Pekár & Toft 2009). In the previous study to evaluate the diet of *T. haemorrhoidale* in the field (chapter 1), termites were not present in any web (although these insects were frequently caught by other species of spiders – pers. obs). Since they are not a common prey type, it is possible that termites may really not be a suitable item to be included in its diet. Other cases of unsuitability of certain insects to feeding other spider species have already been reported in the literature. For example, a diet based only on fly *D. melanogaster*, has a negative effect on development and fertility in different species of the genus *Lycosa* (Lycosidae) apparently because these insects do not have linoleic acids, which are essential nutrients for these spiders (Uetz *et al*. 1992). Therefore, spiders can present metabolic adaptations that allow increase extraction or efficiency in nutrient utilization when feeding on their preferred prey (Toft *et al*. 2010).

The impact of a low-quality diet can also have important consequences on the mortality rate of predators (Mayntz & Toft 2001). When the spider *Portia fimbriata* (Doleschall, 1859) (Salticidae) was fed with the preferred prey (only spiders), most individuals survived to maturity (Li & Jackson 1997). However, when it was fed with other types of prey (mixed diets or just insects), the development time was longer, and the survival rate dropped dramatically. In our study, we did not find a relationship between diet quality and longevity. The monotypic diet of termites did not increase the mortality rate. Therefore, spider can obtain suffient nutrients to survive, and negative effects may only appear in a longer period of time. It is possible that there is a trade-off between longevity and fecundity in *T. haemorrhoidale* with spiders below their optimum weight investing mainly in their physiological maintenance and saving energy for a future opportunity to obtain the biomass required to egg production. Although eggs and ovaries are not normally considered as tissues for nutrient storage, females of some species are able to reabsorb egg nutrients to invest in their metabolism if they are under food limitation (Hawley *et al.* 2014).

Our results confirm the existence of different responses on weight maintenance and fecundity according to the type of diet. The mixed diet can guarantee good results in weight maintenance and egg production, however, for an oligophagic species such as *T. haemorrhoidale*, monotypic diets can also satisfy its nutritional requirements, ensuring a good performance. Nutritional analyzes indicated that ants are a poor quality food item, but because the spider is a specialist in the capture of these insects it may present adaptations that allow a very effective exploitation of this food type. The same has been observed in other spider species. The jumping spider *Portia quei* (Żabka, 1985) (Salticidae), for example, has developed specific capturing behaviors that lead to a restrict diet (Toft *et al.* 2010). According to the authors, there may be a mechanism that works in the short term to extract and utilize nutrients from their favorite prey and that guarantees survival, growth and fertility.

We conclude that two monotypic diets composed of the main prey types (beetles and ants) previously reported as common items captured by *T. haemorrhoidale* have similar effects on fecundity and weight maintenance than compared to a mixed diet. On the other hand, a monotypic diet of termites leads to the production of a reduced number of eggs. These results indicate that a diversified diet is not required for *T. haemorrhoidale* to achieve its maximum reproductive potential. Regarding future studies, a longer experiment might be needed to assess the effects of a suboptimal diet on the longevity and total egg production of these spiders. In addition, experimental studies using nutrient injections, controlling the quality of prey, together with behavioral studies involving the capture of the most common prey, can increase knowledge on the physiological requirements of these animals and the ecological consequences of different types of diets (Hawley *et al.* 2014).

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References

Barry, K.L. & Wilder, S.M. (2013) Macronutrient intake affects reproduction of a predatory insect. *Oikos*, **122**, 1058–1064.

https://doi.org/10.1111/j.1600-0706.2012.00164.x

Bilde, T. & Toft, S. (2000) Evaluation of prey for the spider *Dicymbium brevisetosum* Locket (Araneae: Linyphiidae) in single-species and mixed-species diets. *Ekologia Bratislava*, **19**, 9–18.

Breene, R.G., Meagher, R.L. & Dean, D.A. (1993) Spiders (Araneae) and ants (Hymenoptera: Formicidae) in Texas sugarcane fields. *Florida Entomologist*, **76**, 645–650.

https://doi.org/10.2307/3495799

Compêndio Brasileiro de Alimentação Animal. São Paulo: Sindirações, 2013.

