



Web architecture, dynamics and silk investment in the social spider *Stegodyphus sarasinorum*

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Animal architecture is diverse in form and structure, and extraordinarily intricate, often facilitated by the collective behaviour of several individuals. Social spider webs are one such example of animal architecture, robustly supporting the collective colony weight and intercepting prey for the entire colony. Thus, these webs are interesting, yet little studied from architectural and behavioural perspectives. In the social spider *Stegodyphus sarasinorum* we examined the spatiotemporal dynamics of web architecture and tracked web development in different group sizes through controlled experiments and image analysis. Geometrical parameters including coordination number, and pore size remained constant across group sizes. Silk density was highest near the retreat (nest) and decreased with radial distance for all group sizes. We tested the silk conservation hypothesis, a proposed benefit for the evolution of group living, by asking whether (1) total silk investment increases with group size and (2) per capita silk investment decreases with group size. Our results indicate that while larger colonies produced more silk than smaller ones, per capita silk investment did not decline in larger groups. We propose further investigations into the roles of ecological factors and body condition in shaping individuals' silk investment with consequences for web architecture and colony fitness.

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Structures built by animals have fascinated and inspired biologists, engineers and architects. Animals display tremendous diversity in form, structure and choice of material in building these structures (Von Frisch 1974). Sociable weaver bird nests, termite mounds and honey bee colonies are fascinatingly complex examples of such structures, and are several orders of magnitude larger than the individuals themselves (Hansell, 2007; Ireland & Garnier, 2018). These gargantuan structures built by the collective behaviour of hundreds of individuals living in groups can result in larger nests and increased foraging efficiency and vigilance against predators and parasites (Deneubourg & Goss, 1989; Pinter-Wollman, Fiore, & Theraulaz, 2017). Studies on nest construction behaviour in ants, wasps, bees and termites have provided an evolutionary underpinning for the emergence of collective behaviour (Buhl, Deneubourg, Grimal, & Theraulaz, 2005; Couzin, 2009; Franks & Deneubourg, 1997; Pinter-Wollman, 2015). Various facets of the dynamics of nest building, including choice of materials,

location, spatial extent of the nests and group size have been the focus of several studies. Collective construction behaviour is also the result of self-organization of several individuals with access only to local information (Aleksiev, Longdon, Christmas, Sendova-Franks, & Franks, 2007; Buhl et al, 2002, 2005; Sasaki & Pratt, 2013; Zachariah, Das, Murthy, & Borges, 2017). Nests may be built largely by using extraneous material; however, in some species, individuals expend body reserves to build entire or large parts of the nest; a well-known example is hive construction from wax produced by honey bee workers. Webs built by social spiders are yet another interesting and little studied example of collectively built structures using internally produced silk.

Sociality in spiders is rare, as only around 25 of 45 000 known species of spiders are permanently social (Avilés, 1997; Lubin & Bilde, 2007). Group sizes in social spiders range from tens to hundreds of individuals, and females exhibit collective behaviour in web construction, prey capture and brood care, which are performed by the same individuals. Sociality is suggested to bring benefits such as the ability to capture larger prey (Nentwig 1985; Rypstra 1990; Pasquet & Krafft, 1992), higher feeding efficiency, lower desiccation rate

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(Vanthourmout et al., 2016) and a decrease in per capita investment in silk (Riechert, 1985; Tietjen, 1986). Social spider webs are strong, extensible and resilient structures. Unlike the well-studied orb webs, social spider webs are built over many days by the collective effort of multiple individuals. Although webs get damaged by heavy winds, rain and entangled prey, they are regularly repaired and maintained over time by multiple generations.

Several aspects of webs are known to be important for prey retention and capture. For example, size, orientation and location of webs are known to influence prey interception (Eberhard, 1986; Craig, 1987; Opell, Bond, & Warner, 2006). In addition, material properties (stiffness, toughness and extensibility of silk strands) and architecture (density, topology and silk decoration) of webs also influence prey capture (Harmer, Blackledge, Madin, & Herberstein, 2011; Blackledge, Kuntner, & Agnarsson, 2011). Investigations into the construction and structure of social spider webs are rare, while much is known about the ecological, behavioural and biomechanical factors influencing prey capture in orb- and cobweb-building spiders (Swanson, Blackledge, Beltrán, & Hayashi, 2006; Blackledge & Zevenbergen, 2006; Blackledge & Eliason, 2007; Blackledge et al., 2011). Furthermore, although the dynamics of nest construction in social insects such as bees (Seeley, Camazine, & Sneyd, 1991; Seeley & Visscher, 2004; Smith, Ostwald, & Seeley, 2015), ants (Franks & Deneubourg, 1997; Theraulaz, Gautrais, Camazine, & Deneubourg, 2003) and termites (Bonabeau, Theraulaz, Deneubourg, Aron, & Camazine, 1997; Zachariah, Singh, Murthy, & Borges, 2020) has been extensively studied, the spatiotemporal development of web building in social spiders has remained largely unexplored.

