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LEONARDO PALLONI ACCETTI RESENDE

**O PAPEL DA CONSTRUÇÃO DE NICHOS NA EVOLUÇÃO E
ECOLOGIA DA SOCIALIDADE EM ARANHAS**

Salvador- BA

Outubro de 2020

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ECOLOGIA DA SOCIALIDADE EM ARANHAS**

**THE ROLE OF NICHE CONSTRUCTION IN THE EVOLUTION AND ECOLOGY OF
SOCIALITY IN SPIDERS**

Tese apresentada ao Programa de Pós-Graduação em
Ecologia: Teoria, Aplicação e Valores da Universidade
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Orientador: Dr. Hilton Ferreira Japyassú

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"A ciência se compõe de erros que, por sua vez, são os passos até a verdade."

Júlio Verne

A EMARANHADA CONEXÃO ENTRE A TEIA E A SOCIALIDADE NAS ARANHAS

Leonardo Palloni Accetti Resende

No mundo das aranhas, o comportamento social é raro, apenas 19 espécies dentro do universo de mais de 48 mil são consideradas sociais. Os dois gêneros de aranhas sociais mais bem estudados são *Stegodyphus*, da família Eresidae, que ocorre na África e Ásia, e *Anelosimus*, da família Theridiidae, cujas espécies sociais ocorrem nas Américas Central e do Sul.

As sociedades das aranhas são grandes famílias, com elevado grau de parentesco entre os indivíduos. Elas constroem grandes teias tridimensionais, onde podem viver até mais de 10 mil indivíduos que cooperam na captura das presas, no cuidado com ovos e filhotes e na manutenção da teia. Não há castas reprodutivas, como nas sociedades de formigas e abelhas, sendo todas as fêmeas capazes de se reproduzir. Além disso, essas aranhas são, em geral, menos agressivas e possuem maior variação comportamental entre os indivíduos que suas parentes não sociais.

A hipótese mais aceita, para explicar a evolução da socialidade nas aranhas, apresenta os benefícios da vida em grupo na redução dos custos com a manutenção das teias e na proteção garantida pela permanência na teia natal. Além disso, outros benefícios da vida social incluem a especialização comportamental no desempenho de tarefas específicas dentro do grupo e o acesso a presas maiores.

Apesar de serem bem estudados esses aspectos da aptidão das teias sociais, os mecanismos evolutivos, por trás de sua origem, foram pouco investigados. Em uma série de estudos recentes, os pesquisadores Leonardo Resende, Vitor Rios e Hilton Japyassú, integrantes do Núcleo de Etologia e Evolução da Universidade Federal da Bahia, e colaboradores testaram, a partir de experimentos realizados em campo e através de modelagem computacional, uma hipótese a respeito do mecanismo evolutivo que teria atuado na origem dessas características das aranhas sociais.

A hipótese dos pesquisadores é a de que as aranhas ancestrais das espécies sociais, de maneira ativa, mudaram as pressões seletivas que atuavam sobre elas, através da construção das teias coletivas.

As teias, com maior volume protegido contra o ataque de predadores e intempéries climáticas, permitiram a sobrevivência de indivíduos menos agressivos que a média. Isso promoveu o aumento na diferença comportamental entre os indivíduos, criando a base para a divisão de tarefas dentro do grupo. Esse processo aumentou a aptidão dessas agregações que evoluíram para as espécies sociais.

Ao processo evolutivo que considera a atuação da própria espécie na mudança das pressões seletivas que atuam sobre ela, gerando um ciclo de retroalimentação sobre sua própria evolução, é dado o nome de “construção de nicho”. Foi a verificação desse processo sobre a origem da socialidade nas aranhas que consistiu na grande novidade trazida pelos trabalhos dos pesquisadores da UFBA.

Segundo os resultados das pesquisas, uma mudança sutil no tamanho do volume protegido e no nível de proteção da teia tridimensional teria sido suficiente para promover o surgimento e manutenção dos indivíduos menos agressivos e gerar a cascata de eventos consecutivos que culminaria com o surgimento de sociedades estruturadas. Além disso, eles mostraram que as teias maiores e mais heterogêneas, de fato facilitaram, o processo de divisão de trabalho, atuando sobre a disposição espacial das tarefas para serem realizadas pelos diferentes indivíduos.

Em conjunto, os estudos revelaram o papel central da teia na evolução do comportamento social das aranhas, da mesma maneira que estudos realizados com outros organismos sociais, como cupins e formigas, têm demonstrado a grande influência das estruturas construídas por esses animais tanto na própria origem como na manutenção e organização de seus grupos sociais. Tal evidência torna mais expressivo o fato de que as teias construídas pelas aranhas sociais, assim como os cupinzeiros e formigueiros não são apenas frutos da vida social desses animais, mas sim promovedores da própria socialidade.

RESUMO GERAL

A socialidade nos animais evoluiu, independentemente, em diversos táxons, apresentando diversos níveis de complexidade, partindo das agregações para reprodução nas aves até sociedades altamente organizadas com divisão de trabalho e castas reprodutivas e estéreis, como nas formigas cortadeiras. As aranhas constituem um grupo especial, no sentido de que a socialidade é um fenômeno muito raro, ocorrendo apenas em 19 espécies dentro do universo de mais de 48 mil que já foram descritas. A hipótese mais aceita, para explicar a evolução da socialidade nas aranhas, apresenta os benefícios da vida em grupo na redução dos custos relacionados com a manutenção das teias e na proteção garantida pela permanência na teia natal. Além disso, a especialização comportamental no desempenho de tarefas específicas e o acesso a presas maiores são outras vantagens da vida coletiva para as aranhas. Apesar de serem bem estudados esses aspectos da aptidão das teias sociais, os mecanismos evolutivos, por trás de sua origem, foram pouco investigados. Essa tese apresenta a investigação de uma hipótese a respeito dos mecanismos evolutivos, que levaram a origem da socialidade nas aranhas e dos mecanismos ecológicos, que promovem a organização dessas sociedades. Essa hipótese baseia-se na premissa de que as aranhas são engenheiras de ecossistemas que modificam o ambiente para ajustá-lo às suas necessidades através da construção das teias. As teias, como um ambiente modificado, alteram o cenário evolutivo, alterando as pressões seletivas que agem sobre as populações que as habitam. Quando o ambiente transformado pela ação das aranhas promove mudanças que perpassam gerações causando mudanças evolutivas, temos a ação da construção de nicho como processo evolutivo. E nos três capítulos que compõem este trabalho, investigamos a ação da engenharia de ecossistemas, da construção de nicho como agentes do processo evolutivo da socialidade e orientadores na organização das sociedades. O primeiro capítulo apresenta um modelo teórico sobre a evolução da socialidade nas aranhas por meio da construção de nicho. Esse modelo teórico definiu a hipótese central, apresentando seus pressupostos e previsões. O modelo foi testado através da técnica de “Modelagem Baseada em Agentes” (ABM) desenvolvido no programa *NetLogo*, que nos permitiu criar simulações nas quais os parâmetros de nosso modelo teórico ditavam as regras. Os resultados das simulações nos mostraram que as teias com maior volume protegido contra o ataque de predadores e intempéries climáticas, permitiram a sobrevivência de indivíduos menos agressivos que a média. Isso promoveu o aumento na diferença comportamental entre os indivíduos, criando a base para a especialização comportamental e divisão de tarefas dentro do grupo. Esse processo aumentou a aptidão dessas agregações, dado que as colônias com maior amplitude de variação comportamental sobreviveram mais, evoluindo para as espécies sociais. O segundo capítulo apresenta um segundo modelo teórico com foco nas previsões ecológicas da hipótese geral, que explica como pode emergir a divisão de tarefas entre os indivíduos, dentro do grupo, a partir de diferenças na personalidade entre os mesmos de acordo com contextos ambientais específicos. Esse modelo também foi testado, via ABM, e desenvolvido no programa *NetLogo*. A partir dos resultados das simulações, pudemos testar estatisticamente o efeito das diferenças comportamentais individuais e do contexto espacial, na propensão de realização de tarefas específicas dentro do grupo. Encontramos que o efeito da personalidade, na determinação das tarefas executadas, foi muito fraco, mesmo com um número grande de amostras indicando que esse efeito deve ser praticamente nulo para determinar a tarefa que um indivíduo irá executar. Porém, talvez a personalidade não tenha, de fato, sua importância sobre a determinação direta das tarefas que um determinado indivíduo irá executar, sendo esse talvez o papel da experiência social através das redes de interação e da aprendizagem. Por outro lado, tenha sua importância em um aspecto mais fundamental, como na geração das condições iniciais para que os outros fatores possam emergir e promover a especialização e a divisão de tarefas em si. O terceiro capítulo apresenta um estudo empírico, manipulativo com foco nas previsões ecológicas da hipótese

central, que foi desenvolvida em campo com colônias de aranhas em seu ambiente natural. Aqui o objetivo principal foi observar, na natureza, as colônias de aranhas sociais, registrar os padrões de distribuição espacial e de realização de atividades dos indivíduos. Os dados coletados foram analisados estatisticamente, através de modelos lineares generalizados mistos (GLMMs), para testar se a distribuição espacial dos indivíduos na teia e as tarefas que eles realizavam na colônia se aproximava das previsões obtidas pelos modelos computacionais. Os modelos mostraram que as personalidades dos indivíduos influenciam a distribuição deles sobre a teia, sendo os ousados mais frequentemente observados na vela e os tímidos no cesto, porém não influenciam nas atividades que eles desempenham. Concluímos que os indivíduos se segregam espacialmente na teia, de acordo com as suas personalidades, porém, ao contrário do previsto, a personalidade não se mostrou importante na determinação da tarefa desempenhada pelo indivíduo. A personalidade parece ter um papel indireto na divisão de tarefas, dentro do grupo, ao influenciar a distribuição espacial dos indivíduos. Finalmente, propomos que a heterogeneidade ambiental, incluindo àquela criada por engenharia de ecossistemas, pode gerar pressões seletivas sobre as propriedades inerentes dos indivíduos, como a personalidade, em favor da fidelidade espacial e da especialização de tarefas em grupos sociais. Tal aspecto traz mais evidências de que as grandes teias construídas pelas aranhas sociais não são apenas fruto da vida social desses animais, mas também promovedoras da própria socialidade.

Palavras Chave: Aranhas; Socialidade; Teoria da Construção de Nicho; Personalidade Animal.

GENERAL ABSTRACT

Sociality in animals evolved independently in different taxa, presenting different levels of complexity, from aggregations for reproduction in birds to highly organized societies with division of labor and reproductive and sterile castes as in leaf-cutting ants. Spiders consists a special group in the sense that sociality is a rare phenomenon, occurring only in 19 species within the universe of more than 48 thousand described species. The most accepted hypothesis to explain the evolution of sociality in spiders presents the benefits of group living in reducing costs related to the maintenance of the webs and in the protection guaranteed by the permanence in the natal web. Besides, behavioral specialization in the performance of specific tasks and access to larger prey. Although these aspects of the fitness of social webs have been well studied, the evolutionary mechanisms behind their origin have been little investigated. This thesis presents the investigation of a hypothesis regarding the evolutionary mechanisms that led to the origin of sociality in spiders and the ecological mechanisms that promote the organization of these societies. This hypothesis is based on the assumptions that spiders are ecosystems engineers that modify the environment to adjust it to their needs through the construction of webs. The webs as a modified environment, change the evolutionary scenario, modifying the selective pressures that act on the populations that inhabit them. When the environment modified by the action of spiders promotes changes that pass-through generations causing evolutionary changes, we have the action of niche construction as an evolutionary process. And in the three chapters that make up this work, we investigate the action of ecosystem engineering and niche construction as agents of the evolutionary process of sociality and as drivers for social organization. The first chapter presents a theoretical model on the evolution of sociality in spiders through niche construction. This theoretical model defined the central hypothesis, presenting its assumptions and predictions. The model was then tested through the technique of “Agent Based Modeling” (ABM) and developed in the computer program *NetLogo*, which allowed us to create simulations in which the parameters of our theoretical model dictated the rules. The results of the simulations showed us that the webs with a larger protected volume, against the attack of predators and weather conditions, allowed the survival of individuals less aggressive than the average, this promoted an increase in the behavioral difference between the individuals, creating the basis for the behavioral specialization and division of tasks within the group. This process increased the fitness of these aggregations, as showed by the greatest survival rate of colonies with more behavioral variance, that evolved on to social species. The second chapter presents a second theoretical model focusing on ecological predictions of the general hypothesis, which explains how the division of tasks between individuals within the group can emerge from differences in personality under specific environmental contexts. This model was also tested via ABM and built in the *NetLogo* program and from the results of the simulations we were able to statistically test the effect of individual behavioral differences and the spatial context, on the propensity to perform specific tasks within the group. We found that the effect of personality in determining the tasks performed was very weak, even with a large number of samples, which indicates that this effect must be practically null to determine the task that an individual will perform. However, perhaps personality does not really have its importance in determine the tasks that a certain individual will perform directly, being this the role of social experience through networks of interaction and learning perhaps, but on the other hand it has its importance in a more fundamental aspect, as in the generation of the initial conditions for the other factors could emerge and promote the specialization and the division of tasks. The third chapter presents an empirical, manipulative study focusing on ecological predictions of the central hypothesis, which was developed in the field with spider colonies in their natural environment. Here the main objective was to observe in the nature the colonies of social spiders and to register the patterns of spatial distribution and performance of individuals activities. The collected data were then statistically

analyzed using mixed generalized linear models (GLMMs) to test whether the spatial distribution of individuals on the web and the tasks they performed in the colony approached the predictions obtained by computational models. In summary, our study shows that there is a spatial segregation of individuals in the web of a colony, and that it is influenced by individual differences in the tendency to accept the risk of being exposed. However, contrary to what was expected, personality proved to be not important in determining the rate of activity or the type of activity the spiders performed given the location that they were in. Personality traits may instead indirectly influence task specialization through dictating an individual's location within a group. Finally, we propose that environmental heterogeneity, including that produced by ecosystem engineering such as nest and web building, could generate selective pressures on the inherent properties of individuals, such as personality in favor of spatial fidelity and specialization of tasks within social groups, bringing more evidence that the huge webs built by social spiders, are not only the result of the social life of these animals, but also acts as a driver of their own sociality.

Key Words: Spiders; Sociality; Theory of Niche Construction; Animal Personality.

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ESTRUTURA DA TESE

A tese está orientada em torno de uma hipótese central que permeia todos os estudos que compõem o trabalho. Essa hipótese baseia-se na premissa de que as aranhas são engenheiras de ecossistemas que modificam o ambiente para ajustá-lo às suas necessidades através da construção das teias. Estas, como um ambiente modificado, alteram o cenário evolutivo, modificando as pressões seletivas que agem sobre as populações que as habitam. Quando o ambiente alterado pela ação das aranhas promove transformações que perpassam gerações, causando mudanças evolutivas, temos a construção de nicho como processo evolutivo. Assim, nossa hipótese central considera a construção de nicho como processo evolutivo principal que promoveu o surgimento da socialidade nas aranhas e gera os mecanismos ecológicos da organização dessas sociedades.

Com o intuito de discutir essa hipótese central a tese é organizada em três capítulos, cada um com seu enfoque e estrutura próprios, para tornarem-se publicações independentes. Porém todos estão encadeados e conectados entre si formando uma unidade maior.

Capítulo 1- *The survival of the shyest: a computational model shows the effect of web structure on the origins of social spiders.*

Nesse artigo, apresentamos um modelo teórico sobre a evolução da socialidade nas aranhas através da construção de nicho. Esse modelo teórico define a hipótese central da tese, apresentando seus pressupostos e previsões. O modelo foi testado através da técnica de “Modelagem Baseada em Agentes” (ABM na sigla em inglês) no programa *NetLogo*, que nos permite programar simulações de “mundos virtuais” nos quais os parâmetros de nosso modelo teórico ditam as regras. Os resultados das simulações nos mostram distintos cenários que podem emergir a partir das condições iniciais por nós programadas. Por fim, através de rigorosos testes estatísticos, selecionamos, desses resultados, aqueles

que foram mais plausíveis para explicar como o processo evolutivo pode ter de fato ocorrido na natureza.

Capítulo 2- *Personality is necessary but not sufficient for task division in simulated social spiders.*

Nesse artigo, apresentamos um segundo modelo teórico que testa a hipótese da construção de nicho social como mecanismo de geração da especialização de tarefas e divisão de tarefas dentro do grupo. Essa hipótese apresenta previsões ecológicas, explicando como pode emergir a divisão de tarefas entre os indivíduos a partir de diferenças na personalidade entre os mesmos dados contextos ambientais específicos. Esse modelo também foi testado através de “ABM”, sendo construído no programa *NetLogo*. A partir dos resultados das simulações, pudemos testar estatisticamente o efeito das diferenças comportamentais individuais e do contexto espacial, na propensão dos indivíduos na realização de tarefas específicas dentro do grupo.

Capítulo 3- *There is spatial segregation due to personality in spider colonies, but no task specialization.*

Este artigo apresenta um estudo empírico e manipulativo com foco também nas previsões ecológicas da hipótese da construção de nicho social como o principal mecanismo atuando na organização das sociedades das aranhas. O estudo foi desenvolvido, em campo, com colônias de aranhas em seu ambiente natural. Aqui o objetivo principal foi observar, na natureza, as colônias de aranhas sociais, registrando os padrões de distribuição espacial e de realização de atividades dos indivíduos com diferentes personalidades. Os procedimentos experimentais foram conduzidos por uma equipe de quatro pessoas ao longo de cinco dias de trabalho de campo. Os dados coletados foram analisados estatisticamente, através de Modelos Lineares Generalizados Mistos (GLMM), para testar se a distribuição espacial dos indivíduos na teia e as tarefas que eles realizavam na colônia se aproximavam das previsões da hipótese de construção de nicho social.

Considerando que este trabalho versa sobre a evolução da socialidade nas aranhas através do processo de construção de nicho, considerando que os processos ecológicos atuam na organização dessas sociedades através da construção de nicho social e considerando que a personalidade dos indivíduos tem papel preponderante na constituição do nicho social dos indivíduos, nessa introdução geral, faço uma apresentação concisa dos principais pontos de cada teoria e hipóteses gerais nas quais baseio os estudos que compõem o trabalho. Iniciamos com as hipóteses que explicam a evolução da socialidade nos animais, dando ênfase sobre esse aspecto no táxon das aranhas, passando pela teoria da construção de nicho, da engenharia de ecossistemas e finalizando com a hipótese da construção de nicho social.

A evolução da socialidade nos animais

A maioria das espécies animais apresenta períodos de seus ciclos de vida nos quais se encontram em agregações, seja como juvenis antes da dispersão de seu local de nascimento (Buskirk, 1981; Galliard et al., 2003; Krafft, 1969; Ronce et al., 2001), como adultos que se agregam para forragear (Beauchamp and Giraldeau, 1997; Giraldeau and Caraco, 2000; Rypstra, 1979), ou como adultos que se juntam em grupos para procriar e cuidar de suas ninhadas (Danchin et al., 2008, 2004; Doligez et al., 2004; Valone e Templeton, 2002).

Entretanto, há espécies que permanecem em agregações por todo seu ciclo de vida, sendo chamadas de espécies sociais, variando de grupos familiares até eusociedades com sistemas de castas (Wilson, 2000). A evolução e manutenção desses sistemas sociais é uma das questões mais intrigantes da ecologia e biologia evolutiva, devido às interações antagonistas entre os processos “egoístas” da seleção natural e a manutenção de comportamentos “altruístas” nas sociedades (Costa e Fitzgerald, 1996; Fisher, 1930; Hamilton, 1964; West-Eberhard, 1975; Wilson, 1971).

Crespi e Choe, 1997 e Crespi e Yanega, 1995 caracterizaram cinco formas básicas de socialidade: Reprodução Solitária- os indivíduos não apresentam cooperação parental ou cuidado parental, ou apenas se limitam a ajudar o parceiro reprodutivo no cuidado com as crias; Reprodução Colonial- muitos pares reprodutivos se juntam em um local comum de procriação, sem ajuda mútua entre eles; Reprodução Comunitária- pares reprodutivos ajudam um ao outro a cuidar dos filhotes; Reprodução Cooperativa- há indivíduos que se especializam em cuidar das crias, sendo esses comportamentos específicos reversíveis e podem ser alterados e Eusocialidade- mais complexa forma de socialidade, nas quais há indivíduos reprodutivos e indivíduos estéreis que se dividem em castas de trabalho.

De acordo com a abordagem funcional, a manutenção da socialidade está associada com o balanço entre os custos e os benefícios de se viver em grupo (Danchin et al., 2008; Krause e Ruxton, 2002). Os custos da vida em grupo incluem: i) o risco de transmissão de patógenos e parasitas (Brown e Brown, 1996, 1987), ii) parasitismo de ninho (Birkhead e Moller, 1993; Westneat e Sherman, 1997) e iii) a elevada competição intraespecífica por alimento, locais para reprodução e parceiros reprodutivos (Moller, 1987). Dentre os benefícios estão: i) proteção contra predadores (Darling, 1938; Endler, 1995) e ii) sucesso no forrageamento (Fernández-Juricic et al., 2004).