Fritz, R.S. & Morse, D.H. (1985) Reproductive success and foraging of the crab spider Misumena vatia. *Oecologia*, **65**, 194–200.

https://doi.org/10.1007/BF00379217

Gonzaga, M.O., Leiner, N.O. & Santos, A.J. (2006) On the stick cobwebs of two theridiid spiders (Araneae: Theridiidae). *Journal of Natural History*, **40**, 293–306.

https://doi.org/10.1080/00222930600703433

Hawley, J., Simpson, S.J. & Wilder, S.M. (2014) Effects of prey macronutrient content on body composition and nutriente intake in a web-building spider. *PLoS ONE*, **9**, e99165.

https://doi.org/10.1371/journal.pone.0099165

Head, G. (1995) Selection of fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae). *Evolution*, **49**, 776–781.

https://doi.org/10.1111/j.1558-5646.1995.tb02313.x

Hooker, O.E., Van Leeuwen, T.E. & Adams, C.E. (2017) The physiological costs of prey switching reinforce foraging specialization. *Journal of Animal Ecology*, **86**, 605–614.

https://doi.org/10.1111/1365-2656.12632

Jensen, K., Mayntz, D., Toft, S., Raubenheimer, D. & Simpson, S. (2011a) Prey nutrient composition has different effects on *Pardosa* wolf spiders with dissimilar life histories. *Oecologia*, **165**, 577–583.

https://doi.org/10.1007/s00442-010-1811-1

Jensen K, Mayntz, D. Toft, S., Raubenheimer, D. & Simpson, S. (2011b) Nutrient regulation in a predator, the wolf spider *Pardosa prativaga*. *Animal Behaviour*, **81**, 993–999.

https://doi.org/10.1016/j.anbehav.2011.01.035

Knoflach, B. & Harten, A.V. (2006) The one-palped spider genera *Tidarren* and *Echinotheridion* in the Old World (Araneae, Theridiidae), with comparative remarks on *Tidarren* from America. *Journal of Natural History*, **40**, 1483–1616.

https://doi.org/10.1080/00222930600940993

Li, D. & Jackson, R.R. (1997) Influence of diet on survivorship and growth in *Portia fimbriata*, an araneophagic jumping spider (Araneae: Salticidae). *Canadian Journal of Zoology*, **75**, 1652–1658.

https://doi.org/10.1139/z97-792

Líznarová, E., Sentenská, L., García, L.F., Pekár, S. & Viera, C. (2013) Local trophic specialisation in a cosmopolitan spider (Araneae). *Zoology*, **116**, 20–26.

https://doi.org/10.1016/j.zool.2012.06.002

Mayntz, D. & Toft, S. (2001) Nutrient composition of the preys diet affects growth and survivorship of a generalist predator. *Oecologia*, **127**, 207–213.

https://doi.org/10.1007/s004420000591

Mayntz, D., Toft, S. & Vollrath, F. (2003) Effects of prey quality and availability on the life history of a trap-building predator. *Oikos*, **101**, 631–638.

https://doi.org/10.1034/j.1600-0706.2003.12408.x

Moreno-Mendoza, S.D., Nunez-Ibarra, G., Chame-Vazquez, E.R. & Valle-Mora, F.J. (2012) Gama de presas capturadas por cuatro especies de aranas tejedoras (Arachnida: Araneae) en un agroecosistema de cacao en Chipas, Mexico. *Tropical and Subtropical Agroecosystems*, **15**, 457–469.

Nyffeler, M., Dean, D.A. & Sterling, W.L. (1988) Prey records of the web-building spiders *Dictyna segregata* (Dictynidae), *Theridion australe* (Theridiidae), *Tidarren haemorrhoidale* (Theridiidae), and *Frontinella pyramitela* (Linyphiidae) in a cotton agroecosystem. *The Southwestern Naturalist*, **33**, 215–218.

https://doi.org/10.2307/3671897

Oelbermann, K. & Scheu, S. (2002) Effects of prey type and mixed diets on survival, growth and development of a generalist predator, *Pardosa lugubris*. *Basic and Applied Ecology*, **3**, 285–291. https://doi.org/10.1078/1439-1791-00094

Paradise, C.J. & Stamp, N.E. (1990) Variable quantities of toxic diet cause different degrees of compensatory and inhibitory responses by juvenile praying mantids. *Entomologia Experimentalis et Applicata*, **55**, 213–222. https://doi.org/10.1111/j.1570-7458.1990.tb01365.x

Pêgo, P.T. (2014) Especialização individual em *Tidarren haemorrhoidale* (Bertkau, 1880) (Araneae, Theridiidae). Dissertação (Mestrado em Ecologia e Conservação de Recursos Naturais) – Universidade Federal de Uberlândia). Uberlândia, MG. Brasil.

