

A simpler way to organize society: response to a risky stimulus is related to the spatial distribution of the individuals within a spider colonial web

Leonardo P. A. Resende^{1,2,3}, David N. Fisher⁴, Isabelle O. L. Luz^{1,2}, Hilton F. Japyassú^{1,2}

¹Núcleo de Etologia e Evolução, Instituto de Biologia, Universidade Federal da Bahia, Salvador, Bahia, Brasil.

²Instituto Nacional de Ciência e Tecnologia em Estudos Interdisciplinares e Transdisciplinares em Ecologia e Evolução, Universidade Federal da Bahia, Salvador, Bahia, Brasil.

³Instituto Federal de Educação, Ciência e Tecnologia Baiano, Xique-Xique, Bahia, Brasil.

⁴School of Biological Sciences, University of Aberdeen, Aberdeen, Scotland, UK.

Leonardo Resende ORCID: 0000-0001-5386-7618.

Hilton Japyassú ORCID: 0000-0002-9788-5460.

David Fisher ORCID: 0000-0002-4444-4450.

Corresponding author- E-mail: biologo.leonardoparesende@gmail.com; Phone: +55 71 991114690; Adress: Rua Britoaldo Miranda, 241, Polivalente, Xique-Xique-BA, Brasil. CEP 47400000.

Acknowledgments

We thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) grant (nº 1583297) that supported this work. We also thank all Núcleo de Etologia e Evolução (NuEVo) colleagues that gave insights and precious suggestions to improve the work. We finally thank Rafael Paulino and Sidnei Sampaio for their help during field work.

Abstract

Animals living in social groups often need to conduct certain tasks, such as prey capture or nest maintenance. We might expect individuals to specialize in these tasks, as specialization 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 behavior may drive task specialization. We tested this prediction in groups of the social spider *Anelosimus eximius*, through experiments conducted on natural colonies in the field. We measured the response to a risky stimulus of individual spiders and then tested whether this predicted their location and/or activity when placed back in a colony. We found the more risk-prone individuals were more likely to be in the more exposed areas of the colony used for capturing prey. Irrespective of the risk-taking ~~behaviour~~behavior, individuals rest and care for young in the protective region of the colony, while in the exposed area of the web individuals are more active and more likely to be walking. Therefore, individual's responses to risk showed an influence on where an individual would settle within the colony but had no effect on its activity. Our results support previous work that suggests adult *A. eximius* do not specialize in tasks. Indirect pathways for individual traits, via differences in spatial location or activity levels, may help to explain variation among-individuals in task participation.

Key Words: Sociality, division of labor, social niche, behavioral traits

Statements and Declarations

Funding

This study was financed by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) grant n° 1583297.

Conflicts of interest

The authors declare no conflict of interest.

Availability of data and material

Data publicly available in a data repository: https://github.com/NuEVo-Ufba/Resende_etal_EximiusTask_R.git

Code availability

Code publicly available on Github repository: https://github.com/NuEVo-Ufba/Resende_etal_EximiusTask_R.git

Ethics approval

In Brazil there is no legislation that regulates the manipulation of invertebrate animal species for experimental studies.

Introduction

Social species live in cohesive groups which can maintain stability for long periods. Within these groups there may be an 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 specialized, as specialization should increase efficiency (Bergmüller and Taborsky 2010; Araújo et al. 2011; Montiglio et al. 2013; Boomsma and Gawne 2018).

Increased group efficiency due to task specialization should be associated with improved performance of the task, resulting in increased group productivity and ultimately fitness, since more efficient and productive groups have greater chances of survival and of producing more descendants who will found new colonies or groups (Wilson 1975; Oster and Wilson 1978; Wallace 1982). Several mechanisms can promote task specialization, such as polyethism (division of tasks based on age), polymorphism (division of tasks based on distinct developmental paths) (Schmid-Hempel 1992), and sex and body size (Schwander et al. 2005; Seeley and Kolmes 2010). Furthermore, environmental, and genetic factors can predispose individuals to perform certain tasks (Schwander et al. 2010).

In the cases of societies in which group members are morphologically similar and belong to the same generation and sex, variation in personalities among group members may lead to task differentiation (Réale and Dingemanse 2010). Personality, also called temperament or coping style, refers to the phenomenon that individual behavior tends to be repeatable across time, while varying consistently between individuals (Gosling 2001;

Stamps and Groothuis 2010; Koolhaas et al. 2010; Japyassú and Malange 2014; Brommer and Class 2017).

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 (Theraulaz et al. 1998; Bergmüller and Taborsky 2010; Montiglio et al. 2013). Furthermore, if personalities change the spatial distribution of individuals within the colony, further contributions to task specialization would ensue (Franks et al. 2002; Johnson 2009; Richardson et al. 2011; Mersch et al. 2013; Pamminger et al. 2014). This is because some tasks can only be performed (or only performed efficiently) at specific locations, and cues that indicate the demand for a specific task are only available to individuals in the direct vicinity (Johnson 2009).

While most spiders are solitary, some species have evolved to be social, living in social colonies and cooperating while capturing prey or rearing offspring (Avilés and Guevara 2017). In social spider colonies there are no morphological castes, so polymorphism is not a likely mechanism to promote task specialization and spatial organization of individuals (Lubin and Bilde 2007; Avilés and Guevara 2017). 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), which have been considered as potential factors in social organization (Settepani et al. 2013).

What was known about the effect of different individuals' personalities on the social organization of spider colonies is in the process of being revised. In this work, we measured the spiders' response to a risky stimulus, (note we do not refer to this as a

“personality” trait such as “boldness” as we did not quantify the repeatability of this trait across time or contexts). The response to the risky stimulus was used to test whether we find any spatialization of individuals in the web and whether they show some tendency to perform specific tasks.

Our general hypothesis is that behavioral traits, such as the degree of risk taking, can be a preponderant factor in determining the spatial distribution of individuals in the colony, as has been demonstrated for other social organisms, such as fish, ants and birds (Wagner et al. 2001; Bergmüller and Taborsky 2007; Johnson 2009; Mersch et al. 2013; Pamminer et al. 2014). Specialization in ~~perflinormingperforming~~ specific tasks would also be a prediction given the social niche hypothesis, and may be a good explanation for how spider societies are organized. We therefore expected to find an association between the response of the spiders to the risky stimulus and the kind of ~~behaviour~~behaviors they display in the web.

