

Ontogenetic and sexual differences in exploration and web construction in the spider *Physocyclus globosus* (Araneae: Pholcidae)

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Summary

Differences in reproductive interests between the sexes can affect web construction behaviour, which can vary across ontogeny. This study tested whether exploration and web building behaviour varies with age and sex in *Physocyclus globosus* (Pholcidae), a spider that weaves an irregular, domed sheet web with a tangle above. Spiders were placed in cages with four interconnected chambers. Most fifth instar juveniles and adult females (but only half adult males) wove a sheet in only one chamber. Adult females built the denser sheets. Although adults attached more threads to the walls than juveniles, the latter attached more new threads there over time. Juveniles laid 91% of their threads in the sheet chamber, compared to adult females (55%) and adult males (41%). All spiders (especially adult males) attached many exploration threads throughout 18 days, suggesting repeated abandonments of the web. The reduced rate of exploration by juveniles suggests that they establish webs more quickly to increase the possibility of prey capture, intense foraging, and rapid growth. Exploration or web construction did not differ between the sexes in juveniles. Adult males explored more often, perhaps looking for mates, while adult females modified their web structure after establishing, perhaps to improve prey capture rates.

Introduction

Differences in the costs of gametes (anisogamy) in males and females explain differences not only in the sexual secondary characters, but also in behaviour and physiological activity (Andersson 1994). In spiders sexual size dimorphism is common in many families, and size differences between males and females can reach up to three orders of magnitude (Foelix 1996). Adult males and females also differ in behaviour (Walker & Rypstra 2002; Li & Kuan 2006). Adult female spiders are generally less mobile and more likely to stay in the same place for longer periods than males. Males are more mobile, frequently do not build webs after maturity, and feed less intensively than females (Foelix 1996; Li & Kuan 2006).

In families with little size dimorphism (such as Pholcidae) males continue building webs and hunting after maturity (Eberhard & Briceño 1983; Kirchner 1986; Edwards 2011). Adult pholcid females receive adult males, copulate, and oviposit in the same web; and spiderlings even stay a few days in the maternal web after emerging (Jakob 1991; Eberhard 1992a). In a population of *Physocyclus globosus* (Taczanowski, 1874) inhabiting large, underground tunnels, adult females stayed in the same site for several (2–8) days, but adult males stayed in the web of adult females less than two days, and one adult male moved 50–60 m (Eberhard 1992a). In *Pholcus manueli* (Gertsch, 1937) a high dispersal of adult males and adult females in the first 24 hours was found when they were released at a new site (Edwards 2011).

Both males and females dispersed in the same proportion, especially when the sex ratio of the population was biased toward males; and the density of individuals had no effect (Edwards 2011).

During exploration, an animal leaves its retreat, nest or burrow, ventures forth, and walks further from a central place, acquiring a cognitive map of the surrounding objects or the environment (Shettleworth 2010). Exploration of an environment and web construction differ during the ontogeny of some spider species. This behavioural shift between juveniles and adults may be due to previous experience (Shettleworth 2010), the costs of finding another appropriate site and building another web (Tanaka 1989; Switzer 1993) in terms of energy and nutrients to attach silk relative to body size (Foelix 1996), or a delayed dispersal from the maternal web in juveniles (Jakob 1994). Traditionally, spider juveniles are thought to behave similarly in their foraging and web construction patterns between sexes until they reach sexual maturity (Foelix 1996). However, behavioural differences have been found between male and female juvenile spiders (Singer & Riechert 1994; Persons 1999). In the pholcid *Pholcus phalangioides* (Fuesslin, 1775), newly emerged juvenile males were active for a longer time than female juveniles. Also, juvenile females ate more prey than juvenile males when prey was offered daily (Hoefler *et al.* 2010). These authors suggested that males disperse more to avoid inbreeding and to increase the number of females with which they can mate in the future. I consider this unlikely, because newly emerged spiderlings would aim to feed on as many prey as possible, and differences in reproductive behaviours would not necessarily affect their decisions prior maturity. Hence, I decided to look for behavioural differences between sexes and juveniles of another pholcid, *Physocyclus globosus*. I did so by analysing exploration and web construction, which may be different between sexes in adults, in a way that allowed me to determine gender differences in behaviour among juveniles.

The web of *P. globosus* is an irregular and concave dome-shaped sheet that is approximately horizontal, with a tangle of abundant threads attached to the substrate, that are mostly above the sheet (similar to a *Modisimus* species; Eberhard 1992b). Webs occur in man-made structures such as houses, buildings, markets, and even pipes and tunnels (Eberhard 1992a; Huber 1997; Peretti *et al.* 2006). Webs are often built in the intersections between walls and ceilings, as well as in gaps between furniture and walls (González 2007).