Essa abordagem funcional da evolução da socialidade prediz que as sociedades se mantêm estáveis sob condições nas quais os benefícios superam os custos, aumentando a aptidão em relação aos ganhos que os indivíduos teriam se vivessem sozinhos (Danchin et al., 2008; Sumpter, 2010).

Nesse sentido, uma das questões mais fundamentais no estudo da evolução da sociabilidade é a natureza adaptativa dos comportamentos cooperativos, como eles se originam e se mantêm (Danchin et al., 2008; Korb e Heinze, 2016, 2008). Comportamentos cooperativos são caracterizados por atividades coletivas nos quais todos os envolvidos se beneficiam (Connor, 1995). Essa cooperação pode ser assimétrica, como no caso das sociedades de insetos, nas quais há trabalhadoras estéreis e

rainhas férteis, ou simétricas nas quais os indivíduos se beneficiam mutuamente sem restrições reprodutivas (Danchin et al., 2008).

Uma das teorias mais aceitas para explicar a existência e a evolução dos comportamentos cooperativos é a Teoria da Seleção de Parentesco (Griffin, 2003; Hamilton, 1964; Smith, 1964; West, 2002). De acordo com ela, um organismo pode garantir um aumento em sua aptidão diretamente, através de sua própria progênie ou indiretamente, quando um indivíduo auxilia no aumento da aptidão de algum parente próximo, como um irmão ou primo, já que eles compartilham muitos genes (Hamilton, 1964; Smith, 1964).

Esse aumento indireto na aptidão individual é denominada aptidão inclusiva e está correlacionada com a relação entre os indivíduos (nível de similaridade genética), assim, um indivíduo tende a cooperar com outro (favorecendo sua aptidão) na proporção do grau de parentesco entre eles (Regra de Hamilton (1995)). Essa hipótese apresenta forte apoio de evidências empíricas, já que muitos estudos vêm corroborando a correlação que existe entre a frequência de comportamentos cooperativos e o grau de parentesco entre os indivíduos (*e.g.*: Crespi e Choe, 1997; Emlen, 1982; Griffin, 2003; Koenig e Dickinson, 2016; West, 2002).

Outras hipóteses complementares à seleção de parentesco, que explicam a evolução e manutenção dos comportamentos cooperativos em organismos sociais, são a seleção de grupo e sua versão mais recente, a seleção em múltiplos níveis (Alexander e Borgia, 1978; Goodhart e Williams, 1968; Hamilton, 1963; Leigh, 1999; Okasha, 2004; Reeve e Keller, 1999), a teoria dos jogos, nos casos de comportamentos cooperativos entre indivíduos não relacionados (Axelrod e Hamilton, 1981; Trivers, 1971) e a teoria do mutualismo como subproduto na qual há custos imediatos para os indivíduos que não cooperam em uma interação social (Connor, 1995). Nessa introdução geral, não serão detalhadas as estruturas de todas essas teorias, pois não faz parte dos objetivos desta tese fazer uma revisão a respeito da literatura da Sociobiologia e teorias correlatas.

Todos esses modelos gerais que se desenvolveram para explicar a evolução da socialidade mostraram que os custos e benefícios da vida em grupo são muito similares em uma ampla variedade de táxons, sendo consideradas características ecológicas sem especificidade taxonômica (Whitehouse e Lubin, 2005). Em adição a esse caráter universal, os padrões encontrados no estudo dos seres sociais têm sido aplicados de forma bem sucedida na compreensão de comportamentos coletivos nas mais variadas entidades naturais, em diversas escalas e níveis de organização (Sumpter, 2010).

A socialidade nas aranhas

A grande maioria das mais de 48 mil espécies conhecidas de aranhas (World Spider Catalog 2019) apresentam um estilo de vida solitário, com encontros ocasionais apenas para reprodução (Foelix, 2010). Mesmo sendo um fenômeno raro, a socialidade aparece dentro do táxon das aranhas em diversos níveis, partindo das agregações de teias orbiculares, como por exemplo as que ocorrem nos gêneros *Parawixia* (família Araneidae) e *Philoponella* (família Uloboridae), passando pelas teias comunais das espécies subsociais, nas quais as fêmeas e seus filhotes cooperam entre si na captura de presas e manutenção da teia até a dispersão pré-reprodutiva, que engloba cerca de 70 espécies em 16 famílias de aranhas, até chegarmos às espécies sociais em senso estrito, nos quais ocorre sobreposição de gerações e divisão de trabalho, sendo reconhecidas atualmente 19 espécies em 5 famílias (Avilés e Guevara, 2017).

As espécies sociais, apesar de reduzidas em diversidade, são amplamente distribuídas geograficamente, ocorrendo em regiões tropicais e subtropicais de todos os continentes, com uma particular concentração na região amazônica da América do Sul (Avilés e Guevara, 2017; Guevara e Avilés, 2015).

As aranhas sociais são distinguidas das subsociais e das coloniais porque apresentam teias comunais, forrageamento coletivo, cuidado aloparental, ausência de dispersão dos juvenis e elevada taxa de endocruzamento (Avilés e Guevara, 2017; Lubin e Bilde, 2007; Whitehouse e Lubin, 2005).

Há evidências que suportam a hipótese de múltiplas origens da socialidade dentro dos grupos nos quais ocorrem, sendo aceitas atualmente 18 origens independentes dentro das 5 famílias nas quais a socialidade evoluiu (Agnarsson et al., 2007). Apenas dentro da família Theridiidae, que é o grupo de aranhas com o maior número de espécies sociais (12 espécies), há nove origens independentes reconhecidas na literatura (Agnarsson et al., 2007; Avilés et al., 2006). Assim, as aranhas sociais podem ser vistas como modelos ideais para estudos ecológicos e evolutivos, com a presença de réplicas independentes tanto dentro como entre diversas famílias de aranhas (Avilés e Guevara, 2017; Lubin e Bilde, 2007).

A condição de sociedade cooperativa nas aranhas surgiu, de acordo com os modelos mais aceitos atualmente, de uma condição subsocial com a presença de cuidado maternal estendido e cooperação entre os juvenis antes da dispersão (Avilés e Guevara, 2017; Bilde et al., 2005; Lubin e Bilde, 2007).

Fortes restrições impostas pelo endocruzamento em uma sociedade podem ser superadas por restrições ecológicas na capacidade de dispersão dos indivíduos, associada com um aumento nos recursos energéticos e redução da mortalidade, ampliando os benefícios da vida em grupo (Avilés, 1997; Bilde et al., 2005; Waser et al., 1986).

Algumas características dos organismos podem evoluir porque elas possuem vantagens seletivas em curto prazo, mas em longo prazo acabam gerando baixas taxas de especiação ou elevadas taxas de extinção, tais características são chamadas de “becos sem saída evolutivos” (Normark et al., 2003). Esses fenômenos são ainda pouco compreendidos, sendo considerados pontos de conflito entre características que são vantajosas para as espécies individuais porém desvantajosas entre espécies distintas (Agnarsson et al., 2006). São considerados becos sem saída evolutivos: i) a partenogênese (Normark et al., 2003); ii) auto-fertilização (Takebayashi e Morrell, 2001) e iii) especialização ecológica (Stireman, 2005).

As características ecológicas e padrões filogenéticos apresentados pelas linhagens de aranhas sociais denotam um caminho evolutivo que apresenta benefícios em curto prazo, porém deficiências a longo prazo na manutenção das linhagens, caracterizando a socialidade nesses animais como um beco sem saída evolutivo (Avilés, 1997; Agnarsson et al., 2006).

Além de apresentarem todas as características que foram citadas acima, as espécies sociais de aranhas possuem algumas peculiaridades comportamentais, sendo, em geral, menos agressivas e possuindo uma maior variação comportamental entre os indivíduos que suas parentes subsociais e solitárias (Pruitt et al., 2012). Todas essas características tornam as aranhas sociais um excelente modelo para estudos ecológico-evolutivos do comportamento social nos animais (Avilés e Guevara, 2017).

A teoria da construção de nicho

A teoria da construção de nicho surgiu de ideias introduzidas na biologia evolutiva, durante a década de 1980, pelo biólogo evolucionista, geneticista e matemático Richard Lewontin (1983). Por construção de nicho referimo-nos às modificações no ambiente biótico ou abiótico dos organismos, através de interações tróficas e intervenções diretas desses organismos sobre os componentes do ambiente, por meio de seu metabolismo, dos comportamentos e das atividades fisiológicas, assim como das suas escolhas em relação ao habitat (Laland et al., 2016).

Essa nova perspectiva entende que os organismos modificam seu ambiente, que essas modificações são passadas adiante no tempo e espaço (herança ecológica), promovendo mudanças evolutivas através de alterações nas pressões seletivas sobre os nichos desses organismos e com aqueles com os quais eles compartilham o ambiente (Lewontin e Bendall, 1983; Odling-Smee et al., 2003).

A literatura ecológica reconhece várias categorias de espécies que realizam construção de nicho, sendo: i) as engenheiras de ecossistemas (que modificam o ambiente através de interações não tróficas); ii) espécies chave (que promovem efeitos desproporcionais, no ambiente, em relação à sua

abundância nas comunidades e ecossistemas nos quais ocorrem); iii) espécies dominantes (que apresentam grande efeito nas comunidades e ecossistemas nos quais ocorrem dada a sua grande abundância através de competição) e iv) espécies fundadoras ou facultativas (que criam habitats).

Assim, a herança ecológica se refere ao fenômeno da continuidade dessas mudanças nas comunidades e ecossistemas por várias gerações, modificando as pressões seletivas sobre os organismos descendentes, sendo considerada uma segunda rota de herança para os processos evolutivos, além da genética (Odling-Smee et al., 2003).

Há três aspectos nos quais a construção de nicho é importante dentro dos processos evolutivos. Primeiro, por modificarem seus próprios ambientes e deixando um legado para as futuras gerações, por meio das pressões seletivas modificadas por herança ecológica, as populações podem influenciar a direção e as taxas de sua própria evolução gerando, por exemplo, respostas temporalmente deslocadas aos efeitos da seleção natural (Laland et al., 1999). Segundo, por modificar a estrutura populacional, ela pode reduzir o efeito da deriva e aumentar a longevidade das espécies, a despeito da direcionalidade da seleção. Terceiro, através do processo de modificação de seus próprios nichos, os organismos podem promover mudanças no nicho de outras espécies com as quais compartilham o ambiente, criando um processo difuso de coevolução (Odling-Smee et al., 2003).

Esse processo de interação entre nichos que são compartilhados por diferentes espécies pode acontecer de uma para muitas, de várias para uma ou ainda de muitas para várias espécies (Odling-Smee et al., 2003). Esses processos podem promover não apenas mudanças nas pressões seletivas sobre os construtores de nicho, mas também alterar o processo evolutivo de outras espécies.

Engenharia de ecossistemas e a seleção modificada

A modificação do ambiente realizada por construtores de nicho é associada com o processo ecológico de engenharia de ecossistemas, proposto por Jones et al. (1994). Eles descreveram dois tipos de engenheiros de ecossistemas: i) o tipo alogênico (aqueles que transformam materiais para modificar o ambiente, *e.g.*: vespas que constroem ninhos de papel); e ii) o tipo autogênico (aqueles que

modificam o ambiente transformando a si mesmos, e.g.: árvores, que com seus corpos modificam as condições do ambiente em seu redor).

Essas duas classes podem, por sua vez, ser divididas de acordo com o tipo de transformação provocada pelo organismo no ambiente, como por exemplo, os engenheiros estruturais, químicos, e luminosos, os perturbadores, os atenuadores de vento e os consolidadores (Berke, 2010; Jones et al., 1994).

As consequências ecológicas da construção de nicho são as mesmas que as apresentadas pela engenharia de ecossistemas, mas a teoria da construção de nicho foca mais sua atenção sobre as mudanças que alteram a seleção natural para afetar a evolução das populações (Odling-Smee et al., 2013).

Com a finalidade de integrar a ecologia de ecossistemas e a biologia evolutiva, os proponentes da teoria da construção de nicho definiram uma variável ecológica denominada “R”. Esta pode ser modificada pela ação dos organismos e influenciar a seleção natural que atua sobre as populações. A variável “R” é dividida em três tipos: i) componente abiótico (e.g.: solo); ii) componente biótico (e.g.: organismos) e iii) artefatos (e.g: ninhos). Esses três tipos de variáveis ecológicas podem carregar três tipos de conteúdo, um material, um energético (R_p) ou um conteúdo informacional (R_i). Construtores de nicho podem causar modificações tanto no conteúdo físico-energético como no informacional, e as consequências evolutivas dessas modificações são moduladas pelo tipo de variável e conteúdo que estão sendo modificados (Barker e Odling-Smee, 2014).

Por exemplo, como o componente abiótico dos ecossistemas apresenta apenas o conteúdo físico, ele pode apenas sofrer modificações em sua estrutura ou composição química. Geralmente, recursos abióticos, sobre constante modificação por muitas gerações de construtores de nicho, vão exibir condições que desviam muito de seu estado de equilíbrio termodinâmico (e.g.: solo). Essas mudanças no componente abiótico dos ecossistemas podem persistir por longos períodos de tempo e

avançar muito além da expectativa de vida do construtor de nicho que a produziu (Barker e Odling-Smee, 2014; Odling-Smee et al., 2013).

No que tange ao componente biótico, ele pode ser modificado tanto fisicamente como informacionalmente, sendo as mudanças físicas feitas nas redes tróficas, modulando os ciclos dos nutrientes nos ecossistemas e aumentando ou reduzindo o tamanho das populações nos diferentes níveis tróficos. Esse processo, em cascata, chamado de cadeia trófica (Barker e Odling-Smee, 2014; Odling-Smee et al., 2013).

Além de modificar o conteúdo físico, através da construção de nicho é possível transformar o conteúdo informacional do componente biótico por meio da troca horizontal de genes (*e.g.*: transferência de plasmídeos bacterianos que fazem cepas inofensivas de bactérias se tornarem resistentes a antibióticos) e mediante à transmissão de informação social e cultura (*e.g.*: aprendizado).

Finalmente, a produção de artefatos pode também ser modificada em seu conteúdo físico ou informacional. Nesse caso, os artefatos são, dentre as mudanças causadas por construção de nicho com consequências mais efêmeras, muito complexos e custosos, requerendo manutenção constante para que suas propriedades sejam mantidas (Barker e Odling-Smee, 2014; Odling-Smee et al., 2013).

Através de todos esses fenômenos, os processos da construção de nicho podem atuar, causando mudanças nos componentes ecológicos por meio do tempo e em distintas escalas espaciais. A permanência no tempo é a chave para que esses efeitos ecológicos possam ser significativos em termos evolutivos.

Caminhos de retroalimentação ecológico-evolutivos

Para ser significativa, em termos evolutivos, qualquer alteração em alguma variável ecológica promovida por construção de nicho deve se traduzir em uma mudança em pelo menos uma pressão seletiva sobre uma população em um dado ecossistema (Odling-Smee et al., 2013). Esse processo só é possível se essa variável modificada for parte da herança ecológica da população. Se tais mudanças nas variáveis ecológicas se dissiparem muito rapidamente na população (se não houver transmissão

dessas mudanças através das gerações), ou se forem suplantadas por efeitos mais poderosos causados por outros processos, então, não haverá efeitos evolutivos de construção de nicho (Odling-Smee et al., 2013).

A intensidade dos efeitos causados por construção de nicho depende de alguns fatores regulatórios: i) o ciclo de vida do organismo que é construtor de nicho; ii) a densidade populacional da espécie construtora de nicho; iii) a distribuição local e regional das populações; iv) o tempo de permanência da população em um dado local; v) o tipo e processo de estrutura modificadora do ambiente que a espécie produz; vi) a quantidade e tipos de recursos que são mobilizados no processo de construção das estruturas (Odling-Smee et al., 2013).

Não é difícil imaginar que a intensidade dos efeitos será maior conforme o tamanho e a densidade das populações forem maiores, conforme mais tempo as populações passarem em um local e quanto mais recursos e energia forem despendidos durante a construção das estruturas.

Esses fatores reguladores de intensidade estão conectados com os processos ou caminhos alternativos que permitem retroalimentações ecológico-evolutivas. Dentre essas vias, a mais simples é a do fenótipo estendido (Dawkins, 1982), no qual um genótipo em uma população expressa uma adaptação modificadora do ambiente, tais como as “casas” construídas pelas larvas de trichoptera. Mutações nesses genótipos alteram a forma como o ambiente é modificado pela larva, resultando em mudança nas pressões seletivas sobre o próprio genótipo, o que altera sua aptidão.

Em um segundo caminho, proposto em versões mais antigas dos modelos de construção de nicho e outros arcabouços de modelagem (Laland et al., 1999, 1996), um genótipo expressa um traço modificador de ambiente que modifica uma variável ecológica (ΔR), tornando-se uma mudança em alguma pressão seletiva sobre a população. Nesse segundo cenário, em adição, a promoção de mudanças retroalimentadoras sobre os alelos que promovem os traços modificadores do ambiente (como no caso do fenótipo estendido), outros alelos podem ser também afetados, causando

modificações mais amplas na composição genotípica das populações construtoras de nicho (Odling-Smee et al., 2013).

Um terceiro caminho alternativo, similar ao caminho dois, possui um fator adicional no qual as mudanças nas pressões seletivas afetam não apenas as populações construtoras de nicho, mas também populações de outros organismos, que são afetados pelas mudanças nas variáveis ecológicas, causando processos de coevolução difusos (Odling-Smee et al., 2013). Um quarto caminho alternativo, no qual os efeitos da construção de nicho, promovidos por uma população, interagem com as consequências da construção de nicho realizados por outra população. Essa rede de interações pode ser analisada da perspectiva de uma espécie para muitas; de muitas para uma única ou de muitas para muitas espécies, produzindo cenários extremamente complexos de mudanças nas pressões seletivas sobre as populações envolvidas (Odling-Smee et al., 2013).

Os dois últimos caminhos, que consideram os efeitos da construção de nicho de uma população afetando outras populações em uma cadeia de reações ou em um sistema cíclico de retroalimentação, contém um mecanismo interno que considera as mudanças na disponibilidade de recursos e nas alterações das condições ambientais promovidas por algumas espécies sobre as outras com as quais elas compartilham os habitats. Esses mecanismos que promovem modificações no fluxo de energia e nos ciclos ecossistêmicos de matéria são coletivamente denominados de “associações genotípicas mediadas pelo ambiente” (EMGA na sigla em inglês).

A principal característica dos EMGAs é que eles mapeiam as fontes de seleção resultantes dos genes de uma população sobre o genótipo de outra população que evolui em resposta a essas fontes de modificação e são, dessa forma, fundamentais para testar cenários de coevolução difusa promovidas por esses caminhos de interação entre mudanças nas variáveis ambientais (Odling-Smee et al., 2013).

Processos, como esses, enfatizam que a interação entre processos ecológicos e evolutivos não pode sempre ser reduzida ao nível genético e que um foco mais apropriado poderia ser sobre as “associações fenotípicas mediadas pelo ambiente”.

Como colocado por Odling-Smee et al. (2013):

“Uma das vantagens da perspectiva da construção de nicho é que ela enfatiza os fenótipos como sendo reconstruídos em cada geração por diferentes recursos de desenvolvimento (genéticos e não-genéticos), ao invés de apenas pela expressão de informação codificada geneticamente. O foco de algumas metodologias (e.g.: genética de comunidades) exclusivamente na variação genética do fenótipo, excluindo a variação não herdada geneticamente (e.g.: plasticidade, epigenética, estrutura populacional, herança ecológica) perdem muitos processos ecológico-evolutivos interessantes” (Ellner et al., 2011; Palkovacs et al., 2012; Uller, 2008).

Construção de nicho e socialidade: a importância dos fatores ecológicos

A literatura ecológica apresenta uma série de fatores que se mostram fundamentais para a evolução e manutenção da socialidade nos animais, tendo sido organizados em hipóteses tais como a “das restrições ecológicas” proposta por Emlen (1982) e a “dos benefícios da filopatria” apresentada por Stacey e Ligon (1991). Vamos olhar um pouco mais de perto essas duas hipóteses, pois ambas apresentam, em suas estruturas, os elementos dos quais a construção de nicho se utiliza para realizar a conexão entre a ecologia e a evolução das espécies sociais.

A teoria das restrições ecológicas apresenta três fatores que favorecem a permanência dos juvenis em seu local de nascimento: i) a limitada disponibilidade de locais para construção de ninhos; ii) custos elevados relacionados com a dispersão e iii) fatores demográficos, tais como a densidade e o tamanho do grupo.

Desses três o que se apresenta mais amplamente distribuído entre diferentes táxons que apresentam níveis elevados de socialidade é o da elevada taxa de mortalidade ligada a dispersão (Korb e Heinse, 2008). Em Hymenoptera e Termitoidea, a dispersão para reprodução e fundação de novas colônias está associada ao comportamento de enxamear, que aumenta as chances de sobrevivência dos indivíduos por efeito de diluição. Até mesmo microrganismos apresentam fenótipo social quando entram na fase de reprodução e dispersão, como é o caso de *Dictyostelium discoideum*, que se agregam formando um corpo de frutificação para produzir esporos e dispersar (Newell et al., 1969).