Material and Methods

Study object and study area

Anelosimus ~~Simon 1891~~ is a cosmopolitan genus of spiders of the family Theridiidae, with 53 described species occurring mainly in subtropical and tropical habitats of all continents, except Antarctica (Agnarsson and Zhang 2006; Agnarsson et al. 2006, 2007). Among the *Anelosimus* social species, the Neotropical *A. eximius*, occurs in low land forest areas of Panama to southern Brazil (Levi 1963; Avilés and Guevara 2017; Silva et al. 2020). Colonies of this species may vary from only a single pair of reproductive females and their offspring (a high altitude subsocial behavioral phenotype)

to enormous communal webs with several cubic meters containing tens of thousands of individuals (Venticinque et al. 1993; Avilés 1997; Avilés and Guevara 2017). The 13 colonies used in this study (1 colony as source of individuals, and 12 experimental colonies) were medium sized colonies (ranging from 0.07 to 0.75 m³ of basket volume), 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 select individuals to test. The source colony was used only to collect individuals that were subsequently used for risk-taking ~~behaviour~~behavior assessments and behavioral observations. We collected the entire colony, wrapping it in a plastic bag and cutting the branches of vegetation to which the web was attached. We selected the biggest adult females, placing them in 15 mL Falcon type plastic tubes, prior to the ~~behaviour~~behavioral assay. We took only the largest adult females to minimize the effects of mass and age variation on behavior.

The response to risky stimulus assay we performed is an established assay designed to simulate the approach of an aerial predator (Riechert and Hedrick 1993), and is similar to ~~behaviour~~behaviors often referred to as “boldness” in the animal ~~behaviour~~behavior literature (Dall et al. 2004; Réale and Dingemanse 2010; Sih et al. 2014).

Response to a risky stimulus was measured a single time for each individual by placing a spider in the middle of a Petri dish (15 cm in diameter) and, after a 30s acclimation period, administering 2 puffs of air to the anterior prosoma, using an infant nose-cleaning bulb (Riechert and Hedrick 1993). In response to this stimulus the spider stands still and pull their legs close to the body. The spiders' response was measured as the latency to resume movement, when spiders stretch their legs to walk again, after the air puffs. The test time limit of 600s follows the standard protocol found in the literature (Pinter-Wollman et al. 2017). Because more risk-prone individuals resume movement faster, the smallest values correspond to the most risk-taking individuals.

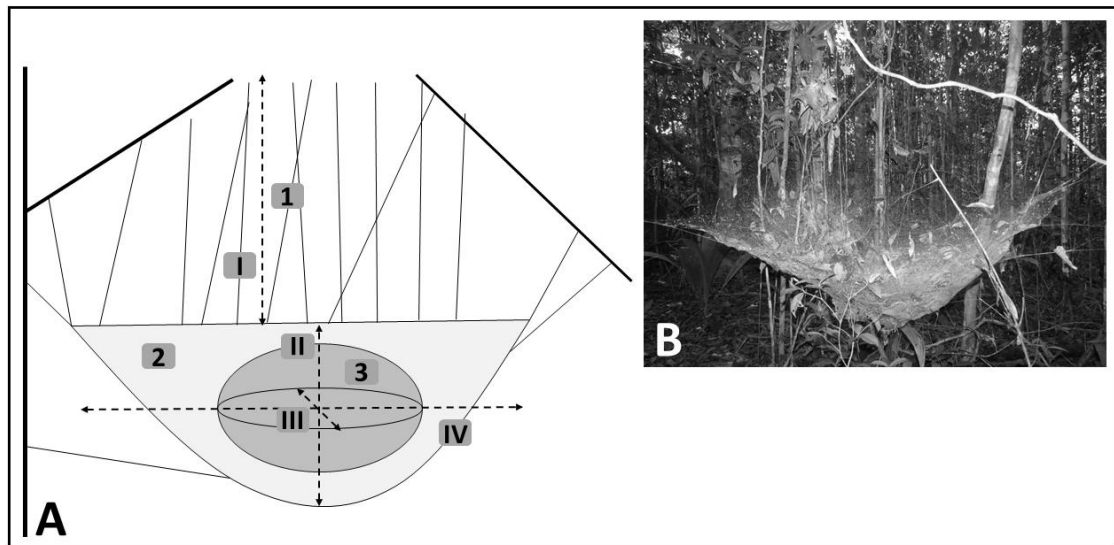
Tested individuals were marked in the abdomen with ink (using permanent oil-based ink marker pens), using a three-color code to uniquely mark each individual. In total, we tested and marked 168 adult female spiders. Next, we randomly introduced 14 marked individuals into each of 12 experimental colonies (Appendix 1). These colonies were located in the low branches of trees and bushes, at a maximum distance of 10 meters from the trails and selected by having a well-defined basket region (Figure 1). Since social spiders do not recognize kin from non-kin, the foreign individuals are accepted into the colony without aggression (Pasquet et al. 1997; Krafft and Cookson 2012), and therefore should be free to engage in typical tasks. We did not observe any atypical interaction between newcomers and residents. Observations began following a 24h acclimation period.

Behavioral scans (Altmann 1974), in which observers inspect colonies as a whole in search of marked individuals for a pre-determined period of time, in the 12 experimental colonies allowed the description of the behavior of the marked individuals

that survived and that could be located after the acclimation time. It was not possible to record data blind because our study involved focal animals in the field. Each colony was scanned three times by two observers for 10 min_per scan, being each observer responsible for finding and recording the location and behavior of 7 of the 14 individuals that were added to each test colony, always in the afternoon, between 2:00 pm and 5:00 pm, yielding in a total of 30 min of observations for each of the 12 experimental colonies. Colonies from ID 1 to 5 were scanned twice on 25th and once on 26th while colonies from ID 6 to 12 were scanned twice on 27th and once on 28th, in June 2019. The minimum time interval between two scans in a colony was 60 min. which occurred when colonies were sampled twice on the same day.

Following previous web morphometric studies (Avilés 1997; Purcell et al. 2012), we registered spiders as being in one of three web regions: “middle of the basket”, “basket edge”, and “sail” (Figure 1). We recorded which of eight activities the spider was engaged in, such as walking or taking care of young (see Table 1 for a description of each behavior).

Fig. 1 Morphometric variables of the web. A= Scheme of the web illustrating its parts and morphometric variables. Legend: 1= Capture web (sail); 2= Basket edge; 3= Basket middle; I= Sail height; II= Basket depth; III= Basket width and IV= Basket length. B= Picture of a natural web. Photo by: Leonardo Resende, Reserva Ecológica da Michelin, Bahia, 2017



Statistical analysis

We built in R (ver. 4.1.2; R Core Team 2020) two sets of binomial models, in the package “*glmmTMB*” (Brooks et al. 2017a), as shown in a schematic outline of the analysis (Figure 2). 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). The odds ratio was extracted from the fixed factors of the models using the “*fixef*” function of the “*glmmTMB*” package and the values extracted were exponentiated through the “*exp*” function.