We examined the collective web-building behaviour in colonies of the social spider *S. sarasinorum* (Eresidae). This species builds one or a few sheets of capture web attached to a nest-like retreat at one end and to vegetation or any other support structures such as fences at multiple points (Fig. 1a). The web is made of dragline silk, which forms the supporting scaffold, and highly coiled cribellate silk, which is laid in a zigzag pattern to facilitate prey capture (Fig. 1b). In the present study, through a series of controlled experiments, we examined the changes in web geometry and topology over time across group sizes. An often-purported benefit of sociality is a reduction in per capita silk investment (Riechert, 1985; Tietjen, 1986). We tested the silk conservation hypothesis by asking

whether (1) overall silk investment increases with group size and (2) per capita silk investment decreases with group size.

METHODS

Collection and Experimental Set-up

In nature, *Stegodyphus* species build webs on fences or on vegetation, which provide different physical environments (Kamath et al., 2019, T. Beleyur, D. Uma & H. Somanathan, personal observations). *S. sarasinorum* webs built on fences are two-dimensional (Fig. 1a) and those built on vegetation are topologically complex and multidimensional. The architecture of both types of web have not been characterized before. This study is restricted to two-dimensional webs since standardization of methods formed a major part of the work involved and two-dimensional webs, which are less complex, suited this purpose.

Small- to medium-sized *S. sarasinorum* colonies were collected from Bangalore, India from March to April 2015. To examine the effect of group size on web building, we categorized spiders into four group sizes: 1, 5, 10 and 25 subadult individuals. Spiders belonging to a particular group came from the same colony, and each group had three to six replicates ($N = 19$ colonies in total) each of which lasted 6–10 days (Table 1). Group sizes of 5–25 typically constitute small to medium spider colonies in the field. We also included a single spider as an experiment treatment: retreats with single spiders are not uncommon, as individuals often disperse solitarily from their natal colonies to found new colonies (Parthasarathy & Somanathan, 2018). To control for the effect of body size on web building, we selected similar-sized spiders, with comparable cephalothorax widths (mean \pm SD = 2.34 ± 0.23 mm, $N = 178$ spiders) and weights (mean \pm SD = 65.1 ± 15.8 mg, $N = 178$ spiders). Cephalothorax width is a reliable indicator of developmental stage, and spider weight indicates recent feeding history (Lubin, Koltzman, & Ellner, 1991; Pasquet, Leborgne, & Lubin, 1999). Individuals were marked with unique colour codes to record any changes in their body masses before and after the experiment.

Each group (1, 5, 10 and 25 spiders) was housed in a black square cardboard pocket lined with nest material (spider silk and debris) obtained from the original colonies to serve as an artificial retreat. These retreats were clipped on to the left-hand corner of a thin

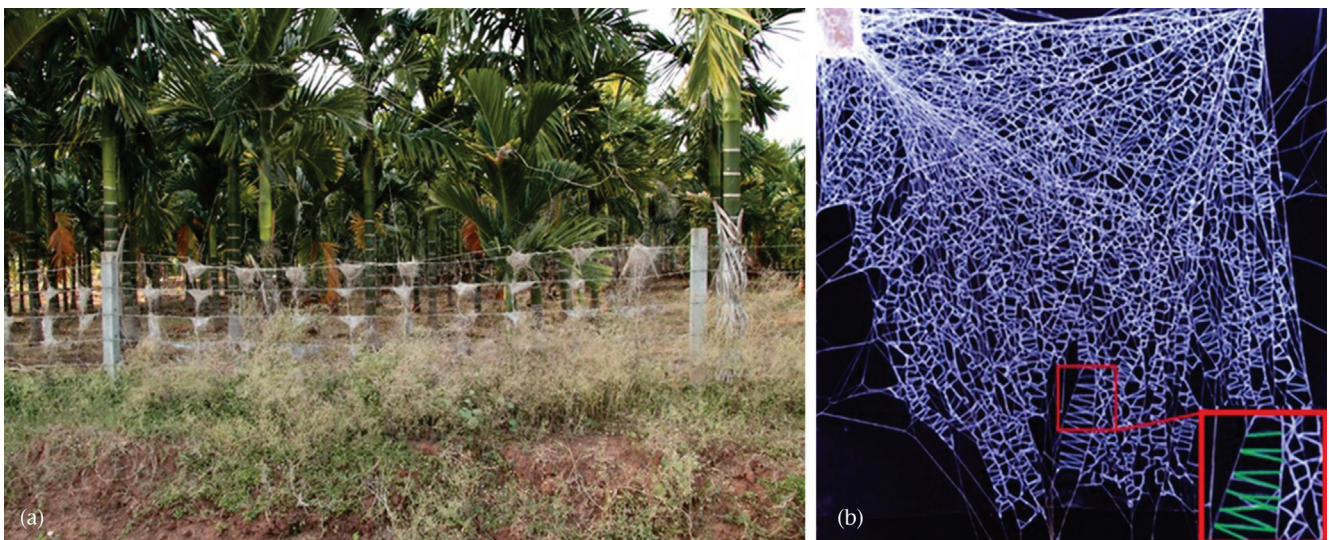


Figure 1. (a) Web of the social spider *S. sarasinorum*. Multiple retreats or nests seen as dense structures on the fence are connected by a two-dimensional web. Photo credit: H. Somanathan. (b) Processed image of social spider web used for image analysis. Insert depicts scaffolding silk highlighted in white and zigzag cribellate silk highlighted in green, which is often laid over the scaffolding structure.