Little is known about web construction behaviour in pholcids. Initially, *Modisimus guatuso* Huber, 1998 attaches threads to the substrate forming a web skeleton, which is afterwards extended and filled, and the sheet is completed by adding more lines (Eberhard 1992b). Some pholcids build gumfoot threads in the substrate (Japyassú & Macagnan 2004). The web of *P. globosus* captures both walking and flying prey (Eberhard 1992a).

Most studies (Eberhard 2007; Herberstein & Tso 2011) compared finished webs (mostly orb webs, and mostly of mature females). However, pholcids and other sheet-weaving spiders keep adding new lines to the substrate and threads with glue drops in the sheet over time, even after the sheet is already functional (Pholcidae: Kirchner 1986; Japyassú & Macagnan 2004; Theridiidae: Blackledge &

Zevenbergen 2007; Agelenidae: Rojas 2011). To my knowledge, no previous study has addressed the changes in web structure over several days between juveniles, adult females, and adult males. Since sex and age affect behaviour, investigating both factors would elucidate the plasticity of spiders in exploration and web construction during different life stages in the two sexes.

I tested the hypothesis that the exploration of an environment and web construction is associated with age and sex in *P. globosus*. This hypothesis predicted that juveniles would explore less than adults because juveniles would aim to establish quickly and build a web to capture prey and mature faster. Additionally, I tested exploration and web structure change throughout 18 days, reflecting a continuous process in expanding the web and maintaining it. Also, differences were expected in the exploration and web construction between sexes in adults, but not in juveniles. Adult females were predicted to be more sedentary than adult males, while juvenile males or juvenile females were not expected to differ, as both would aim to feed and grow. Additionally, I asked whether the spiders would choose to build their sheets in large or small spaces when both options were provided.

Material and methods

Adult males and adult females were collected from March 2010 to June 2011 on buildings of the campus of the Universidad de Costa Rica in San José, Costa Rica (84°03'N 9°56'W; 1160 m a.s.l.). I kept adult spiders in round plastic containers (7 cm upper diameter, 5 cm base diameter and 14 cm height), under laboratory conditions (mean of 20°C and 80% relative humidity) and fed them once a week with a stingless bee (*Tetragonisca aungustula*; Meloponinae). I bred 33 pairs of adults to obtain juveniles and then reared them until the fifth instar (out of 7–9 instars) to perform observations. The juveniles were then reared to maturity to determine their sex. I used virgin and already mated adults, and some females that had already oviposited. Mating status was not distinguished, however, so it was not possible to test for possible effects of mating status. Specimens were deposited in the Museo de Zoología of the Escuela de Biología, Universidad de Costa Rica.

Cages and observations. Spiders were placed individually in one of 20 cages, made out of cardboard shoe boxes lined with black matte construction paper. The cages had a mean (± 1 SD) of 31.6 ± 1.3 cm long, 20.9 ± 1.2 cm wide and 11.6 ± 0.6 cm tall (Fig. 1A–C), with an average volume of 7650 ± 810 cm³. The cages were covered with a transparent plastic sheet, to which spiders seldom attached lines. Each cage was divided into four chambers by adding four cardboard walls (7 cm long, 12 cm wide and 0.5 cm thick). Two walls were placed in the middle of the narrow sides of the cage, and two on the wider sides, in which the position of the wall varied (Figs. 1A–C). Cages with design A had four chambers of the same size (Fig. 1A). Chambers were asymmetric in cages with design B, in which diagonally opposite corners had chambers of the same size (small or large chambers; Fig. 1B). One wall was at 70% and the other at 30% of the length of the wider side. Cages of design C had adjacent chambers of the same size, where both walls were at 70%