In the first set of models, we aimed to test predictors for spider position 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

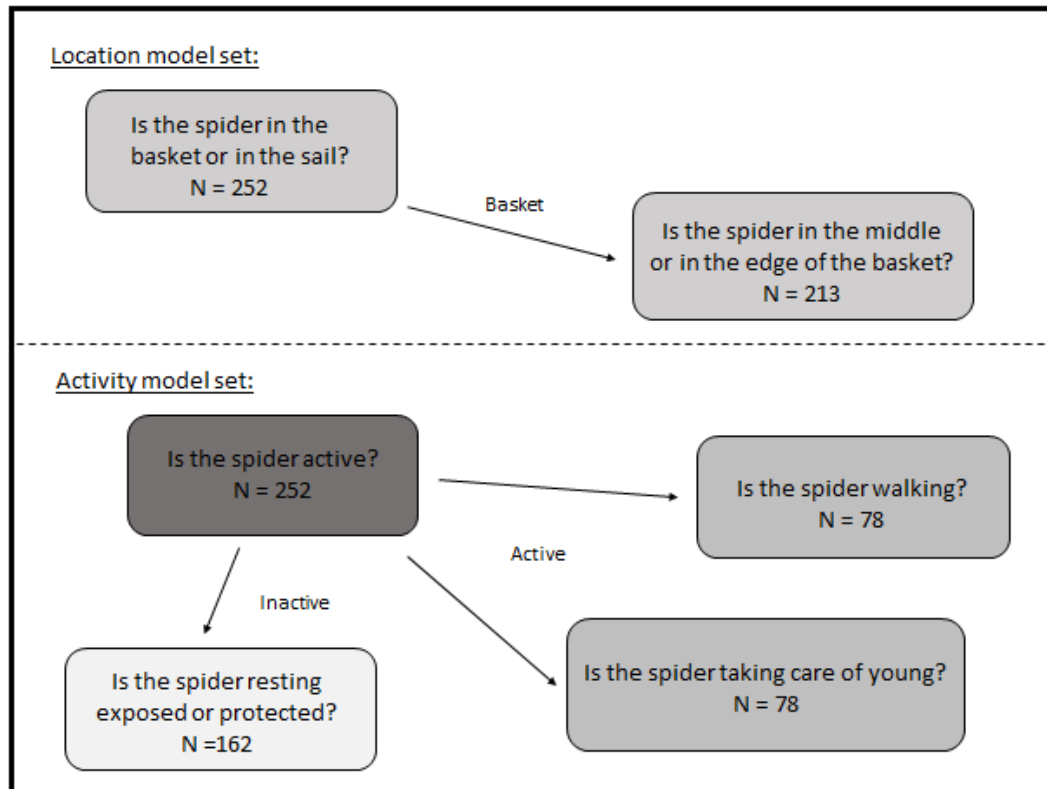
individual's response to the risk stimulus and the log of the volume of the basket as fixed effects (both mean centered and scaled to unit variance) as well as the random effects of colony ID, spider ID nested within colony ID, and date of observation. We used the variable "volume of the basket" to assess the importance of the size of the protected area of the web on the spatial distribution of individuals because individuals could passively be more abundant in larger areas just because of area size, instead of actively choosing them. 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 as in the first location model.

The second set of models focused on predictors of spider activity. The first model in the activity model set had a binary response of "spider was resting or active", with a 0 indicating rest (either exposed or protected), and a 1 indicating activity (n = 252). We fitted as fixed effects the individual's response to the risky stimulus, the log of the volume of the basket (mean centered and scaled to unit variance), the location of the spider (edge of basket, middle of basket, capture web), and the interaction between the spider behavioral trait and location. We fitted as random effects the colony ID, the spider ID nested within colony ID, and date of observation. 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 protected or exposed", 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 (either egg sacs or young spiders). Note that this behavior was never observed in the sail (Table 1), and so the effect of location tests for the difference between the edge and middle of the basket. 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. The other behaviors listed in Table 1 (grooming, fighting, capturing prey) were not frequent enough to analyze in their own right.

In total we fitted 6 models (two models in the location model set, and four models in the activity model set, see Fig. 2). We confirmed model convergence based on glmmTMB’s default output, and we tested each model for under- or over-dispersion using the DHARMA package (Hartig 2021). For models with a non-zero among-individuals variance, we re-fitted the model in the rptR package (Stoffel et al. 2017) to estimate repeatabilities on the original data scale of spider location and the activity it was performing. Repeatability on the data scale is preferable to on the latent scale as it allows better comparison across traits with different distributions (Nakagawa and Schielzeth 2010). In these models we also removed any random effects that had estimates of < 0.001 , to aid convergence.

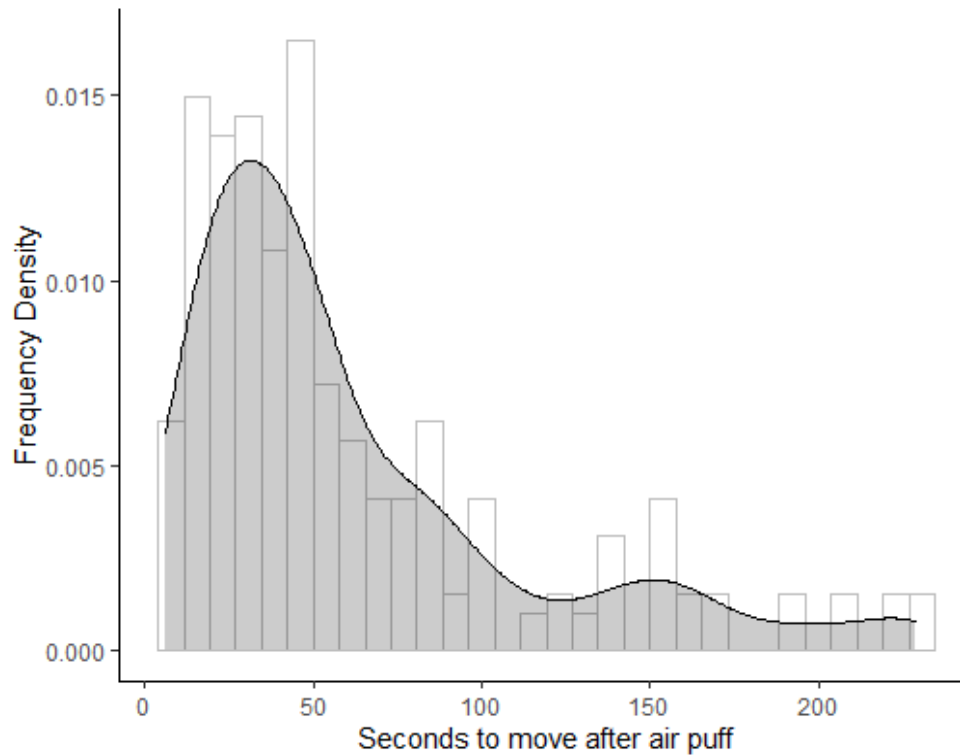
Fig. 2 Scheme outlining the sets of binomial models built to test predictors of the location and activity of the spiders. The fixed predictors of the models are risk-taking ~~behaviour~~behavior and basket volume, and the random predictors are colony ID, spider ID and sampling date.



