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SHORT COMMUNICATION

Influence of prey availability on web-building in the social spider *Stegodyphus sarasinorum* (Araneae: Eresidae)

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Abstract. Spider webs are characteristic of a species, yet web architecture, the amount of silk laid, and silk mechanics are plastic at an individual level. These different web parameters are influenced by the spiders' own intrinsic state as well as biotic and abiotic conditions. When compared to satiated spiders, hungry spiders are known to build bigger webs, alter the mesh width of the web or increase the frequency of web-building. Although the influence of hunger on web architecture is known in solitary spiders, it has not been studied in social spiders. Here, we examine how prey availability affects the amount of web and cribellate silk laid in the social spider *Stegodyphus sarasinorum,* Karsch, 1892 (Eresidae). In a laboratory setup, we observed that unfed spiders invest more in web-building, compared to fed spiders. Unfed social spider colonies laid more silk, particularly cribellate silk, than fed colonies. Our results help to shed light on the plasticity of web architecture in social spiders with respect to changes in prey availability.

Keywords: Cribellate silk, hunger, collective behavior

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Sit and wait predators such as web-building spiders make excellent model organisms for studying foraging: the web facilitates prey capture, and web-building itself is a foraging decision influenced by spiders' own internal state and external factors (Foelix 2011; Scharf et al. 2011 and references therein). Web-building spiders can respond to these cues by altering the web size, different parameters of the web or relocating the web altogether.

Although the web is characteristic of a species, the web architecture, the amount of silk invested in the web, or the protein composition of the web is often plastic within the individuals of the same species (Boutry & Blamires 2013). Web architecture, i.e., geometry of the web and mechanical properties of individual silk strands, is influenced by both abiotic (humidity, wind etc), and biotic factors (spiders' own internal state, ontogeny, predation risk, etc.) (Foelix 2011; Herberstein & Tso 2011). Plasticity in web architecture is fairly well documented in solitary spider species. For example, the orb-weaving spiders *Argiope trifasciata* (Forsskål, 1775) (Araneidae) are known to adjust the mechanical properties of silk depending on the external environment, such as the height of the web from the ground (Garrido et al. 2002); *Nephila pilipes* (Fabricius, 1793) (Araneidae) alter their mesh size, thickness and stiffness of the silk strands depending on the prey type (Tso et al. 2005); the cob web spiders *Parasteatoda tepidariorum* (CL Koch, 1841) (Theridiidae) altered the thickness and stiffness of their supporting threads based on prey type (Boutry & Blackledge 2008). Internal state and body condition of spiders also influence other web parameters—hungry orb-weaving spiders, *Araneus diadematus* Clerck, 1757 (Araneidae) increase web-building frequency and adjust the mesh width and area covered by sticky web compared to satiated spiders (Vollrath & Samu 1997). Fed black widow spiders, *Latrodectus hesperus* Chamberlin & Ivie, 1935 (Theridiidae), reallocated their silk from gum-foot threads that help in prey capture to supportive threads that enhance protection (Blackledge & Zevenbergen 2007). The satiated sub-social desert spiders, *Stegodyphus lineatus* (Latreille, 1817) (Eresidae), build smaller webs compared to hungry spiders (Pasquet et al. 1999). Although there is considerable information about the effect of prey availability and the internal state of solitary spiders on web parameters, little is known about their effect on the webs of permanently social spiders.

Sociality in spiders is rare, as only around 25 out of 48,918 known species of spiders are permanently social (Aviles 1997; Lubin & Bilde 2007). Group sizes in social spiders range from tens to hundreds of individuals, and females exhibit collective behavior in web-construction, prey capture and brood care (Lubin & Bilde 2007). Unlike most orb webs, social spider webs are built over many days, and are regularly repaired and maintained by the collective effort of multiple individuals. How prey availability influences web architecture is very interesting as the web is not built by one spider, but by collective behavior of multiple individuals in a colony. The amount and type of silk contributed by a spider in a colony may depend on its own internal state, as well as relative contributions made by others in the colony. For example, some individuals may capture prey more than others (Settepani et al. 2013; Beleyur et al. 2015), resulting in spiders with different hunger levels even within a colony. Hungry individuals may contribute to web-building much more than satiated individuals within a colony.

