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Aggression in a western Amazonian colonial spider, *Philoponella republicana* (Araneae: Uloboridae)

Catherine Wu[1,*], **Chaiti Bhagawat**[1,*], **Modan R. Goldman**[1,*], **Nihal A. Punjabi**[1,*], **Debra M. Shier**[1,3], **Roxana P. Arauco-Aliaga**[2], and **Gregory F. Grether**[1]: [1]Department of Ecology and Evolutionary Biology, University of California Los Angeles, 612 Charles E. Young Drive E, Los Angeles, CA, 90095, USA; E-mail: catherinedwu@gmail.com; [2]Cocha Cashu Biological Station, San Diego Zoo Global-Peru, Cusco, Peru; [3]San Diego Zoo Institute for Conservation Research, Recovery Ecology, 15600 San Pasqual Valley Road, Escondido, CA, 92027, USA; * These authors contributed equally to this work.

Abstract. Group-living spiders are rare, and can be divided into multiple subcategories based on their tolerance of group mates. While social spiders are cooperative, colonial spiders are often antagonistic towards conspecifics. We examined colony dynamics in a colonial species, *Philoponella republicana* (Simon, 1891), focusing on aggressive behaviors to further understand this understudied species. We studied whether web region, sex ratio, web size, or spider size affected aggression. We also tested whether colony members discriminate against conspecific intruders, since this behavior, known as group closure, is prevalent in many other group-living animals but had not yet been tested in colonial spiders. Colony mates were often aggressive due to competition for limited resources, such as mates and orb webs, yet several characteristics of this species may reduce these competitive forces. First, female-biased secondary sex ratios appear to reduce male-male and female-male competition. Moreover, although some individuals defended orb webs, other areas in the communal web were not defended. *Philoponella republicana* also did not exhibit group closure. Our results further confirm that aggression between males decreases in colonies with more female-biased secondary sex ratios, and larger individuals correlate with a higher frequency of aggressive interactions. Moreover, we raise new questions concerning the evolutionary pressures that shape coloniality in spiders.

Keywords: Uloboridae, orb-weaver, social evolution, territoriality, group closure

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Of the over 50,000 spider species identified, fewer than 0.1% display social behavior (Avilés & Guevara 2017; World Spider Catalog 2022). Sociality is hypothesized to evolve when the benefits of group-living outweigh the costs (Krause & Ruxton 2002). As compared to solitary web-building spiders, group-living web-builders can occupy larger areas of open space, which increases the likelihood that prey will intercept the colony web; cooperate to secure larger prey; capture a greater proportion of arriving prey due to insects getting caught in surrounding webs while attempting escape (i.e., the ricochet effect); and obtain earlier predator warnings (Uetz 1989). Group-living spiders, however, have webs more conspicuous to predators, are more susceptible to parasites and disease, and are exposed to higher levels of within-group resource competition (Alexander 1974; Nentwig 1985; Uetz & Hieber 1997).

Group-living spiders are commonly classified by two criteria: territoriality, or the lack thereof, and duration of sociality—permanent or periodic (Avilés & Guevara 2017). Non-territorial permanent and periodic group-living spiders, referred to as social or sub-social spiders, respectively, cooperate in prey capture, brood care and web construction (Schneider 1995; Avilés 1997; Avilés & Guevara 2017). Territorial permanent and periodic group-living spiders, referred to as colonial spiders, cooperate only to maintain the shared structural framework of the colony web and often display aggression towards colony mates (Lubin & Bilde 2007). The evolutionary pathways to territorial or non-territorial group-living are thought to be distinct; that is, non-territorial social spider species generally arise in lineages with extended maternal care of offspring, and have subsocial sister species, whereas territorial colonial behavior appears to arise more sporadically, when favored by ecological conditions (Agnarsson et al. 2006).

Aggression levels may vary within colonial spider colonies in predictable ways because different regions within the communal web offer different fitness payoffs (Rayor & Uetz 1990). The most common colonial spiders are orb weavers that embed orb-shaped hunting webs guarded by an individual (hereafter, orb webs) within a network of interconnecting webs that are anchored to the surrounding vegetation (hereafter, connecting webs) (Binford & Rypstra 1992; Avilés & Guevara 2017). Individuals move to communal retreats, which are distinct sections of connecting web, for protection when they are not hunting, especially at night (Lubin 1980; Binford & Rypstra 1992). While colony members cooperate to build the connecting webs, they work individually to either construct their own orb webs or usurp another individual's orb web (Buskirk 1975a; Uetz & Hieber 1997). In one well-studied tetragnathid orb weaver, *Metabus ocellatus* (Keyserling, 1864), (formerly *Metabus gravidus* Pickard-Cambridge, 1899), many individuals do not have orb webs and orb-web holders respond aggressively to intruders (Buskirk 1975b). In another colonial spider, *Metepeira incrassata* F. O.Pickard-Cambridge, 1903 (Araneidae), the outermost layer or periphery of a three-dimensional colony offers the greatest access to prey but also the most exposure to predators (Rayor & Uetz 1990, 1993; Rayor 1996), and thus regions in the center or semi-periphery may optimize the trade-off between prey capture and predation risk. For the colonial spider *Cyrtophora citricola* (Forskål, 1775) (Araneidae), there was a higher frequency of prey captures, as well as conspecific aggressive interactions in the middle layers of the web as opposed to the innermost and outermost regions (Rypstra 1979). Thus, orb webs in the semi-periphery may be at the heart of territorial disputes in the colony.