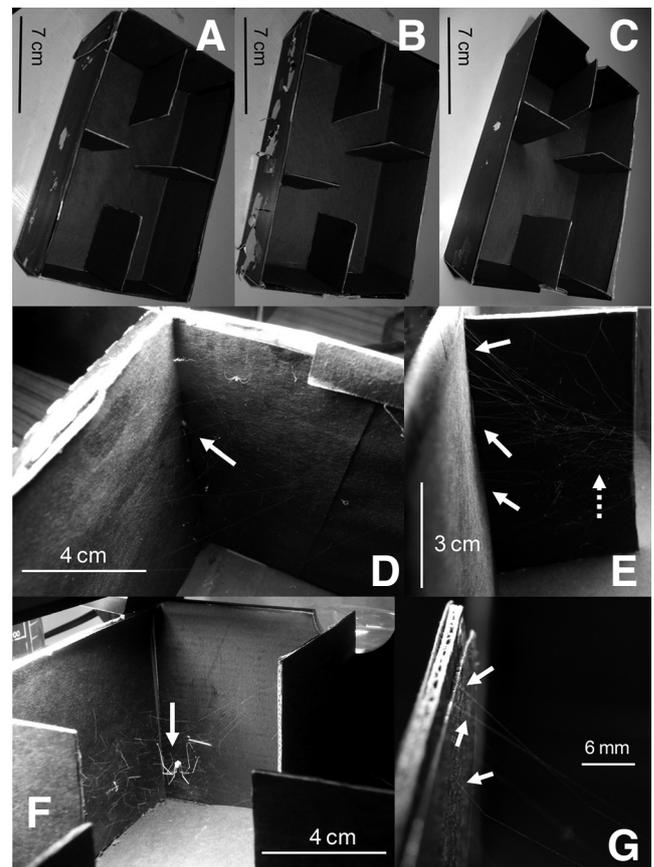


Fig. 1. *Phycocylus globosus* spiders and the cages where they built webs. **A** Symmetric chambers cage; **B** Asymmetric cage with chambers diagonally opposite; **C** Asymmetric cage with adjacent chambers the same size; **D** Female (arrow) resting in a corner prior to sheet construction; note threads attached to walls; **E** Threads attached to the wall (left, solid arrows) and a sheet (right, dashed arrow); **F** Female (arrow) resting upside down in centre of sheet web; **G** Close-up of threads attached to the wall (arrows).

of the wider side length (Fig. 1C). The small chambers had an area of 140 ± 15 cm², and large chambers were 193 ± 14 cm². This cage design allowed me to test whether spiders preferred spaces of certain sizes to build their sheets. The sizes of the chambers were designed to bracket web measurements in natural conditions: adult female ($n = 14$) sheet webs are 202 ± 25 cm², and sheet webs of unknown (but advanced) instar juveniles ($n = 13$) are 115 ± 54 cm². The cages were always stored on a bookshelf, hence two chambers were always next to the wall and the other two closer to the front of the shelf, having more exposure to artificial and natural light.

Measurements of exploration and web structure. Once a spider was placed in a cage, I observed it for five minutes. I observed three adult males and three adult females for 30 minutes, and then for five minutes every hour for six hours during the day. I recorded body and leg positions and movements, and the thread-attaching behaviour.

I analysed the exploration by counting the number of substrate threads the spider attached, which reflects its past activity. Specifically, it reflects the places where they have travelled, because pholcids and other spiders tend to leave a thread attached to the substrate where they have walked (Vollrath 1992; Eberhard 1992b). Every three days over 18 days I checked whether the spider had built a sheet. Also, I counted the number of threads attached (as seen in

figs. 12 & 13 of Schütt 1996) to the walls (most common; Fig. 1E,G) of each chamber of the cage and to the floor. For that purpose I lifted the plastic sheet and illuminated the cage with a mobile fluorescent light (following Blackledge & Zevenbergen 2007). Spiders eventually built a sheet web in one of the four chambers, and rested in it during the day (Fig. 1D,F). I named this the “sheet chamber”, in which most threads were added in the following days. Spiders also added threads in the other three chambers, but there was never a complete sheet web in another chamber. Thus, I considered all the threads outside the sheet chamber as exploration threads, and each set of new exploration threads to represent the abandonment of the sheet (at least once in those three days, which could underestimate the number of times the spider abandoned the sheet). These new threads represent a combination of the number of explorations outside the sheet, and the amount of movement made by the spider (assuming that spiders did not remove previous threads as they moved). To quantify exploration behaviour I calculated the proportion of threads in the sheet chamber over the total number of threads in the cage. A proportion of 1.0 meant that all threads were attached in the sheet chamber; if a spider placed equal number of threads in all four chambers the proportion was 0.25.

To measure the density of lines in the sheet, I placed four small, round, wooden sticks (2 mm in diameter, 14 cm long) on the top of each chamber, separated 3 cm from each other, and placed them at the same points each time a given sheet was measured, every three days. I observed directly from above and counted the number of silk lines that crossed each stick. I took the average number of lines crossing the four sticks in the sheet chamber as a measure of sheet density. Hereafter “web” refers only to the irregular group of threads attached to the substrate, mostly in the chambers other than the sheet chamber; and “sheet” refers to the dense, domed structure where spiders rested (Eberhard 1992b).

I made a preliminary test to determine whether feeding affected exploration behaviour, comparing adult males that were fed with a *T. aungustula* stingless bee *versus* unfed adult males ($n = 6$ and 5 , respectively). The number of threads and sheet density did not differ between the two groups. The fed adult males had 49.3 ± 9.7 threads attached in the sheet chamber, a proportion of those threads in the cage of 0.5 ± 0.1 , and sheet density of 20.7 ± 12.3 threads/cm. For unfed males, the corresponding numbers were: threads = 35.0 ± 15.4 , proportion = 0.5 ± 0.3 , sheet density = 16.4 ± 17.9 threads/cm (Mann-Whitney U comparisons $P > 0.10$ for all comparisons). Therefore, for practical reasons, I decided not to feed the juveniles, adult females or the rest of adult males during the 18 day observation period.