Em aranhas, as restrições à dispersão se manifestam até mesmo na morfologia das espécies, de acordo com o nível de socialidade. Os indivíduos de espécies sociais possuem menor capacidade de

produzir as “pontes” com os fios guia de teia e apresentam menor razão entre o comprimento das patas e o comprimento do corpo, condições anatômicas que limitam a capacidade dos indivíduos de se deslocar no ambiente (Corcobado et al., 2012).

Ligadas às limitações ecológicas sobre a dispersão dos indivíduos, estão as possíveis vantagens em termos de aptidão aos indivíduos que permanecem no ninho, tais como: i) cooperação no cuidado com as crias (cuidado aloparental); ii) defesa dos familiares contra predadores e parasitas; iii) aumento da aptidão direta por meio da herança do ninho e/ou aquisição de experiência e iv) ganhos diretos e indiretos na aptidão através da monopolização de recursos alimentares contra competidores.

O cuidado aloparental é extensivamente documentado nas colônias de aranhas sociais (Samuk e Avilés, 2013; Schneider, 2002; Viera e Agnarsson, 2017), promovendo o aumento da sobrevivência dos filhotes e garantindo que, mesmo no caso de morte da mãe, os seus filhotes tenham chances de se desenvolver (Avilés e Guevara, 2017).

A defesa de familiares contra predadores e parasitas é uma vantagem menos ubíqua dentre os animais sociais, sendo pouco importante entre as aves por exemplo (Korb e Heinse, 2008), embora comportamentos de alarme, como a presença de sentinelas, ocorre tanto em grupos de mamíferos quanto em grupos de aves (Clutton-Brock et al., 1999; Sherman, 1977; Zahavi, 1990). Dentre os invertebrados, a proteção contra predadores e parasitas é uma importante pressão seletiva em favor da socialidade. No caso das aranhas, além da proteção garantida pelas grandes teias tridimensionais, a presença de outros indivíduos para alertar sobre a possibilidade de ameaças ou a cooperação na defesa ativa contra os inimigos, promovem o aumento das chances de sobrevivência das colônias (Avilés e Guevara, 2017; Straus e Avilés, 2018; Uetz et al., 2002; Yip e Rayor, 2011).

Os padrões ecológicos, apresentados anteriormente, mostram como a construção de um ambiente mais favorável, onde há mais proteção e maior garantia de recursos alimentares pode favorecer a permanência dos indivíduos em seu local de nascimento. E quanto maior for a diferença entre os custos e riscos oferecidos pelo ambiente do entorno e os benefícios do ambiente construído

pela população parental, maiores as chances de se permanecer no local de nascimento e tornar a sociedade maior e mais complexa. Dentro dessa lógica, podemos dizer que as espécies construtoras de nicho são fortes candidatas a criarem condições para a evolução da socialidade.

Nicho social e personalidade: a organização das sociedades

Os indivíduos de uma população nunca são exatamente idênticos, mesmo aqueles que compartilham o mesmo material genético (clones), vão apresentar, ao longo de seu desenvolvimento, diferenças na morfologia e no comportamento dadas as experiências distintas que vivenciarem em contato com o ambiente. Uma importante fonte de variação, dentro das populações das mais diversas espécies, é a personalidade, que se configura como uma consistência no comportamento dos indivíduos ao longo do tempo e dentro de diferentes contextos (Gosling, 2001; Stamps e Groothuis, 2010).

Apesar de se reconhecer que a personalidade é uma propriedade inerente dos animais, pois já foi identificada nos mais distintos táxons, a origem e a manutenção dessa consistência no comportamento dos indivíduos, dentro das populações, ainda é um campo pouco investigado (Stamps e Groothuis, 2010).

O arcabouço da especialização de nicho social promove uma possível explicação adaptativa para a existência de diferenças na personalidade dos indivíduos dentro de um contexto social, baseada na dinâmica dos efeitos das interações entre eles ao longo de suas vidas (Bergmüller e Taborsky, 2010). Essa hipótese se apoia na premissa de que os indivíduos aumentam sua aptidão ao escolherem estratégias comportamentais que reduzem o conflito com os demais membros do grupo. A seleção natural deve favorecer traços que promovam soluções efetivas contra os conflitos sociais, sendo a consistência comportamental dos indivíduos ou sua personalidade uma dessas estratégias, pois reduz a sobreposição dos nichos sociais entre os indivíduos que utilizam os mesmos recursos, em uma condição análoga ao “distanciamento de caracteres”, presente na ecologia de comunidades (Bergmüller e Taborsky, 2010).

Uma das mais importantes consequências da hipótese da especialização de nicho social baseada na personalidade se refere à existência da divisão de tarefas dentro dos grupos, um fenômeno que, por muitos, é considerado uma das mais importantes adaptações da vida em sociedade. A presença de indivíduos especializados na realização de tarefas vitais para a organização e sobrevivência do grupo, tais como, cuidar dos filhotes, forragear e defender o ninho, aumenta a eficiência e a produtividade das colônias (Boomsma e Gawne, 2018; Nowak et al., 2010).

Os mecanismos envolvidos nesse processo de especialização dos indivíduos na execução de determinadas tarefas em detrimento de outras, envolvem processos genéticos, interações genótipo-ambiente (polifenismo observado nas colônias de formigas com castas morfológicas), fatores de desenvolvimento (polietismo observado nas colônias de cupins, nas quais os indivíduos mudam de casta conforme se desenvolvem) e também predisposições comportamentais, como seria o caso da divisão de tarefas baseada na personalidade (Grinsted et al., 2013; Ravary et al., 2007; Spaethe e Weidenmüller, 2002; Theraulaz et al., 1998; Tripet e Nonacs, 2004).

Como a presença de polifenismo (castas morfológicas) e polietismo (diferentes fases do desenvolvimento realizam tarefas distintas), são pouco comuns dentro da imensa diversidade de sistemas sociais que existem na natureza, a divisão de tarefas baseada em predisposições comportamentais dos indivíduos (personalidade) parece ser um mecanismo mais universal (Grinsted et al., 2013). Dessa forma, possivelmente, a evolução de sistemas sociais pode estar de forma sistemática ligada a uma maior amplitude da variação comportamental dos indivíduos, gerando um fenômeno que, a princípio, parece paradoxal, segundo o qual, para viver em grupos, os indivíduos precisam ser mais diferentes entre si (Bergmüller e Taborsky, 2010; Grinsted et al., 2013; Montiglio et al., 2013; Pamminger et al., 2014; Pruitt et al., 2012).

Essa tese apresenta a investigação de hipóteses a respeito dos mecanismos evolutivos que levaram a origem da socialidade nas aranhas e dos mecanismos ecológicos que promovem a organização dessas sociedades. Essa investigação é desenvolvida amparada sob a estrutura da Teoria

da Construção de Nicho como agente do processo evolutivo da socialidade e da Hipótese de Construção de Nicho Social como mecanismo principal na organização das sociedades.

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CAPÍTULO 1

The survival of the shyest: a computational model shows the effect of web structure on the origins of social spiders

A sobrevivência do mais tímido: um modelo computacional mostra o efeito da estrutura da teia sobre a origem das aranhas sociais

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The survival of the shyest: a computational model shows the effect of web structure on the origins of social spiders

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For social life to emerge, the benefits of group living must overcome its costs, a balance that depends on the life history of the organisms and may occur more easily in some taxa than in others. Among spiders, sociality is uncommon. Social species evolved several times independently through the subsocial route, a process connected to a mean reduction in the aggressiveness and boldness of the individuals, with a simultaneous increase in the variability of personality. Personality variability is at the root of spider's division of labor, but the mechanism for its increase is yet poorly studied. One possible mechanism for the evolution of the variability in personality would be the creation of a new selective regime by the newly evolved, larger colonial webs, which could offer a mix of more protected and predator-exposed areas. To evaluate this hypothesis, we present an ecological-evolutionary model in which heterogeneous, spatially explicit variation in predatory selective pressures appear through changes in niche construction. Our model shows that social webs, by providing areas of greater protection against predators, increase the survival of the shyest variants, leading to increased intra-colonial variability in personality. We speculate that this greater protection allowed social species the possibility of colonizing otherwise inhospitable environments, and that larger intra-colonial personality variance, associated with social web spatial heterogeneity provided the basis for social organization through division of tasks among colony members.

Keywords: Social spiders, inceptive niche construction, relaxed selection, animal personality

To understand how social systems evolved, it is necessary to start with the selective forces that led to the formation of aggregations of individuals in the first place. One of these forces is the limitation in the dispersal capacity of individuals, a trade-off among the benefits of leaving the family against the risks inherent to this strategy, such as predation (Clobert *et al.*, 2004; Clobert *et al.*, 2009). Natal philopatry is selected when the environmental properties required for survival are rare or too costly to achieve. If organisms, through ecosystem engineering, are able to change the environment around them to make conditions more favorable, for instance, by constructing a nest, and if habitat modification is selected for a higher benefit/cost ratio, then natal philopatry may be further selected for (Jones *et al.*, 1994; Odling-Smee *et al.*, 2003).

Ecological engineering, such as the construction of galleries, chamber systems (in the soil or in the wood), fortified nests or webs, can thus modify selective pressures on the present and future generations, generating evolutionary feedback loops known as inceptive niche construction (*sensu* Odling-Smee *et al.*, 2003), a phenomenon connected to social life in a large number of invertebrate taxa (see a brief list in Appendix 1). In these cases, the level of sociality is related to the severe ecological restrictions to dispersion caused by the construction of the sophisticated structures required for colony maintenance. For a given individual, the chances of leaving the colony and building a new structure elsewhere are so small that it is more advantageous to stay at the natal site and cooperate with the group (Emlen, 1982; Emlen, 1997; Korb and Heinze, 2008).

Once a social system has been established, there is selection for a well-structured internal organization, and the division of labour is one of the most important organizational adaptations for social life (Boomsma and Gawne, 2018; Nowak *et al.*, 2010; Wilson, 1970). Task specialization is typical of eusocial societies, such as in Hymenoptera and Blattodea, in which polyphenism and polyethism characterize morphological and behavioral between-caste variation (Boomsma and Gawne, 2018; Nowak *et al.*, 2010; Wilson, 1970). Recently it has been shown that there is also repeatable inter-individual variability, that is, personality variability within each working caste

(Chapman *et al.*, 2011; Jandt *et al.*, 2013; Pamminger *et al.*, 2014), and personality differences within the colony could also explain asymmetries in task distribution, even in species without a caste system. Although the tasks could potentially be done by any individual in these casteless societies, there is a clear tendency for task specialization based on individual personalities (Grinsted *et al.*, 2013; Holbrook *et al.*, 2009; Wright *et al.*, 2014).

A possible mechanism linking personality with task performance is the direct influence of the constructed niche's architecture on the interaction networks between individuals. Recent studies have shown the fundamental role of the configuration of the environment on the structure and social organization in various animal societies (He *et al.*, 2019; Penn and Turner, 2018).

Long-lasting and repetitive interactions with individuals of one same behavioral type reinforce the expression of behaviors that characterize this very same behavioral type (Laskowski and Pruitt, 2014; Modlmeier *et al.*, 2014). If the spatial structure of the nest increases social modularity, shaping the interaction network of the groups, for instance, by promoting cliques of interaction between individuals of similar behavioral types, this spatially structured interaction network would create a feedback loop reinforcing the distinction between behavioral types within the colony. Evidence of a similar feedback loop has been recorded in ants and social spider colonies (Hunt *et al.*, 2018; Mersch *et al.*, 2013; Pamminger *et al.*, 2014).

Enhanced ecosystem engineering could in this way promote the spatial heterogeneity necessary for the development and maintenance of distinct personalities within a social group, and subsequent evolution through inceptive niche construction would permanently change the organization of these social systems.

The Case of Social Spiders

Sociality is rare among spiders, since only 30 species are social, with 30 other species displaying gregarious behavior (Lubin and Bilde, 2007; Whitehouse and Lubin, 2005), among a total of more than 47 thousand species described for the taxon (World Spider Catalog, 2018).

The transition from subsocial to social life occurred through the transformation of several behavioral characteristics, such as: i) the loss of premating dispersal (Corcobado *et al.*, 2012; Jones and Parker, 2002; Jones *et al.*, 2007); ii) the emergence of a highly inbred mating system (Agnarsson and Avilés, 2013; Avilés and Bukowski, 2006; Bilde *et al.*, 2005); iii) the emergence of allomaternal care and allomatriphagy (Jones and Parker, 2000; Junghanns *et al.*, 2017; Kim *et al.*, 2000; Schneider, 2002; Salomon *et al.*, 2005; Salomon and Lubin, 2007); and iv) the increase in the variance of personalities, with a reduction in aggressiveness and boldness (Pruitt *et al.*, 2011c; Pruitt *et al.*, 2012b).

For a subsocial species it is advantageous to be aggressive and bold, because the single colony founder must capture prey items, maintain the web and care for the offspring always alone, making decisions quickly and efficiently, and incurring in elevated risks, otherwise the mother and their offspring will either starve or be preyed upon (Hardwood and Avilés, 2018; Pruitt *et al.*, 2012b).

In turn, permanent social life demands low levels of aggressiveness to reduce intra-colonial competition for food and space, while diluting among group mates the risks of decisions related to prey or threats, thus opening opportunities for the shyest individuals (Hardwood and Avilés, 2018). Notwithstanding these considerations, the question of the emergence of the shyest variants within social species still constitutes an unanswered question (Pruitt and Avilés, 2017). Here we propose an evolutionary mechanism implemented in a spatially explicit model that simulates the change in inter-individual behavioral variation in personality traits, showing that the survival of the shyest could be modulated by niche construction.

THE THEORETICAL MODEL

Web Structure, Climate Conditions and Predation Pressure Effects on Sociality

Spider social behavior evolved not only through decreases in dispersal coupled to inbreeding and maternal care increases, but also through web size increase coupled to changes in dietary composition. These later changes have resulted in a distinct spatial distribution across the levels of sociality at both the local and the biogeographical scales (Guevara and Avilés, 2017; Hoffman and Avilés, 2017;

Purcell *et al.*, 2012). At a local scale, subsocial species predominate at higher altitudes (from 600 to more than 3000 meters), while social species predominate at lower altitudes (from 0 to 2000 meters) (Avilés *et al.*, 2007). At a biogeographical scale, there is a clear latitudinal gradient to spider sociality, with subsocial species distributed throughout subtropical areas while social species live in the tropics (between 23.5° S and 23.5° N) (Guevara and Avilés, 2015).

The three main ecological factors that cause this distributional pattern are: i) occurrence of heavy rains; ii) predation intensity and iii) occurrence of large prey (Guevara and Avilés, 2015; Hoffman and Avilés, 2017). Precipitation is more intense in the tropical lowlands, decreasing at higher latitudes and altitudes. Precipitation limits the distribution of subsocial species because constant and intense rain damages the web, increasing excessively web repair costs for the single adult female in the colony (Hoffman and Avilés, 2017; Avilés *et al.*, 2007; Purcell and Avilés, 2008). These same costs are relatively lower for social spiders, that live in a more resistant web, and share the maintenance costs with their nest mates.

Predation pressure for subsocial and social spiders is higher at lower latitudes and altitudes, and the majority of predation is caused by ants (Hoffman and Avilés, 2017; Purcell and Avilés, 2008). Predation rate decreases 9.6% for every 100 meters increase in altitude, and 3.5% for every 1° latitude moved away from the equator (Roslin *et al.*, 2017). Experimental increases of predation pressure led to significant decreases in the survival rate of subsocial nests, leaving unaffected the social nests (Hoffman and Avilés, 2017).

Finally, larger prey items are vital to the maintenance of large colonies, since they provide the necessary amount of energy to support the group, as well as reinforcing group hunting behavior, because they require the cooperative activity of many individuals to be killed (Guevara and Avilés, 2015).

Although it is becoming clear that the evolution of permanent sociality in *Anelosimus* spiders allowed the colonization of otherwise inhospitable habitats, by increasing social spiders' abilities to

cope with enhanced predation pressures and inclement weather (Hoffman and Avilés, 2017; Purcell and Avilés, 2008), while simultaneously facilitating the capture of large prey items (Guevara and Avilés, 2015), we have so far no hypothesis about the mechanisms that could promote these increased abilities. Considering the close association between inceptive niche construction and social life (Appendix 1), it remains an open possibility that more complex social spider webs could provide this mechanism, by increasing the heterogeneity of selective pressures within the colony.

Here we develop a model to evaluate this possibility, testing the effect of different evolutionary scenarios at the origin of sociality and of different changes of selection pressures due to the evolution of larger and more complex webs. This capacity to tolerate high predation rates and more severe precipitations is, in our model, attributed to aspects of the collective web (*degree of refuge protection* and *refuge size*) that, with a denser mesh of silk and the incorporation of vegetal debris in its structure, promotes an effective line of defense against ecological limiting factors, while promoting intra-colony spatially heterogeneous sources of selective pressures for the increase of personality trait variation.

Evolutionary Model for the Increase in Personality Variation Modulated by Niche Construction

Here we use the genus *Anelosimus* (Theridiidae) as a biological model for our evolutionary hypothesis and computational simulations because it is well studied, with well-known phylogenetic relationships (Agnarsson et al., 2006; Agnarsson, 2012; Pruitt *et al.*, 2012b), and with a wealth of information concerning its ecological niche and sociality levels (Guevara and Avilés, 2015; Hoffman and Avilés, 2017; Purcell *et al.*, 2012). The central axis of our evolutionary hypothesis (see Appendix 2) is niche construction: the construction of increasingly more complex gregarious webs would promote an intra-colony diversification of the selective pressures upon behavior.

The appearance of three-dimensional, larger, more complex, and consequently costlier webs in the subsocial ancestors of social species would be the key to the generation of a more aggregate distribution of the population in the landscape, through increased dispersion costs. Larger nests reduce the individual cost of web maintenance (Purcell and Avilés, 2008; Riechert, 1985; Riechert *et al.*,

1986) and allow the capture of larger prey (Guevara and Avilés, 2015; Hardwood and Avilés, 2013; Nentwig, 1985). The clumpy distribution opens the possibility for further evolution of extended maternal care (Jones *et al.*, 2007; Schneider, 2002; Purcell and Avilés, 2008). Also, larger and more complex webs provide additional protection for residents against predators and adverse climate conditions (Avilés *et al.* 2007; Hoffman and Avilés, 2017; Purcell and Avilés, 2008).

The survival of shyer individuals, that represent the left tail of the distributions of personality, would split behavioral strategies in the subsocial aggregations. Bolder and more aggressive individuals should continue to disperse before reproducing, abandoning their natal colony and founding new webs elsewhere, while the most docile and shy individuals should remain and even reproduce in their natal colony. Over time, the mean aggressiveness and boldness within the group would decrease, due to the permanence of non-dispersing, shyer individuals. This larger group with now permanent residents would produce a larger and more complex web, thus creating a positive feedback to the evolution of web size and complexity. With a progressively higher investment in the web, the corresponding increase in dispersion costs would finally pay for natal philopatry even among the boldest individuals, thus giving rise to the social condition (Figure 1).

The evolutionary outcome of this process is not only a reduction in the average aggressiveness and boldness of social species, but also an increase in the range of variation, allowing individuals to express their behavior in a broader range of personality traits. The more protected areas of the web, with denser silk mesh and with the presence of elements like leaves and twigs that could function as refuges, would provide ideal conditions to the expression of shyer behavioral phenotypes, thus promoting a spatially heterogenous distribution of personality traits, as has been shown for ants (Pamminger *et al.*, 2014). Also, the concentration of protected areas in the center of the web would let shyer individuals in constant contact with other similarly shy individuals, and in closer contact with the offspring whose care eventually evolves as their main function. Meanwhile, the more aggressive and bolder individuals would be more frequent in the peripheral regions of the web, where contact with other bold individuals

and with potential prey and enemies, such as predators and parasites, would reinforce their aggressive and daring behavior.

THE COMPUTATIONAL MODEL

Agent-Based Model of the Effect of Web Structure on Personality Variability

A complete model description is presented in the ODD protocol (see Appendix 3), and the full model is available for download at (<https://github.com/NuEVo-Ufba/spider-personalities-paper>). Here we present a summary of the model, that was developed in *NetLogo* software (Wilensky, 1999).

We have represented the web as a planar structure, with different regions having different levels of exposure to predation danger. The more elaborate the tridimensional structure of real webs, the higher the level of protection they offer. We can simulate the effects of different, non-planar real web geometries, which give different gradients of protection to the spiders, varying the danger level in different areas of the modelled web. To test the effect of different levels of protection on the distribution of personalities, we ran simulations with different web configurations (different distributions of predation danger throughout the web).