The frequency of aggressive behaviors may also be governed by colony-level characteristics, such as the physical size of the colony, the size and size distribution of the spiders, and the colony sex ratio. Since larger colony webs generally capture a greater number of prey due to the ricochet effect (Uetz 1988, 1989), we assume that larger colony webs may have greater prey biomass per capita and consequently less within-colony competition for prey. As a result, we expected to observe less intra-colony aggression in larger colony webs while controlling for the number of individuals (colony size), provided that colony size and web size vary independently. Larger individuals generally are more likely to win contests and thus have more to gain by challenging conspecifics (Potter et al. 1976; Riechert 1978; Christensen & Goist 1979; O'Neill 1983). Therefore, the overall level of aggression may depend on individual size or size distribution in a colony. As in other taxa, variation in sex ratio is likely to affect the intensity of competition among males for mates and the level of mating harassment experienced by females (Clutton-Brock & Parker 1995; Kvarnemo & Ahnesjö 1996). Among social spider species, those having a more female-biased secondary sex ratio generally exhibit less male-male and female-male aggression (Avilés 1997; Lubin & Bilde 2007; Avilés & Purcell 2012; Avilés & Guevara 2017), but to the best of our knowledge, this prediction has not been tested by comparing aggression levels between colonies with different sex ratios within a colonial species.

Conspecific familiarity is negatively correlated with aggression in diverse taxa (Ydenberg et al. 1988). In general, individuals that are more familiar—because of genetic similarity or spatial proximity—exhibit lower levels of aggression towards each other compared to unfamiliar conspecifics. This phenomenon, known as group closure, is hypothesized to occur because an individual's inclusive fitness increases by cooperating with kin (Pasquet et al. 1997). Under certain conditions, group closure can evolve when between-group competition outpaces within-group competition (Lehmann et al. 2007; Gardner & Grafen 2009; Lion et al. 2011; Marshall 2011). The way groups are formed may indicate the presence or absence of group closure. Social spiders tend to remain at their natal sites and inbreed, and therefore groups can reach nearly clonal levels of relatedness (Avilés & Guevara 2017). Many colonial spider species tend to disperse as competition in their natal colony intensifies, which reduces within-group relatedness (Smith 1983). Unlike the many social insects that exhibit both high levels of relatedness and group closure, social spiders have not been found to discriminate against unfamiliar conspecifics under normal conditions (Pasquet et al. 1997). However, groups have been found to discriminate against unrelated spiders during environmental stress (e.g., starvation conditions) (Yip & Rayor 2014). In general, social spiders are not known to be aggressive to conspecifics. To the best of our knowledge, no study has examined group closure in the more aggressive colonial spiders.

We studied aggression in *Philoponella republicana* (Simon, 1891) (Uloboridae), a colonial, orb-weaving spider found in secondary and mature forests of the Amazon Basin, and in a geographic area ranging from Panama to Bolivia (Opell 1979). Like other uloborids, *P. republicana* lack poison glands and capture prey using extensive silk wrapping (Opell 1979). They construct three-dimensional colonial webs close to the ground, with support lines attached to vegetation, individual orb webs interspersed throughout, and a centrally located communal retreat (McCook 1889). Within the communal retreats, individuals demonstrate limited forms of cooperation: some large prey items are occasionally caught in an orb web but wrapped in the communal retreat by more than one spider. Once wrapping is complete, however, only one spider consumes the prey (Masumoto 1998).

To assess whether *P. republicana* compete for specific spatial positions within the colonies, we compared aggression frequencies between spiders in web types (i.e., orb vs. connecting webs which include communal retreats) and among regions within the colony (i.e., periphery, semi-periphery, and core). To directly examine how the spiders respond to approaching colony members, and whether this depends on the resident's web type (i.e., orb vs. connecting), we measured responses to staged intruders. Based on the hypothesis that larger colonial web volumes result in increased prey capture and reduced competition within colonies, we tested the prediction that colony web size correlates negatively with aggression, while controlling for the number of spiders in the colony. We also examined whether female size class (i.e., small, medium, and large) affected the frequency of aggression and kleptoparasitism (i.e., prey snatching). To test the hypothesis that female-biased colony sex ratios reduce mating competition among males and mating harassment between females and males, we tested for effects of colony sex ratio on levels of male-male and female-male aggression. Finally, we conducted a translocation experiment to test for group closure. All studies were completed in the field using naturally occurring colonies.

METHODS

Study site.—We studied *P. republicana* in intact, lowland Amazonian rainforest at Cocha Cashu Biological Station in Manu National Park, Peru (11.8880°S, 71.4078°W, elevation 340 m, average annual temperature 24 °C) during the rainy season from 26 January to 11 February 2019.

Colony census and behavior observations.—We recorded the locations of 20 *P. republicana* colonies within 10 m of established trails (Fig. 1) and observed each colony once within three weeks of discovery in a randomized order, between 0800 and 1800 hours. Fifteen colonies were in intact forest, while the other 5 colonies were in treefall gaps, near the edge of an oxbow lake, or near streams. To characterize colony web size dimensions, we measured the longest horizontal, the widest width perpendicular to the horizontal, and the height from the lowest to the highest point (Alves-Costa & Gonzaga 2001). Because some spiders moved in response to our presence, we waited 10 min, which appeared to be sufficient time for any disturbed spiders to return to their original position, before collecting census data (sex, size class, and web region). Sex was determined based on color markings