Statistical analyses. To investigate if exploration and web structure differed with the age and sex of spiders throughout the days, I performed generalized linear models (GLMs). I used the spider groups (adult males, adult females, and juveniles) and the days after entering the cage as fixed-factor predictor variables, and the spider identity as a random factor, and to control for the repeated measures on the same individuals. As response variables, I used the number of threads in the sheet chamber, their proportion, the number of exploration threads, and the sheet density; one model for

each response variable. I performed four additional GLMs using the sex of juveniles as predictor fixed factor.

I tested whether the number of spiders that built a sheet in large or small chambers was different with one χ^2 test for each spider group. I performed a similar analysis to test the effect of the light versus dark locations. I compared the proportion of adult females, adult males, and juveniles that had built a sheet three and 15 days after entering the cage with an independence χ^2 test comparing proportions (Zar 1999). With another proportion χ^2 , I tested whether the spider groups differed in the number of individuals that attached exploration threads after three days. I also tested whether the proportion of spiders in each group that had abandoned their sheets changed between observation periods with proportion χ^2 . I tested whether the groups differed in the number of times they abandoned their web with a one-way analysis of variance. Finally, I performed three sets of simple linear correlations between the four response variables, one set for each spider group. I used the values of nine-day old sheets, since most spiders had already built a sheet by that time. All analyses were performed with STATISTICA 8.0 (StatSoft, Inc. Oklahoma, USA, 2007).

Results

All the spiders ($n = 98$) attached threads to the walls during the first three days, but some spiders did not build a sheet (see below), and instead rested in a corner (Fig. 1D). After 6–9 days most spiders had built a clearly identifiable and dense sheet, with silk lines in many directions (as described for *M. guatuso* by Eberhard 1992b). Spiders built the sheet in the centre of the chamber, or halfway between the centre and a corner, and rested under it, upside down, during the day (Fig. 1F). Juveniles and adult females in the cages made sheets that were apparently similar in size and in general structure to those in a room (pers. obs.). After three days, the percentage of spiders that had built a sheet was greater in adult females (83% of 30 individuals) and juveniles (67% of 39 individuals) than in adult males (41% of 34 individuals) (proportion $\chi^2 = 12.51$; $df = 2$; $P = 0.002$). That pattern was also present after 15 days ($\chi^2 = 25.53$; $df = 2$; $P < 0.001$), and most adult females (93%) and juveniles (97%), but only half of males (52%) had built a sheet.

Almost all adult males (97%) and adult females (90%), but only 45% of juveniles, attached exploration threads in the first three days (proportion $\chi^2 = 28.41$; $df = 2$; $P < 0.001$). Therefore, either the adults explored more thoroughly before building a sheet, or they were more likely to explore after having built a sheet compared to juveniles. After six days, 57% of adult females had abandoned their sheet and built new exploratory threads, and that percentage increased to 80% after 18 days ($\chi^2 = 12.78$; $df = 4$; $P = 0.01$). In adult males that percentage remained between 35–67% and did not change for 18 days ($\chi^2 = 6.58$; $df = 4$; $P = 0.16$). Juveniles also abandoned their sheets often (41–58%), but that proportion did not change over time ($\chi^2 = 3.52$; $df = 4$; $P = 0.48$). Finally, the mean number of three-day periods in which an individual abandoned its sheet at least once was not different between adult females (2.9 ± 1.5 times),