Results

Latencies for the response to the risky stimulus were continually distributed between 6 and 229 seconds, with most scores falling in the range of 25 s (1st Qu.) to 80 s (2nd Qu.), with no bimodal structure or formation of separate categories that could suggest qualitatively distinct ~~behaviour~~behavioral phenotypes (Figure 3).

Fig. 3 Frequency distribution of the response to the risky stimulus of the 168 adult females collected from the source colony used for the observations, quantified as the latency time to resume movement after an air puff (low values indicate more risk-prone).



Observed behaviors

We observed eight distinct behaviors, which we separated into four categories. The assigned nomenclature, the description of the behaviors and the number of observations made on each area of the web can be seen in Table 1.

Table 1 Classification and description of the observed behaviors, with the respective frequency of observations for each web area. Legend: Beh.Cat.= Behavior category; Beh.Type= Behavior type; T.Obs.= Total observations; Obs.Sail= Observations in the

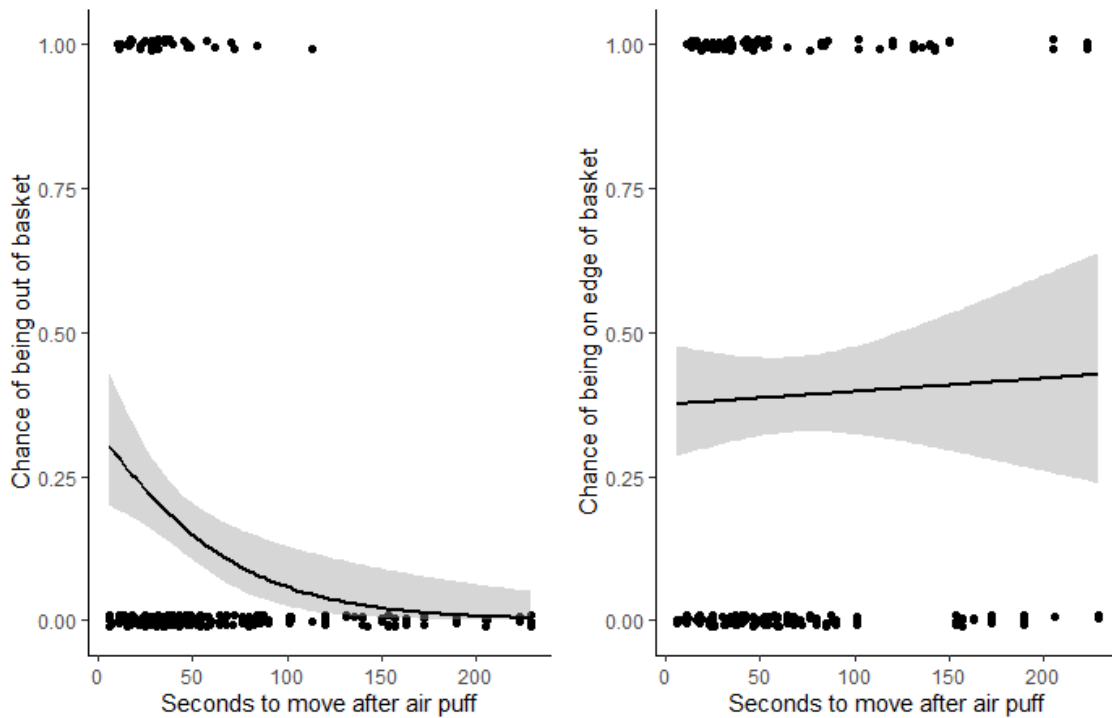
Sail; Obs. M.bask= Observations in the Middle Basket and Obs.E.bask= Observations in the Edge Basket

Beh.Cat.	Beh.Type	Description	T.Obs.	Obs. Sail	Obs. M.bask	Obs. E.bask
Resting	Resting Protected	Remaining motionless under the cover of leaves, twigs or any detritus.	143	0	93	50
	Resting Exposed	Remaining motionless away from any type of coverage.	31	12	7	12
Grooming	Grooming	Repeatedly rubbing the legs and pedipalps between the chelicerae.	3	0	3	0
Care of Young	Care of Egg sac	Staying close to the egg sacs, sometimes with legs over them.	18	0	12	6
	Care of Young	Staying close to young spiders.	7	0	4	3
Action	Walking	Walking on the web leaving a guideline along its path.	46	25	10	11
	Catching prey	Grasping and tangling prey in silk.	3	1	0	2
	Fighting	Two individuals aggressively tap each other's prosoma with front legs.	1	1	0	0

Predictors of spider location

We found that risk-avoiding individuals were more likely to be in the basket (Figure 4a), with the chance of remaining in the basket being 0.17 times greater for each additional second in the latency time of the individual risk-avoidance score. There was variance among individuals but none among colonies or dates. Additionally, we found that the greater the volume of the web, the greater the chance of individuals remaining inside the basket, in which the chance of being in the basket increases by a factor of 0.4 for every unit increase in the log of basket volume (Table 2).

Fig. 4 Logistic regressions corresponding to the location models set. The solid black lines indicate the estimated mean response for a given latency, with the grey areas showing the 95% confidence intervals around these estimates. 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 nor web volume affected the choice between being in the edge or in the middle of the basket (Figure 4b) (Table 2). There was variance among individuals in whether they were in the middle or edge of the basket, but less among colonies and none among dates.