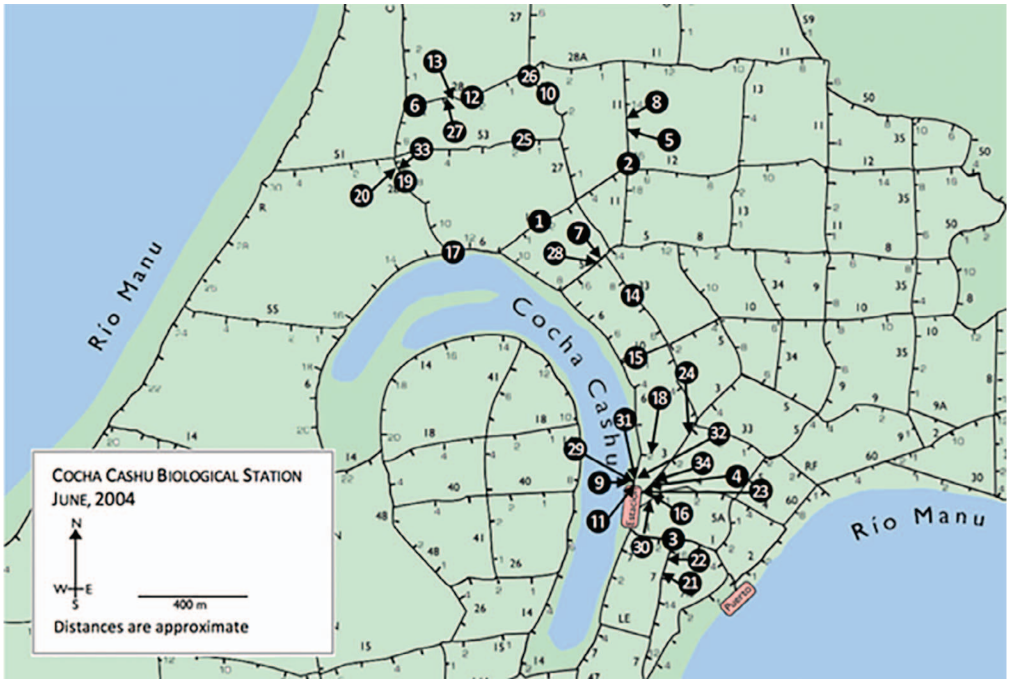

Figure 1.—A map of the 34 colony sites, created using the 2004 map of the Cocha Cashu trail system, courtesy of the Cocha Cashu website, accessed 29 April, 2020, https://cochacashu.sandiegozooglobal.org/maps/

and size: females are orange, black or brown with white markings, while males are solid red-orange and smaller than all but the smallest females (Opell 1979). We visually assessed the size class of the female spiders (small: bottom 15%; medium: middle 60%; and large: top 25%). Small and medium size class females are likely to be juvenile and subadult females. Few very small immatures were observed, and these were not counted at all, as males and females at that age/size are not easily distinguishable. We also did not attempt to classify males by size due to the lack of variability in their size. To avoid disrupting the web, we did not measure the length of each spider, so we used relative size difference classification. Finally, we counted the number of females within three concentric web regions: the innermost core, the semi-periphery and periphery. The periphery includes the outermost edges of the web structure (e.g., colony web support lines attached to vegetation, small orb webs imbedded between support lines or not surrounded by other orb webs), the core contains the communal retreat (as described in Lubin 1980; Smith 1983; Breitwisch 1989; Binford & Rypstra 1992), and the semi-periphery is comprised of the interstitial space between the core and periphery (Fig, 2). Two observers counted the spiders, categorized spiders into size classes, and determined each spider's web region independently and then compared notes. When discrepancies between the observers' counts could not be reconciled, the average count was used in the data analysis. Inter-observer reliability before reconciliation was 0.69 (Spearman rank correlation, $P < 0.001$, $n = 240$ counts).

After each colony census, we observed and recorded aggressive behaviors ad libitum for 80 minutes using the ethogram in Table 1. For each behavior, we recorded the time of occurrence, the web region, the sex and size class of initiator and recipient, and the winner of the interaction. We classified spiders as winners if they displaced the opponent. Repeated behaviors, such as continuous web plucking, were recorded once per minute.

Intra-colony intrusion experiment.—To examine how the spiders respond to approaching colony members and to examine how the type of web occupied by the resident (i.e., orb vs. connecting) affects the responses, we carried out simulated intruder tests at 20 colonies in randomized order. In a given trial, one female was captured and immediately presented to another female of the same size class. We excluded females of the smallest size class (because they rarely occupy orb webs), females that were actively hunting or consuming prey, and males. Otherwise, our choice of "intruders" and residents was based primarily on accessibility, i.e., whether we could capture and release the spiders without touching the web and disturbing the whole colony. The type of web occupied by the resident and intruder varied throughout each trial. We used an entomological aspirator to gently suction a spider off the web. We then blew the intruder out to within 15 cm of the resident, and in the same 2-dimensional web plane as the resident. We recorded all interactions between the resident and intruder for 5 min., using the ethogram in Table 1, and recorded whether the resident had returned to its original position by the end of the trial. We used each colony for two trials and conducted a total of 21 orb web tests and 19 connecting web tests.

Translocation experiment.—We performed inter-colony translocations to determine whether *P. republicana* treat colony mates and conspecifics from other colonies differently, and whether the distance (and possibly relatedness) between colonies affects the occurrence of aggression. We used a repeated-measures design in which medium-sized females from each of 10 source colonies were assigned to three translocation

Table 1.—Ethogram of *Philoponella republicana* behaviors. Aggressive behaviors are marked with an asterisk.

Behavior	Definition
Approach	Individual walks towards another individual
Chase*	Focal individual runs towards and follows another individual, and the other individual runs away
Displace*	Focal individual approaches another individual, and the other individual moves away while the focal individual stays, taking the original place of the other individual
Prey Ball Snatch*	Focal individual takes a food ball of crushed prey from another individual
Leg Attack*	Focal individual quickly forces leg onto another individual's body, physically moving them away
Leg Tap	Focal individual slowly touches another individual with one of their front legs, without moving the other individual
Prey Snatch*	Focal individual takes prey item away from another individual
Throw*	Focal individual grabs and tosses another individual away
Web Cut*	Focal individual breaks web between itself and another individual
Shake*	Focal individual quickly pulls on web between itself and another individual, often performed in a series of plucks
Web Pull*	Focal individual pulls on web between itself and another individual, decreasing the distance between the focal and the other individual
Web Vibrate	Individual vibrates web by tapping the strands directly at another individual