Pekár, S. (2004) Predatory behaviour of two European specialized ant-eating spiders (Araneae, Zodariidae*). Journal of Arachnology*, **32**, 31–41. https://doi.org/10.1636/S02-15

Pekár, S., Coddington, J.A. & Blackledge, T.A. (2012) Evolution of stenophagy in spiders (Araneae): evidence based on the comparative analysis of spider diets. *Evolution*, **66**, 776–806. https://doi.org/10.1111/j.1558-5646.2011.01471.x

Pekár, S. & Haddad, C.R. (2011) Trophic strategy of ant-eating *Mexcala elegans* (Araneae: Salticidae): looking for evidence of evolution of prey-specialization. *Journal of Arachnology*, **39**, 133–138. https://doi.org/10.1636/Hi10-56.1

Pekár, S., Líznarová, E., Bočánek, O. & Zdráhal, Z. (2018) Venom of prey-specialized spiders is more toxic to their preferred prey: A result of prey-specific toxins. *Journal of Animal Ecology*, **87**, 1639–1652. https://doi.org/10.1111/1365-2656.12900

Pekár, S., Mayntz, D., Riberio, T. & Herberstein, M.E. (2010) Specialist ant-eating spiders selectively feed on different body parts to balance nutrient intake. *Animal Behaviour*, **79**, 1301–1306. https://doi.org/10.1016/j.anbehav.2010.03.002

Pekár, S., Šobotník, J. & Lubin, Y. (2011) Armoured spiderman: morphological and behavioural adaptations of a specialised araneophagous predator (Araneae: Palpimanidae). *Naturwissenschaften*, **98**, 593–603.

https://doi.org/10.1007/s00114-011-0804-1

Pekár, S. & Toft, S. (2009) "Can ant-eating Zodarion spiders (Araneae: Zodariidae) develop on a diet optimal for euryphagous arthropod predators?" *Physiological Entomology*, **34**, 195–201.

https://doi.org/10.1111/j.1365-3032.2009.00672.x

Pekár, S. & Toft, S. (2014) Trophic specialisation in a predatory group: the case of prey-specialised spiders (Araneae). *Biological Reviews*, **90**, 744–761.

https://doi.org/10.1111/brv.12133

Pekár, S., Toft, S., Hrušková, M. & Mayntz, D. (2008) Dietary and prey-capture adaptations by which *Zodarion germanicum*, an ant-eating spider (Araneae: Zodariidae), specialises on the Formicinae. *Naturwissenschaften*, **95**, 233–239.

https://doi.org/10.1007/s00114-007-0322-3

R Development Core Team, R. (2018) R: A language and environment for statistical computing.

Svanbäck, R. & Bolnick, D.I. (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory model. *Evolutionary Ecology Research*, **7**, 993–1012.

Sigsgaard, L., Toft, S. & Villareal, S. (2001) Diet–dependent survival, development and fecundity of the spider *Atypena formosana* (Oi) (Araneae: Linyphiidae) implications for biological control in rice. *Biocontrol Science and Technology*, **11**, 233–244.

https://doi.org/10.1080/09583150120035657

Terraube, J., Arroyo, B., Madders, M. & Mougeot, F. (2011) Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos*, **120**, 234–244.

https://doi.org/10.1111/j.1600-0706.2010.18554.x

Toft, S. (1999) Prey choice and spider fitness. *Journal of Arachnology*, **27**, 301–307.