The protection afforded by the web is represented by two parameters: *degree of protection* and *refuge size*. *Degree of protection* is a measure of the level of protection from predators that the protected areas provide. Higher values indicate a sharper drop in the predation probability offered by the refuge, as compared to non-refuge areas. *Refuge size* is the proportion of the web that is protected by the refuge. See Figure 2 for a graphical representation of these parameters.

Spiders in the model have a *personality* trait, varying from 0 (shyest) to 1 (boldest) which describes their propensity to seek risk: higher levels in this parameter indicate that the spider is more likely to move to a spot where it is more exposed to danger.

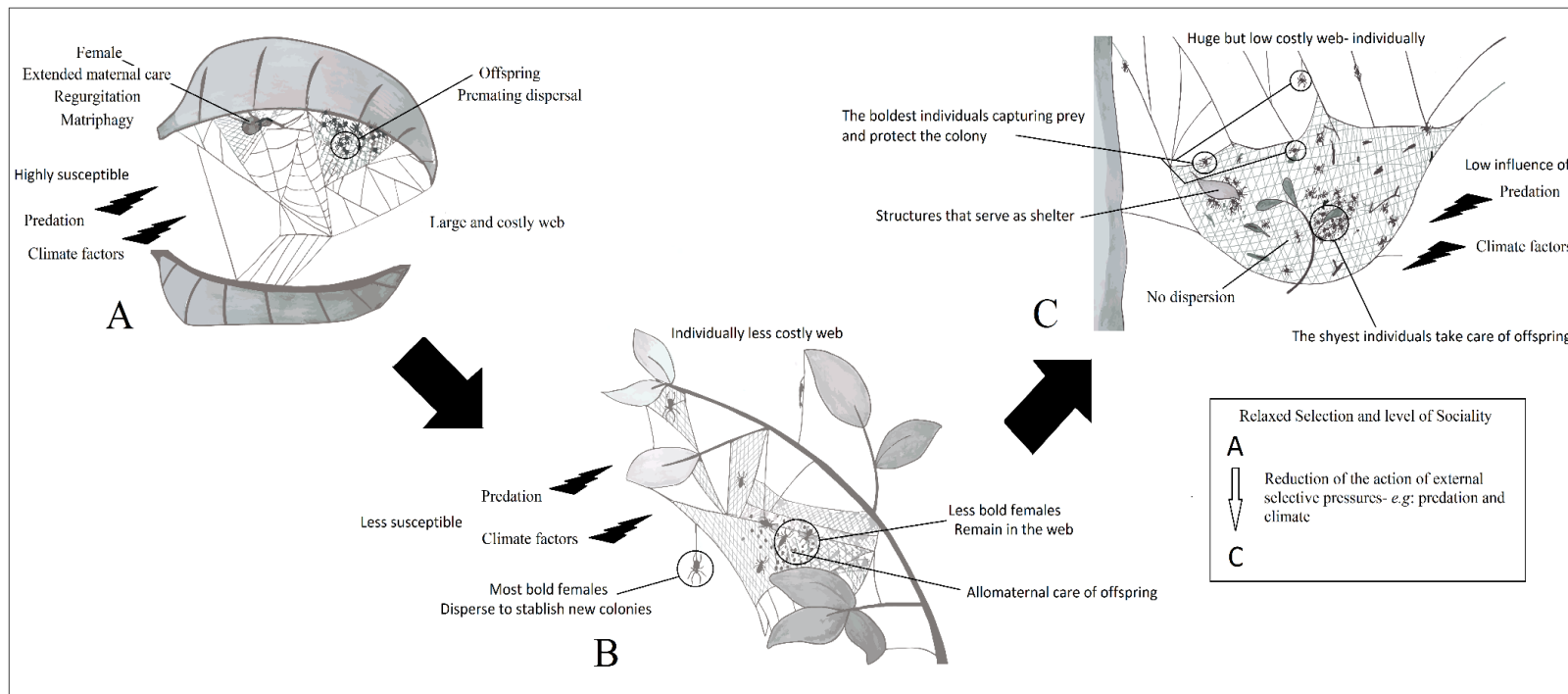


Figure 1: Evolutionary sequence of increase in the sociality level in spiders. Beginning in the subsocial condition (A), the investment in larger webs enhances the costs of dispersal. The resulting densely populated web feeds back (evolutionarily) into larger, and more complex webs (B). More complex webs promote a diversification of intra-colonial selective pressures, with sheltered and unprotected areas selecting for diverse behavioural profiles and setting the stage for the emergence of disparity among individual personalities generating the social condition (C).

Spiders can reproduce, and the personality trait is inherited as the average of that of the parents, with a small random mutation probability. This is based on the fact that personality related traits, such as aggressiveness, has been shown to be a heritable trait in spiders (Sih *et al.*, 2004; Riechert and Johns, 2003; Pruitt *et al.*, 2008). To evaluate distinct evolutionary scenarios representing possible ancestral states, we evolved the system from distinct initial conditions with regard to within-colony personality distributions:

- a) Normal-bold: The *personality* of each spider is randomly drawn from a normal distribution with mean = 0.9 and standard deviation 0.1;
- b) All bold: All spiders have *personality* equal to 0.9;
- c) Normal: The *personality* of each spider is randomly drawn from a normal distribution with mean = 0.5 and standard deviation 0.1;
- d) Uniform distribution: The *personality* of each spider is randomly drawn from a uniform distribution between zero and one;

Each *set of simulations* was composed of 501 independent replicates for each combination of web parameters (*refuge size* and *degree of protection*) and personality distributions, essentially modelling a population of 501 similar but independent webs developing in time. At the end of the simulation, we analyzed the distribution of personalities in each set of simulations, that is, for each web parameters' configurations and initial conditions (personality distributions).

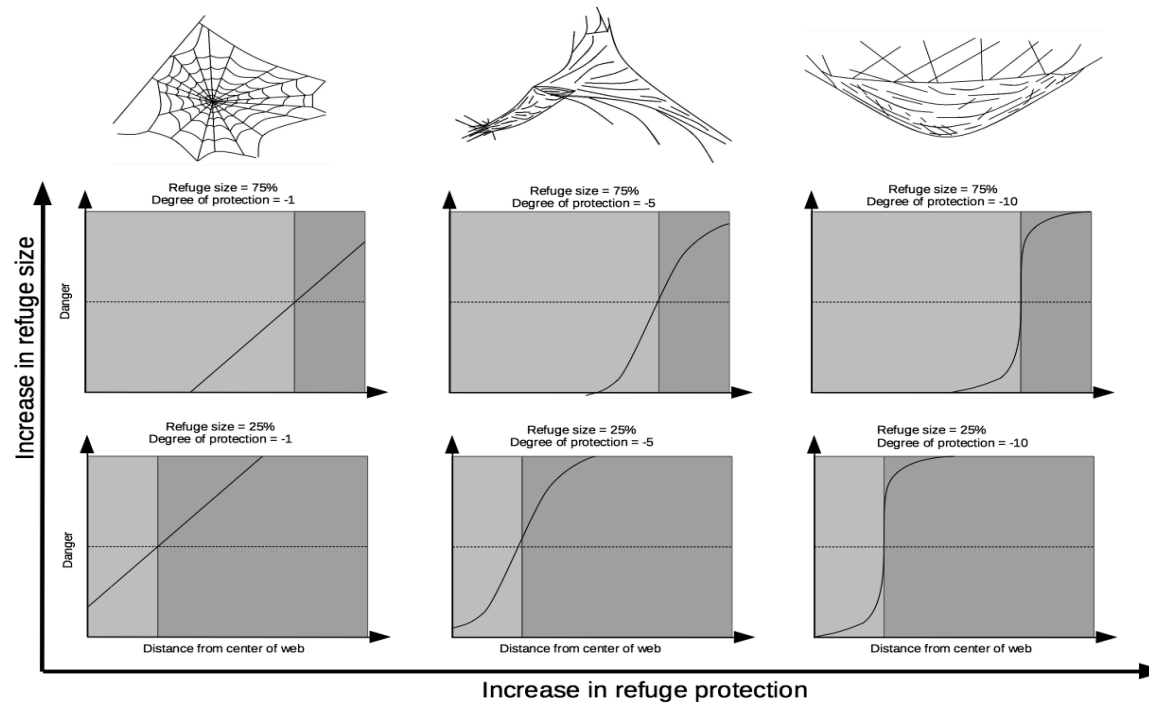


Figure 2: Simulation parameters: *Refuge size* is the proportion of protected (lighter grey) versus unprotected (darker grey) regions in the web. The higher this proportion (top panels), the bigger the refuge is. *Refuge protection* is a measure of the efficiency of the protection, a parameter that impacts the danger level, the response variable in each panel. Highly protective refuges (right panels) are simulated through a sharp increase of danger at the border of the refuge area, with danger levels approaching asymptotically to the maximum, at periphery of the web, and to the minimum levels, at the centre of the web. Lowly protective refuges (left panels) are simulated through a linear danger function increasing from the center to the periphery of the web (straight inclined lines), while intermediate levels of refuge protection (middle panels) are simulated by intermediate danger functions.

STATISTICAL ANALYSES AND RESULTS

We found that increases in web protection allow the presence of a greater proportion of shy individuals. This differential survival is caused by boldness correlating with a preference for exposed areas and with survival from direct predation. The result is positive for shy spiders in more protected webs that is, webs in which the spiders have larger and/or more protective refuges, which diminish their exposure to predation, while in less protected webs this is reversed, favoring bolder spiders, which can survive predation with higher probability. This causes shy spiders to remain within protected areas, while bolder spiders are distributed among protected and exposed web areas.

In our model, probability of surviving a predation event is dependent on personality: the bolder the spider is, the higher its chances of surviving a predation event are. (see Appendix 3, section 3.2 for details). Thus, if the web is more exposed, shy survive less than their bold counterparts, causing the colonies' personality distribution to have a small variance.

Protected webs cause greater survival of shy spiders in the protected areas, also increase the variance of the colonies' personality distribution. By far, the greatest effect was that of the increase in percentage of protected area (controlled by the parameter "*refuge size*"). In fact, when this value was as low as 0.3 (30% protected areas), colonies survived for only a few simulation sets (see Figure 3). We also found that the presence of shy individuals allowed the colonies to survive in harsher (more dangerous) situations.

The simulation sets with a higher proportion of shy individuals at the start (sets *Uniform* and *Normal*) survived in conditions whereas bold colonies (sets *Normal Bold* and *All Bold*) did not, as evidenced by Figure 3. This is due to the risk-seeking behavior of bold spiders, which move to less-protected areas more frequently than shy ones, and thus are more exposed to predation. If all spiders tend to move to risky areas, eventually all are predated, and the colony perishes. The shy spiders remain in the protected regions, and thus survive and are able to breed, replenishing the colony.

Because of the survival differences between sets of simulations, we compared only within each set, and even so, the difference in survival between groups makes standard analysis difficult (levels are extremely unbalanced). We opted not to do a standard linear model regression to compare these differences in distribution (with original *personality distribution*, "*degree of refuge protection*" and "*refuge size*" as predictors of *final personality distribution*), as the levels are extremely unbalanced, and do not meet the assumptions of homoscedasticity. Balancing could be achieved by randomly sampling from levels with surviving colonies, but we believe that this discards important information: in more dangerous situations, colony survival probability is extremely small. Thus, we modelled the number of surviving colonies with a linear model, using "*refuge size*", "*degree of refuge protection*", and "*original personality distribution*" as predictors.

We found that the effect of "*original personality distribution*" is significant ($F(3, 54) = 10.24$, $p < .001$) and can be considered as large (Partial Omega-squared = 0.31), that the effect of "*degree of refuge protection*" is significant ($F(3, 54) = 15.28$, $p < .001$) and can be considered as large (Partial Omega-squared = 0.40) and that of "*refuge size*" is significant ($F(3, 54) = 32.24$, $p < .001$) and can be considered as the largest (Partial Omega-squared = 0.60).

In other words, as the web gets safer, with higher "*degree of refuge protection*" and "*refuge area*", more colonies survive, with "*refuge area*" having the largest effect. This means it is better for the colony if the web has a larger, but less protected refuge, than if the web has a small, but very protected one, even if the smaller refuge offers more protection per unit of area. Combined with this, distributions which have a higher proportion of shy spiders have a higher chance of survival.

All analyses were performed with R software (R Core Team, 2018), using the packages: *purrr* (Henry and Wickham, 2018), *dplyr* (Wickham *et al.*, 2018), *ggplot2* (Wickham, 2016), *ggthemes* (Wilke, 2018), *psycho* (Makowski, 2018) and *forcats* (Wickham, 2018).

DISCUSSION

As seen in Figure 3, moderate levels of refuge area are sufficient to allow the existence of shy individuals and thereby increase the survival and personality variance of the colonies. This shows that structural web changes in ancestral gregarious species could pave the way for the emergence of the social condition in *Anelosimus* spiders. It is interesting to note that, according to our model, for very high levels of predation risk (represented by small *degree of refuge protection*), even bold individuals do not survive. This phenomenon has been observed in nature with subsocial species, which, even though they are more aggressive and bolder than their social relatives, cannot survive in low-land tropical forests, where predation rates are very high (Guevara and Avilés, 2015; Hoffman and Avilés, 2017).

Our model brings fundamental implications for the current state of knowledge about the evolution of sociality in spiders. As Pruitt and Avilés (2017) show, the mechanisms favoring the transition from subsociality to sociality in spiders, the actual mechanisms connecting environmental factors to these evolutionary processes, comprise one of the most intriguing and exciting lines of research in this field.

It is becoming clear that unfavorable climatic conditions and high predation rates of the tropical forests are probably the two main environmental factors that guide this transition (Guevara and Avilés, 2015). In addition to this, access to large prey is also an important factor (Hardwood and Avilés, 2013; Nentwig, 1985; Guevara and Avilés, 2007). These ecological factors would thus preclude the colonization of tropical areas by subsocial spiders but, as our model shows, increased, collective ecological engineering of larger and more protective webs could overcome these difficulties.

Collectively constructed webs, besides being less costly individually in terms of maintenance, can be bigger, and thus have properties that guarantee greater structural stability, being more resistant to adverse climatic conditions, while offering greater protection against predator

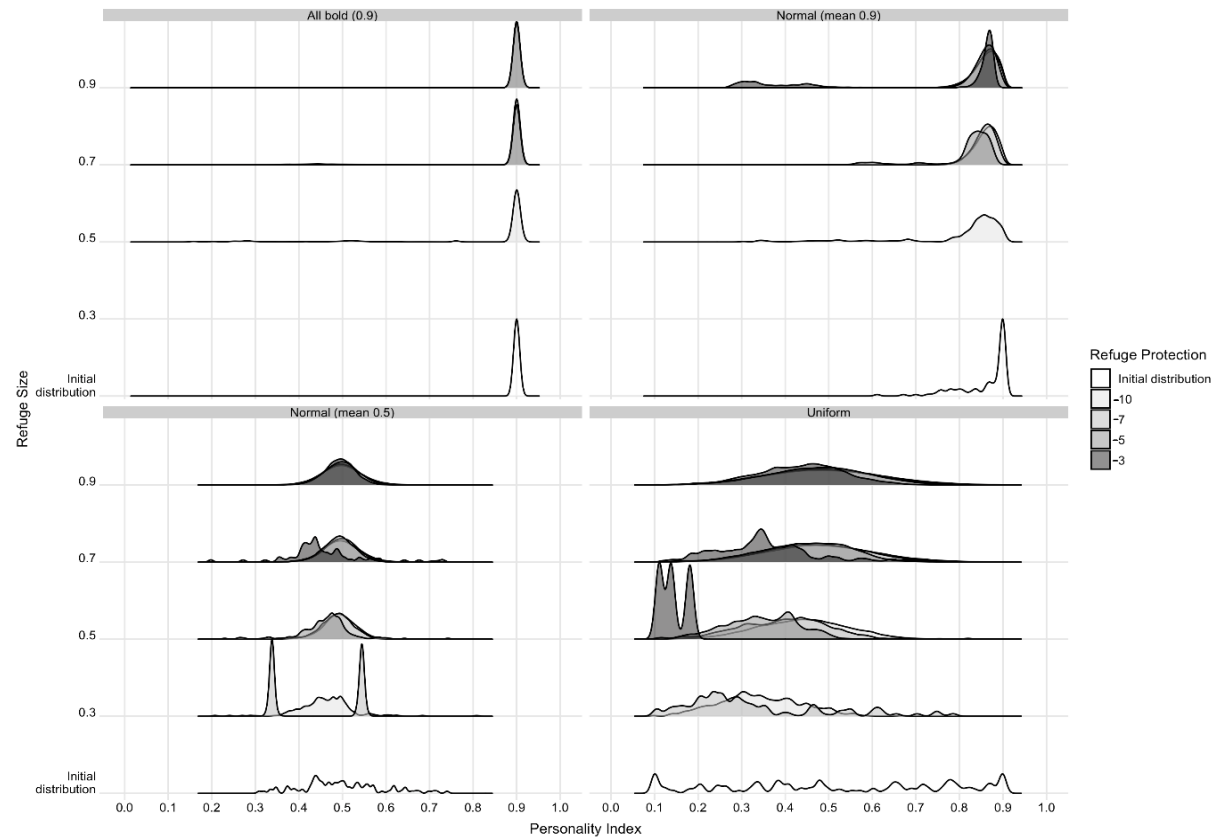


Figure 3: Summary of the results from 32064 simulations, showing the final personality distributions for the surviving colonies. Each of the four panels summarizes the results for a set of simulations under one initial personality distribution (All bold - 0.9; Normal - mean 0.9; Normal - mean 0.5, and Uniform). The initial personality distribution is shown at the bottom level of each panel. Within each panel, each level summarizes the results for a value of refuge area, that increases from the bottom to the top of the panel (0.3; 0.5; 0.7 and 0.9 of the web's area). For each refuge area value and initial personality distribution, darker shaded curves represent progressively lower levels of refuge protection. Absence of a coloured curve at a given level means that no colonies survived that combination of parameters.

attacks and thus, as our model shows, selecting for shyer individuals and larger personality variance.

Once the colonies experience the increase in personality variance among individuals afforded by web structure, they can gain the advantages of this new social condition. Colonies that have individuals occupying a greater range of personality variation (mixed colonies) have higher fitness than colonies with lower variation. They are more successful in capturing prey (Laskowski *et al.*, 2016; Pruitt and Riechert, 2011a), and more efficient in the conversion of prey into colony biomass (Lichtenstein and Pruitt, 2015; Lichtenstein *et al.*, 2016). They possess a more efficient defence system against predators and parasites (Pruitt and Riechert, 2011b) while also presenting greater durability (Pruitt, 2012).

The emergence of shy individuals in the colonies could be considered an important adaptation of social life (Pruitt and Avilés, 2017; Riechert and Jones, 2008). Indeed, Pinter-Wollman *et al.* (2017) have shown in *Stegodyphus dumicola* that shy individuals are more important for colony robustness than bold ones, with colonies where shy individuals were replaced having a seriously degraded performance when compared to colonies where the bold ones were replaced.

The authors attribute this to increased levels of positive social interactions between shy individuals having a positive effect on colony stability, and to the fact that *S. dumicola* colonies may have been selected to be resistant to the loss of bold individuals. In agreement with this, our model shows that, for the same levels of “refuge size” and “degree of refuge protection”, simulation sets with few or no shy individuals had much smaller survival rates than sets with higher proportions of shy spiders. In the most extreme cases, all-bold sets had no survivors at all (Figure 3).

All these benefits are related to a phenomenon that is intrinsically linked to the increase in the behavioral variation of the individuals, the social organization provided by the division of labor (Grinsted *et al.*, 2013; Holbrook *et al.*, 2014; Pamminger *et al.*, 2014; Settepani *et al.*, 2013; Wright *et al.*, 2014). The division of tasks based on personality would promote a separation of social niches within the colonies, reducing intraspecific competition thus increasing the energetic gains of the group (Bergmuller and Taborsky, 2010; Holbrook *et al.*, 2014). Our model shows that the presence of shy

spiders is crucial to colonization of dangerous environments, suggesting that there may be a personality-based division of tasks. Another prediction of the model is the spatial segregation of the personalities within the web. According to this prediction, the shyest individuals would be more frequent in the innermost protected areas of the web, while the boldest ones would be more frequent in the more external and less protected areas.

This prediction is in accordance with the personality-based social niche construction models proposed by (Bergmuller and Taborsky, 2010) and (Montiglio *et al.*, 2013), in which they propose that personality can determine the social function of an individual, but the social function can affect the expression of personality over time. Individuals with distinct personalities may not do well in all social environments, so individuals with distinct personalities would seek to perform certain social functions over others. The search for an appropriate social environment within the structured environment constructed by the social group would segregate spatially the personality types, and spatial web heterogeneity would reinforce the behavior of each behavioral type.

Heterogeneous spatial distribution of personalities occurs in social ants, such as *Myrmica rubra* (Pamminger *et al.*, 2014), with certain behavioral syndromes tending to specialize in specific functions, such as taking care of the eggs, or following foraging trails. Our model predicts that niche construction would select for personality specialization and spatial segregation, promoting a strong association between the behavioral traits of individuals, the tasks they play in the colony and the region of the colony they occupy. Such spatial structure of the personalities in the colonies of social spiders has not yet been observed, constituting a promising avenue for future investigations.