treatments: same colony, < 300 m from the source colony (proximal), and > 800 m from the source colony (distal). Distances were selected based on logistical feasibility because the dispersal abilities of *P. republicana* have not been well studied. All colonies used in this experiment as either source or receiving colonies contained ≥ 15 females. Source colonies were selected at random from a sample of 20 such colonies and visited in randomized order. Proximal and distal receiving colonies for each source colony were selected at random from the colonies available, with the restriction that no receiving colony could be used more than once for a given translocation treatment. We captured focal spiders by placing a transparent plastic cup near the spider and gently closing the lid with the spider inside. Regardless of the translocation treatment, we marked the focal spider with a drop of acrylic paint on the abdomen and held the focal spider in the container for 20 minutes, to account for the travel time required for distal-colony translocations. After placing the focal spider on the web of the receiving colony, we recorded all interactions involving the focal spider for 1 hour, using the ethogram in Table 1. The focal spider was then recaptured and immediately returned to its original colony.

Statistical analysis.—To compare the frequency of aggressive interactions among female size classes and between regions within the webs, we used a Friedman test with trials matched by source colony, followed by Wilcoxon signed-rank tests with p-values adjusted for multiple comparisons based on an extension of the method of Holm (1979). The Friedman test is the standard non-parametric equivalent of a repeated measures ANOVA for making comparisons among three or more groups (Sprent & Smeeton 2007). Holm's (1979) method, also known as the sequential Bonferroni method (Rice 1989) is more powerful than the original Bonferroni method but more conservative than most other methods, including the false-discovery rate method (Hochberg & Benjamini 1990; Verhoeven et al. 2005). To obtain a measure of heterogeneity of size classes of females in each colony, we calculated female size class variability using the measure 'unalikeability' from Kader & Perry (2007), which is a measure between zero and one that indicates how unalike or different observations are from each other, with zero meaning all are identical, and one meaning all are different. To determine whether females of different size classes were distributed non-randomly across regions within webs, we compared observed frequencies to expected frequencies based on the proportion of all females found in each region, using a goodness-of-fit G test. To determine whether aggression occurred non-randomly with respect to female size class, we compared the observed frequency of aggressive interactions within and among size classes to expected frequencies based on the expansion of $(s + m + l)^2$ where s, m and l are the proportions of females in each size class. Expected frequencies were generated for each colony by multiplying the expected proportion of aggressive interactions of each type by the total number of aggressive interactions observed in that colony, and then summing observed and expected frequencies across colonies for an overall goodness-of-fit G test.

We carried out a Principal Component Analysis (PCA) of the three web-size dimensions (length, width and height) to find the primary axis of variation in web size (PC1). To test predictions about how colony metrics (web size, sex ratio, female size, colony size, web region, and web type) affect different types of aggression (total aggression, prey snatch events, female-female aggression, female-male aggression and male-male aggression), we constructed the five linear models shown in Table 2 ($n = 20$ colonies). To properly account for the dispersion of these count-based dependent variables, we used General Linear Models in the negative binomial family (glm.nb in the R package Stats).

For the intra-colony intrusion experiment, we tested if the total number of vibrations, shakes, and leg taps differed between web types using a Wilcoxon rank sum test with continuity correction. To test for an association between web type and the resident's final position, we used Fisher's exact test (Fisher 1930).

For the inter-colony translocation experiments, behaviors were grouped together as aggressive interactions, non-aggressive interactions, as indicated in the ethogram (Table 1). We tested for treatment effects on the number of these grouped behaviors using a Friedman test with trials matched by source colony. We used the R base package, and the packages ggplot2, ggpubr, reshape, ragree, MASS and cowplot (Ven-

Table 2.—Effects of colony characteristics on the frequency of aggressive interactions (negative binomial GLMs) in *Philoponella republicana* colonies. N = 20 colonies.

Model	Estimate	*P*	*df*
Total aggression			
Web size (PC1)	-0.03	0.6	16
Colony size (number of spiders)	0.02	**0.02**	
Female size class variability	2.35	**0.02**	
Female-female aggression			
Web size (PC1)	0.02	0.39	13
Number of large females	0.11	**0.01**	
Number of medium females	0.29	**0.03**	
Number of small females	0.22	0.19	
Female-male ratio	0.28	0.35	
Female size class variability	-0.15	0.92	
Prey Snatch Frequency			
Web size (PC1)	0.01	0.77	14
Number of large females	0.17	**0.02**	
Number of medium females	0.34	0.08	
Number of small females	0.28	0.32	
Female size class variability	-0.10	0.97	
Female-male aggression			
Web size (PC1)	0.24	0.44	16
Female-male ratio	-0.61	**0.04**	
Female size class variability	2.09	0.10	
Male-male aggression			
Web size (PC1)	0.03	0.92	16
Female-male ratio	-1.36	**0.01**	
Female size class variability	4.68	**0.01**	

Table 3.—Web size PCA loading matrix.

Web dimension	PC1	PC2	PC3
Length	0.177	-0.793	-0.584
Width	0.258	-0.535	0.804
Height	0.950	0.292	-0.110
Proportion of Variance	0.623	0.301	0.076

ables and Ripley 2002; Wickham 2007, 2016; Wilke 2019; Kassambra 2020; R 2020; Redd 2021).

RESULTS

Colony web characteristics.—We found that colony webs were amorphous structures with a median height of 173 m, median length of 1.77 m, and median width of 1.53 m. The first principal component (PC1) of colony web size dimensions accounted for 62% of the variance and had positive loadings for all three colony web size variables, and thus provided a suitable measure of variation in overall web size (Table 3). Colony Web size (PC1) was not a significant predictor of intra-colony aggression while controlling for the number or sex ratio of spiders in the colony (Table 2). Fig. 2 is a representative diagram of a colony web.