Toft, S. (2013). Nutritional aspects of spider feeding. *Spider Ecophysiology* (eds W. Nentwing), pp. 373–384. Springer press, Berlin, Heidelberg.

https://doi.org/10.1007/978-3-642-33989-9_27

Toft, S., Li, D. & Mayntz, D. (2010) A specialized araneophagic predator's short-term nutrient utilization depends on the macronutrient content of prey rather than on prey taxonomic affiliation. *Physiological Entomology*, **35**, 317–327.

https://doi.org/10.1111/j.1365-3032.2010.00746.x

Toft, S. & Wise, D.H. (1999a) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia*, **119**, 191–197.

https://doi.org/10.1007/s004420050776

Toft, S. & Wise, D.H. (1999b) Behavioral and ecophysiological responses of a generalist predator to single and mixed species diets of different quality. *Oecologia*, **119**, 198–207.

https://doi.org/10.1007/s004420050777

Uetz, G., Bischoff, J. & Raver, J. (1992) Survivorship of wolf spiders (Lycosidae) reared on different diets. *Journal of Arachnology*, **20**, 207–211.

Wilder, S.M. & Rypstra, A.L. (2008) Diet quality affects mating behaviour and egg production in a wolf spider. *Animal Behaviour*, **76**, 439–445.

https://doi.org/10.1016/j.anbehav.2008.01.023

Wilder, S.M. (2011) Spider nutrition: an integrative perspective. *Advances in Insect Physiology*, **40**, 87–136.

https://doi.org/10.1016/B978-0-12-387668-3.00002-7

Wise, D.H. (1993) Spiders in Ecological Webs. Cambridge University Press.

https://doi.org/10.1017/CBO9780511623431

Zschokke, S., Henaut, Y., Benjamin, S.P. & Garcia-Ballinas, J.A. (2006) Prey capture strategies in sympatric web-building spiders. *Canadian Journal of Zoology*, **84**, 964–973.

https://doi.org/10.1139/z06-074

Figures

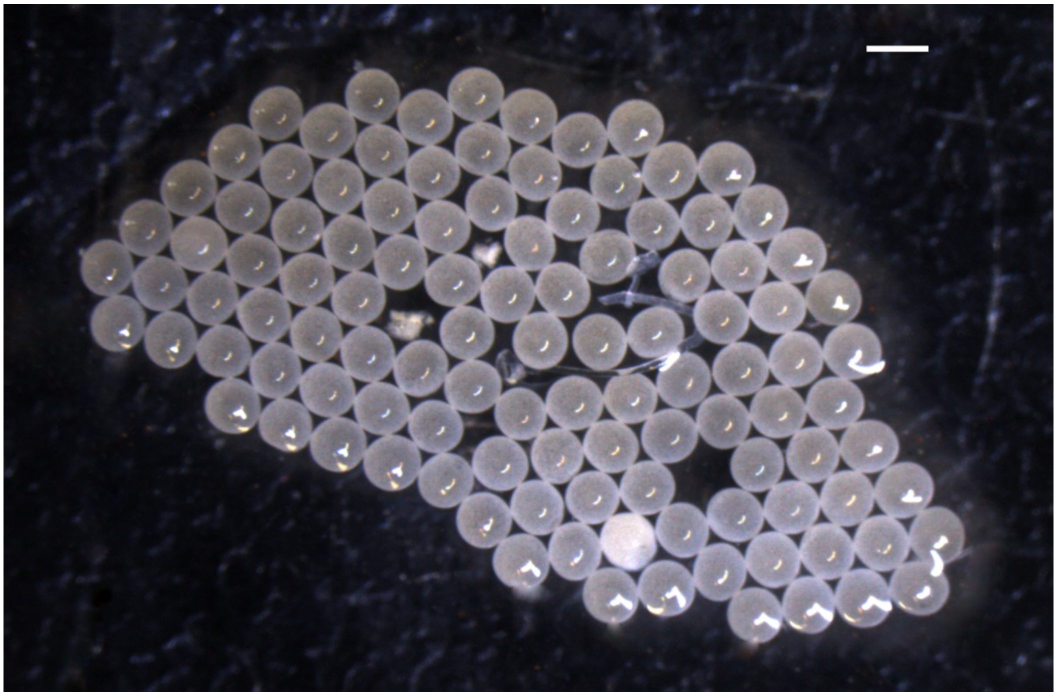

Fig. 1. Eggs contained in a *T. haemorrhoidale* eggsac. Scale of one millimeter.