Conclusions

Our model presents a possible evolutionary mechanism for the increase of personality variance in the transition from the subsocial to the social condition in spiders. Under the subsocial condition there is little behavioral variance between individuals, they are mostly aggressive and bold, because shy individuals do not survive in a subsocial, unprotected web. However, subsocial species are not able to

survive in tropical lowland forests because the occurrence of torrential rains increases the costs of web maintenance, and because they cannot survive the higher levels of ant predation, even if they are more audacious and aggressive.

We show that a small increase in the size of the web, even without an expressive increase in its degree of protection, would be enough for the variance in the behavior to increase. This increase in the size of the refuge could be at first achieved via aggregations, that would give rise to a more complex, compounded web structure, followed evolutionarily by the complex social web. More complex tridimensional web aggregations (or social webs) would offer more protection, allowing the survival of the shyer variants within the colonies, with an expressive increase in the personality variance in relation to the subsocial ancestors.

Colonies with high behavioral variance survived better than those that contained mostly bold individuals, because bold individuals do not avoid risky areas, thus exposing themselves to high predation levels. This means that the emergence of shy spiders in the colonies was an important adaptation, increasing the success of the colonies in environments with high rates of predation.

Finally, the collective webs, by means of larger refuges and higher protection, allowed the survival of the shyest spiders. This in turn can give rise to an increased social organization, in which individuals with distinct personalities play different roles within the group. This high variance of personality types can possibly allow the colonies to dominate lowland forests, where environmental conditions and high rates of predation do not allow the survival of subsocial species, nor of webs with homogeneous personality traits. Our model opens new avenues of research highlighting the triggering role of the architectural structure of the collective webs in the emergence and organization of spider societies.

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Appendix 1. Social invertebrates with extensive ecosystem engineering:

Taxon	Structure	Reference
Araneae		
Theridiidae: <i>e.g.</i> : <i>Anelosimus</i> spp.	tridimensional web	Bernard and Kraft, 2002; Kraft and Cookson, 2012
Eresidae: <i>e.g.</i> : <i>Stegodyphus</i> spp.		Avilés and Guevara, 2017;
Blattodea		
Termitoidae	wood galleries;	Korb, 2008; Korb and Heinze, 2008
	fortified nests;	
Coleoptera		
Scolytidae	wood galleries	Kirkendall <i>et al.</i> 1997; Eggertand and Muller, 1997
Platypodidae		Schuster and Schuster, 1997; Nowak <i>et al.</i> 2010
Passalidae		

Hemiptera

Sternorrhyncha: Hormaphididae

galls

Stern and Foster, 1997; Pike and Foster, 2008;

Pemphigidae

Aboot and Chapman, 2017;

Hymenoptera

Apoidea

soil galleries;

Korb and Heinze, 2008; Field, 2008;

Formicoidea

fortified nests;

Nowak et al. 2010; Wcislo and Fewell, 2017;

Vespoidea

wood galleries;

Hunt and Toth, 2017; Heinze *et al.* 2017;

Thysanoptera

Tubulifera: Phlaeothripidae

galls

Cresp and Mound, 1997; Aboot and Chapman, 2017

Appendix 2. Model: assumptions; hypothesis and predictions

Assumptions: In order for the structure of the social web to play a role in the emergence and maintenance of shy individuals in the colonies, it is necessary that- i) in isolation, extremely shy individuals should have a lower chance of survival from a predator attack than bold individuals; ii) the social web should promote effective protection against predators; iii) the chances of being predated within the more densely knit central areas should be smaller than the chances of being preyed upon on the edges, or outer areas of the social web.

Hypothesis: The structure of the social web allowed the emergence and maintenance of shyer variants in the social groups, promoting the increase in the variation of the personality traits among the individuals of the colonies.

Predictions: Shyer individuals should concentrate in the most central regions of the social webs, whereas bolder individuals should walk on its edges. We expect microhabitat heterogeneity to select for an asymmetrical distribution of personalities in the web. The presence of shy individuals are essential to the survival of the colony due to the elevated mortality rate among the bolder ones.

Appendix 3. ODD protocol

1. Purpose

The model's purpose is to investigate the effects of web structure on the spatial distribution of personalities inside the web, from an evolutionary perspective

2. Entities, state variables, and scales

There are two entities in the model, the web and the spiders

Spiders: spiders have seven state variables:

- ID: each spider has its own individual identifier
- Location: represents the spider's position in the XY plane
- personality: A proxy for risk-seeking behaviour. Bolder spiders tend to move to a patch with higher risk, with probability equal to its personality score. Varies between 0 and 1
- mutation-prob: represents the probability of offspring personality score mutations. It is equal for all spiders
- mutation-rate: represents the amount of change in an offspring personality mutation. The change can be positive or negative (an increase or a decrease in personality value), and the direction is selected randomly, with equal probability. It is equal for all spiders
- mating-radius: This represents, in abstract units of space, how far the spider looks to find a mate.
- Age: How old the spider is. When a spider reaches age 5, it dies

Spatial units (e.g., grid cells).

- *Web*: the simulations happens within the web. The web is represented as a rectangular plane of 10 by 40 units of space, called *patches*. Each patch has a given amount of protection, determined by the distribution of danger in the environment. Time and space are arbitrary units

- *Environment:*
- The only important trait of the environment is the *danger level*, which represents the attack probability for any given spider
- *Collectives:*
- There are no collectives in the model

3. Process overview and scheduling

Time passes in discrete steps, and each simulation lasts a hundred rounds. Agents act in a randomised order, and their internal state is updated, at the beginning of their turn, with information from the current state of the world. This simulates an asynchronous update process (Caron-Lormier et al. 2008). The model runs according to the following pseudo-code:

1. Simulation starts, the *danger level* of the patches is updated according to the chosen distribution, agents are created and distributed randomly throughout the web
2. Start of time-step, agent order is randomised by the NetLogo Observer agent
3. On its turn, each agent does the following, in order:
 1. Move: the agent draws a random number between 0 and 1 and compares it to its personality score. If the random number is lower, the spider moves to one of the neighbouring patches with a danger level higher than the one it is currently in, otherwise, it moves in a random direction, as in brownian motion.
 2. Test survival: the agent tests if it suffers a predation event, with probability equal to that patch's danger level
 1. If attacked, the spider has a survival probability equal to its *personality*, which represents an attempt to evade predation. If preyed upon, the agent dies, if not, it proceeds to the reproduction event

3. Reproduce: the spider tests against its mating probability. If successful, if there are any other spiders in its *mating radius*, the spider picks one at random and they reproduce. Each mating event produces one offspring. The offspring's *personality* is the average of its parents' *personality*
 1. Mutation: if a mutation event happens, the offspring's *personality* is altered by an amount equal to its *mutation rate*, randomly determined to be an increase or a decrease
 2. The offspring is randomly placed somewhere in the web
4. Ageing and death: the agent's *age* is updated by one. If the age is greater than 5, the agent dies
4. End of turn: the simulation time-step counter is updated. If the set limit is reached, the simulation stops.

4. Design concepts

- *Basic principles.* The spiders' *personality* is a proxy for risk-seeking behaviour: bolder spiders tend to seek danger more often than shyer ones. The danger level represents the protection afforded by the web's structures, with danger increasing from the centre of the web to its borders. Different web structures are represented as different distributions of danger level.

Danger can increase linearly, as found for instance in planar webs, or it can vary highly, presenting a secluded, protected area, with an exposed outer rim, as in the complex webs of *Anelosimus* sp.. We model this exposure to danger as the web patches' danger level (see equation 1 in submodels)

- *Emergence.* We also expect that a mixed bold-shy population will emerge from a pure bold population, due to the protection given by the web

- *Adaptation.* The agents have no adaptive traits, as they do not make choices based on the environment or presence of other agents.
- *Objectives.* Agents do not have stated objectives
- *Learning.* Agents do not learn
- *Prediction.* Agents make no predictions
- *Sensing.* The agents sense the number of neighbours when they reproduce, and sense the danger level of the web patch they are in and its immediate neighbourhood
- *Interaction.* The only interaction is reproduction
- *Stochasticity.* Almost all processes are stochastic. Movement is randomly decided. At every turn there is a 30% chance that each spider will reproduce. Death can happen by age, or by predation events. The probability of a predation event is the danger level of each patch
- *Collectives.* There are no collectives
- *Observation.* At the end of the simulation, the position and personality of each agent is collected, and appropriate statistics are calculated outside the model

5. Initialisation

At time zero, the danger level of each patch is assigned, according to the chosen distribution, and 100 spiders are randomly generated, each with a personality drawn from a given distribution between 0 and 1. Each replicate has a different random seed. Parameters "degree of refuge protection" and "refuge size" x (see submodels) are varied in different combinations in the ranges given in *submodels*

6. Input data

The model does not depend on external data

7. Submodels

The danger level (y) of each web patch is determined by its position (x) from the centre of the web and the danger distribution of the given simulation, according to the following equation, where

"degree of refuge protection" varies between -15 and 0, and "refuge size" varies from 0.1 to 1 $y =$

$$1/(1 + \exp(\text{"degreeofrefugeprotection"} * (x - \text{"refugesize"}))$$

where "refuge size" corresponds to proportion of the web inside the refuge, and "degree of refuge protection" corresponds to the size of the concavity in the sigmoid danger function. In biological terms, a larger "refuge size" imply a larger, central protected area in the web; a larger "degree of refuge protection" corresponds to a more stepped, more abrupt danger increase from the centre to the periphery of the web.

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**Personalities are necessary but not sufficient for task division in
simulated social spiders**

**Personalidade é necessária, mas não suficiente para divisão de tarefas
em aranhas sociais simuladas**

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Personalities are necessary but not sufficient for task division in simulated social spiders

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Social spiders are characterized by presenting alloparental care, cooperating in the activities of the colony, and absence of dispersion after sexual maturity. Since there are no working castes with morphological differentiation in social spiders, one of the possible determinants of the task division is personality, defined as consistent behavioral differences between individuals that persist over time in different contexts. Considering this, we investigated the effects of personality on the task division in colonies of social spiders using an Agent Based Model (ABM). To perform tasks such as hunting, breeding, parental care or web repair, each simulated spider analyzes the context around it and decides what to do. Task distribution was measured as the proportion of time spent by each individual on each task and the effect of personality was calculated from the percentage of times that each spider performed each task. We divided the spiders into three levels of personality: shy (personality ≤ 0.4), moderately bold ($0.4 < \text{personality} < 0.6$) and very bold (personality ≥ 0.6). A Welch ANOVA was performed, due to the different variances observed between groups ($p < 0.01$ for all activities), then a separate ANOVA was performed for each task and a Games-Howell *post-hoc* test to verify differences

between personality levels for each type of action. Although statistically significant effects were found, the small effect size and high variation indicate that significance is probably an artifact of the large number of samples. These results indicate that the effect of personality alone is not sufficient to allow the task division seen in social spider colonies. Other factors such as the environmental context and social relationships must also be considered to paint a more complete picture of the phenomenon.

Key Words: Individual differences, behaviour, division of labour, colony-living

Introduction

Spiders are predominantly solitary animals, with sociality occurring in a reduced number of taxa (Avilés and Guevara, 2017; Whitehouse and Lubin, 2005). Sociality is a multifactorial characteristic, with several different levels of expression. Spiders can be classified as: i) colonial, when they aggregate in web conglomerates but maintain their territoriality and do not cooperate directly; ii) subsocial, when they live in family groups composed of mother and offspring that, when close to reaching sexual maturity, develop aggression towards siblings and disperse from the natal web; and finally iii) social, that not develop aggressiveness towards co-specifics after sexual maturity, and cooperate in performing tasks within the colony (Avilés and Guevara, 2017; Whitehouse and Lubin, 2005). According to Kullmann (1972), social individuals need to tolerate and interact with their co-specifics and participate in collective activities, in addition to interacting through sexual behavior.

The ancestral stage of sociality in spiders seems to be one of subsociality, the so-called “subsocial route” (Agnarsson et al., 2006). In this type of colony, cooperation between members can occur in tasks such as catching prey and expanding the web (Yip and Rayor, 2014), however this behavior only occurs among juveniles, and is lost when they reach adulthood, when they disperse from the maternal web. As a result, this colony configuration does not normally present the task division seen in social spiders (Settepani et al., 2015).

In order for animals to aggregate into a society, the benefits need to be large enough to offset the costs of being in a group (Hamilton, 1970, 1964, 1963). Such benefits may include a greater protection offered by a pre-existing nest, and the possibility of inheriting an already successful web (Avilés and Gelsey, 1998).

The geographic distribution of social spiders can play a crucial role in enabling such aggregations, since they occur predominantly in tropical environments (Avilés and Guevara, 2017), which have large predation pressure and heavy rains (Guevara and Avilés, 2015; Hoffman and Avilés, 2017), but which also have large prey availability to support a large number of individuals (Guevara and Avilés, 2007; Harwood and Avilés, 2013; Powers and Avilés, 2007). These factors may have facilitated the evolution of group life in these spiders (Avilés and Gelsey, 1998; Avilés and Guevara, 2017).

Task division is a pattern of specialization in cooperative individuals, where each one performs different tasks or functions in a society (Wilson, 1985, 1975). This phenomenon is present in many animals, such as social insects, which even exhibit morphological differentiation of castes, with different castes performing different functions, with rare exceptions in which reproductive caste change occurs (Beshers and Fewell, 2001). It is inherently multifactorial in its presentation, and, as we will explore in this paper, probably also in its causes.

Task division in social spiders is different than the one seen in social insects. The structure of the colony is based on an “egalitarian” system, in which all members of the group are totipotent, that is, everyone has, in principle, the ability to perform any task, and what determines the task division is not morphological differentiation or age, but differences in behavioral traits (Réale and Dingemanse, 2010).

Social spiders do not have morphological differentiation between castes, however, there is a behavioral differentiation, with individuals exhibit personality phenotypes from a continuous

spectrum, with the extremes being termed *shy* and *bold* (Parthasarathy et al., 2019; Royauté et al., 2015, 2014; Settepani et al., 2013), and there is some evidence of a correlation between a spider's personality phenotype and the type of task it performs (Dall et al., 2004; Parthasarathy et al., 2019; Settepani et al., 2013).

This correlation indicates that individual behavioral differences may be one of the causes of task division in social spiders. According to Réale and Dingemanse (2010), animal personality has the potential to play an organizing role in virtually any social system, and these consistent individual behavioral differences can provide a general mechanism by which task differentiation emerges in societies without strict morphological functional castes. This suggests that animal personality may be an important factor in orchestrating the division of labor (Jandt et al., 2014; Jeanson and Weidenmüller, 2014). In spiders, personality is an inheritable trait that is also influenced by extrinsic factors, such as social interactions or nutrition (Dall et al., 2004), which points to an additional influence of the environment on the task division.

The most studied personality character in social spiders consists of the *boldness* axis, in which the so-called *bold* individuals are generally more active and aggressive, and the *shy* ones are generally less active and less aggressive. Bold individuals participate more in the defense of the colony, prey capture and construction and web repair, while shy individuals tend to participate more in parental care (Parthasarathy et al., 2019; Royauté et al., 2014, 2015; Settepani et al., 2013).

In addition to inter-individual differences in personality, another factor that can influence an individual's tendencies to perform certain tasks is the individual's position in the web (Mersch et al., 2013; Pamminger et al., 2014; Richardson et al., 2011). The importance of this factor lies in the fact that there are tasks that can only be performed in specific locations, and the clues that trigger these specific tasks can only be perceived by individuals present in that location's immediate vicinity, that is, this type of task depends primarily on spatial context to be performed (Johnson, 2009).

In this paper, we aim to assess the effects of the interaction between the spatial context and personality, that is, how the situation in which the individual is inserted and its personality interact to cause task division within simulated colonies of social spiders. Since personality differences between individuals in social spider colonies can lead to trends in the execution of different tasks, we hope to find that personality-related behavioral differences associated with spatial context can promote task division in the colony.

Material and Methods

An Agent Based Model (MBA), derived directly from the model by (Resende et al., 2019), was developed by programming the behavior of individuals, called agents, enabling the simulation of their interactions in a virtual world (Grimm, Volker and Railsback, Steven F., 2005). This type of model allows the control of the agents' behaviors and attributes, allowing the simulation of persistent individual differences.

The model agents interact with each other and with the programmed world, simulating a web shared by a colony of social spiders. The virtual web is the space where the agents are distributed, and where they interact with each other and with the web. The web is structured in such a way that closeness to the margin increases the level of danger, associated with a higher probability of predation, while closeness to the center of the web decreases the risk of predation. The virtual web suffers damage in random locations at a fixed time interval, simulating the interference of external factors that damage the web, and making repairs necessary.

There are two types of agents on the web, spiders and prey, the latter falling randomly over the web to be preyed upon by spiders. The model starts with 100 adult spiders, with the ability to reproduce and perform tasks. With each timestep, the number of spiders increases or decreases as they reproduce or die. Spiderlings turn into adults after 6 timesteps, and adults die when they reach 20 timesteps of age, or when they are preyed upon.

Task execution is restricted to adult spiders, and spiderlings only move and need to be fed by the adults. At the beginning of the simulation, each spider has its personality randomly determined, with a value between 0.1 (shyer) and 0.9 (bolder). When a spider is born, its personality value is the average of the parents' personality, plus or minus a small random variation. This simulates personality heritability.

Virtual spiders can perform four different tasks: i) parental care; ii) web repair; iii) hunting and iv) reproduction. The agents move randomly and analyze the context in which they are inserted, that is, they collect information about their surroundings and use it to decide which task to perform (Figure 1). The agent randomly decides between the actions available to it at that moment, with equal probability. For example, if when walking through the web the agent finds a spiderling and there is damage in the web nearby, it chooses between taking care of the young and repairing the web.

The model was run for 5000 timesteps, with 500 replicates. Each replica represents an independent colony, with no migration or connection between replicate webs.

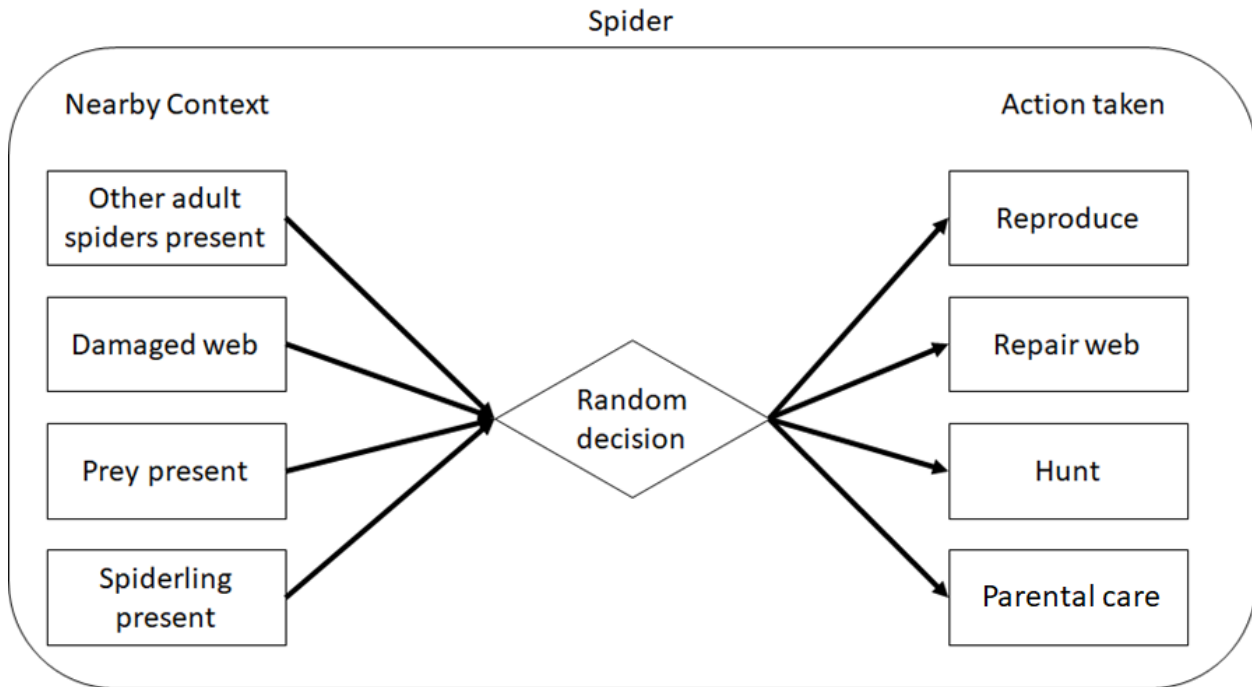


Figure 1. Flowchart representing possible contexts and possible decisions. Each context allows for a specific task, and the spider chooses randomly, according to the present contexts, which one will be performed.

The full description of the model (ODD protocol, Grimm et al., 2010) can be found in appendix 1.