Colony composition.—*Philoponella republicana* colonies ranged from 8–88 individuals (mean ± sd, 411 ± 20.24; $n =$ 20 colonies), including 3 to 16 large females (median = 8.5), 0 to 64 medium females (median 16.5), 0 to 19 small females

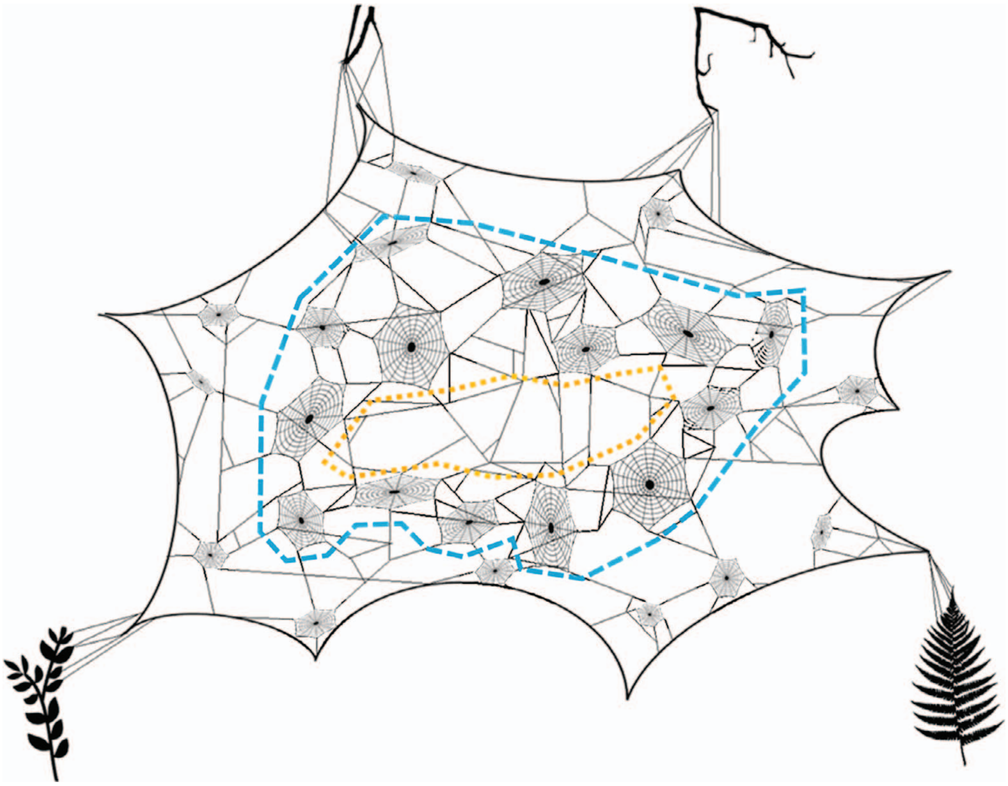

Figure 2.—A composite diagram of a colony web with the three web regions delineated. The dotted orange line encompasses the core, and the dashed blue line minus the dotted orange line equals the volume of the semi-periphery. The periphery covers the remainder of the colony web, including the support lines secured to vegetation.