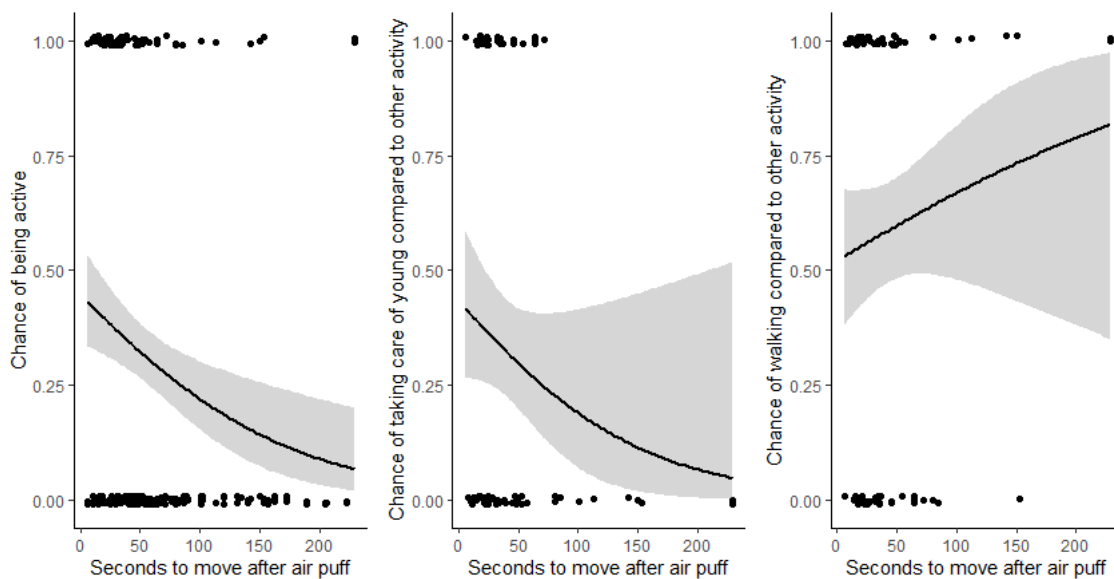
Table 2 Results of the location model set. Chances of being in the basket or in the sail, and chances of being in the middle or in the edge of the basket as a function of latency time and web volume. Legend: Est.= Estimate; S.E= Standard Error; Chisq= Chi-squared; p= P Value; O.R= Odds Ratio; C.I= Confidence Interval

Basket -Sail	Est.	S.E	Chisq	p	O.R	95% C.I	
						Low	High
Latency Time	-1.725	0.642	7.212	0.007	0.178	-2.984	-0.466
Web Volume	-0.866	0.384	5.091	0.024	0.420	-1.618	-0.113
Among individual	2.11	-	-	-	-	0.916	4.87
Among colonies	< 0.001	-	-	-	-	< 0.001	Inf
Among dates	< 0.001	-	-	-	-	< 0.001	Inf
Repeatability	0.331	0.21	-	-	-	0.098	0.726
Middle -Edge							
Latency Time	-0.058	1.052	0.003	0.956	9.440	-2.119	2.003
Web Volume	0.003	0.871	0	0.997	1.003	-1.703	1.709
Among individual	47.4	-	-	-	-	20.6	109
Among colonies	2.32	-	-	-	-	< 0.001	693000
Among dates	< 0.001	-	-	-	-	< 0.001	> 10 x 10 ¹²²
Repeatability	0.371	60.942	-	-	-	0.27	29.81

Predictors of spider activity

We found a significant difference in activity levels between the web regions, with spiders being 14 times more active in the sail than on edge or middle of the basket (Table 3). There was no effect of latency time, either as a main effect or as an interaction with location (Figure 5a - c).

Fig. 5 Logistic regressions corresponding to the activity models set. The solid black lines indicate the estimated mean response for a given latency, with the grey areas showing the 95% confidence intervals around these estimates. 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 taking care of young (est = -0.357, se = 0.777, $\chi^2 = 2.517$, p = 0.113). C= Latency time vs walking (est = 1.363, se = 1.102, $\chi^2 = 3.075$, p = 0.080)



The volume of the basket did not influence activity rates (Table 3). There was more variance in activity levels among individuals than among colonies, and there was none among dates (Table 2).

Table 3 Results of the activity model set. Chances of being resting or active as a function of location and latency time. Legend: Est.= Estimate; S.E= Standard Error; Chisq= Chi-squared; p= P Value; O.R= Odds Ratio; C.I= Confidence Interval

Rest x Active	Est.	S.E	Chisq	p	O.R	95% C.I	
						Low	High
Latency Time	-1.090	0.596	1.337	0.248	0.336	-2.259	0.079
Space	-	-	10.438	0.005	-	-	-
Space Middle Basket	-0.069	0.602	-	-	0.933	-1.248	1.111
Space Sail	2.658	1.033	-	-	14.26 5	0.633	4.681
Web Volume	0.310	0.306	1.025	0.311	1.362	-0.289	0.908
Latency Time: Space	-	-	4.318	0.115	-	-	-
Space Middle Basket	1.043	0.678	-	-	2.838	-0.285	2.371
Space Sail	-1.407	1.412	-	-	0.244	-4.173	1.360
Among individual	1.77	-	-	-	-	0.929	3.38
Among colonies	0.474	-	-	-	-	0.067	3.35
Among dates	< 0.001	-	-	-	-	< 0.001	Inf
Repeatability	0.311	0.12	-	-	-	0.064	0.521

For the analysis of resting protected vs resting exposed, the model failed to converge unless some of the fixed or random effects were removed, and even upon convergence the model showed underdispersion (DHARMA nonparametric dispersion test via comparison of *sd* of residuals fitted vs. simulated, dispersion = 0.6055, $p = 0.016$), and so we do not report the results.

Regarding whether the individual was taking care of the juveniles or doing something else, we found no latency time-location interaction, and the main effect of location was non-significant (Table 4). Both risk-taking ~~behaviour~~behavior and the volume of the web did not influence tendency to care for young (Table 4). There was variance among colonies in the tendency to take care of young but none among individuals or dates.

Table 4 Results of the activity model set. Chances of taking care of young vs doing other activity as a function of latency time and location. Legend: Est.= Estimate; S.E= Standard Error; Chisq= Chi-squared; p= P Value; O.R= Odds Ratio; C.I= Confidence Interval

Care x Other Activity	Est.	S.E	Chisq	p	O.R	95% C.I	
						Low	High
Latency Time	-0.391	0.923	2.091	0.148	0.67 6	-2.199	1.417
Space	-	-	0.485	0.486			
Space Middle Basket	-1.107	1.321	-	-	1.38 5	-1.314	1.966
Web Volume	0.322	0.485	0.440	0.507	1.37 9	-0.629	1.273

Latency Time:							
Space	-	-	0.701	0.402	-	-	-
Space Middle					0.33		
Basket	-1.107	1.321	-	-	0	-3.696	1.483
Among individual	< 0.001	-	-	-	-	< 0.001	Inf
Among colonies	0.988	-	-	-	-	0.277	3.53
Among dates	< 0.001	-	-	-	-	< 0.0001	Inf

Finally, we found that locations differed in whether spiders were walking compared to doing other activities, with spiders being 20 times more likely to be walking if they were in the sail compared to middle or edge of the basket. There was no latency time-location interaction (Table 5). Web volume did not influence whether the spider was walking or not. There was variance among individuals but none among colonies or dates.