Statistical analysis

To investigate the effect of personality on the task division, at the end of the simulation, we calculated the percentage of times that each spider alive at that moment performed each task during its life, and performed a Welch ANOVA to investigate the effect of personality level on the performed task proportion. We chose a Welch ANOVA instead of normal one due to the different variances observed between groups. (Figure 2, Levene's test with $p < 0.01$ for all activities, see Quinn and Keough, 2002). The dependent variable was the percentage of total actions performed that each task represented, using the arcsine transformation (Quinn and Keough, 2002), and "personality" was the predictor variable. A separate test was run for each type of task.

As a predictor variable, personality was divided into three levels: shy (personality score ≤ 0.4), intermediate ($0.4 < \text{personality} < 0.6$) and bold (personality score ≥ 0.6). Subsequently, a Games-Howell *post-hoc* test (suitable for factor levels with different variances, Quinn and Keough, 2002) was performed to assess differences between personality levels for each type of action.

Results

All tasks but repair were affected by personality level (Table 1). Although significant effects were found, the small effect size (small difference between means) and the high variance found indicate that the significance is probably an artifact of the large number of samples (Figure 2). As re-running the test with a smaller sub-sample of replicates would be equivalent to p-hacking (changing the experimental design until a significant p-value is found), we chose to interpret the results as they are. This means that even though we found a significant effect, the effect size was too small to be considered relevant. This agrees with several criticisms of using the p-value as the only threshold for assessing statistical significance (e.g., Hubbard and Lindsey, 2008; Gelman 2016, Price et al, 2020; Vidgen and Yasseri, 2016).

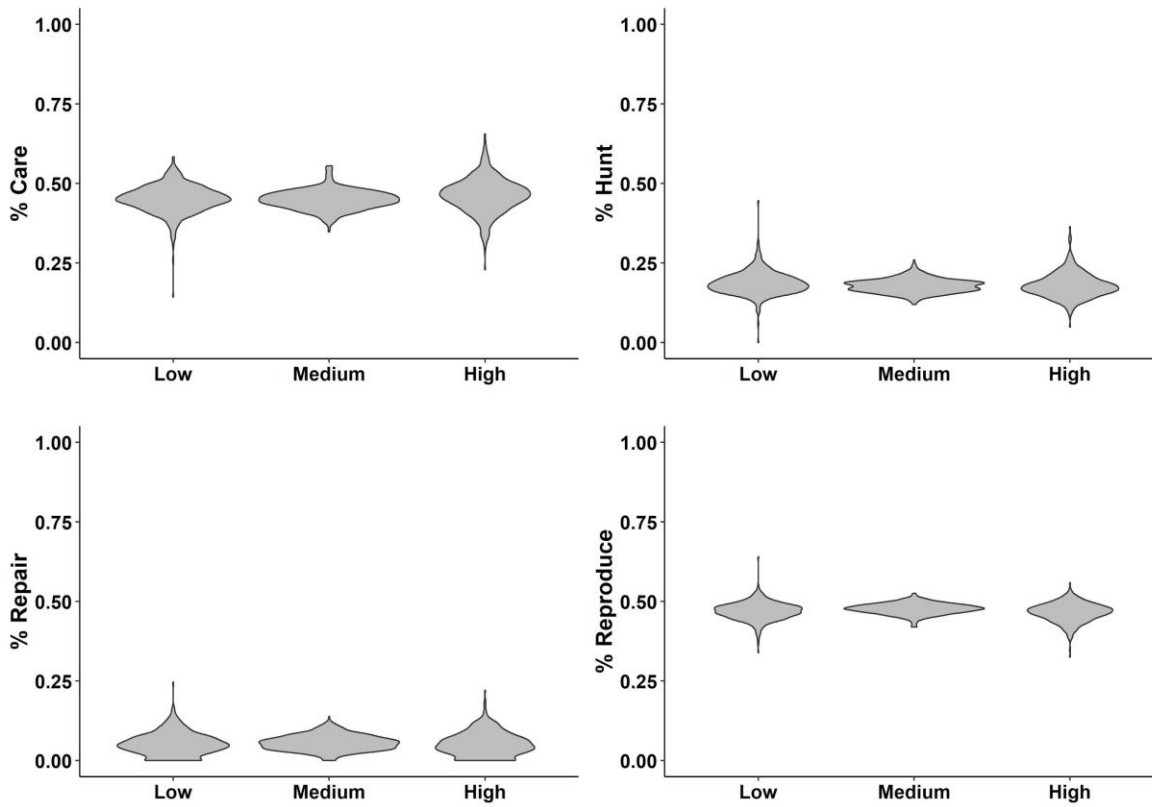


Figure 2. Distribution of task proportion according to the agents' personality level.

Table 1. Results of Welch's ANOVA for the different activities.

Activity	F	num.df	denom.df	p
Reproduce	30.69	2	912.79	< 0.01
Repair	2.46	2	937.95	0.09
Care	11.44	2	919.61	< 0.01
Hunt	9.69	2	904.67	< 0.01

Table 2. P-values for comparisons between personality levels, for each type of activity, according to the Games-Howell *post-hoc* test.

Comparison	Activities			
	Reproduce	Repair	Care	Hunt
Medium-Low	< 0.01	0.20	0.76	< 0.01
High-Low	0.1	0.98	< 0.01	< 0.01
High-Medium	< 0.01	0.15	< 0.01	0.92

Discussion

The social niche specialization hypothesis predicted that, within social groups, internal conflicts over resources could be mitigated via differentiation of traits of individuals, who would specialize in performing a specific task, creating more-or-less segregated social niches, which reduce competition and consequently increases the fitness of social groups (Bergmüller and Taborsky, 2010, 2007; Réale and Dingemanse, 2010).

In order to determine the social niche specialization in any social species, some components and their respective connections must be considered as subjects for investigation: i) Niche preference, which assesses how strong the relationship between the behavioral predisposition of individuals and the social role of their predisposition is; ii) Character displacement, which assesses the role of density and frequency-dependent factors in niche diversification; iii) Social experience, which assesses the role of learning over the social role played by individuals and iv) The fitness consequences, which

assesses how much niche segregation reduces internal conflicts and how it affects group performance and fitness (Bergmueller and Taborsky 2010).

Note that personality or behavioral predisposition of individuals can be included as a variable for investigation of all these components, and the effect strength of each one of them will be different, because it will interact with other factors, which can either reinforce their effect or obscure it (Bergmueller and Taborsky 2010; Réale and Dingemanse 2010).

In this study, the niche specialization component modeled was "Niche Preference", in the sense that we modeled the effect of individual predisposition in choosing to perform a specific task. As we can see in the results section, the effect of personality was very weak, even with a large number of samples, which indicates that this trait, as modelled, bears practically no influence in determining which tasks an individual will perform in spider societies.

These results do not mean that there is no specialization of social niche and task division in some social spider colonies, a phenomenon that has been observed empirically (Parthasarathy et al., 2019; Royauté et al., 2015, 2014; Settepani et al., 2013), but it shows us that factors other than personality must have a more important role in the formation of social niches and task specialization in this taxon.

In a recent study, Resende et al. (2019) showed that the evolution of group life (using structural complexity of shared webs as a proxy) and the increase in personality variance in spider colonies were phenomena that happened simultaneously in a positive feedback process, with more social (more complex webs) group showing a greater personality variation between its members, which directly impacted colony survival. In addition, other studies have shown that more heterogeneous groups have greater fitness, which corroborates the main argument of the social niche hypothesis (Blight et al., 2016; Brommer and Class, 2017).

A possible mechanism that can act on niche specialization in spider societies is the spatial segregation of individuals with different behavioral tendencies, a phenomenon that was correlated with the division of tasks in a study with ants (Pamminger et al., 2014). In another recent study, Resende et al. (*in prep*) found a marked spatial segregation among individuals in natural spider colonies, in which individuals determined as shy tended to be found more frequently in a more protected region of the web called basket, while individuals determined as bolder were found more often in a more exposed region of the web called sail.

This points to the possibility that the importance of personality may not be in directly determining which task a particular individual will perform, but that it may be in a more foundational aspect, for instance, generating the initial conditions on which other factors, such as spatial segregation can act and promote the niche specialization and task division we see in natural colonies. Task determination could be due to social experience, based on an individual's interaction networks or learning that is limited by the spatial segregation of the individuals.

Conclusions

Even though we found significant differences in the distribution of activities between agents, we still cannot affirm that the difference in the boldness levels alone is decisive in the division of tasks. We represent personality as the tendency to be exposed to risk of predation, with bolder spiders being more prone to it, and the context was determined mainly by the spider's position in the web. Thus, we expected the differences in personality to expose individuals to different contexts, forcing a differentiation in the tasks performed. This effect was found to be significant, but with a very small effect size, which leads us to interpret the results with caution. This statistical significance with small effect size may be an artifact of the large number of replicates. Thus, we cannot conclude that personality alone is capable of causing division of tasks in colonies of social spiders, with some other factor being necessary to explain the marked differences that are observed in real colonies.

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Appendix 1 - ODD protocol

1. Purpose

The model's purpose is to investigate the effect of personality on task division in a colony of simulated spiders

2. Entities, State Variables, and scales

The models presents three entities: web, spiders and prey

Web: the web is the world where interactions happen. It provides protection from predation, but this protection varies according to the region where the spider is located. Regions closer to the left edge of the web (representing the center region of real webs) have a higher protection, which means spiders in these regions have a lower predation risk (represented by the variable *danger-level* in the code). The web can also suffer *damage*, in which case that area will be unavailable to be used by the spiders until it is fixed.

Prey: prey are agents which fall on random places on the web, and can be eaten by the spiders. Prey do not move or perform any activities, and die when they reach 5 timesteps of age

Spiders: spiders are the main agents of the simulation. They have the following traits, represented as variables in the code:

Id: each spider has an individual identification number

Location: the spider's position on the web

Personality: Represents the spider's risk-seeking probability. Varying from 0.1 to 0.9, spiders with higher personality values tend to move to a riskier patch, with probability equal to its personality value.

Mutation-probability: represents how likely a spider's offspring's personality is to differ from the average of its parents. Equal for all spiders.

Mutation-rate: the amount of change in personality value an offspring has if it mutates. Can be either positive (offspring becomes bolder) or negative (offspring becomes shyer), with direction being selected randomly, with equal probability. Equal for all spiders.

Mating-radius: represents the maximum distance, in patches, that a spider can look for a mate.

Age: how long the spider has been alive, in timesteps. A spiderling is born with age 0, and when spiderlings reach age = 5, they become adults. When adults reach age=25, they die

My-energy: A spider's personal energy budget. When it reaches 0, the spiders die of starvation.

Already-ate: whether a spider has its stomach full

Action counters: a series of variables representing the amount of times a spider has performed a particular action. At the end of the simulation, these absolute values are turned into proportions

Scales: Space:

Web: all actions happen within the web, and border conditions are closed (spiders cannot enter or leave the web, nor "go around" it). The web is rectangular, measuring 10 by 40 units of space (patches). Each patch has a *danger-level*. The smaller this values is, the less probable a spider is to be predated there. The web also represents a collective source of food, and all prey captured is considered to be a part of this food deposit.

Time and space are arbitrary units, without direct real world corresponde. Time is divided in discrete timesteps

Environment: the environment is represented by the web. It has a *danger-level*, as described above, and a *damage*, which represents the structural integrity of that particular patch

Collectives: the model has no collectives, nor collective behaviours.

Process overview and scheduling:

Time is represented as a sequence of discrete steps, called *ticks* in the model. Each simulation has duration of up to 5000 timesteps, being interrupted if there are no spiders, or if population reaches over 1000 spiders (for computational limit reasons). Action order is randomized between spiders at the beginning of each timestep. To better approximate a continuous time process, each agent updates its personal state at the beginning of its turn to act, in an asynchronous update process (Caron-Lormier et al. 2008). The simulations proceeds according to the following pseudo-code:

- (1) Start: the web is created, with each patch receiving its respective danger-level. The web starts with no damage. Adult spiders are created in random positions with random personality values.
- (2) Timestep starts: Agent order is randomized, and the following actions are performed, in order:
 - (a) Spiderlings move, in the same way as adults (see below)
 - (b) Adult spiders move: each agent, on its turn, draws a random number between 0 and 1. If the drawn number is smaller than its personality value, the spider moves to one of the neighboring patches with a higher danger-level. Otherwise, the spider moves randomly to a neighboring patch.
 - (c) Adult spiders eat: if the spider is hungry (energy level less than 30), the spider consumes a part of the energy available on the web's food deposit.
 - (d) Adult spiders test for survival: The spider draws a random number between 0 and 1. If it is smaller than the protection afforded by the web on that particular patch, it dies, simulating a predation event
 - (e) Surviving adult spiders decide what action to perform, based on surrounding context. The possible actions are: *reproduce*, *repair web*, *hunt prey*, *care for young*. If there are no available actions, the spider moves again.
 - (f) Web damage: every 20 timesteps, 15 randomly chosen web patches are damaged, and remain so until a spider repairs it.
 - (g) Die of old age: spiders older than 25 timesteps die and are removed from the simulation
 - (h) Prey falls on web: each timestep, 20 prey agents fall on random web patches
 - (i) Prey aging and death: any prey older than 5 timesteps, dies and is removed from the simulation
 - (j) End turn. If there are over 1000 spiders, or over 5000 timesteps have passed, stop simulation. Else, go back to (2)

Action scheduling: each action follows a distinct process scheduling, detailed below

- (1) Reproduce: if there are any other adult spiders in its mating radius, the spider tests against its mating probability. If the random number generated is smaller than the probability, the spider picks one neighbor at random they reproduce, producing on offspring. To determine its personality value, the newborn spiderling takes the average of that of the parents, then tests for a mutation. If the random number generated is smaller than the *mutation probability*, the newborn's personality value altered by an amount equal to the *mutation rate*. The signal of the change (increase or decrease) is determined randomly, with equal probability. The newborn is then placed on a random location in the web

- (2) Repair web: if there is any damaged web patch in the spiders immediate neighborhood, the spider fixes the patches.
- (3) Hunt prey: if there is any prey in a radius of 3 patches, the spider attacks one, chosen at random. The prey is then added to the web's collective food pool.
- (4) Care for young: if there are any spiders with age under 5 timesteps in the immediate vicinity, the adult feeds on the younglings from the webs collective food pool.

Design concepts

Basic principles:

As in Resende et al 2019, the spider's personality represents their propensity to seek or avoid risk, with bolder spiders being more risk-prone than shy ones, that is, they tend to move towards more dangerous areas of the web. Danger (in the form of predation risk), changes across the web following a sigmoid curve, but no region is completely protected. This simulates the type of webs seen in the *Anelosimus* (Araneae, Theridiidae) genus of social and subsocial spiders, which have a protected core region and an exposed periphery.

Emergence:

Our hypothesis is that the differences in risk-taking propensity (personality) will force the spiders to put themselves in different spatial contexts, and these contexts will force task specialization to occur in the spiders.

Adaptation:

The spiders show adaptive behaviour (in the computational sense, not in the biological one), by responding differently to the different contexts it perceives.

Objectives:

Spiders do not have stated objectives

Learning:

Even though agents perceive different context, previous experiences have no bearing on present behaviour, and thus agents do not learn

Sensing:

Agents can perceive a number of conditions around them, and use this information to decide which action to take. Namely, spiders can sense the presence of prey, which can lead to hunting behavior; the presence of other adult spiders, which can lead to reproduction; the presence of youngling, which can lead to parental care; and the presence of damage on the web, which can lead to repairing behaviour. Spiders can also sense whether they are more or less exposed to predation, and can move towards danger or not based on their personality values.

Interactions:

Adult spiders can interact with other adults to reproduce, and with younglings to care for them. They also interact with prey in the form of predation

Stochasticity:

Most processes are stochastic in nature. Direction of movement is decided randomly, based on the spiders personality value. Spiders can also die stochastically depending on the web patch's danger level. Actions are also taken probabilistically, based on the spatial context

Collectives:

Although there is a collective community food resource, there is no collective action of any of the agents

Observation:

When simulation ends, the proportion of actions performed is taken for each spider, and the appropriate statistics are calculated using R software.

Initialization:

When the simulation starts, the web is created and each patch receives its danger level, and 100 spiders are generated at random points in the web. Their personality values are randomly assigned, drawn from an uniform distribution between 0.1 and 0.9. 100 replicates are run, each starting with a different random seed

Input data:

The model does not use any external data as source.

Submodels

The danger level (y) of each web patch is determined by its position (x) from the centre of the web, increasing according to the following equation (see Resende et al 2019 for the reasoning behind the equation):

$$y=1/(1+\exp(-7*(x-0.7)))$$

In biological terms, this is equivalent to a web with a protected center, with exposure rising sharply as one moves towards the outer edges.

ODD references:

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**There is spatial segregation due to personality in spider colonies, but
no task specialization**

**Há segregação espacial devido à personalidade em colônias de aranhas,
mas não especialização de tarefas**

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There is spatial segregation due to personality in spider colonies, but no task specialization

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Abstract

Animals living in social groups often need to conduct certain tasks, such as prey capture or nest maintenance. We might expect individuals to specialise in these tasks, as specialisation should increase efficiency and therefore group performance. In groups that vary in sex, morphology, or generation, these factors often determine task participation. However, in social groups where these factors are invariant, persistent individual differences in behaviour may drive task specialisation. We tested this prediction in groups of the social spider *Anelosimus eximius*. We found the bolder individuals were more likely to be in the capture web of the colony, as opposed to within the dense, protective web at the base of the colony. In the protective region of the colony, individuals rest and care for young, while in the capture web individuals are more active and more likely to be walking. Therefore, behavioral differences showed a more robust influence on where in a group the individuals are found and little or no influence on the activity they were performing. We conclude that personality has a more indirect role on task participation, via influencing where in the web individuals are. Furthermore, colonies

varied in whether they had young to take care of or not, and if they did then there was no variation among-individuals in their tendency to take care of them. Our results support previous work that suggests adult *A. eximius* do not specialise in tasks. There was however variation among-individuals in activity levels and movement rates. Indirect pathways from individual traits, via differences in spatial location or activity levels, may help to explain variation among-individuals in task participation.

Key Words: Sociality, task specialization, social niche, animal personality,

Introduction

Social species live in cohesive groups which, unlike simple aggregations, can be maintained for long periods. Within these groups, there may be the overlap of generations and some type of internal organization, such as hierarchy or division of labor among the members of the group (Wilson, 1971; Wilson and Holldobler, 2005). When groups of organisms need to complete a series of tasks as part of daily living, we might expect individuals to trade-off doing some tasks for others, i.e. for them to become specialised, as specialisation should increase efficiency (Araújo et al., 2011; Bergmüller and Taborsky, 2010; Boomsma and Gawne, 2018; Montiglio et al., 2013).

Increased group efficiency due to task specialization should be associated with improved performance of the task, resulting in increased group productivity and ultimately fitness (Oster and Wilson, 1978; Wallace, 1982; Wilson, 1975). Several mechanisms can promote task specialization: differences in age, sex and body size (Schwander et al., 2005; Seeley and Kolmes, 2010), that could lead to discrete polymorphisms (Schmid-Hempel, 1992) while environmental and genetic factors can predispose individuals to perform certain tasks (Schwander et al., 2010). In the absence of these factors, the driver of task specialisation remains unclear.

In the cases of societies in which group members are morphologically similar and belong to the same generation and sex, variation in personalities (consistent behavioral tendencies at multiple

contexts and over time Dall et al., 2004) among group members can lead to task differentiation (Réale and Dingemanse, 2010). Personality can play this role in task differentiation if it influences the probability an individual performs a specific task, modulating the “task threshold” of the individual (Bergmüller and Taborsky, 2010; Montiglio et al., 2013; Theraulaz et al., 1998). Furthermore, if personalities change the spatial distribution of individuals within the colony, further contributions to task specialisation would ensue. The spatial distribution of individuals can be a fundamental factor for generating division of labor (Franks et al., 2002; Johnson, 2008; Mersch et al., 2013; Richardson et al., 2011). Its importance is based on the fact that some tasks can only be performed at specific locations, and cues that indicate the demand for a specific task are only available to individuals in the direct vicinity (Johnson, 2009). Therefore, differences in personality could generate task specialisation both directly, changing task thresholds, and indirectly, through influencing an individual’s spatial location.

While most spiders are solitary, some species have evolved to be social, living in stable colonies, and cooperating in prey capture and the rearing of offspring (Avilés and Guevara, 2017). In social spider colonies there are no morphological castes, so polymorphism is not a likely mechanism to promote task specialisation and spatial organization of the individuals (Avilés and Guevara, 2017; Lubin and Bilde, 2007). Specialization of tasks may instead be based on age (“age polyethism”) (Ebert, 1998; Settepani et al., 2013). There are however typically differences in personality traits among individuals of the same age (Parthasarathy et al., 2019). Thus, even when age polyethism is present, personality could still be a mechanism promoting the specialization of tasks and the spatial organization of the colonies.