In this study, we examine the influence of prey availability on the web architecture of the social spider *Stegodyphus sarasinorum* Karsch, 1892 (Eresidae) in a controlled lab setup. *Stegodyphus sarasinorum* build 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 at multiple points (Fig. 1). The capture web is made up of dragline silk that forms structural support and highly coiled cribellate silk that is laid in a zigzag pattern to facilitate prey capture. Cribellate silk is composite structure that consists of larger axial fibers and nano-scale cribellate fibers (Vollrath 2006). We asked if the density of the web and incorporation of cribellate silk strands change with prey availability. Based on what is seen in solitary spiders, we hypothesized that unfed spiders would spin more web and have more cribellate silk compared to well-fed spiders.

Stegodyphus sarasinorum colonies ($n = 19$) consisting of adult spiders were collected from Sarjapur area, Bengaluru, India in May–June 2018 and 2019. From these, spiders were randomly divided to form 33 small-sized colonies of 13 female spiders of comparable weights (0.1 ± 0.06 g). Thus, individuals that formed new colonies did not come from the same original colony. Each colony was provided with adequate nest material (silk and debris) and was attached to the corner of a thin square metallic frame (0.6 m^2, Fig. 2). The frames

Figure 1.—A dense aggregation of colonies of the social spider *Stegodyphus sarasinorum* in their natural habitat in Sarjapur, Bangalore. Red circles indicate nests/retreats made of dense silk within which a colony resides. Nests are built on branches and are connected to multiple sheet webs.

Figure 2.—Social spider colonies attached on thin metal frames hung by ropes inside a laboratory setup. Spiders readily build two-dimensional webs on these metal frames that can be easily photographed.