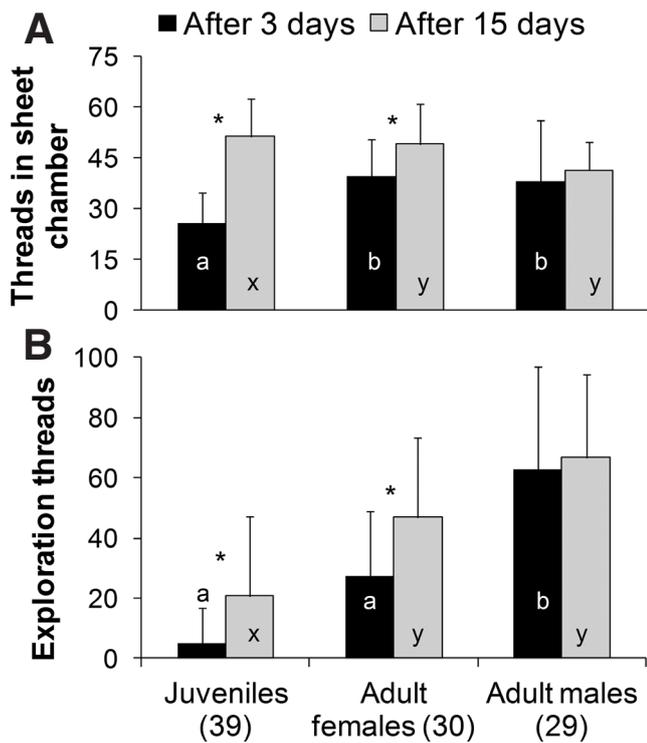


Fig. 2: **A** Mean (± 1 SD) of number of threads attached to the walls in the chamber where *P. globosus* built their sheet after three and 15 days; **B** Number of exploration threads (attached outside the sheet chamber) built in the cages. Sample size shown in parentheses. Letters inside bars represent statistically different groups within the three or 15 days comparisons. * = significant changes within a spider group from three to 15 days after spiders entered the cage.

adult males (2.4 ± 0.9 times) or juveniles (2.3 ± 1.5 times) ($F_{2/92} = 2.40$; $P = 0.10$).

Age/sex differences and changes through time. Juveniles differed from adults in web-building behaviour and web density pattern. Differences according to sex were found in adults, but not in juveniles. In general, most of the threads in the walls and in the sheet were attached during the first three days. The number of threads in the sheet chamber after three days was greater in adult females and adult males than in juveniles (GLM spider group \times days interaction: $F_{10/450} = 10.42$; $P < 0.001$; Fig. 2A). However, after 15 days, juveniles and adult females attached more new threads to the sheet chamber than did adult males (Fig. 2A). Adult males attached most of their threads outside the sheet chamber, and the total number of these threads was greater in adult males than in adult females and juveniles (GLM spider

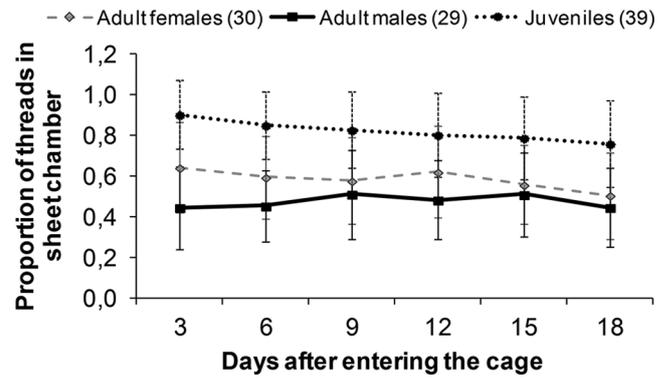


Fig. 3: Mean proportion (± 1 SD) of threads attached to the walls of the chamber where *P. globosus* built their sheet, relative to the total threads in cages, throughout 18 days. Sample size shown in parentheses. Juvenile and adult females decreased their proportion throughout the days, but adult males did not (see text for statistical results).

group \times days interaction: $F_{10/450} = 4.18$; $P < 0.001$; Fig. 2B). This pattern remained constant throughout the observation period, but juveniles and adult females attached more exploration threads after 15 days compared to adult males (Fig. 2B). The proportion of threads in the sheet chamber was greater in juveniles than in adults, which laid proportionally more threads outside the sheet chamber (GLM spider group \times days interaction: $F_{10/450} = 2.66$; $P = 0.004$; Fig. 3). In juveniles and adult females, that proportion decreased with time, but did not change in adult males (Fig. 3). In juveniles, the exploration was delayed because the average thread proportion attached in the sheet chamber was high (> 0.60) during the first 12 days (Fig. 3). Finally, the sheet density was greater in juveniles and adult females than in adult males after three days (GLM spider group \times days interaction: $F_{10/450} = 1.42$; $P = 0.17$; Fig. 4). After 15 days, the sheet density of adults increased slightly, and adult females had denser sheets than those of juveniles and adult males (Fig. 4).

All the exploration and web structure variables varied between individuals. The spider identity factor in the GLMs was significant in the models using threads in the sheet chamber: $F_{82/450} = 7.42$; $P < 0.001$; proportion of threads in the sheet chamber: $F_{82/450} = 13.97$; $P < 0.001$; exploration threads: $F_{82/450} = 4.17$; $P < 0.001$; and sheet density: $F_{82/450} = 6.93$; $P < 0.001$.

Juvenile exploratory and web construction behaviour did not differ according to sex. Juvenile females ($n = 25$) and juvenile males ($n = 14$) did not differ in the total number of

Variable	Days after entering cage	Juvenile females (n = 25)	Juvenile males (n = 14)
Threads in sheet chamber	three	27.92 ± 9.56	22.43 ± 7.52
	fifteen	52.72 ± 10.91	51.86 ± 13.26
Exploration threads	three	6.12 ± 13.38	1.29 ± 2.63
	fifteen	26.68 ± 30.70	11.14 ± 11.19
Proportion of threads in sheet chamber	three	0.90 ± 0.17	0.95 ± 0.12
	fifteen	0.74 ± 0.23	0.84 ± 0.14
Sheet density	three	30.18 ± 15.33	28.29 ± 11.83
	fifteen	24.11 ± 15.02	24.59 ± 14.35

Table 1: Mean (± 1 SD) of the exploration and sheet structure variables according to sex in *P. globosus* juveniles. Sample size is shown in parentheses.