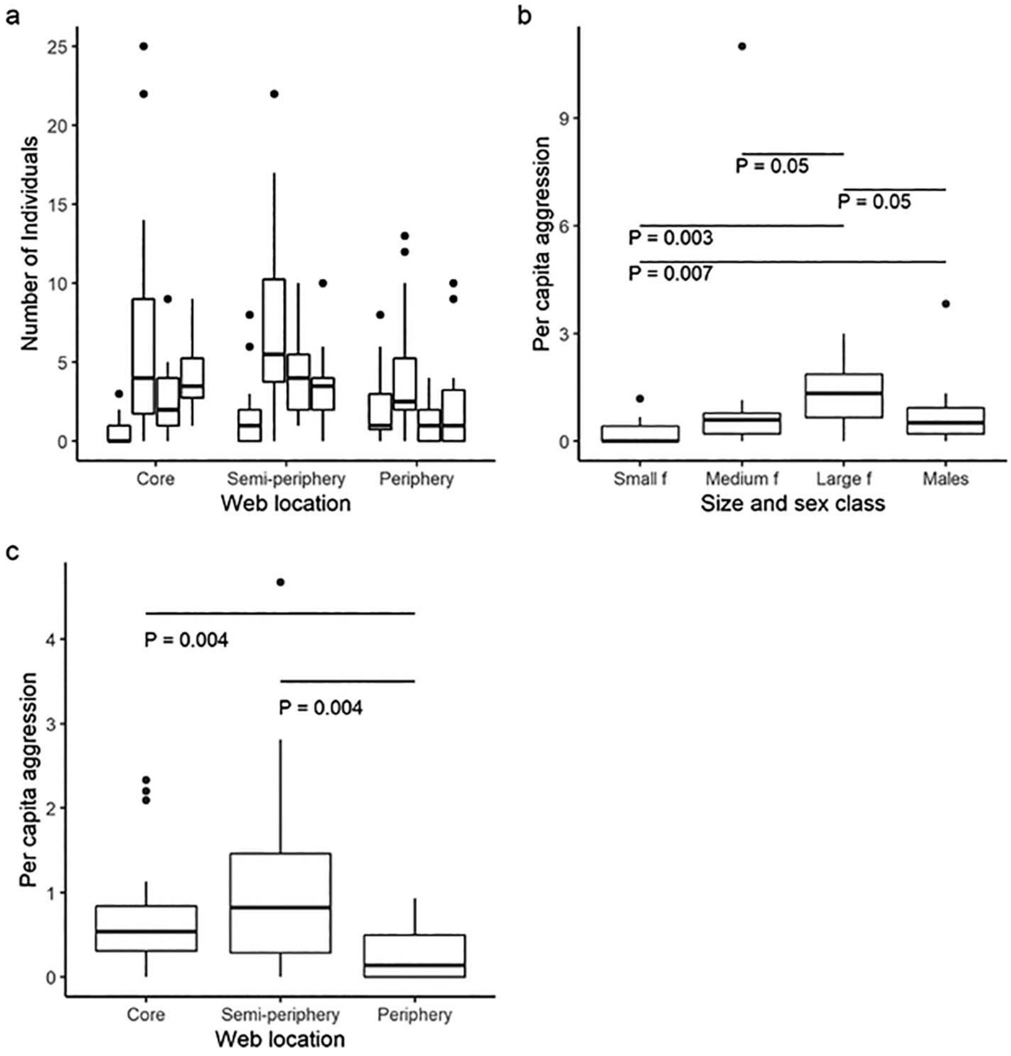

Figure 3.— (a) Distribution of size and sex classes of spiders by region within the colony webs. For each web region, size and sex classes are in the same order, from left to right, as shown in (b). (b) Variation in the frequency of aggression per individual by size and sex class ($n = 14$ colonies). Six colonies were excluded from this analysis because one or two female size classes were absent. (c) Observed rates of aggression per capita in relation to colony web region. Box plots show the following statistical values: the thick horizontal line indicates the median, the lower and upper boundaries of the box indicate the 25th and 75th percentile values (Q1 and Q3) respectively, the box represents the interquartile range (IQR), the whiskers represent the minimum (Q1 – 1.5(IQR)) and maximum (Q3 + 1.5(IQR)) values without outliers, and the circles represent outlier values.

(median = 3), and 3 to 21 males (median = 6) (Fig. 3a). Female size class variability ranged from of 0.00 to 0.66 (mean ± SE = 0.48 ± 0.03, median = 0.49, $n = 20$ colonies), where 0 would be totally homogeneous and 1 would be maximally heterogeneous.

The number of spiders varied among regions in the web (Friedman test, $\chi 2 = 16.13$, df = 2, $P = 0.0003$), with fewer spiders in the periphery (median = 9, $n = 20$) than in the semi-periphery (median = 16, $n = 20$, Wilcoxon signed rank test with Holm's adjustment for multiple comparisons $P = 0.0003$) but no significant difference between the number of spiders in the core (median = 13) and semi-periphery ($P = 0.16$) or core and periphery ($P = 0.08$) (Fig. 3a). Median percentages for spiders in the three web regions were 31.70% in the core, 40.45% in the semi periphery, and 20.64% in the periphery.

The distribution of female size classes across web regions differed significantly from chance expectations (G-test, $P = 0.0004$). Small females were found in the periphery more often than expected (44.0 observed and 27.0 expected) and in the core less often than expected (16.0 observed and 29.2 expected), and large females were found in the periphery less often than expected (27.0 observed and 40.2 expected) (Table 4).

Females outnumbered males in every colony (Wilcoxon signed rank test, $P = 0.0001$, $n = 20$), and the female to male sex ratio ranged from 1.05 to 14 (median = 2.98, $n = 20$).

Colony aggression.—The number of aggressive interactions per individual (total number of aggressive interactions initiated by the female class divided by the total number of females of the size class) varied among the three female size classes (Friedman test, $\chi 2 = 2226$, df = 3, $P < 0.0001$, $n = 20$

Table 4.—Observed frequencies and expected frequencies based on proportions of *Philoponella republicana* females of different size classes in relation to regions within webs. N=20 colonies.

Region	Small Females	Medium Females	Large Females
Core			
Observed	16	129	54
Expected	29.17	113.47	56.37
Semi-periphery			
Observed	38	149	87
Expected	44.09	158.52	71.39
Periphery			
Observed	44	81	27
Expected	27	87.01	40.24

Table 5.—Frequency of female-female aggression within and between size classes. Observed frequencies are below the diagonal and expected frequencies are above the diagonal and in **boldface**. Data from all 20 colonies are combined here.

	Small Females	Medium Females	Large Females
Small Females	**10.51** 7	**47.44**	**18.11**
Medium Females	11	**109.67** 93	**86.65**
Large Females	16	53	**33.6** 124

colonies) (Fig. 3b). Large females were involved in more aggressive interactions (median = 1.33, $n = 20$ colonies) than medium-sized females (median 0.59, $n = 19$, Wilcoxon signed-rank tests with Holm's adjustment for multiple comparisons, $P = 0.05$) and small females (median = 0, $n = 15$, $P = 0.003$), but medium-sized and small females did not differ in aggression levels ($P = 0.07$, $n = 15$). Males were involved in more aggressive interactions (median = 0.52, $n = 20$) than small females (Wilcoxon signed rank test with Holm's adjustment for multiple comparisons, $P = 0.007$, $n = 15$), and fewer aggressive interactions than large females ($P = 0.05$, $n = 20$) but there was no significant difference between males and medium-sized females ($P = 0.98$, n =19). Sample sizes vary among tests because five colonies had no small females and one colony had no medium-sized females. Female size class variability was a significant positive predictor of total aggression and male-male aggression in the colony (Table 2).

Observed female-female aggression totals differed significantly from the expected (G-test, $P<0.0001$). The largest differences in expected and observed totals were in large female-large female aggressive interactions (124 observed and 33.6 expected), medium female-medium female aggressive interactions (11 observed and 47.44 expected), and large female-medium female aggressive interactions (53 observed and 86.65 expected, Table 5).

The number of aggressive interactions per individual varied among regions within the web (Friedman test, $\chi2 = 16.57$, df = 2, $P = 0.0003$) and tended to be highest in the semi-periphery, where most orb webs are located, and lowest in periphery (Fig. 3c). The number of aggressive interactions was lower in the periphery (median = 0.14, $n = 19$) than in the semi-periphery (median = 0.82, $n = 20$, Wilcoxon signed rank test with Holm's adjustment for multiple comparisons, $P = 0.004$) and core (median = 0.54, $n = 20$, $P = 0.004$), but did not differ significantly between the core and semi-periphery ($P = 0.28$). Sample sizes vary among tests because there were no spiders in the periphery of one colony.