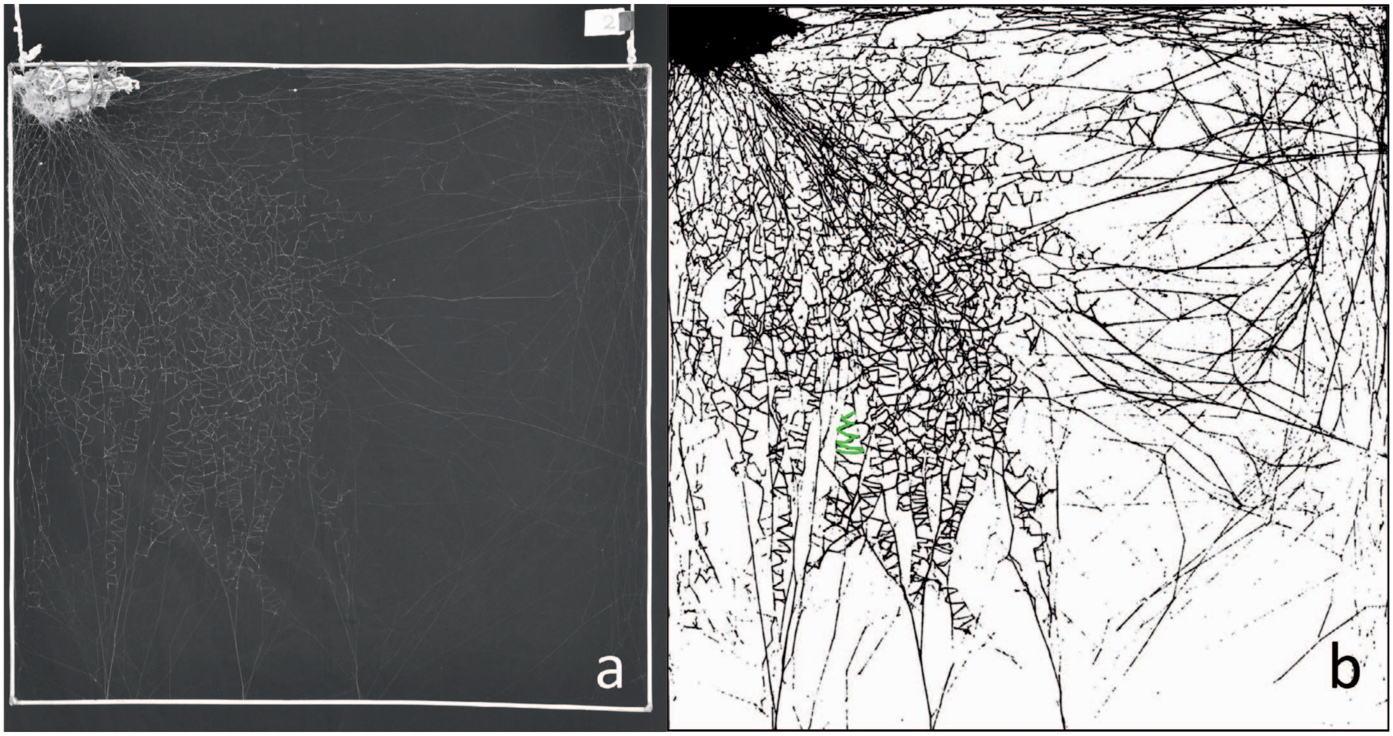

Figure 3.—(a) Raw image of unfed colony on day 7. (b) Negative of the same raw image with cribellate silk highlighted in green. The black area on the left corner of the image is the retreat.

were suspended by strings from a rope railing inside a room with natural lighting. To minimize the number of spiders that put out silken threads to move away from their colonies, all windows and doors were kept closed to block out any drafts. To prevent spiders from escaping from the rope railings, petroleum jelly was applied to the string tied to the frame. Webs were misted daily with water to provide moisture to the spiders.

We examined the influence of prey availability on web-building by performing the following experiment: to ensure that all the spiders had similar hunger levels in the beginning, we first fed each colony with 8–9 field-caught grasshoppers or crickets (2–3.5cm), until no spiders came out to hunt. After this, the colonies were randomly divided into 2 treatment groups: 'fed' (15 colonies) and 'unfed' (18 colonies). We continued feeding the 'fed' group for a week with one large grasshopper or cricket per colony/per day and did not feed the 'unfed' group for a week. At the end of this treatment period, we completely removed the existing web, and allowed the spiders to build a new web for the next 7 days.

Each frame containing a web was photographed against a black background daily for the 7 days of the treatment period using a DSLR camera (Nikon D7200 camera with a AF-S Micro NIKKOR 60mm f/2.8G ED lens) from a fixed distance (3.35m), and fixed settings that captured the entire frame. Monochrome images with low ISO and high clarity were taken (Fig. 3a). Images were analysed using ImageJ (version: 1.8.0_66). The original image was inverted and converted into an 8-bit image (Fig. 3b). The top 5 cm of the image that included the retreat was excluded from further analysis to facilitate thresholding. Each image was converted into a binary image using a manually set threshold. The image was then 'skeletonized' using the in-built ImageJ function. Skeletonization allowed us to preserve the most important features of the image such as the topology, while reducing the noise in the image. In the skeletonized image, the total amount of silk laid down was measured by the number of black pixels against the white background. Total number of black pixels divided by total number of pixels in the image was used as a proxy for web density.

Preliminary analysis showed that the average distance between two zigzag cribellate strands made by adult spiders were ~1 cm. To measure the area occupied by cribellate silk, a 1cm^2 grid was overlaid on the image of the web. Any grid square that contained 1 or more strands of cribellate silk was manually counted and used as a proxy for area occupied by cribellate strands. The total amount of silk and that of cribellate strands of fed and unfed colonies on the 7th day were compared using the Wilcox rank sum test. All statistical analysis was conducted on 'R' (R Core Team 2017; version: 1.0.153).