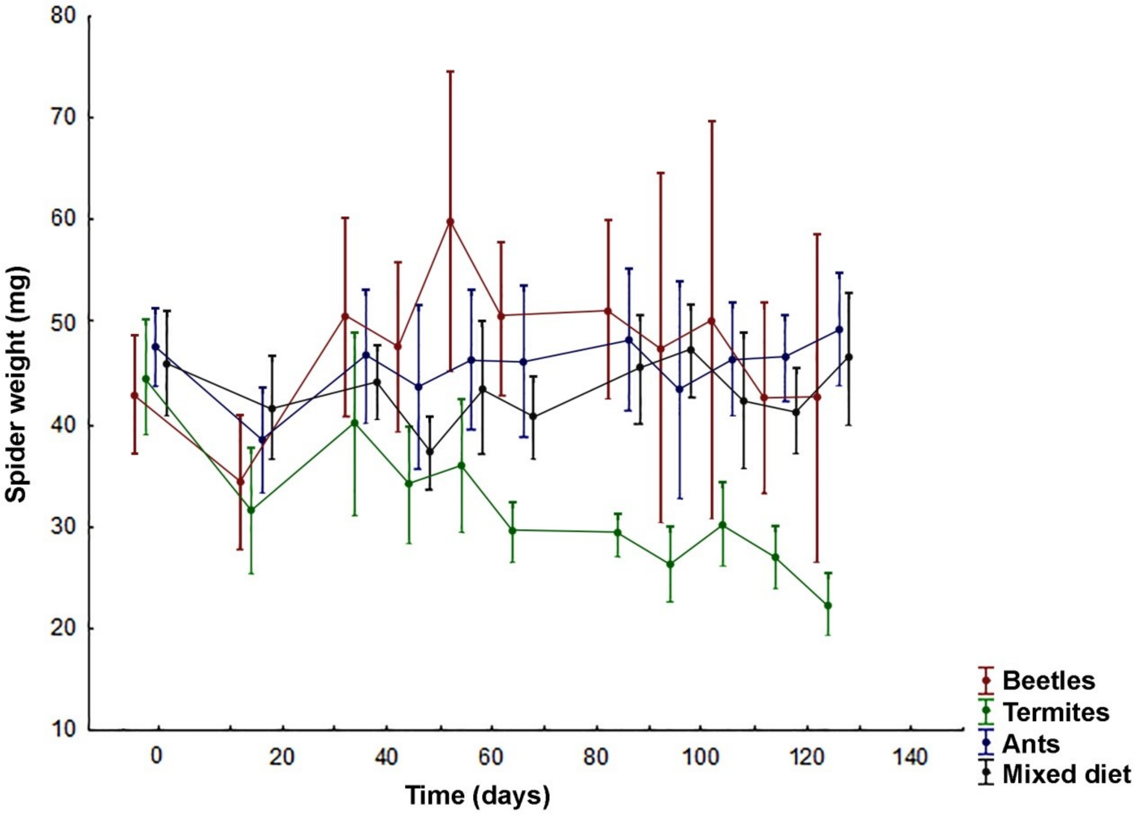

Fig. 2. Effect of diet on weight change of *T. haemorrhoidale*.