While controlling for web size (PC1), the total number of aggressive interactions increased with colony size and female size class variability. The frequency of female-female aggression increased with the number of medium-sized and large females, and the number of prey snatch events also tended to increase with the number of large females in the colony (Table 2).

As predicted, the frequencies of male-male aggression and female-male aggression both decreased with the female-to-male sex ratio (Table 2). Female-to-male sex ratio had no effect on female-female aggression (Table 2). Male-male aggression also increased with an increase in female size class variability.

Intra-colony intrusion experiment.—We consistently observed high levels of aggression from resident females in orb webs and almost no aggression from resident females in connecting webs toward the simulated intruder females. In 17 trials, the resident stayed in the center of the orb web and shook and vibrated the web until the intruder withdrew. In the remaining 4 trials, the resident left the center and aggressively fought with the intruder until she moved off the orb web. The connecting web trials typically unfolded in one of the following ways: the two females sat very close together but did not interact, moving either very little or not at all (2 trials); the females did not interact overtly and slowly moved apart over the course of the 5-minute trial (8 trials); or the females came into very close contact, even physically touching through leg taps but did not display aggression (5 trials). In the four connecting-web trials in which aggression was observed, the duration of the behaviors was shorter than in the orb web trials. Resident females from orb webs performed more shakes (Wilcoxon test, $W = 0$, $P < 0.01$, $n_1 = 21$ orb webs, $n_2 = 19$ connecting webs; Fig. 4a) and vibrates ($W = 7$, $P < 0.01$, Fig. 4b) than resident females from the connecting web. The number of leg taps performed by the two groups did not differ significantly ($W = 214$, $P = 0.57$). The orb-web residents were also more likely than the connecting-web residents to be in the same position at the end of the trial with respect to their position at the beginning of the trial (Fisher's exact test, $P< 0.01$, Fig. 4c).

Translocation experiment.—We found no differences among translocation treatments in any of the behaviors recorded (Friedman tests, $P \geq 0.05$, $n = 10$ colonies; Table S1, online at https://doi.org/10.1636/JoA-S-20-093.s1). Whether the translocated spiders were taken from the same web, a proximal web, or a distal web, members of the receiving colonies in general did not interact with the translocated females very often. Across treatments, the median number of interactions ranged from 1 to 2.5 (Fig. 5a; for specific interactions, see Table S2, online at https://doi.org/10.1636/JoA-S-20-093.s2).

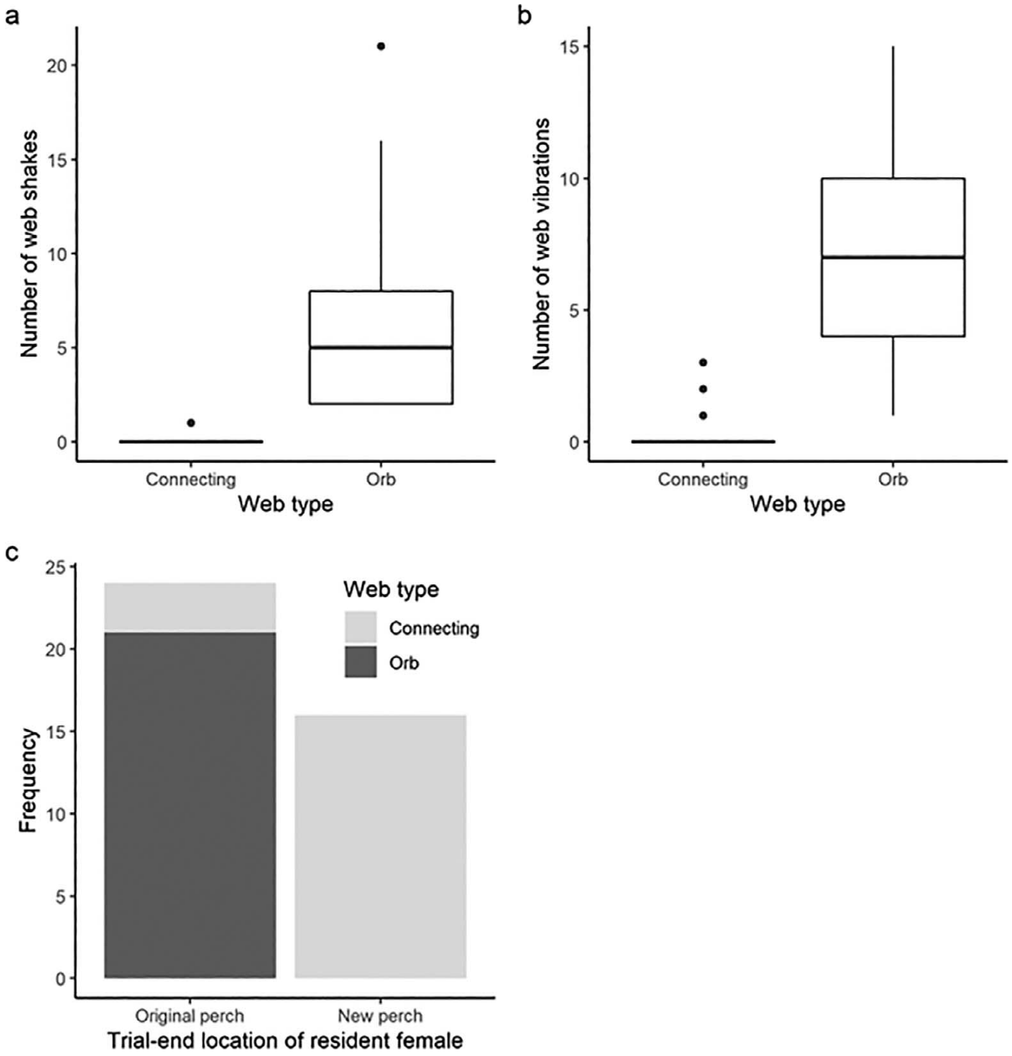

Figure 4.— Effects of web type on the responses of resident females to simulated intruders. In (c) the height of the bars represents the total number of resident females observed in each ending position across all trials. Box plot definitions as in Fig. 3.