Both unfed and fed spider colonies built a web over the course of a week. Spiders in the unfed colonies had denser webs and laid 1.43 times more silk than the fed colonies by the end of our experiment, although the difference was not significant (Fig. 4; Wilcoxon rank sum $W = 92$, $P = 0.125$). The total amount of silk includes both the dragline, as well as cribellate silk, as these could not be differentiated in the image analysis.

By measuring the grids covered by cribellate strands, our results clearly show that unfed spider colonies incorporated 2.38 times more cribellate strands in their webs compared to fed colonies over time (Fig. 5; Wilcoxon rank sum $W = 247$, $P = 1.083\text{x}10^{-5}$).

Social spider webs are built collectively and are maintained over several months. Understanding how the web geometry and architecture changes with foraging needs of spiders is an interesting problem, as it is dependent on not just one individual, but by collective conditions of multiple individuals. In our controlled study, we manipulated hunger levels of *S. sarasinorum* spiders to examine the silk investment of starved and well-fed spiders. Even in just one week of a feeding-starving regime, unfed spider colonies invested more in web building, particularly in cribellate silk, compared to the fed spider colonies. Solitary web-building species are known to alter their web architecture, geometry, and silk protein in response to external conditions such as prey availability, predator presence or reproduc-

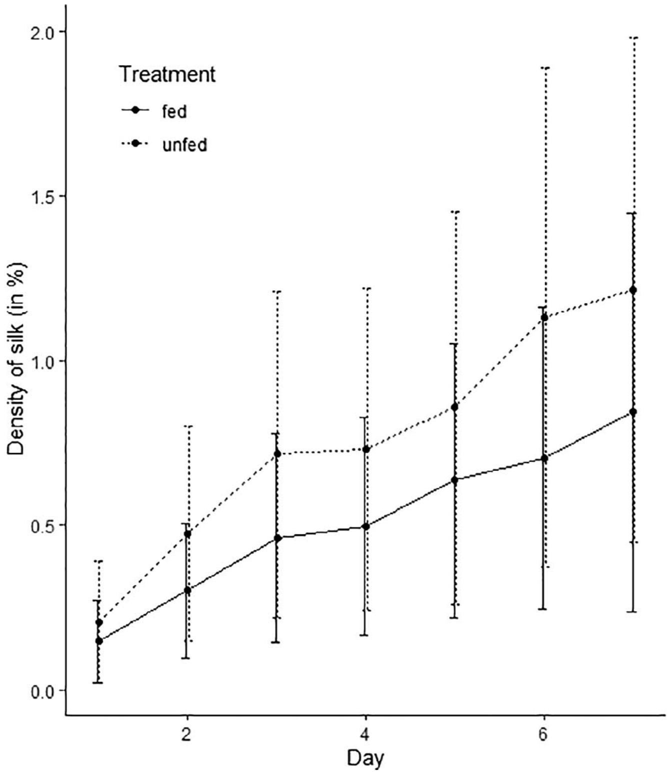

Figure 4.—Density of silk laid over time by unfed (dotted line) and fed colonies (solid line). Vertical bars show standard deviations.