Within spider colonies there are differences among-individuals in their degree of tolerance to risk, in which more tolerant individuals are called bold and those less tolerant are called shy, and these behavioral tendencies emerge very early in the development of social spiders (Parthasarathy et al., 2019; Settepani et al., 2013). Since neither polymorphism nor age polyethism represent likely

mechanisms in determining the division of tasks and spatial organization of individuals in spider colonies, we hypothesise that personality differences between individuals are directly linked to task specialization. Additionally, personality type could indirectly influence task participation by first influencing where individuals are positioned spatially in a colony. We therefore first aimed to determine whether personality traits are associated with an individual's spatial position in a colony, and then whether this position, the personality, or a combination of the two, predict the tasks the individual engages in.

We predicted that the boldest individuals would occupy the most exposed areas and the shyest the most protected areas. Furthermore, we predicted that individuals in the most exposed areas would mostly be walking and capturing prey, while in the most protected areas individuals would rest and care for young. Finally, we predicted that bolder individuals would be more active, more likely to be moving around the colony, and would be less likely to be taking care of young.

To test these hypotheses, we studied colonies of the social spider *Anelosimus eximius* (Keyserling, 1884) in the Northeast region of Brazil. We marked individuals, assayed their behaviour, and observed their activity when returned to natural colonies. This allowed us to test whether the behavioral trait predicted both where a spider was positioned in a colony, and also the tasks it was performing.

Material and Methods

Study object and study area

Anelosimus Simon 1891 is a cosmopolitan genus of spiders of the family Theridiidae, with about 53 described species occurring mainly in subtropical and tropical habitats of all continents (Agnarsson et al., 2007, 2006; Agnarsson and Zhang, 2006; World Spider Catalog, 2020). Among the *Anelosimus* social species there is the Neotropical *A. eximius*, which occurs in low land forest areas of Panama to southern Brazil (Avilés and Guevara, 2017; Levi, 1963; Silva et al., 2020). Colonies of this

species may vary from only a single pair of reproductive females and their offspring (a subsocial behavioral phenotype that can be found in the upper limit of altitude occurrence of the species) to enormous communal webs with several cubic meters containing tens of thousands of individuals (Avilés, 1997; Avilés and Guevara, 2017; Venticinque et al., 1993). The 12 colonies used in this study were medium sized colonies (ranging from ~600 to 2000 adult females), located in a fragment of Atlantic Forest on a farm in the municipality of Catu (12° 24' S/ 38° 29' W), around 156 m above sea level, in Bahia state, Northeast Brazil (see Appendix 1).

Experimental Design

The first step in the field was to collect a single source colony, from which we would collect individuals to test. The source colony was used only to collect individuals and was not one of the 12 colonies selected for observations. We collected an entire colony, wrapping it in a plastic bag and cutting the branches of vegetation to which the web was attached. Next, we collected all the biggest adult females we found, placing them in 15 mL Falcon type plastic bottles in order to proceed with the boldness assay.

The boldness assay is designed to simulate the approach of an aerial predator using puffs of air from a baby nose cleaner. The individual's boldness level is measured by the time in seconds it takes to resume movement following the stimulus (Riechert and Hedrick, 1993). Then, the tested individuals were marked with ink, using a three-color code to uniquely mark each individual. In total, we tested and marked 168 adult female spiders. Next we randomly introduced 14 marked individuals into each of the 12 colonies selected for the observations. After being placed in the colonies we gave them 24 hours for acclimatization. Following the 24 hours we began the observations.

In order to record the location of the marked individuals on the webs, and to describe the behavior they were performing at the moment they were observed, we performed scans for behaviours (Altmann, 1974). We scanned each web for 10 minutes, recording for the location and activity of

marked individuals. We carried out three scans in each of the 12 colonies, so the marked individuals that were found later were sampled at least once and at most three times. Observations were always performed in the afternoon, from 2 pm to 5 pm, and we conducted two scans on one day and the third scan on the next day.

In order to register the position of individuals, we divided the webs into three regions: middle of the basket, basket edge and sail (see: Figure 1). This spatial division is based on morphometric analysis of the social *Anelosimus* webs that were carried out in previous studies (Avilés, 1997; Purcell et al., 2012; Vasconcellos-Neto et al., 1995).

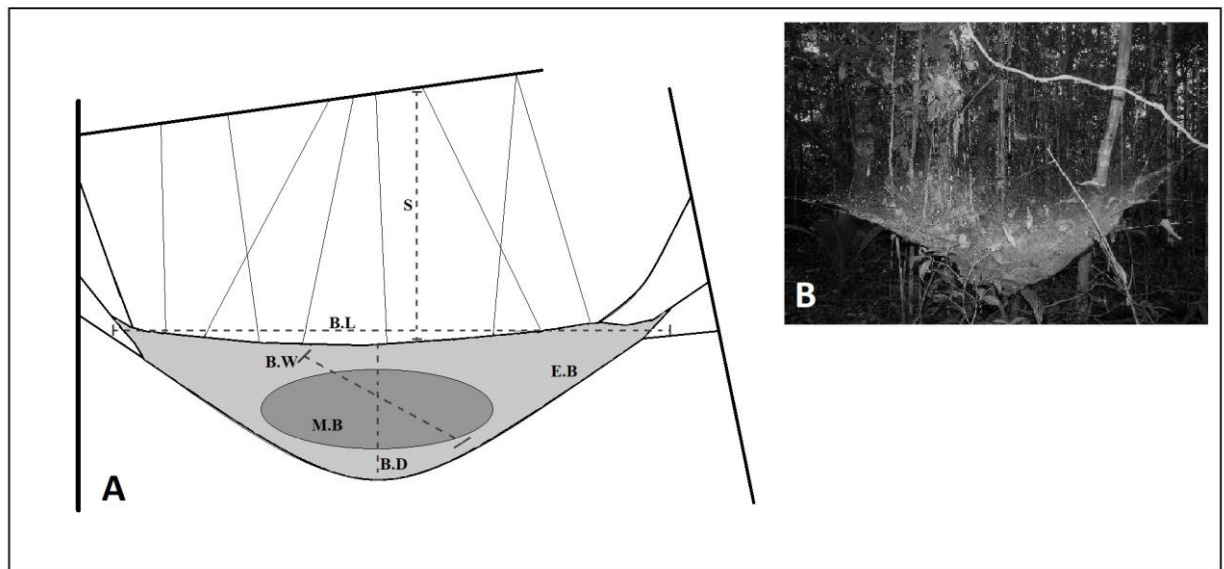


Figure 1: Morphometric variables of the web. A= Scheme of the web illustrating its parts. Legend: B.L= Basket length; B.D= Basket depth; B.W= Basket width; S= Sail height; M.B= Middle basket; E.B= Edge basket. B= Picture of a natural web. Photo by: Leonardo Resende, Reserva Ecológica da Michelin, Bahia, 2017.

Statistical analysis

To answer our questions we built two sets of binomial models, all in R (R Core Team, 2020) in the package “glmmTMB” (Brooks et al., 2017). See Figure 2 for a schematic outline of the analysis. In all cases we extracted model coefficients from the full model and used the “*Anova*” function in the “*car*” R package (Fox and Weisberg, 2019) to calculate p-values of fixed effects, using type-II sum of squares. For random effects we report estimates and confidence intervals using the Wald method calculated with the “*tidy*” function of the “*broom.mixed*” R package (Dushoff et al., 2019).

In the first set of models we aimed to test predictors for spider location in the web. The first model in the location model set had a binary response of “in or outside the basket”, with a 0 indicating inside and a 1 indicating outside ($n = 252$). We fitted an individual’s boldness score and the log of the volume of the basket as fixed effects (both mean centred and scaled to unit variance) as well as the random effects of colony ID, spider ID nested within colony ID, and date of observation. For the second model in the location model set we fitted a model for only the spiders in the basket ($n = 213$), with a binary response of “was the spider in the edge or in the middle of the basket”, with a 0 indicating the middle and a 1 indicating the edge. The predictor variables (both fixed and random) were the same in this model as for the first model in the location model set.

The second set of models focused on predictors of spider activity. The first models in the activity model set had a binary response of “spider was resting or active”, with a 0 indicating resting, and a 1 indicating active ($n = 252$). We fitted an individual’s boldness score and the log of the volume of the basket (mean centred and scaled to unit variance), the location the spider was in either edge of basket, middle of basket, or in capture web, and the interaction between the behavioural trait and location as fixed effects. We fitted random effects of colony ID, spider ID nested within colony ID, and date of observation for both models. The second model in the activity model set included spiders that were resting in the basket ($n = 162$), and had a binary response variable of “spider was resting

exposed or protected”, with a 0 indicating resting protected and a 1 indicating resting exposed. The third model included spiders that were active ($n = 78$), and a binary response variable of “spider was taking care of young (eggs or juveniles) or not”, with a 0 indicating not taking care of young, and a 1 indicating that they were taking care of young. The fourth model included spiders that were active ($N = 78$, the same dataset as for the third model), and a binary response variable of “spider was walking or not”, with a 0 indicating not walking, and a 1 indicating walking. In all cases the fixed and random effects of these three models were the same as for the first model in the activity model set, except that the fixed effect of web volume could not be included in the fourth model (taking care of young or not) as it resulted in a non-positive definite Hessian matrix.

In total we fitted 6 models (two models for the location model set and four models in the activity model set, see Fig. 2). Each model was checked for convergence and overdispersion.

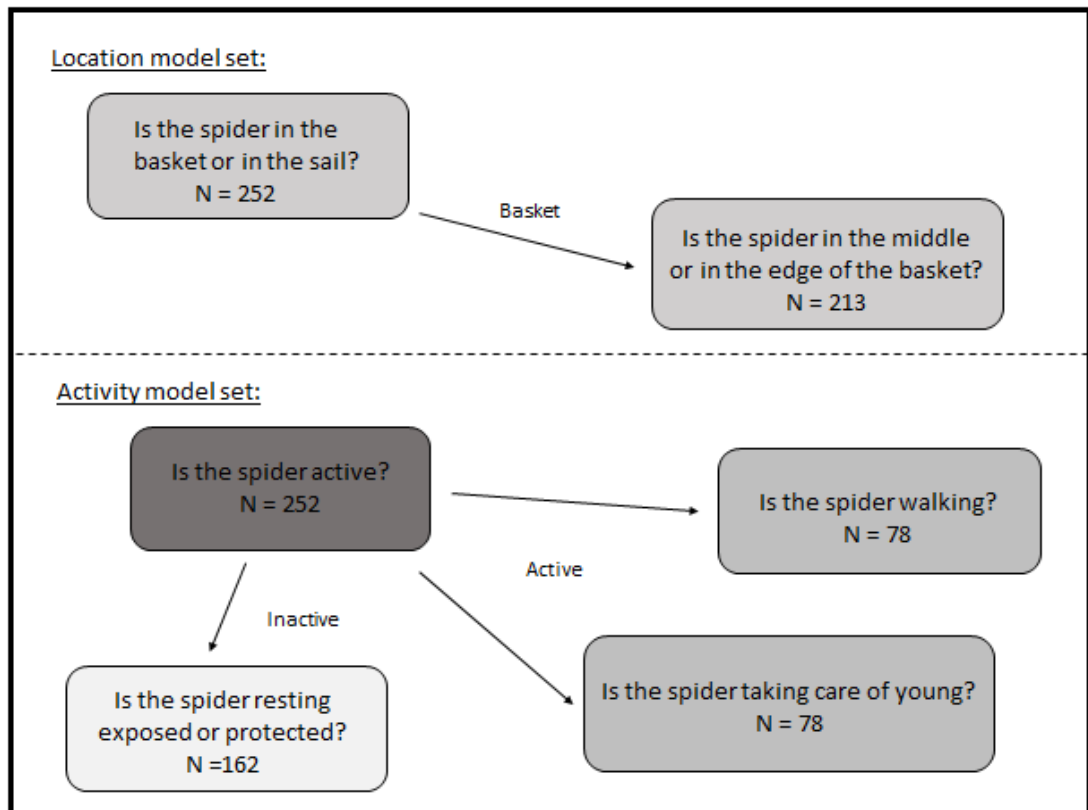


Figure 2: Scheme outlining the sets of binomial models built to test predictors of the location and activity of the spiders.

Results

Predictors of spiders location

We found the shyer individuals were more likely to be in the basket (est = -1.725, se = 0.642, $\chi^2 = 7.212$, $p = 0.007$) (Figure 3a). There was variance among individuals (2.11, 0.916 to 4.87, referring to the estimate and its 95% confidence intervals respectively) but none among colonies (< 0.001 , 0 to Inf.) or dates (< 0.001 , 0 to Inf.). Additionally, we found that the greater the volume of the web, the greater the chance of individuals remaining inside the basket (est = 0.866, se = 0.384, $\chi^2 = 5.091$, $p = 0.024$).

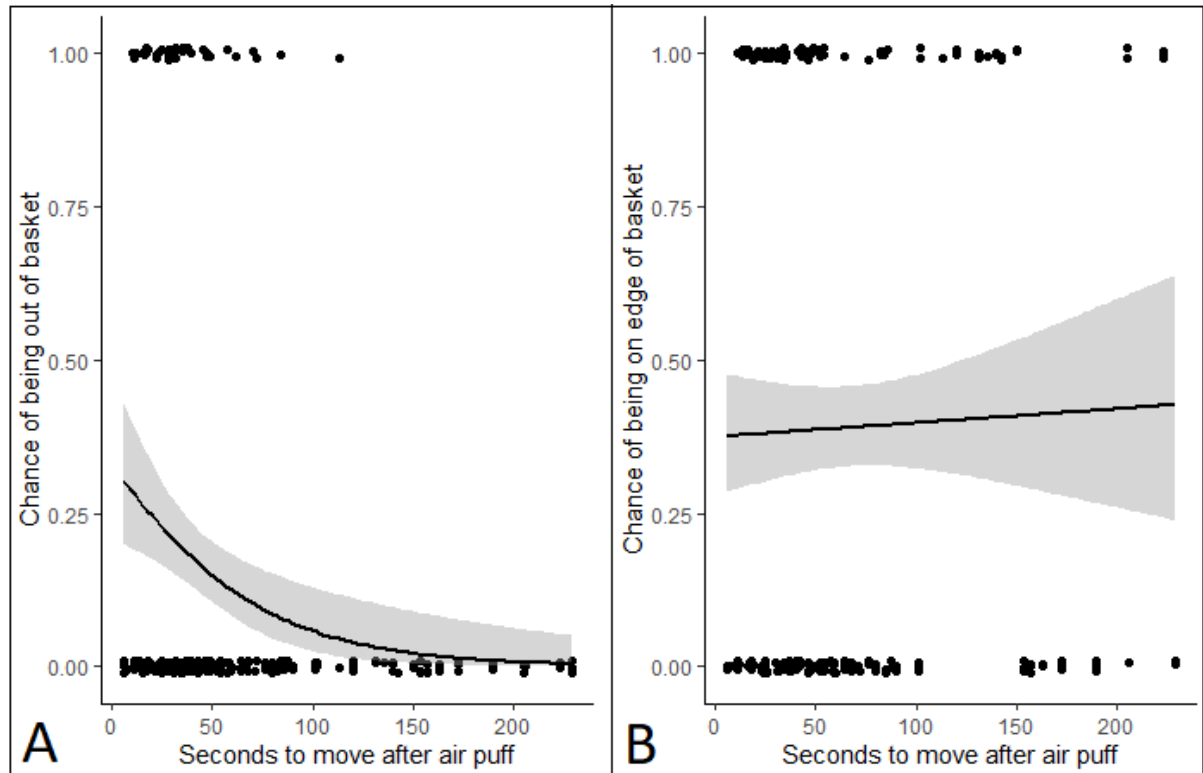


Figure 3: Logistic regressions corresponding to the location models set. A= Latency time vs being in the basket or in the sail (est = 1.725, se = 0.642, $\chi^2 = 7.212$, p = 0.007). B= Latency time vs being in the middle or on the edge of the basket (est = -0.058, se = 1.052, $\chi^2 = 0.003$, p = 0.956).

Neither latency time (est = -0.058, se = 1.052, $\chi^2 = 0.003$, p = 0.956) or web volume (0.0034, se = 0.871, $\chi^2 = 0.000$, p = 0.997) had an effect on being in the edge or in the middle of the basket (Figure 3b). There was variance among individuals (47.4, 20.6 to 109) in whether they were in the middle or edge of the basket, but less among colonies (2.32, < 0.001 to 693000) and none among dates (< 0.001, < 0.001 to > 10e122).

Predictors of spiders activity

We found a significant difference in activity levels between the web regions ($\chi^2 = 10.438$, df = 3, p = 0.0054), with spiders being less likely to be resting if in the sail than on edge or middle of the basket (Table 1). There was no effect of latency time, either as a main effect (est = -1.092, se = 0.597,

$\chi^2 = 1.337$, $p = 0.248$) or as an interaction with location ($\chi^2 = 4.318$, $df = 2$, $p = 0.115$) (Figure 4a - d). The volume of the basket did not influence activity rates (est = 0.310, se = 0.306, $\chi^2 = 1.025$, $p = 0.311$). There was more variance in activity levels among individuals (1.77, 0.929 to 3.38) than among colonies (0.474, 0.0671 to 3.35), and there was none among dates (<0.001, 0 to Inf).

For the analysis of resting protected or resting exposed there was no latency time-location interaction ($\chi^2 = 0.0074$, $df = 1$, $p = 0.931$), and no effect of latency time (est = -1.280, se = 2.318, $\chi^2 = 0.426$, $p = 0.514$) or location ($\chi^2 = 0.567$, $df = 1$, $p = 0.451$) as main effects. The volume of the basket did not influence whether spiders were resting exposed or protected (est = -1.070, se = 1.106, $\chi^2 = 0.935$, $p = 0.334$). There was variance among individuals for whether the spider was resting in an exposed or protected position (12.1, 5.49 to 26.5) but not among colonies (< 0.001, 0 to Inf.), or dates (< 0.001, 0 to Inf.).

Regarding whether the individual was taking care of the juveniles or doing something else, we found no latency time-location interaction ($\chi^2 = 0.883$, $df = 2$, $p = 0.643$), and the main effect of location was not significant ($\chi^2 = 0.836$, $df = 2$, $p = 0.658$). The main effect of latency time was non-significant either, but suggested a trend of bolder individuals to be more likely to be caring for young (est = -0.357, se = 0.777, $\chi^2 = 2.517$, $p = 0.113$). The effect of web volume could not be estimated for this model. There was variance among colonies in the tendency to take care of young (1.01, 0.290 to 3.50) but none among individuals (<0.001, 0 to Inf), or dates (< 0.001, 0 to Inf.).

Finally, we found that locations differed in whether spiders were walking compared to doing other activities ($\chi^2 = 8.652$, $df = 2$, $p = 0.0132$) with spiders being more likely to be walking if in the sail compared to middle or edge of the basket (Table 1). There was no latency time-location interaction ($\chi^2 = 0.381$, $df = 2$, $p = 0.827$). Web volume did not influence whether the spider was walking or not (est = 0.199, se = 0.390, $\chi^2 = 0.260$, $p = 0.610$). There was variance among individuals (0.947, 0.116 to 7.75) but none among colonies (<0.001, 0 to Inf) or dates (< 0.001, 0 to Inf.).

Table 1: Number of observations recorded for each pair behaviors we compared in each of the three web regions.