Table 1
Number of replicates for each group size and experimental duration

Group size (no. of replicates)	Experimental duration (days)
1 (6)	7,7,7, 8,9,10
5 (3)	6,9,9
10 (6)	6,7,8,9,9,10
25 (4)	7,7,8,9

square metallic frame (60 × 60 cm). The size of the artificial retreat differed according to the size of the experimental group; for group sizes 1 and 5, the retreat size was 2.5 × 2.5 cm and for group sizes 10 and 25, the retreat size was 5 × 5 cm. The frames were suspended by two strings from a rope railing connected to the opposite walls of the temperature-controlled experimental room with ambient light conditions. To prevent spiders from escaping by walking up the strings, we coated the strings with petroleum jelly (Paraffin). Since adult *Stegodyphus* spiders are known to disperse by ballooning (*S. dumicola*: Schneider, Roos, Lubin, & Henschel, 2001, *S. sarsinorum*: D. Uma, personal observation), we kept all the windows and doors shut to prevent any air draft that can facilitate ballooning. Spiders are known to tolerate long periods of starvation and desiccation (Bodasing, Crouch, & Slotow, 2002; Nakamura, 1987; Seibt & Wickler, 1990). Hence, we did not feed or spray spiders with water for moisture during the period of the experiment (10 days) for two reasons: (1) to avoid any confounding effects on web building arising from food competition between individuals which could result in unequal rates of weight change and (2) to prevent damage to webs due to prey capture. The webs thus built by the experimental spider groups were similar to *S. sarsinorum* webs in the field. The study abides by the animal ethics laws of India. Spiders that were used in the experiment were released back in the field after the experiment.

Image Analysis

Each frame containing a spider web was photographed every 24 h for 10 days, against a dark background lit with consistent LED lighting that illuminated the entire plane of the web. We used a DSLR camera (Nikon D700 with a 16–85 mm AF-S Nikkor lens) placed on a tripod at a fixed distance (1.78 m) and at a fixed focal setting that captured the entire frame. The amount of silk on the web was quantified using AngioQuant (Niemisto, Dunmire, Yi-

Harja, Zhang, & Shmulevich, 2005), which was custom adapted for this study. AngioQuant is an image analysis algorithm that skeletonizes the original image and is implemented on a MATLAB platform. Skeletonizing is a technique that reduces the image of a complex object to extract the skeleton or the framework of the object, while preserving the object's original topology (Fig. 2). In our case, we extracted the skeleton of the web and obtained a simplified outline of the web's structure.

Extensive details of the geometry and topology of the web, including the total length of silk laid by each group, the spatial distribution of the laid silk, the mean coordination number (CN) and mean pore size were quantified through imaging and image analysis. CN was calculated as

$$2 \times \text{total number of edges} \div \text{total number of nodes}$$

Each silk strand constitutes an edge, and the point where two strands attach constitutes a node. CN is typically used in graph theory in building networks or in understanding how many atoms/molecules are connected to its nearest neighbours in a crystal/solid. We used CN here to calculate how silk strands are connected to each other. Given the spatial distribution of the attachment point of the strands, CN helps us understand the density of a web, where a CN of 3 or higher implies a dense web. Pore size is simply the space enclosed by silk strands. Mean pore size is the average size of the nonoverlapping pores or mesh size of the web. Hence, denser webs will have smaller pore size. Pore size was calculated in a fixed region of the web (125 × 125 pixels for single spiders; 300 × 300 pixels for the remaining group sizes) below the retreat. To understand the temporal development of silk distribution through the web, the image was divided into 4096 (64 × 64) grids and the length of silk in each grid was calculated individually. Density of silk, measured at a radial distance of 0.25 and 0.75 m from the retreat, was analysed. These results are represented as contour plots using the plot3D package (Soetaert, 2013).