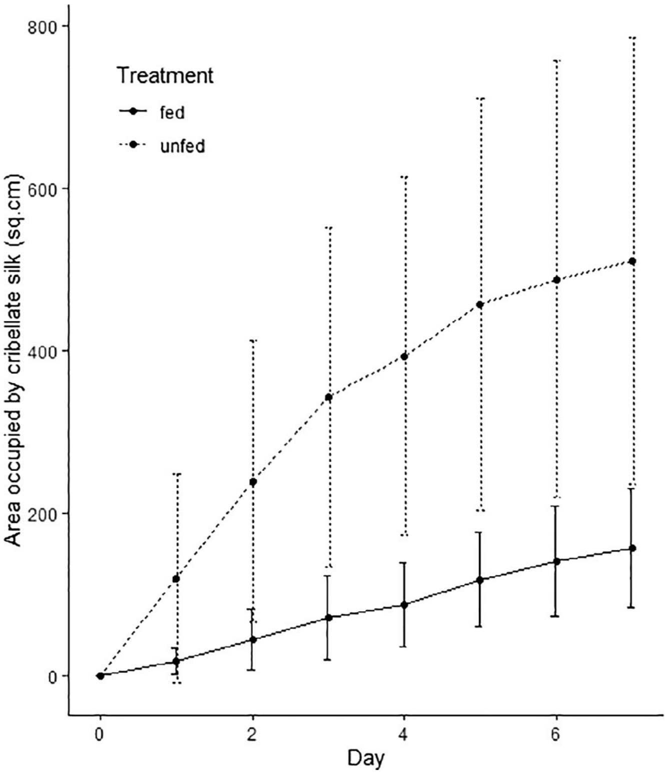

Figure 5.—Area occupied by cribellate silk strands in unfed (dotted line)and fed spider colonies (solid line). Vertical bars show standard deviations.

tion (Rayor & Uetz 1990; Sherman 1994; Vollrath & Samu 1997; Tso et al. 2005; Blackledge & Zevenbergen 2007; Blamires et al. 2010). Prey availability influenced both time to build/renew web, and total size of the web in the sub-social spider *S. lineatus* (Pasquet et al. 1999). As hypothesized, we showed that *S. sarasinorum* individuals in starved colonies invested in more cribellate silk than those in fed colonies. However, we did not find any difference in the total amount of silk laid (dragline and cribellate) between the fed and unfed colonies.

The density of silk laid by fed spiders was not significantly different from that of unfed spider colonies (Fig. 4). This result could be attributed to the fact that the measurement of total silk could not differentiate between cribellate and dragline silk. More importantly, deduced from the photos (not shown here), fed spider colonies had many more dragline strands, and very little cribellate silk in the first few days of the experiment. Towards the end of the experiment, fed spiders had some amount of cribellate strands, suggesting that hunger may induce incorporation of the cribellate silk. Alternatively, individuals within a colony may invest in different amounts of dragline and cribellate silk. Such unequal investment may be influenced by their own internal state, and/or colony needs. In our experimental colonies, we had all fed or all starved spider groups. However, in nature, the proportion of starved-satiated spiders within a colony may vary.

Starved spiders clearly invested in more amount of cribellate silk than well fed spiders (Fig. 5). Cribellate silk is energetically expensive and time consuming to produce (Pasquet et al. 1999; Vollrath 2006), yet starved spiders spun more cribellate strands. Solitary spiders are known to move foraging sites, fine-tune different components of their web, and even change silk protein composition based on changes in their internal state and prey availability (Higgins 1995; Vollrath & Samu 1997; Tso et al. 2005; Mayntz et al. 2009). Some spiders are also known to reallocate energy to reproduction: *Larinioides cornutus* (Clerck, 1757) (Araneidae) increased thread length and web area when prey was low, but built smaller webs, and relocated energy to egg production when prey was abundant. (Sherman 1994). Silk can be used also to protect egg sacs, line the interiors of the colony, or in post-mating dispersal, to start a new colony (Parthasarathy & Somanathan 2018). Furthermore, in the fed group, we observed some amount of cribellate silk towards the end of the experiment, suggesting that foraging responses of these spiders are indeed dynamic, reflecting intra-individual differences in silk investment.

Individual spiders within a colony may have different internal states due to a number of reasons: individuals may differ in their feeding history prior to group establishment; their molting times may be different; since our experimental groups were formed by mixing individuals from multiple colonies, individuals' familiarity with neighbours (and hence, response) may also vary. We examined the changes in dragline and cribellate silk up to a week after altering prey availability. In nature, *S. sarasinorum* webs are maintained for several months, and food availability is not uniform. Future work should track these dynamic changes in web architecture over long periods of time.

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