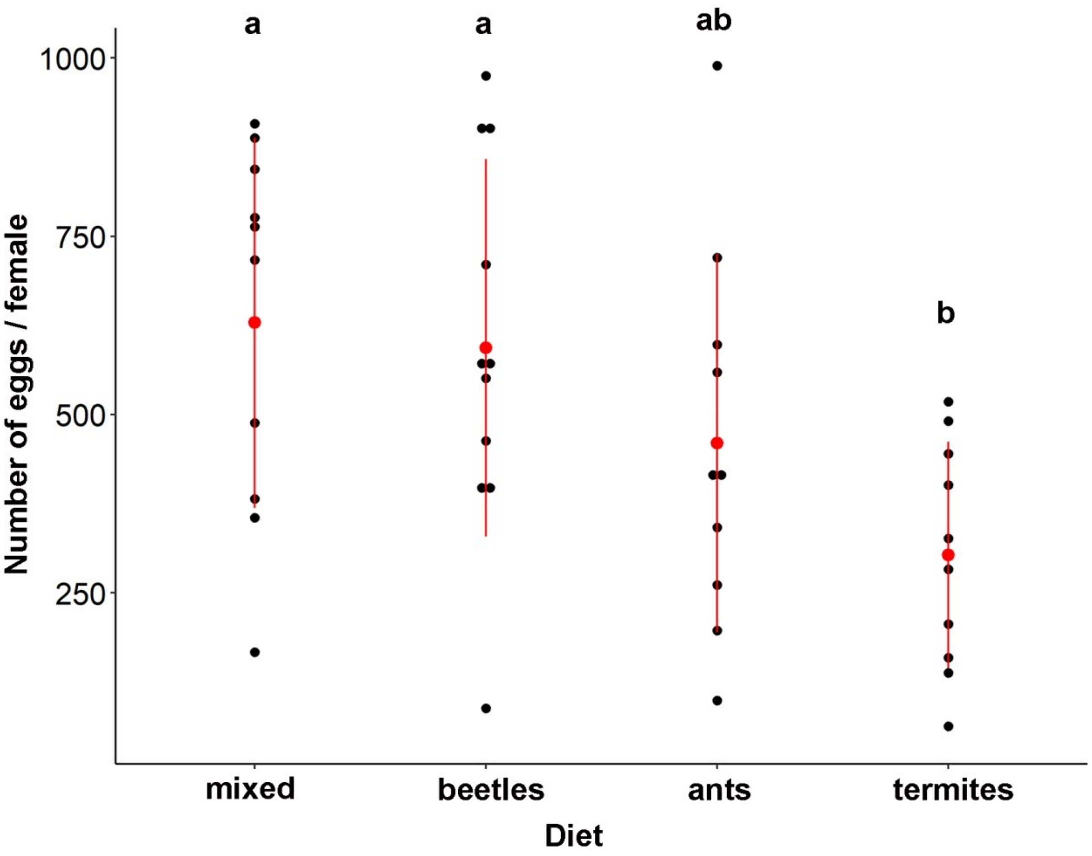

Fig. 3. Effect of diet on egg production of *T. haemorrhoidale*.

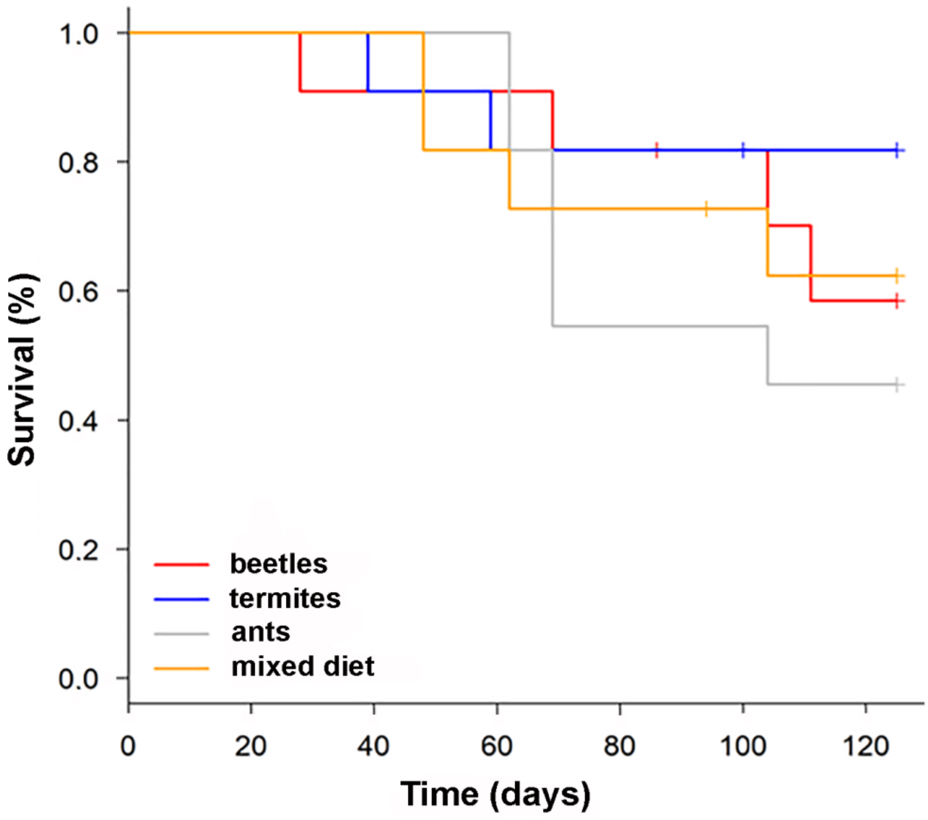

Fig. 4. Survival of *T. haemorrhoidale* females submitted to four distinct diets in captivity along 125 days**.**

Table 1. Mean weight (mg) of each prey before and after consumption by the spiders. The difference between these values were considered as the biomass consumed.