Low- and high-threshold grey scale intensity values of 220 and 230 were used in the image analysis as it allowed accurate recovery of the web structure. Total length of silk was measured from the number of connected pixels in the skeletonized image. We did not differentiate between scaffolding dragline silk and cribellate silk strands while calculating the total length of silk. Cribellate silk strands were often laid over scaffolding silk, making it impossible to differentiate between them. Additionally, we also calculated per capita silk investment, where the total silk invested was

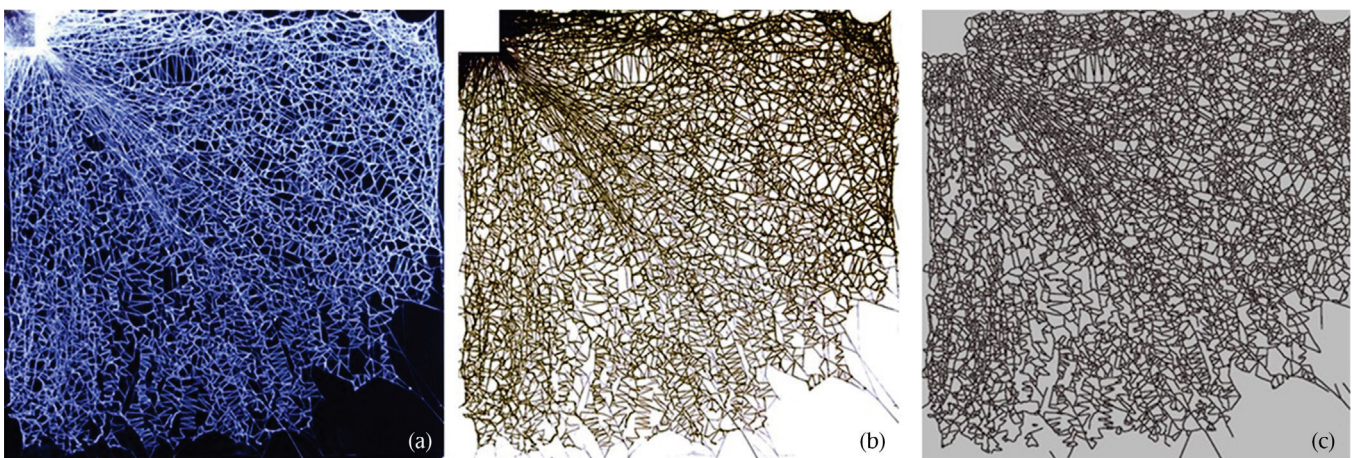


Figure 2. Image analysis of the web of social spider *S. sarsinorum*: (a) raw image of a 25-spider group, (b) negative of the raw image and (c) skeletonized image where black lines are silk strands. The retreat (nest) is present at the top left corner in the raw image and is manually edited out in the negative and skeletonized images to avoid spurious silk detection during image analyses.

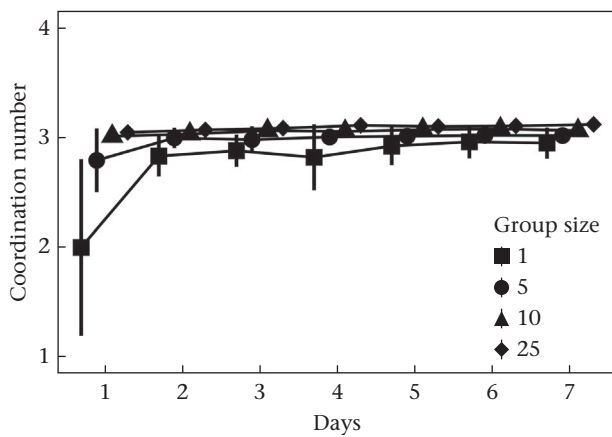


Figure 3. Mean (\pm SD) coordination number across group sizes over time.

normalized with respect to group size. The methods used to analyse web parameters such as CN, pore size, density of silk, length of silk and per capita silk are reported in Table 2.

Statistical Analysis

To examine the effect of group size on the total quantity of silk (length) and the per capita silk investment, we used nparLD (nonparametric analysis of longitudinal data, Noguchi 2012). Effect of group size on web geometrical parameters such as coordination number and pore area were also analysed using nparLD. Although the figures are plotted for 7 days, we analysed all the silk investment for 1–5 days as beyond this the webs built by the 25-spider group size showed reduced growth due to spatial limitation of the experimental frame provided. During a fixed time, spiders in a large group are more likely to fill up a fixed space than spiders in a small group. Thus CN, pore size, length of silk and per capita silk investment were plotted for 7 days but analysed for the first 5 days. Figures and tables for the entire data set up to 10 days are provided in the Appendix (Figs A1, A2, Table A1). To analyse the total length of silk and per capita silk investment for the entire length of the experiment, we used liner mixed models.

Since spider weights can change over time, we examined weight change in individuals during the experiment in relation to cephalothorax width (size), colony identity, group size and time using linear mixed models.

All statistical analyses were performed using R 3.2.0 (R Core Team, 2015) and plots were made using the ggplot2 package (Wickham, 2009).