Activity / Location	Middle basket	Edge basket	Sail
Resting vs Active	100 vs 30	62 vs 21	12 vs 27
Resting exposed vs Resting protected	7 vs 93	12 vs 50	Excluded from model
Taking care of young vs Other	16 vs 14	9 vs 12	0 vs 27
Walking vs Other	11 vs 19	10 vs 11	25 vs 2

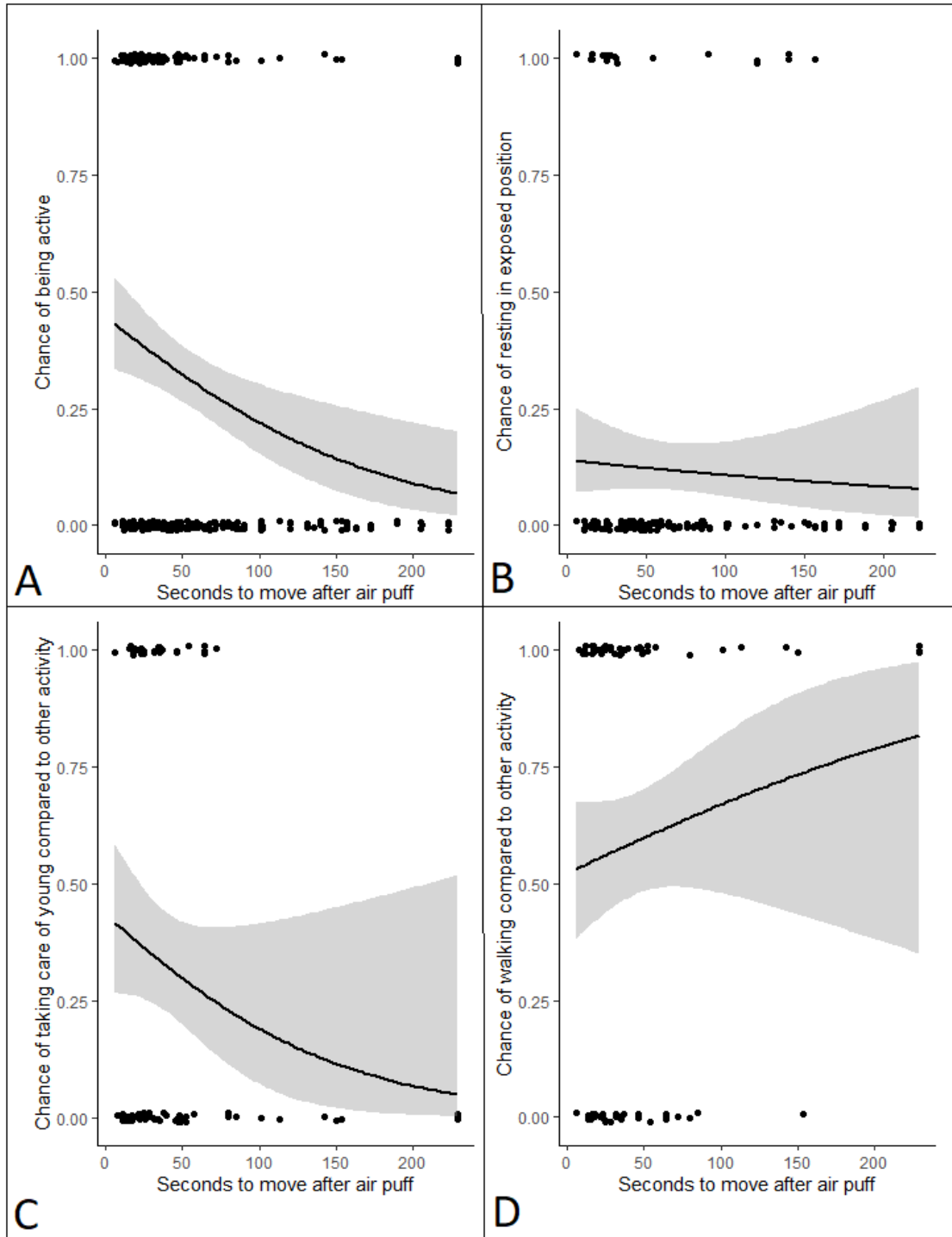


Figure 4: Logistic regressions corresponding to the activity models set. A= Latency time vs being active or resting (est = -1.092, se = 0.597, $\chi^2 = 1.337$, p = 0.248). B= Latency time vs resting protected or exposed (est = -1.280, se = 2.318, $\chi^2 = 0.426$, p = 0.514). C= Latency time vs taking care of young (est = -0.357, se = 0.777, $\chi^2 = 2.517$, p = 0.113). D= Latency time vs walking (est = 1.363, se = 1.102, $\chi^2 = 3.075$, p = 0.080).

Discussion

We aimed to determine whether variation in personality could explain variation in task specialisation, either directly, or indirectly through influencing the spatial location a spider would be in. We found that personality did not influence activity in any direct way. We did however find that personality influenced the spatial location of individuals. Here we present the results of our experiments in contrast to the social niche hypotheses and elaborate the proposal for an alternative hypothesis.

There is no task specialization on *A. eximius* colonies

Individuals that showed more bold behaviours were more likely to be in the sail, an exposed region of the web that functions as a prey capture area. In contrast, shy individuals were more often observed inside the basket, a more protected area of the nest. These results corroborate those found for other taxa of social animals. For example, studies with species of ants showed that more active and aggressive individuals are more often found in the outermost regions of the nests, while less active and docile individuals were found in the inner chambers of the nests (Mersh et al., 2013; Pamminer et al., 2014). Similarly, in sticklebacks, bold individuals tend to not join the shoals and maintain a leadership position, benefiting from primary access to food but exposing themselves more to predation (Ward et al., 2004), a situation similar to that of spiders on the sail of the web. In colonial birds, individuals determined to be more aggressive and bold in general gain access to the most internal and protected regions of the breeding colonies, while more docile individuals stay on the less protected edges (Verbeek, 1999) an inverted pattern to that found in spiders, ants and fish but which reinforces the hypothesis that personality influences the position that individuals occupy within a group.

The findings of this study support our hypothesis that there is a spatial organization of the individuals in relation to their personality, however, our results fail to support several of our predictions, as behavior had no direct impact on activity levels and did not influence the type of activity an individual was engaged in. Behavioural traits never significantly influenced what tasks an

individual was conducting, given it was active. There was among-individual variation in whether an individual was walking or not, but there was no among-individual variance for whether an individual was taking care of young. Therefore, we cannot say whether the lack of predictive power of personality is due to a general lack of specialisation by individuals in *A. eximius* colonies, an irrelevance of the personality we measured for the tasks we were able to observe, or something else. Two other studies have investigated task specialization in *A. eximius*. Settepani et al. (2013) also found a lack of task specialisation for attacking prey and web maintenance, while Fisher et al. (*in prep*) found bolder spiders were more active. Therefore, in aggregate there appears to be variation among individual *A. eximius* in how active they are, but not in the particular tasks they do.

Additionally, we only had enough observations to analyse the most common behaviours we saw. We occasionally recorded individuals attacking prey, or removing debris from the web, but not frequently enough to fit a mixed-effects model. Behaviours such as these might be more specialised, and so could be candidates for detecting a link with other behavioural traits, if one could collect enough data to examine the relationship (albeit Settepani et al., 2013 found no evidence for task specialisation in attacking prey or web maintenance).

Previous authors (Ebert, 1998; Settepani et al., 2013) have suggested that body size drives differences in task participation in *A. eximius*. Studies of bumblebees have also shown that the size of individuals is related to the ability of them to perform certain tasks within the colony (“alloethism”; Kapustjanskji et al., 2007; Spaethe, 2002). We did not measure body size here, since we selected only the largest females found in the source colony, assuming that the variation in mass between them would be too small and not significant to affect their behavior. Additionally, Fisher et al. (*in prep*) found no influence of body mass on the location, activity levels, and activity type in artificial colonies of *A. eximius*. Therefore, task specialisation in terms of taking care of young may not extend beyond the age polyethism observed in Ebert (1998) and Settepani et al. (2013).

In contrast, whether a spider was active or resting, given it was resting in an exposed or protected position, and whether an individual was walking or not, all showed a degree of among-individual variation. Therefore, some individuals are consistently more active than others. These were not the more bold or shy individuals however. Instead, differences in some unmeasured or unobservable factor, like motivation, energy levels, or residual reproductive value may underpin the differences in activity levels. Variation in energy levels and metabolic rates of individuals has often been suggested to underpin differences in their behavioral phenotypes (Biro and Stamps, 2008, 2010; Careau et al., 2008). While we are yet to identify a specific pathway, we think it likely that the inter-individual variation observed in this study is associated with the physiological properties of the individuals.

Task specialization is determined by environmental heterogeneity

The colonial web presents some degree of heterogeneity in the environmental conditions between its two main regions, the more protected basket and the more exposed sail. Broadly in line with our predictions, we found that the shyest individuals who are risk averse are most often found in the basket and the boldest ones who are risk tolerant are seen most often in the sail.

This is likely because, in a heterogeneous space, where there are locations with different characteristics, the possible tasks that can be efficiently performed will vary between locations (He et al., 2019; Johnson, 2009). This type of spatial organization of tasks is already documented for a wide variety of social organisms, from ants and bees to cichlid fish (Bergmuller and Taborsky, 2007; Johnson, 2009; Mersh et al., 2013; Pamminger et al., 2014; Wagner et al., 2001). We found substantial variation among individuals in their location, suggesting a degree of spatial fidelity. However, this is only over two days, data over longer periods are required to determine whether individuals are rigid in their choice of locations throughout their adult life. What also remains to be investigated is whether there is a relationship between the size or volume of the web and the degree of heterogeneity between their regions, which might promote greater differences among individuals. We found that larger webs

have proportionally more individuals in the basket (see Appendix 2), which indicates web size can influence the distribution of individuals, but does not necessarily support or contradict our above suggestion.

Thus, it is evident that the different personalities, when promoting the spatial distribution of individuals, expose them to a certain set of tasks that they can perform in that particular location. However, both shy and bold individuals performed the same activities when they were in the same parts of the web, the opposite of what we expected based on the social niche hypothesis.

Our study presents evidence that there is no task specialization in *A. eximius* groups. Several studies conducted with other taxa have also found no association between division of labor and specialization in performing tasks (Bennet and Faulkes, 2000; Johnson, 2009; Lacey and Sherman, 1991; Robinson et al., 2009; Thorley et al., 2018; Ulrich et al., 2018; Zottl et al., 2016a, b, 2018; Ward et al., 2004). However there is empirical evidence in the literature that supports the existence of division of labor and specialization among a variety of taxa (Bergmuller and Taborsky, 2007; Dolezal et al., 2012; Jarvis, 1981; Kather et al., 2011; Mersh et al., 2013; Mooney et al., 2015; Pamminger et al., 2014; Ravary et al., 2007; Tizo-Pedroso et al., 2018).

To synthesise these results, we suggest that there is a gradient in the relationship between division of labor and task specialization in social groups, and this gradient is established by the degree of heterogeneity of the space occupied by the group (see Figure 5). In ants, which is the taxon in which there is more evidence in favor of task specialization, there is a great variation among the environmental conditions present within the internal environment of the complex nest, and these conditions will also differ from the external environment. These environmental differences may create very different selective pressures among regions, favoring spatial fidelity and specialization in the execution of specific tasks, generating the development of different individuals in both behavioral and morphological phenotypes. On the other hand, in social species that live in more homogeneous environments and or in less complex nests, there is no such selective pressure acting to strengthen

spatial fidelity and or specialization in the performance of tasks, so it is inexpensive to be generalist and individuals are totipotent in relation to the tasks available to be performed.

In this way, the differences between the environments designed by social groups (*e.g.*: subterranean nests) and the surrounding environments, could favor the evolution of development processes that would promote greater differentiation and specialization of individuals who are subjected to one or another environmental condition.

We advocate that social spiders are at an intermediate position along this gradient, since colonial webs have a degree of modularity that promotes the spatial separation of individuals with different personalities, generating a condition in which bold and shy individuals are more likely to perform certain tasks, but the web is not heterogeneous enough to have promoted the evolution of distinct developmental pathways between these individuals, therefore they are morphologically similar and not specialized in the performance of any tasks.

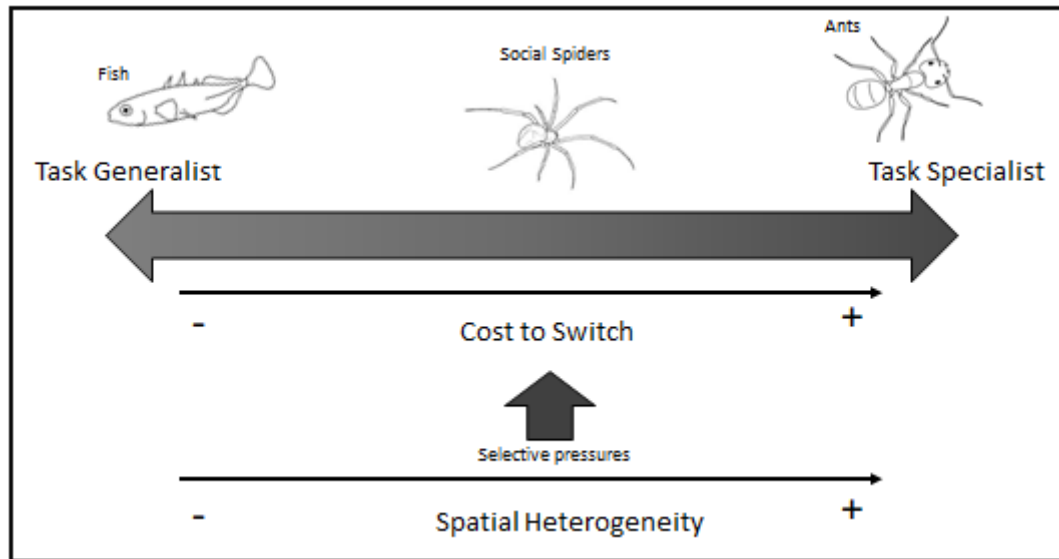


Figure 5: Scheme illustrating a hypothesis that relates the tradeoff between being a generalist or an specialist in performing tasks according to the degree of heterogeneity of the environment. Spatial heterogeneity, promoted by the complexity of the nest and / or the external environment occupied by the group, promotes selective pressures that modulate the cost of being a generalist or specialist in carrying out specific tasks. If heterogeneity is small (homogeneous environments) it is not expensive to be generalist, if heterogeneity is high it becomes costly to be generalist, favoring task specialization.

Although, as presented above, several studies present different degrees of spatial fidelity and task specialization in different taxa, few studies specifically explore the role of spatial heterogeneity on social organization (He et al., 2019; Penn and Turner, 2018) and there are no studies that directly test the effect of spatial heterogeneity on task specialization, being an open path for future investigation.

In summary, our study shows that there is a spatial segregation of individuals in the web of a colony, and that it is influenced by individual differences in the tendency to accept the risk of being exposed. However, contrary to what was expected, personality proved to be not important in determining the rate of activity or the type of activity the spiders performed given the location that they were in. Personality traits may instead indirectly influence task specialisation through dictating

an individual's location within a group. Finally, we propose that environmental heterogeneity, including that produced by ecosystem engineering such as nest and web building, could generate selective pressures that favor spatial fidelity and specialization of tasks within social groups.

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Appendix 1

Location and morphometric measurements of the 12 natural colonies utilized on the field experiments.

Legend: bask.len= basket length; bak. wid= basket width; bask.dep= basket depth; sail h.= sail height;

bask. vol.= basket volume.

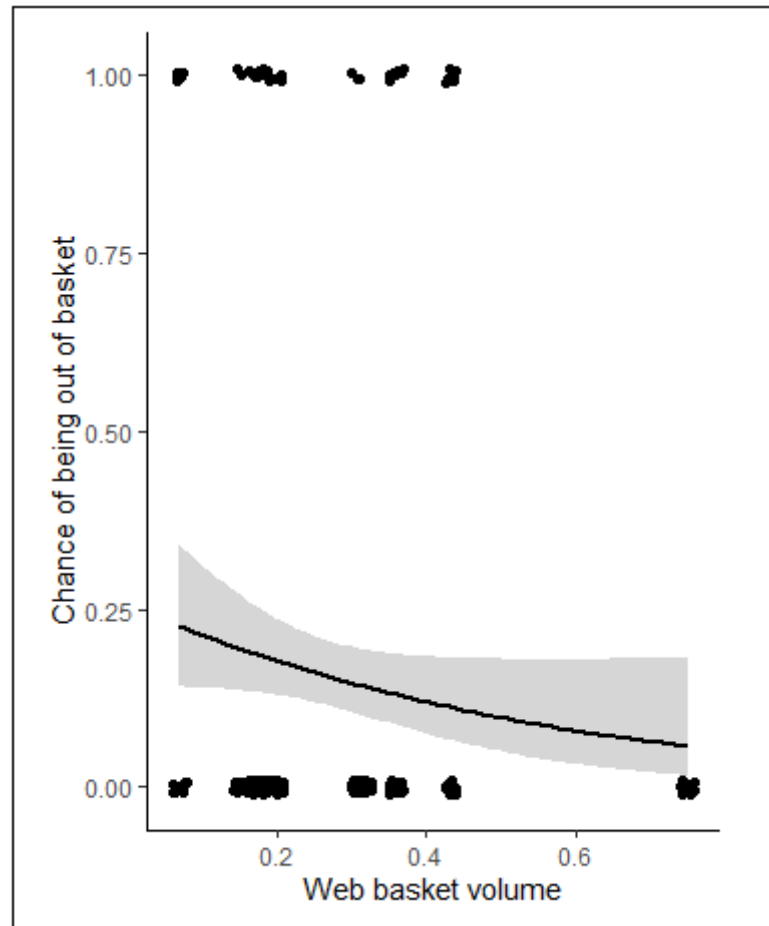
Morphometrics

Colony	Location	bask. len. (cm)	bask. wid. (cm)	bask. dep. (cm)	sail h. (cm)	bask. vol. (m ³)
1	Catu (12° 24' S/ 38° 29' W)	120	40	65	175	0.31
2	Catu (12° 24' S/ 38° 29' W)	187	55	42	350	0.43
3	Catu (12° 24' S/ 38° 29' W)	336	45	24	500	0.36
4	Catu (12° 24' S/ 38° 29' W)	148	150	34	400	0.75
5	Catu (12° 24' S/ 38° 29' W)	117	75	23	360	0.2
6	Catu (12° 24' S/ 38° 29' W)	103	20	73	400	0.15
7	Catu (12° 24' S/ 38° 29' W)	70	38	73	255	0.19
8	Catu (12° 24' S/ 38° 29' W)	93	20	40	200	0.07
9	Catu (12° 24' S/ 38° 29' W)	100	57	32	300	0.18
10	Catu (12° 24' S/ 38° 29' W)	450	37	22	240	0.36

11	Catu (12° 24' S/ 38° 29' W)	78	62	35	187	0.17
12	Catu (12° 24' S/ 38° 29' W)	172	50	38	196	0.32

Appendix 2

Logistic regression corresponding to the location model set. Here the volume of the basket determines that more spiders remain inside the basket (est = 0.866, se = 0.384, $\chi^2 = 5.091$, p = 0.024).



CONSIDERAÇÕES FINAIS

Esse trabalho investigou hipóteses que tratam da evolução da socialidade e da organização social, divisão de tarefas e especialização de tarefas nas aranhas.

A hipótese mais aceita para explicar a evolução da socialidade nesse táxon apresenta os benefícios da vida em grupo na redução dos custos com a manutenção das teias e na proteção garantida pela permanência na teia natal. Além disso, a especialização comportamental no desempenho de tarefas específicas dentro do grupo e o acesso a presas maiores são outros benefícios advindos da vida coletiva das aranhas. Apesar de serem bem estudados esses aspectos da aptidão das teias sociais, os mecanismos evolutivos por trás de sua origem foram pouco investigados. No primeiro capítulo apresentamos uma hipótese a qual propõe que a evolução da socialidade nas aranhas se deu através do processo de construção de nicho e encontramos o seguinte:

1. As teias coletivas proporcionaram maior proteção aos indivíduos contra o ataque de predadores e intempéries climáticas (engenharia de ecossistemas);
2. Essa proteção que permitiu a sobrevivência de indivíduos mais dóceis que a média, ampliando a variância comportamental das colônias;
3. Colônias com maior variância comportamental (com indivíduos mais dóceis) apresentaram maior taxa de sobrevivência (herança ecológica).

Concluimos que o processo de retroalimentação entre as propriedades das teias coletivas, alterando as pressões seletivas sobre os indivíduos que constroem e vivem nas teias, caracteriza a construção de nicho como processo evolutivo que levou ao surgimento da socialidade nas aranhas a partir de uma condição subsocial.

Investigamos, nos dois capítulos seguintes, a partir do ponto em que o sistema social se estabeleceu, como se dá a organização das sociedades das aranhas, como elas cooperam na realização das tarefas na teia. Para responder a essas perguntas, testamos a hipótese do nicho social, que apresenta mecanismos pelos quais as diferenças interindividuais no comportamento, denominadas como personalidade, enviam os indivíduos a realizarem tipos específicos de atividades dentro da colônia, selecionando nichos sociais de acordo com suas características intrínsecas.

No segundo capítulo, testamos a hipótese do nicho social através de modelagem computacional e encontramos os seguintes aspectos:

1. Não há especialização comportamental na realização de tarefas específicas por indivíduos com diferentes personalidades;
2. A personalidade por si só não é capaz de explicar tendências na realização das tarefas pelos indivíduos nas colônias.

No terceiro capítulo, testamos a hipótese do nicho social através de experimentos realizados com aranhas em teias naturais no campo e encontramos o seguinte:

1. A personalidade não influencia o tipo de tarefa desempenhado pelos indivíduos na colônia;
2. A personalidade influencia o local da teia no qual indivíduos com personalidades diferentes ocorrem com maior frequência;
3. Indivíduos ousados são os que ocorrem com maior frequência na área de captura da teia;
4. Teias maiores têm uma proporção maior de indivíduos nas áreas mais protegidas.

Por fim, propomos uma hipótese que apresenta a heterogeneidade ambiental, incluindo a produzida por engenharia de ecossistemas, como construção de ninhos e teias, que podem gerar

pressões seletivas sobre as propriedades inerentes dos indivíduos em favor de uma maior fidelidade espacial e especialização de tarefas em grupos sociais.

Com isso, concluímos que, segundo nossos estudos, o surgimento das aranhas sociais ocorreu devido a um processo iterativo entre o tamanho das teias e seu grau de proteção contra agentes externos e o aumento da variação comportamental dos indivíduos que viviam nessas teias. As aranhas sociais não apresentam especialização no desempenho de tarefas, a divisão de trabalho se dá mais pela segregação espacial dos indivíduos com personalidades distintas.

Trazendo evidências de que as grandes teias construídas pelas aranhas sociais não são apenas fruto da vida social desses animais, mas sim promovedoras da própria socialidade.