Prey type	Prey weight	Prey weight after consumption	Biomass consumed
Beetle	11.98 ± 0.43	1.83 ± 0.22	10.15 ± 0.34 (84.7%)
Termite	6.03 ± 0.79	0.74 ± 0.14	5.28 ± 0.81 (87.6%)
Ant	14.03 ± 0.61	3.28 ± 1.27	10.75 ± 1.02 (76.6%)

Table 2. Bromatological analysis of prey types.

Prey type	% Moisture	% Proteins	% Lipids
Beetle	51.00 ± 0.06	21.43 ± 0.32	11.5 ± 0.16
Termite	73.25 ± 0.20	15.77 ± 0.23	4.87 ± 0.09
Ant	72.9 ± 0.09	15.18 ± 0.16	2.27 ± 0.17

Table 3. General linear mixed model considering diet as predictive vaiable, spider identity as ramdom variable and the weight as variable response.

Variable	*F*	*df*	$df_{\mathrm{residuals}}$	*P*
Intercept	668.43	1	38.54	<0.001
Diet	13.82	3	39.14	<0.001

CONSIDERAÇÕES FINAIS

Com esses três capítulos foi possível conhecer um pouco mais sobre a complexidade comportamental envolvida nas atividades de forrageamento, os fatores determinantes da amplitude da dieta (em nível populacional e individual) e sobre as consequências da variação da dieta sobre parâmetros da história de vida de uma espécie construtora de teias irregulares da família Theridiidae. *Tidarren haemorrhoidale* constrói teias no mesmo ambiente do que e *Nihonhimea tesselata*, porém essas espécies segregam seus nichos, capturando presas distintas. Pudemos observar diferenças marcantes na posição e arquitetura das teias que possivelmente estão relacionadas à interceptação de diferentes tipos de insetos. Além disso, observamos que não ocorreu especialização individual em nenhuma das espécies estudadas, com os nichos individuais não diferindo do nicho populacional. Finalmente, a variação na dieta dos indivíduos não pode ser explicada pela distribuição espacial diferencial dos recursos, uma vez que indivíduos mais próximos não apresentam maior sobreposição em suas dietas.

Em relação ao comportamento de forrageamento pudemos concluir *T. haemorrhoidale* necessita de mais tempo para realização das rotinas envolvendo aproximação, enrolamento e picada para que uma formiga fosse completamente dominada. Esse resultado se deve à cautela necessária para imobilização de um tipo de presa que oferece riscos de injúria para o predador. A experiência prévia não foi um fator determinante de uma maior eficiência de captura (tempo de manipulação) para *T. haemorrhoidale*, uma vez que os indivíduos não diminuíram os tempos de captura após sucessivas interações com o mesmo tipo de presa. As aranhas testadas conseguiam manipular as presas de forma eficiente desde a primeira tentativa, havendo uma variação que não está relacionada com a sequência de experiências. O tempo necessário para captura mostrou-se dependente do comportamento da presa interceptada e/ou de seu potencial risco de injúria para a aranha. Apesar das presas testadas variarem quanto a esses aspectos, as rotinas comportamentais para captura foram similares, havendo apenas diferenças no tempo necessário para conclusão de partes dessas rotinas. Além disso, experiências prévias (em campo) com besouros e formigas podem ter ajudado na manipulação dessas presas em laboratório, resultando na similaridade entre os tempos e comportamentos desempenhados desde o início até o término dos experimentos.

Finalmente, questões relacionadas à dieta podem ser muito importantes na história de vida de *T. haemorrhoidale*. Nossos resultados confirmam a existência de diferentes efeitos na manutenção do peso e fecundidade de acordo com o tipo de presa consumida. Embora uma dieta mista possa garantir bons resultados na manutenção do peso e na produção de ovos, mostramos que dietas monotípicas também podem satisfazer as necessidades nutricionais da espécie. As análises nutricionais indicaram que as formigas são um item alimentar com qualidade nutricional relativamente baixa, mas é possível que a espécie apresente adaptações fisiológicas que permitam uma exploração muito efetiva desse tipo de alimento.