RESULTS

Group Size and Web Geometry

Mean CN for groups of 1, 5, 10 and 25 spiders was 2.94, 3.01, 3.06 and 3.11, respectively. In the single spider and 5-spider groups, CN

increased in the first 3 days and plateaued thereafter. The CN of groups of 10 and 25 spiders remained constant from Day 1 onwards (Fig. 3). Although there were slight changes in CN, group size or time did not have a significant effect on it (Table 3). Across group sizes, the mean pore size for a fixed region near the retreat initially decreased but stabilized over time (Fig. 4). The unusually large pore size seen in the 5-spider group is primarily due to a single colony in which spiders explored empty areas of the frame to lay silk. As a result, a single strand laid across an empty frame appears to be a large pore. Group size did not have a significant effect on pore size. However, time significantly influenced pore size of webs (Table 3).

Dynamics of Web Structure

Fig. 5 presents the spatial distribution of the silk invested in the experimental frame during the study. At the end of the first day, a moderate amount of silk was invested in the region around the retreat regardless of the group size. In 10- and 25-spider groups as well as over time, the distribution of silk in the frame radiated away from the retreat. In these group sizes, the frame space was initially rapidly filled (i.e. in the first 5 days), after which the quantity of silk produced declined daily and the total quantity of silk invested remained largely constant over the remaining days. Temporal change in the density of silk for different group sizes was represented as a contour map which is informative in understanding the distribution and development of silk invested across the web (see Supplementary movies). These maps indicate that the density was highest near the retreat and declined with radial distance. Specifically, mean density \pm SE at 0.25 m from the retreat for groups of 1, 5, 10 and 25 spiders was 0.002 ± 0.001 , 0.01 ± 0.004 , 0.02 ± 0.003 and 0.03 ± 0.001 m/grid, respectively. Density declined drastically with radial distance from the retreat across all group sizes at 0.75 m from the retreat ($7.46 \times 10^{-5} \pm 4.86 \times 10^{-5}$, 0.001 ± 0.0006 , 0.004 ± 0.001 , 0.01 ± 0.002 m/grid for groups of 1, 5, 10 and 25 spiders, respectively).

Group Size and Total Silk Investment

Group size and the time elapsed had a significant influence on the total length of silk invested on the web (Fig. 6, Table 3). At the end of 5 days, a single spider on average produced 4.72 ± 4.58 m (mean \pm SD) of silk and the 25-spider group produced an average of 88.45 ± 13.40 m of silk. The increase in total silk investment was roughly linear for the first 4–5 days for all group sizes but the slope of the line was shallow for single spiders. Further analysis of the entire data set also showed consistent results for total silk investment (Fig. A1).

Group Size and per Capita Silk Investment

Per capita silk investment as a function of group size is presented in Fig. 7. Interestingly, per capita silk investment of spiders was similar across group sizes, suggesting that, on average, larger groups did not show reduced investment in silk (Table 3). Across group sizes, the mean (\pm SD) per capita silk produced per day was 0.75 ± 0.41 m.

Table 2
Web parameters and mode of measurement

Web parameter	Mode of measurement
Coordination number (CN)	$2 \times$ total number of edges/total number of nodes
Pore size (mesh size)	Space enclosed by silk strands. Measured at a fixed region below the retreat
Silk length	Length of silk measured as number of connected pixels in a skeletonized image
Silk density	Total length of silk in a fixed area. Measured at different radial distances from the retreat
Per capita silk	Total silk invested divided by group size

Table 3

Nonparametric statistic for coordination number, pore size, length of silk and per capita silk investment

		Anova-type test statistic (nparLD)	df	P
Coordination number	Group size	3.01	1	0.082
	Number of days	2.86	1.96	0.058
Pore size	Group size*day	2.86	1.96	0.058
	Group size	0.18	1.83	0.82
	Number of days	3.59	3.46	0.01
Length of silk	Group size*day	1.25	5.58	0.28
	Group size	30.88	2.75	1.59×10^{-18}
	Number of days	50.42	1.79	1.54×10^{-20}
Per capita silk investment	Group size*day	0.88	3.83	0.47
	Group size	0.64	2.20	0.54
	Number of days	0.56	2.55	0.61
	Group size*day	0.68	4.54	0.63

Median values for CN and group size were used, as the distribution within the web was not normal.

This was also found to be true for the whole data set (up to 10 days; Fig. A2) Furthermore, although spiders lost weight (possibly due to desiccation) over the experiment (mean \pm SD = 15.8 ± 5.9 mg), the weight loss was similar within and across group sizes (Table A1), also suggesting a parallel line of evidence for similar per capita silk investment by spiders across group sizes.

DISCUSSION

We studied the web architecture and dynamics of silk investment in the social spider *S. sarasinorum*. Single layered sheet webs of *S. sarasinorum* built on thin experimental frames were similar to those built on fences, and easily lend themselves to high-resolution image analysis. Webs of *S. sarasinorum* are built within days and are maintained over several weeks to months (T. Beleyur, D. Uma & H. Somanathan, personal observation). Our study presents the dynamics of web building especially highlighting the distribution of silk over the first few days when most of the web is constructed. Our results suggest that beyond a particular threshold, spiders do not keep adding silk in a given region, regardless of group size. Furthermore, spiders in larger groups invested more silk compared to smaller groups, but per capita silk investment did not decrease in larger groups.