Table 5 Results of the activity model set. Chances of walking vs doing other activity as a function of latency time and location. Legend: Est.= Estimate; S.E= Standard Error; Chisq= Chi-squared; p= P Value; O.R= Odds Ratio; C.I= Confidence Interval

Walk x Other Activity	Est.	S.E	Chisq	p	O.R	95% C.I	
						Low	High
Latency Time	1.363	1.102	3.075	0.080	3.907	-0.796	3.52
Space	-	-	8.652	0.013	-	-	2

Space Middle Basket	-1.017	0.856	-	-	0.361	-2.695	0.66 1
Space Sail	3.005	1.431	-	-	20.180	0.199	5.81 0
Web Volume	0.199	0.390	0.260	0.610	1.219	-0.565	0.96 2
Latency Time: Space			0.381	0.827	-	-	-
Space Middle Basket	-0.707	1.155	-	-	0.493	-2.971	1.55 6
Space Sail	-0.790	2.426	-	-	0.454	-5.544	3.96 4
Among individual	0.947	-	-	-	-	0.116	7.74
Among colonies	< 0.001	-	-	-	-	< 0.001	Inf
Among dates	< 0.001	-	-	-	-	< 0.001	Inf
Repeatability	0.169	37.61	-	-	-	0	50.0 33

Discussion

Individuals that responded faster to the risky stimulus were more likely to be in the sail, an exposed region of the web that functions as a prey capture area. In contrast, slower responding 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 (Mersch et al. 2013; Pamminer et al. 2014). Similarly, in sticklebacks, bolder individuals tend not to be in

the middle of the school, but rather maintaining a leadership position in front of the school, in its outermost regions, thus benefiting from primary access to food while exposing themselves more to predation (Ward et al. 2004), a situation similar to that of more risk-prone spiders on the sail of the web.

The findings of this study support our hypothesis that there is a spatial organization of the individuals in relation to their ~~behaviour~~behavioral traits. However, our results failed to support several of our predictions, as response to the risky stimulus had no direct impact on whether an individual was active or not, and did not influence the type of activity an individual was engaged in. Risk-taking ~~behaviour~~behavior never significantly influenced what tasks an active individual was conducting. There was among-individuals variation in whether an individual was walking or not, but there was no among-individuals variance for whether an individual was taking care of young.

~~Two~~Other studies have investigated task specialization in *A. eximius*. Settepani et al. (2013), in accordance with our results, also found a lack of task specialization for attacking prey and web maintenance, ~~while Fisher et al. (in prep) found more risk taking spiders were more likely to be active.~~ Therefore, 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 analyze the most common behaviors we observed. We occasionally recorded individuals attacking prey, or removing debris from the web, but not frequently enough to fit a mixed-effects model. Behaviors such as these could still be more specialized, and so could be candidates for detecting a link with behavioral traits, if only one could collect enough data to examine the relationship (albeit Settepani et al. 2013 found no evidence for task specialization in attacking prey or web maintenance).

Concerning whether a spider was active or resting, and whether an individual was walking or not, both showed a degree of among-individual variation. Therefore, irrespective of response to the risky stimulus, some individuals are consistently more active than others. 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 (Careau et al. 2008; Biro and Stamps 2008, 2010), but we are unable to identify which of these mechanisms may be responsible here.

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. Heterogeneous spaces are thought to promote task specialization as locations with different characteristics will differ in how effectively tasks can be performed within them (Johnson 2009; He et al. 2019). Spatial organization of tasks is already documented for a wide variety of social organisms, from ants and bees to cichlid fish (Wagner et al. 2001; Bergmüller and Taborsky 2007; Johnson 2009; Mersch et al. 2013; Pamminger et al. 2014). Additionally, building on the general idea that the spatial organization of task availability generates task specialization, here we show that a behavioral trait (such as risk avoidance) could indirectly, through promoting spatial preferences, lead to task specialization.

We found substantial variation among individuals in their location, suggesting a degree of spatial fidelity. However, this is only over four days; longer duration datasets would be required to determine whether individuals are consistent 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 even 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.

In summary, our study shows that there is a spatial organization of individuals in the web of a colony, and that it is influenced by individual differences in a behavioral trait. However, contrary to what was expected, risk-taking behaviour/behavior proved to be not itself important in determining the rate of activity or the type of activity the spiders performed, given the location that they were in. Behavioral traits may instead indirectly influence division of tasks through dictating an individual's location within a group, thus exposing distinct individuals to distinct task profiles.

Future studies that aim to investigate the social organization of spiders should seek to isolate the different factors that modulate the behavior of individuals (satiety, age, reproductive fitness), in order to reformulate the understanding about the role of individual behavioral traits in the organization of social life. Furthermore, a new avenue for further investigation is the effect of web architecture itself on collective colony behavior (Resende et al. 2019), an approach of the niche construction theory that may yield important insights into the ecology and evolution of sociality in spiders.

References

Agnarsson I, Avilés L, Coddington JA, Maddison WP (2006) Sociality in theridiid spiders: repeated origins of an evolutionary dead end. *Evolution* 60:2342–2351. <https://doi.org/10.1111/j.0014-3820.2006.tb01869.x>

Agnarsson I, Coddington JA, Knoflach B (2007) Morphology and evolution of cobweb spider male genitalia (~~A~~araneae; ~~t~~Theridiidae). *J Arachnol* 35:334–395.
<https://doi.org/10.1636/SH-06-36.1>

Agnarsson I, Zhang J-X (2006) New species of *Anelosimus* (Araneae: Theridiidae) from Africa and Southeast Asia, with notes on sociality and color polymorphism. *Zootaxa* 1147:1. <https://doi.org/10.11646/zootaxa.1147.1.1>

Altmann J (1974) Observational ~~S~~study of ~~B~~behavior: ~~S~~sampling ~~M~~methods. ~~Behaviour~~Behavior 49:227–267

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation: ~~F~~the causes of individual specialisation. *Ecol Lett* 14:948–958.
<https://doi.org/10.1111/j.1461-0248.2011.01662.x>

Avilés L (1997) Causes and consequences of cooperation and permanent-sociality in spiders. In: Choe JC, Crespi BJ (eds) ~~The~~ ~~E~~volution of ~~S~~social ~~B~~behavior in ~~I~~nsects and ~~A~~arachnids. Cambridge University Press, Cambridge, pp 476–498

Avilés L, Guevara J (2017) Sociality in ~~S~~spiders. In: Rubenstein DR, Abbot P (eds) Comparative ~~S~~social ~~E~~volution. Cambridge University Press, Cambridge, pp 188–223