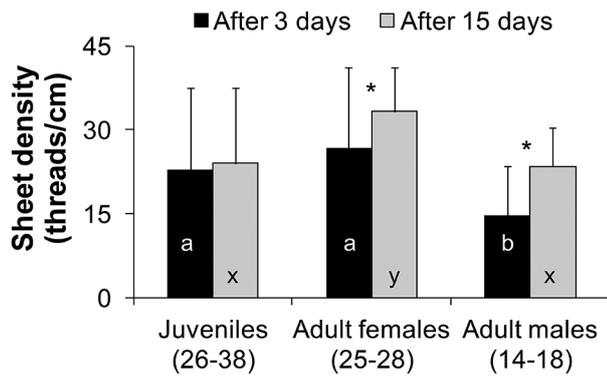


Fig. 4: Mean (+ 1 SD) sheet density (number of silk lines that crossed sticks above the sheet) of *P. globosus*. Sample size for each is shown in parentheses (3–15 days, since the number of individuals that built a sheet increased throughout the days). Letters inside bars represent statistically different groups within the three or 15 days comparisons. * = significant changes within a spider group from three to 15 days after spiders entered the cage.

threads attached in the sheet chamber during 18 days (GLM juvenile sex \times days interaction: $F_{5/186} = 1.79$; $P = 0.12$), the proportion of threads in the sheet chamber ($F_{5/186} = 1.49$; $P = 0.20$), the exploration threads ($F_{5/186} = 0.61$; $P = 0.69$), or the sheet density ($F_{5/186} = 0.42$; $P = 0.84$) (Table 1).

Correlations between threads and sheet density. The three spider groups had a very different web structures (Table 2). Denser sheets correlated positively with the number of exploration threads only in adult males (Table 2). Also, adult males that had most of their threads in the sheet chamber had less dense sheets (Fig. 5A). Only in adult females did denser sheets have a greater number of threads in the sheet chamber (Fig. 5B, Table 2).

Original exploration and thread attachment behaviour. When released into the cage, adults ($n = 12$) walked on the floor and walls, and eventually encountered the plastic ceiling, on which they could not walk easily, and stopped walking. Most spiders visited two chambers in the first five minutes, and then remained immobile in a corner, with their ventral side touching the wall. After 10–15 min the spiders rose and started attaching threads to the wall. For each attachment, the spider lowered the tip of its abdomen and contacted the substrate, then raised the abdomen quickly, walked, and attached it to another wall. As the spider walked it extended one of its legs I forward, and touched the

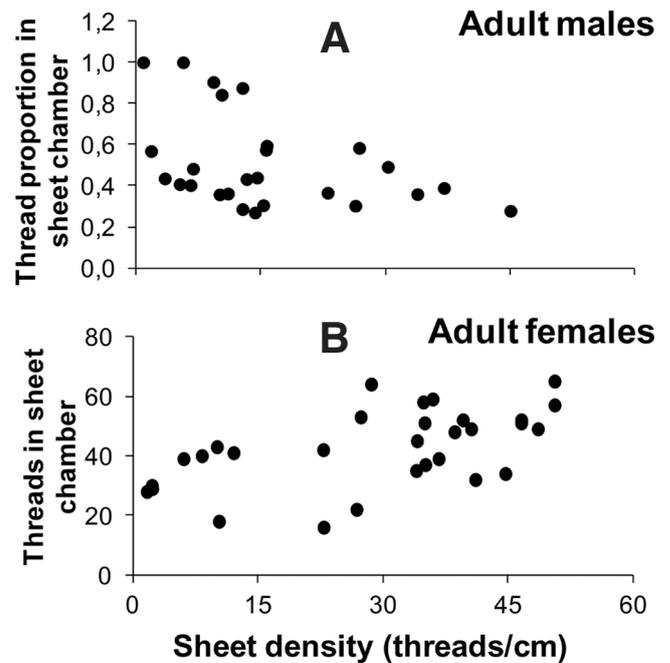


Fig. 5: Simple linear correlations between the sheet density and **A** the thread proportion in the sheet chamber where 34 adult male *P. globosus* built their webs, and **B** the number of threads in the sheet chamber for 30 adult females. Data are from nine days after entering the cage. Correlation coefficients: **A** $r = -0.41$; **B** $r = 0.56$; both are significantly different from 0 at the $P < 0.05$ level.

substrate when it was nearby. The spider also explored by moving their extended leg I from side to side. Movements that appeared to be exploratory were performed alternately, mostly with both legs I, but also with legs II. The third pair of legs was either still or it moved with the advance of the spider. The fourth pair of legs held threads by which the spider supported its weight (similar to fig. 8 in Eberhard 1992b).