In our experiments, CN and pore size remained the same across group sizes (Fig. 3). CN provides an understanding of web density; a highly dense web (less porous) can be thought of as being more stable to any disturbance from prey interception or natural forces such as wind or rain. That CN did not change over time suggests that spiders do not continue adding new silk strands beyond a threshold for different group sizes. This pattern is also reiterated with respect to mean pore size (Fig. 4). Pore size of the web, which was calculated for a region below the retreat where silk density was highest, was similar across group sizes, suggesting spiders do not conserve silk over the range of group sizes used in our study.

Functionality of the web in capturing prey is determined by both web architecture and silk biomechanics, which are in turn shaped by ecological (e.g. prey ecology, spider behaviour, variability in microhabitat) and evolutionary factors (e.g. silk protein diversification; Harmer et al., 2011). Blackledge and Eliaison (2007) and Sensenig, Kelly, Lorentz, Leshner, and Blackledge (2013) suggested that denser webs may be both efficient and stable since they have a narrow mesh width, which is likely to retain larger prey that offer significantly more nourishment than smaller prey. Additionally, owing to their design and molecular structure, orb webs are stable under both localized disturbance (for example insects flying into the web) and more widespread disturbance (for example high

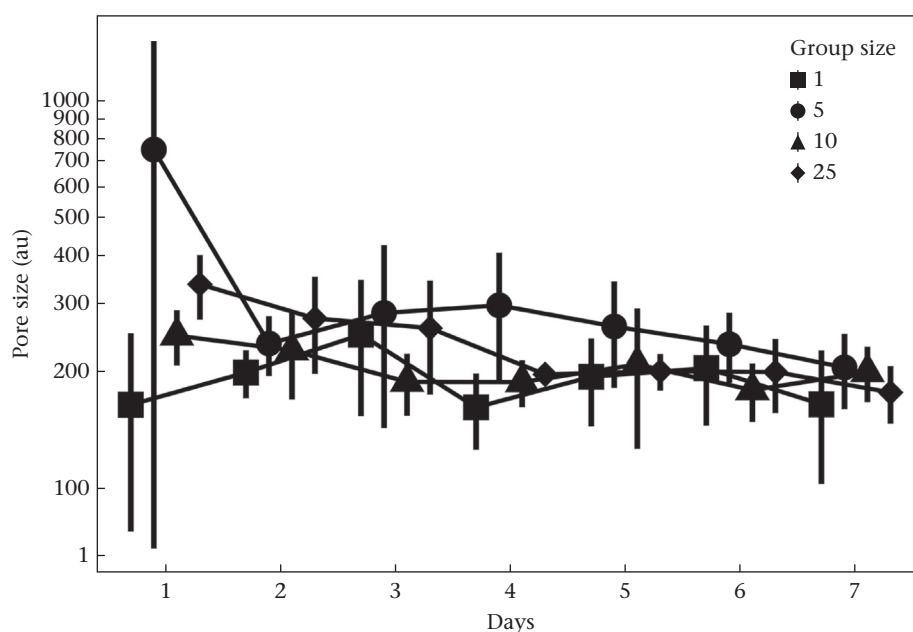


Figure 4. Log mean pore size (\pm SD, measured in pixels; au: arbitrary units) within a fixed region across group sizes.

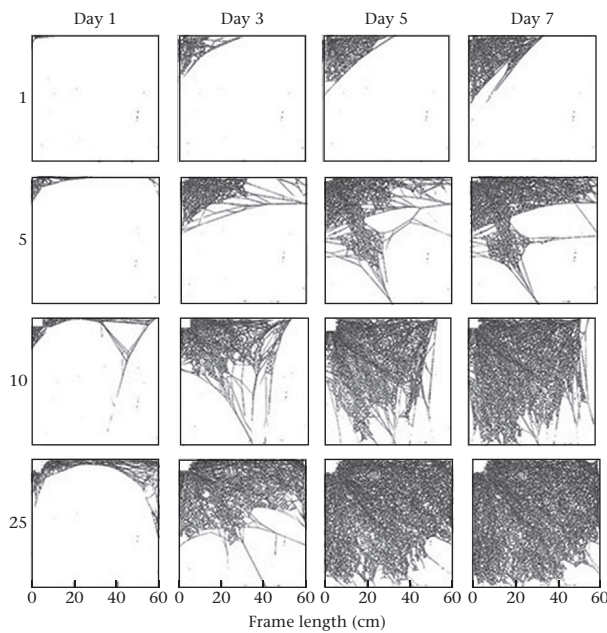


Figure 5. Spatiotemporal dynamics of the web: progression of web architecture over 1–7 days across representative groups of 1–25 spiders. Retreats (nests) are seen as a white square on the top left corner of the 60×60 cm frame on which spiders were allowed to construct webs.

winds; Cranford, Tarakanova, Pugno, & Buehler, 2012). Similar to orb webs, denser social spider webs may be more likely to capture larger prey and to be stable, as any damage from prey impact can be localized to small sections of the web, while the rest of the web remains functional. Although we did not directly measure stability of the webs, parameters of web geometry such as CN and pore size that we calculated help us understand density and, indirectly, the stability of the web.