Bergmüller R, Taborsky M (2010) Animal personality due to social niche specialisation. *Trends Ecol Evol* 25:504–511.
<https://doi.org/10.1016/j.tree.2010.06.012>

Bergmüller R, Taborsky M (2007) Adaptive ~~behaviour~~behavioural syndromes due to strategic niche specialization. *BMC Ecol* 7:12. <https://doi.org/10.1186/1472-6785-7-12>

Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history productivity? *Trends Ecol Evol* 23:361–368.
<https://doi.org/10.1016/j.tree.2008.04.003>

Biro PA, Stamps JA (2010) Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol Evol* 25:653–659. <https://doi.org/10.1016/j.tree.2010.08.003>

Boomsma JJ, Gawne R (2018) Superorganismality and caste differentiation as points of no return: how the major evolutionary transitions were lost in translation: ~~S~~superorganisms, eusociality and major transitions. *Biol Rev* 93:28–54. <https://doi.org/10.1111/brv.12330>

Brommer JE, Class B (2017) Phenotypic correlations capture between-individual correlations underlying behavioral syndromes. *Behav Ecol Sociobiol* 71:50. <https://doi.org/10.1007/s00265-017-2278-4>

~~Brooks ME, Kristensen K, van Benthem KJ, et al (2017) Modeling zero-inflated count data with glmmTMB. *Ecology*~~

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. (2017a) Modeling zero-inflated count data with glmmTMB. *bioRxiv* 132753. <https://doi.org/10.1101/132753>

Careau V, Thomas D, Humphries MM, Réale D (2008) Energy metabolism and animal personality. *Oikos* 117:641–653. <https://doi.org/10.1111/j.0030-1299.2008.16513.x>

Dall SRX, Houston AI, McNamara JM (2004) The ~~behaviour~~behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* 7:734–739. <https://doi.org/10.1111/j.1461.0248.2004.00618.x>

Dushoff J, Kain MP, Bolker BM (2019). I can see clearly now: ~~R~~reinterpreting statistical significance. *Methods Ecol Evol* 10:756–759. <https://doi.org/10.1111/2041-210X.13159>

Ebert D (1998) Behavioral ~~A~~asymmetry in ~~R~~relation to ~~B~~body ~~W~~weight and ~~H~~hunger in the ~~T~~tropical ~~S~~social ~~S~~spider *Anelosimus eximius* (Araneae: Theridiidae). *J Arachnol* 26:70–80

Franks NR, Pratt SC, Mallon EB, et al. (2002) Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philos Trans R Soc Lond B Biol Sci* 357:1567–1583. <https://doi.org/10.1098/rstb.2002.1066>

Fox J, Weisberg S. (2019). ~~An R Companion to Applied Regression, Third~~ 3rd edition. Sage, Thousand Oaks CA.
<https://socialsciences.mcmaster.ca/jfox/Books/Companion/>

Gosling SD (2001) From mice to men: ~~W~~ hat can we learn about personality from animal research? *Psychol Bull* 127:45–86. <https://doi.org/10.1037/0033-2909.127.1.45>

Hartig F (2021) DHARMA: ~~R~~ residual ~~D~~ diagnosics for ~~H~~ hierarchical (Multi-Level / Mixed) ~~R~~ regression ~~M~~ models. R package version 0.4.4.
<http://florianhartig.github.io/DHARMA/>

He P, Maldonado-Chaparro AA, Farine DR (2019) The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behav Ecol Sociobiol* 73:9. <https://doi.org/10.1007/s00265-018-2602-7>

Hunt ER, Mi B, Geremew R, et al. (2019) Resting networks and personality predict attack speed in social spiders. *Behav Ecol Sociobiol* 73:97.
<https://doi.org/10.1007/s00265-019-2715-7>

Japyassú, H-F, Malange, J (2014) Plasticity, stereotypy, intra-individual variability and personality: handle with care. ~~Behaviour~~ Behavioral Processes, 109: 40-47.
<https://doi.org/10.1016/j.beproc.2014.09.016>

Johnson BR (2009) A ~~S~~ self-~~O~~ organizing ~~M~~ model for ~~T~~ task ~~A~~ allocation via ~~F~~ frequent ~~T~~ task ~~Q~~ quitting and ~~R~~ random ~~W~~ walks in the ~~H~~ honeybee. *Am Nat* 174:537–547.
<https://doi.org/10.1086/605373>

Kapustjanskij A, Streinzer M, Paulus HF, Spaethe J (2007) Bigger is better: implications of body size for flight ability under different light conditions and

the evolution of alloethism in bumblebees. *Funct Ecol* 21:1130–1136.
<https://doi.org/10.1111/j.1365-2435.2007.01329.x>

Koolhaas JM, de Boer SF, Coppens CM, Buwalda B (2010) Neuroendocrinology of coping styles: Ftowards understanding the biology of individual variation. *Front Neuroendocrinol* 31:307–321. <https://doi.org/10.1016/j.yfrne.2010.04.001>

Krafft B, Cookson LJ (2012) The Role of Ssilk in the Behaviourbehaviour and sociality of Sspiders. *Psyche J Entomol* 2012:1–25.
<https://doi.org/10.1155/2012/529564>

Levi HW (1963) The American Sspiders of the Genus a*nelosimus* (Araneae:
Theridiidae). *Trans Am Microsc Soc* 82:30. <https://doi.org/10.2307/3223818>

Lubin Y, Bilde T (2007) The Evolution of Ssociality in Sspiders. In: *Advances in the Sstudy of Bbehavior*. Elsevier, pp 83–145

Mersch DP, Crespi A, Keller L (2013) Tracking Individuals Sshows Spatial Fidelity Is a Kkey Regulator of Ant Ssocial Organization. *Science* 340:1090–1093.
<https://doi.org/10.1126/science.1234316>

Montiglio P-O, Ferrari C, Réale D (2013) Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philos Trans R Soc B Biol Sci* 368:20120343. <https://doi.org/10.1098/rstb.2012.0343>

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and Non-Gaussian data: a practical guide for biologists. *Biol. Rev.* 85:935–956.
<https://doi.org/10.1111/j.1469-185X.2010.000141.x>

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Monogr Popul Biol 12:1-352-Princeton

Pamminger T, Foitzik S, Kaufmann KC, et al. (2014) Worker Personality and Its Association with Spatially Structured Division of Labor. *PLoS ONE* 9:e79616. <https://doi.org/10.1371/journal.pone.0079616>