Chamber selection. Adult spiders built their sheets equally in large or small chambers (adult females: $n = 16$; $\chi^2 = 1.00$; $df = 1$; $P = 0.32$; males: $n = 15$; $\chi^2 = 1.67$; $df = 1$; $P = 0.20$). However, more juveniles (14 of 19 individuals in asymmetric cages) built their sheets in small chambers ($\chi^2 = 4.26$; $df = 1$; $P = 0.04$). About half of the spiders that built sheets did so in the dark chambers (farther from direct exposure to light): 16 of 30 adult females ($\chi^2 = 0.13$; $df = 1$; $P = 0.72$), 15 of 38 juveniles ($\chi^2 = 1.68$; $df = 1$; $P = 0.19$), and 18 of 27 adult males ($\chi^2 = 3.00$; $df = 1$; $P = 0.08$).

Group	Variable	Exploration threads	Threads in sheet chamber	Proportion of threads in sheet chamber
Adult females (n = 30)	Threads in sheet chamber	0.14		
	Proportion of threads in sheet chamber	-0.83 *	0.36 *	
	Sheet density	0.15	0.56 *	0.15
Adult males (n = 27)	Threads in sheet chamber	0.03		
	Proportion of threads in sheet chamber	-0.89 *	0.13	
	Sheet density	0.50 *	0.07	-0.41 *
Juveniles (n = 39)	Threads in sheet chamber	0.09		
	Proportion of threads in sheet chamber	-0.95 *	-0.01	
	Sheet density	-0.04	0.08	0.06

Table 2: Correlation coefficients (r) for simple linear correlations between the four response variables, analysed separately by spider groups of *P. globosus*. Data from nine days after the spider entered a cage. Sample size shown in parentheses. * = significant correlation at the $P < 0.05$ level.

Discussion

According to the results of the present study, web building in *P. globosus* continues over several days, and the pattern differs between juveniles and adults, and between sexes in adult spiders. Juveniles and adults add new threads to the sheet chamber and outside of it, and increase their sheet density even 18 days after being placed in the cage. This pattern may reflect the expansion of the capture area of the web to favour higher prey-capture rates (Blackledge & Zevenbergen 2007). Also, spiders may add new threads to the tangle to renew sticky gumfoot lines, because some of them break (pers. obs.), or dry after a few days, as has been reported for *P. phalangoides* (Kirchner 1986). Adding lines outside the sheet chamber once the sheet was built suggests that the spiders abandon their sheet and explore the environment. In natural conditions, they presumably have to spend time and silk when weaving a new sheet after abandoning their sheets unless they are able to return to sheets following explorations (no data are available on this point). The high rate of exploration and the high frequencies of web abandonment found in *P. globosus* presumably balance the benefit of increased capture to the cost of abandoning their webs (Switzer 1993). The relation of these data with behaviour in nature is not clear. However, the increase in sheet threads that occurs following the first exploration after the sheet was built may be an artifact of enclosing the spiders in containers where they eventually encountered their original webs after leaving them to explore. Spiders probably re-encounter their own web only seldom in the field. Nevertheless, *P. globosus* adult females are known to reoccupy abandoned webs in nature (Eberhard 1992a). However, in that study it was not possible to determine if a spider reoccupied its own web.

Adult males of *P. globosus* were more active and exploratory compared to adult females and juveniles. Most adult males laid threads in almost even numbers in all four chambers in the first three days and, additionally, they also made sheets later. Therefore, even though males continue to build sheets and feed when adults, they seem to be more disposed to abandon their sheets and explore more than do juveniles and adult females. In the field, adult males of *P. globosus* remain fewer days in the same webs than adult females (Eberhard 1992a). In addition, adult males of the pholcids *Litoporus lopez* Huber, 2000, *Mesabolivar eberhardi* Huber, 2000, *Modisimus guatuso*, and an unidentified species of *Modisimus*, also change sites often (Eberhard & Briceño 1983). After spiders are placed in already built webs, adult males of *P. manueli* disperse earlier than adult females (Edwards 2011). This suggests that males disperse more to look for mates, since they visit adult females in their webs to copulate (Uhl 1998). Building a sheet and increasing its density would probably not happen every time in males because, in some pholcids, adult males can also capture prey in abandoned webs they encounter, or even in adult females' webs (Eberhard & Briceño 1983). In the opposite pattern, most adult females seem to establish in a chamber during the first three days. The proportion of threads in that chamber positively correlates with denser sheets, as noted for *P. phalangoides* webs (Kirchner 1986), in which web density is related to prey abundance (Roush & Rababaugh

1993). This web structure could increase the possibility of capturing prey.