As expected, we obtained a positive trend between the number of spiders in a group and the amount of silk invested on the web (Fig. 6). Surprisingly, however, and contrary to the silk conservation hypothesis, the mean per capita investment in silk did not decline in larger group sizes. Instead, it remained similar for groups of 1–25 in our study (Fig. 7), although there was variation between colonies within a group size. An additional important observation that we highlight here is that weight loss of individuals across group sizes was similar over the experimental period, suggesting similar levels

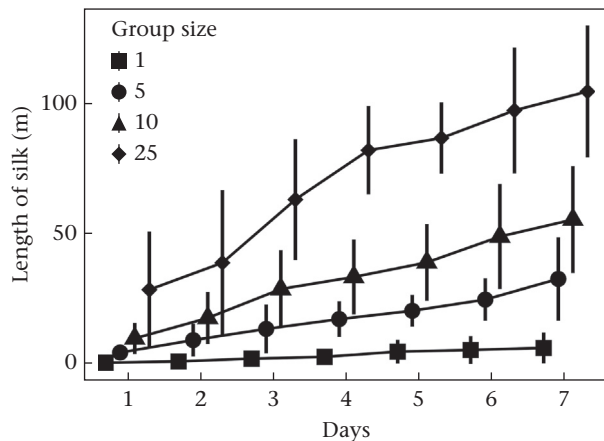


Figure 6. Mean amount of silk (m) laid on experimental frames (\pm SD) across group sizes over time.

of silk investment by them. Since the spiders were not fed or sprayed with water for the duration of the experiment, we can reasonably conclude that individuals must have been in the same state of hunger or satiation.

In nature, prey availability is likely to be sporadic and individuals in a colony may differ in their feeding opportunities (Beleyur, Bellur, & Somanathan, 2015). This could lead to differences in the hunger state of individuals with implications for their investment in silk. However, under the controlled conditions of our experiments, wherein spiders were maintained in the same state, group size did not appear to affect per capita silk investment. The only other laboratory study that examined the effect of group size on web architecture in the social spider *Mallos gregalis* found that larger groups built denser and more complex webs (Tietjen, 1986). In the same study, the relationship between silk density (measured as pixels) and colony size was nonlinear over 5 days. There are several important methodological differences between that study and ours. First, the web of *M. gregalis* is connected to multiple silk-lined tunnels where the spiders rest. Silk density of these tunnels was included in that study, whereas we excluded silk investment of *S. sarasinorum* in or on the retreat in our analysis. Second, all individuals of *M. gregalis* used in experiments were sourced from a single large colony which was further split to form several experimental colonies of different sizes. In contrast, we retained the colony identity of individuals when we formed our experimental groups. Third, *M. gregalis* were housed in small 50 cc petri dishes which could have limited the spatial extent and complexity of webs that spiders built, whereas we provided larger 60×60 cm frames. Thus, a direct comparison cannot be made with our results.

Silk conservation is an often-suggested hypothesis to explain the benefits of group living, but it is important to recognize that there are other advantages of sociality (for example ability to capture larger or more prey; protection from predators; better survival rates and access to mates; Nentwig 1985, Riechert, 1985, Uetz, 1989, Henschel, 1998, Avilés, 1997, bib_Powers_and_Avilés_2007 Powers & Avilés, 2007). Earlier studies in *S. sarasinorum* have shown all or most individuals within colonies engaged in web-building behaviour (Settepani et al., 2013; Beleyur et al., 2015). Silk is nevertheless energetically expensive, and some spiders such as the cooperative agelenid spiders (Riechert, 1985) and pholcid spiderlings (Jakob, 1991) are known to save silk. Individuals' silk investment is not known in social spiders; our study provides estimates of per capita investment as it was not possible to quantify how much silk was produced by each individual or to determine interindividual differences in the amount of silk expended. Web building occurs

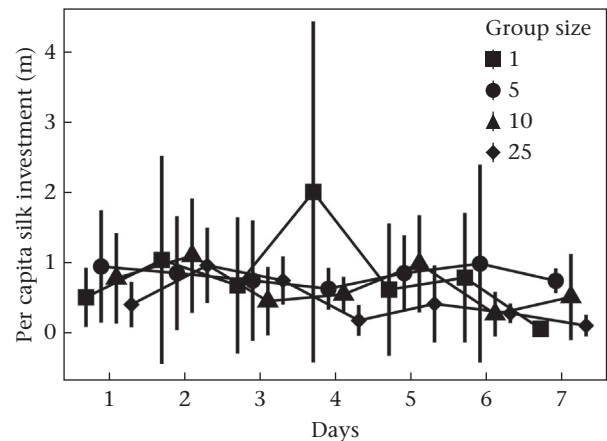


Figure 7. Mean daily per capita amount of silk (m) invested (\pm SD) across group sizes over time.

sporadically from dusk to dawn in a staggered manner, and tracking different individuals' contribution to web building over multiple days was not possible in this study. It is essential for future work to test the silk conservation hypothesis in an ecological context.