- Parthasarathy B, Joshi CH, Kalyadan SS, Somanathan H (2019) Early ontogenic emergence of personality and its long-term persistence in a social spider. *Behav Ecol Sociobiol* 73:35. <https://doi.org/10.1007/s00265-019-2645-4>
- Pasquet A, Trabalon M, Bagnères AG, Leborgne R (1997) Does group closure exist in the social spider *Anelosimus eximius*? ~~Behaviour~~Behavioural and chemical approach. *Insectes Sociaux* 44:159–169. <https://doi.org/10.1007/s000400050038>
- Pinter-Wollman N, Mi B, Pruitt JN (2017) Replacing bold individuals has a smaller impact on group performance than replacing shy individuals. *Behav Ecol* 28:883–889. <https://doi.org/10.1093/beheco/ax054>
- Purcell J, Vasconcellos-Neto J, Gonzaga MO, et al. (2012) Spatio-temporal ~~D~~Differentiation and ~~S~~Sociality in ~~S~~Spiders. *PLoS ONE* 7:e34592. <https://doi.org/10.1371/journal.pone.0034592>
- Réale D, Dingemanse NJ (2010) Personality and individual social specialisation. In: Szekely T, Moore AJ, Komdeur J (eds) *Social Behaviour*~~behaviour~~. Cambridge University Press, Cambridge, pp 417–441
- Resende LPA, Rios VP, Japyassú HF (2019) The survival of the shyest: a computational model shows the effect of web structure on the origins of social spiders. *Animal Behaviour*~~Behav~~, 155:229–239. <https://doi.org/10.1016/j.anbehav.2019.05.029>
- Richardson TO, Christensen K, Franks NR, et al. (2011) Ants in a ~~L~~Labyrinth: ~~A~~A ~~S~~Statistical ~~M~~Mechanics ~~A~~Approach to the ~~D~~Division of ~~L~~Labour. *PLoS ONE* 6:e18416. <https://doi.org/10.1371/journal.pone.0018416>
- Riechert SE, Hedrick AV (1993) A test for correlations among fitness-linked behavioral traits in the spider *Agelenopsis aperta* (Araneae: Agelenidae). *Anim Behav* 46:669–675. <https://doi.org/10.1006/anbe.1993.1243>

Schmid-Hempel P, (1992) B. Holldobler, B. E. O. Wilson EO (1990): “The Aants.”
Springer, Berlin, 732 pp. DM 198.-. J Evol Biol 5:169–171.
<https://doi.org/10.1046/j.1420-9101.1992.5010169.x>

Schwander T, Lo N, Beekman M, et al. (2010) Nature versus nurture in social insect
caste differentiation. Trends Ecol Evol 25:275–282.
<https://doi.org/10.1016/j.tree.2009.12.001>

Schwander T, Rosset H, Chapuisat M (2005) Division of labour and worker size
polymorphism in ant colonies: the impact of social and genetic factors. Behav
Ecol Sociobiol 59:215–221. <https://doi.org/10.1007/s00265-005-0027-6>

Seeley TD, Kolmes SA (2010) Age Ppolyethism for Hhive Dduties in Hhoney Bbees-:
Hillusion or Rreality? Ethology 87:284–297. <https://doi.org/10.1111/j.1439-0310.1991.tb00253.x>

Settepani V, Grinsted L, Granfeldt J, et al. (2013) Task specialization in two social
spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius*
(Theridiidae). J Evol Biol 26:51–62. <https://doi.org/10.1111/jeb.12024>

Sih A, Mathot KJ, Moiron M, Montiglio P, Wolf M, Dingemanse NJ (2014) Animal
personality and state-behaviour-behaviour feedbacks: a review and guide for
empiricists. Trends Ecol. Evol. 30:-50- 60.
<https://doi.org/10.1016/j.tree.2014.11004>

Silva LM, Batalha-Filho H, Japyassú HF, El-Hani CN (2020) Population history of a
social spider reveals connection between South American tropical forests. Zool
Anz 285:139–146. <https://doi.org/10.1016/j.jcz.2020.01.004>

Spaethe J, Weidenmüller A (2002) Size variation and foraging rate in bumblebees
(*Bombus terrestris*). Insectes Sociaux 49:142–146

Stamps J, Groothuis TGG (2010) The development of animal personality: relevance,
concepts and perspectives. Biol Rev 85:301–325. <https://doi.org/10.1111/j.1469-185X.2009.00103.x>

- Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol* 8: 1639-1644. <https://doi.org/10.1111/2041-210X.12797>
- Theraulaz G, Bonabeau E, Deneubourg J-N (1998) Response threshold reinforcements and division of labour in insect societies. *Proc R Soc Lond B Biol Sci* 265:327–332. <https://doi.org/10.1098/rspb.1998.0299>
- Vasconcellos-Neto J, Souza ALT, Marques ESA, Ferraz FFF (1995) Comportamento Social de *Anelosimus eximius* (Theridiidae: Araneae). *Anais de Etologia*, 13: 217-230.
- Venticinque EM, Fowler HG, Silva CA (1993) Modes and Frequencies of Colonization and its Relation to extinctions, Habitat and Seasonality in the Social Spider *Anelosimus eximius* in the Amazon (Araneidae: Theridiidae). *Psyche J Entomol* 100:35–41. <https://doi.org/10.1155/1993/82186>
- Wagner D, Tissot M, Gordon D (2001) Task-related environment alters the cuticular hydrocarbon composition of harvester ants. *J Chem Ecol* 27:1805–1819. <https://doi.org/10.1023/A:1010408725464>
- Wallace B (1982) Phenotypic variation with respect to fitness: the basis for rank-order selection*. *Biol J Linn Soc* 17:269–274. <https://doi.org/10.1111/j.1095-8312.1982.tb02021.x>
- Ward AJW, Thomas P, Hart PJB, Krause J (2004) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol Sociobiol* 55:561–568. <https://doi.org/10.1007/s00265-003-0751-8>
- Wilson EO (1975) Some central problems of sociobiology. *Soc Sci Inf* 14:5–18. <https://doi.org/10.1177/053901847501400601>
- Wilson EO (1971) The Prospects for a Unified Sociobiology: This important branch of behavioral biology should be joined with population biology. *Am Sci* 59:400–403

Wilson EO, Hölldobler B (2005) Eusociality: ~~O~~origin and consequences. Proc Natl Acad Sci 102:13367–13371. <https://doi.org/10.1073/pnas.0505858102>

World Spider Catalog. ~~(2020)~~ World Spider Catalog. Version 21.0. Natural History Museum Bern. ~~online at~~ <http://wsc.nmbe.ch>, doi: 10.24436/2. [Accessed August 2021](#)

Appendix 1

Location and morphometric measurements of the 12 natural colonies utilized on the field experiments. Legend: bask.len= basket length; bask. 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, $\chi^2 = 5.091$, $p = 0.024$).