Age was also associated with exploration and sheet structure throughout the days. Juvenile *P. globosus* spiders established in a chamber and concentrated the threads they added in the sheet chamber (and built dense sheets), rather than exploring the cage. In juveniles, abandoning the sheet to explore was delayed compared with adults. However, subsequent exploration may have occurred because the spiders were not fed. Additionally, juveniles showed a preference for smaller chambers not seen in adults. These findings are in agreement with the likely hypothesis that spider body size affects the site in which they build webs, as also occurs in orb weavers (Waldorf 1976; Gunnarson 1992). The ontogenetic changes in exploration and web construction found here are only subtle and qualitative. This is contrary to spider species in which structural, behavioural, and functional web features differ quantitatively between juveniles and adults (Uloboridae: Eberhard 1977; Araneidae: Eberhard 1985; Hesselberg 2010; Nephilidae: Japyassú & Ades 1998; Tenggellidae: Barrantes & Madrigal-Brenes 2008; Theridiosomatidae: Eberhard 2000; Theridiidae: Eberhard *et al.* 2008; Barrantes & Eberhard 2010). Finally, there was no apparent effect of illumination, since individuals did not show a preference for building a sheet in lighter or darker chambers, as was found in the theridiid *Parasteatoda tepidariorum* (Turnbull 1964).

The sex of juveniles was not associated with the patterns of thread attachment, sheet density, or site tenacity. This is contrary to Hoefler *et al.* (2010) who found that *P. phalangoides* juvenile males were more active, and less willing to hunt than juvenile females. Juvenile *P. globosus* of an advanced fifth instar did not differ in their exploration or sheet construction, so it is unlikely that spiderlings behave differently after their first instar. Also, it is unlikely that juvenile males capture a suboptimal number of prey items in the fifth instar, since immature spiders are expected to eat as much as possible in order to mature sooner and perhaps obtain larger body size as adults (Foelix 1996). The other variable investigated by Hoefler *et al.* (2010) was the amount of time during a 15 min interval that spiderlings spent in walking and moving after being placed in plastic containers. The activity of spiderlings in this context could be caused by their reaction to an unnatural scenario: being released into an artificial substrate, and the need to build silk threads to secure themselves, a behaviour observed in *P. globosus* in the present study after placing the spiders in the cage. Therefore, my results are congruent with the expectation that the behaviour of immature pholcid spiders will not differ according to their sex at maturity. This will be true in Pholcidae (and in other spider taxa) because juveniles do not show exaggerated morphological sexual dimorphism, which can affect their exploration, web-building, and foraging patterns (Foelix 1996).

Individual differences were present during exploration and web construction, suggesting repeatability (Bell *et al.* 2009) in those two biologically different behaviours. For example, some adult males built their sheet after six days and after exploring many times, while others did not build a sheet even though they attached many exploration threads. In adult females and juveniles, individual differences were

more quantitative (more threads attached to the walls, or denser sheets). These differences and repeatability may be caused by genetic and environmental factors (as suggested by Rodríguez & Gloudeman 2011), but my design could not identify them. However, differences in the condition of each spider before entering the cage, the accumulation of past experiences in environment explorations, differences in prey capture success of their webs or sites, an unknown number and type of prey attacked, age and reproductive status in adults (see below), and brood specific variation could also account for the behavioural differences found.

Accumulated hunger affects the pattern of web construction, exploration, and web abandonment in other spiders. In *Latrodectus hesperus* (Theridiidae), well fed adult females build a cloud of silk to avoid predation instead of adding new gumfoot lines to increase prey capture, when compared with unfed adult females (Blackledge & Zevenbergen 2007). Hunger could also make spiders abandon their sheet sooner, especially because web relocation is energetically costly for sheet-weaving spiders (Tanaka 1989). In this project, fed and unfed adult males did not differ in exploration or web-construction behaviours, but my sample sizes were very small, and probably the starvation time was not long enough to cause differences. The reproductive stage of adults can also affect the behaviour of spiders. Adult females of *L. hesperus* after copulation made similar changes to their webs as mentioned above (Blackledge & Zevenbergen 2007). In this project, I included adults of unknown and possible different reproductive status. However, even though hunger and reproductive status could affect the behaviour of *P. globosus*, those factors would have a greater within- than between-group effect. Further examination of the effect of hunger and reproductive status, as well as the individual differences in behaviour of pholcid spiders, are needed to fully understand the biology and natural history of these organisms. To summarize, in this study I report novel findings for Pholcidae spiders, in which ontogenetic and sexual differences in web building and exploration behaviour have never been addressed.

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