In conclusion, within the framework of our study we were unable to find support for the silk conservation hypothesis for the evolution and maintenance of spider sociality. Even in the largest experimental group size of 25 individuals, per capita savings in silk investment were not observed. However, we cannot rule out the possibility of silk conservation being applicable to even larger group sizes as social spiders often occur in much larger colonies (consisting of 100 or more individuals). We also obtained estimates for web geometric properties such as coordination number and pore size which were similar in small and medium-sized experimental groups. This suggests that new colonies founded by solitary dispersers (Parthasarathy & Somanathan, 2020) as well as medium-sized colonies develop certain characters of the web early during web construction. A functional web that is ready for use early on is critical for social spiders, which are sit-and-wait predators that depend on uncertain and unpredictable prey interception events, unlike more mobile stalk-and-chase predator species.

Author Contributions

TB, TM, HS and DU designed the experiment. TB & DU collected data. TB & SS analysed results. TB, TM, SS, HS, DU wrote the paper.

Data Availability

All data and code used to generate the analysis, results and figures in this paper are uploaded in the Zenodo repository <https://zenodo.org/record/4009461#.X1cwMdThXIU> and on GitHub <https://github.com/thejasvibr/stego-web-dynamics>.

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Supplementary Material

Supplementary material associated with this article can be found online

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Appendix

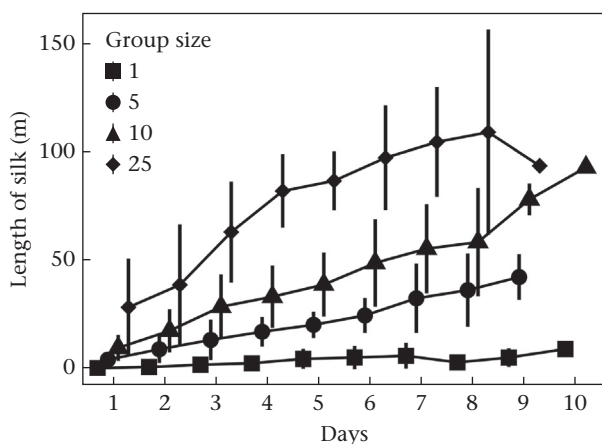


Figure A1. Mean amount of silk (m) laid on experimental frames (\pm SD) across group sizes for the full data set (10 days).

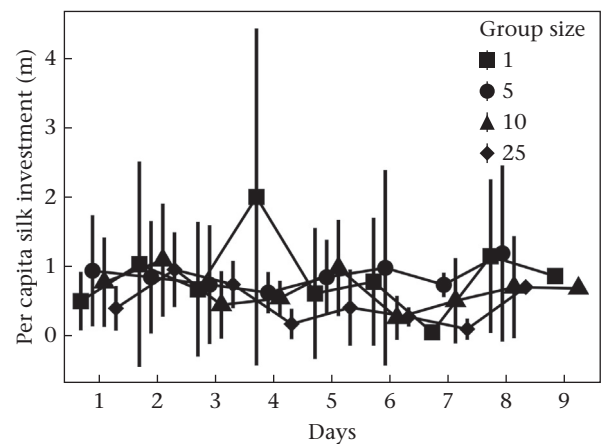


Figure A2. Mean daily per capita amount of silk (m) invested (\pm SD) across group sizes for the full data set (10 days).

Table A1
Effect of variables on weight loss

Variable	Mean	93% highest posterior density interval
Intercept	0.5	2.94–1.85
Standardized body condition	0.56	0.43–0.69
Weighing day	0.05	0.21–0.31
Group size 5	0.34	0.71–1.45
Group size 10	0.08	0.82–0.98
Group size 25	0.39	1.45–0.66

The linear mixed model run was with weight loss (mg) as the outcome variable. The predictors used were (1) standardized body condition, (2) weighing day and (3) group size. Group size was treated as a factor with group size 1 set to the reference group. Colony ID was set as a random intercept. Regressions were performed using the ‘lmer’ function in the ‘lme4’ package (Bates, Maechler, Bolker, & Walker, 2015). All fixed effects are reported with mean and 93% highest posterior density intervals. The mean and the highest posterior density interval of coefficients were estimated with 5000 simulations using noninformative priors through the ‘sim’ function in the ‘arm’ package (Gelman & Su, 2020). One standard deviation of body condition is 0.47 mg/mm.