Most interactions that did occur were aggressive (Fig. 5b, Table S2).

DISCUSSION

Conspecific aggression can be an indicator of cooperation and competition within a group, so examining antagonistic behaviors can help elucidate the balance between these two types of behaviors in colonial spiders (Opell 1979; Binford & Rypstra 1992; Uetz & Hieber 1997; Avilés & Guevara 2017). We studied *P. republicana*, reported to display both tolerance and discrimination towards conspecifics (Opell 1979; Binford & Rypstra 1992), to identify and quantify the impact of aggression on colony dynamics. We studied 34 colonies in total and performed colony censuses and translocation experiments to understand aggression. As in other colonial spiders, aggression between colony members was common (Buskirk 1975a, b; Rayor & Uetz 2000; Lubin & Bilde 2007; Avilés & Guevara 2017). The frequency of aggressive interactions was higher in optimal hunting areas (i.e., orb webs throughout the colony, both web types in the semi-periphery), colonies with less female-biased sex-ratios, and colonies with a greater number of large and medium females. However, *P. republicana* also demonstrated some characteristics that may indicate greater levels of cooperation. All colonies had female-biased secondary sex ratios, and a larger bias was associated with both reduced male-male and female-male competition. Even though spiders individually defended orb webs, they moved freely in the connecting web, which may provide a setting for spiders to jointly accomplish tasks such as colony web construction (Uetz & Hieber 1997). We found no evidence for group closure in *P. republicana* (i.e., the spiders did not discriminate between outsiders and colony mates), but to the best of our knowledge, group closure has not been reported in social spiders either. Overall, the patterns of aggression in *P. republicana* reveal a balance between aggression and tolerance towards conspecifics.

Aggression was concentrated in orb webs and the semi-periphery.—Our intra-colony intrusion experiment uncovered elevated levels of aggression among orb-web holders towards individuals found within their territories. As in the colonial species *M. ocellatus* (Buskirk 1975a, b), *P. republicana* orb web

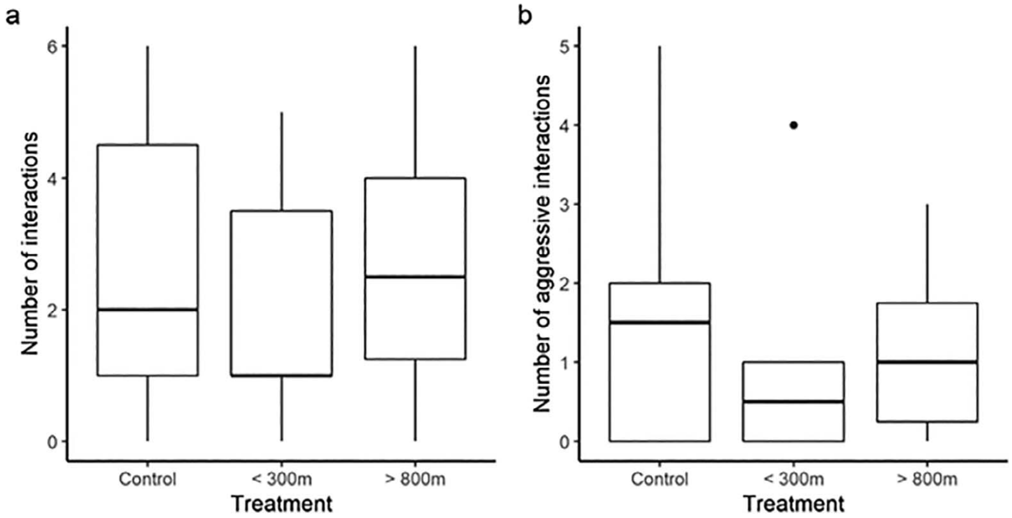

Figure 5.— Translocation experiment results. (a) Variation in the total number of interactions between colony members and translocated individuals. (b) Variation in the total number of aggressive interactions between colony members and translocated individuals. Box plot definitions as in Fig. 3.

holders shook and vibrated their webs in response to approaching conspecifics. However, residents in connecting webs usually only displayed non-aggressive behavior (e.g., leg tapping) toward intruders, if they responded at all.

Our census data showed that the highest levels of aggression occurred in the semi-periphery, suggesting increased competition for this optimal space (Rayor & Uetz 1990). The highest density of orb webs was also found in this region. Although the periphery also contained orb webs, we observed less aggression and more small females in that region (Figure 3). This may be indicative of an adaptive spacing pattern in which smaller individuals avoid competition by building their orb webs in less-contested areas of the web, similar to the colonial spiders *Cyrtophora citricola* and *Metepeira incrassata* (Pickard-Cambridge, 1903) (Rayor & Uetz 2000; Yip et al. 2017). Alternatively, this pattern could be the result of exclusion of smaller spiders from preferred regions by larger spiders.

The lack of aggression in the core and in the connecting webs provides quantitative evidence for the use of communal retreats, consistent with observations from previous studies (Lubin 1980; Binford & Rypstra 1992). *Philoponella republicana* individuals sat in very close proximity to one another in communal retreats without displaying any strong signs of aversion to their nearby neighbors, as they did in orb webs. *Philoponella oweni* (Chamberlin, 1924) (Smith 1983) and an unidentified species of *Philoponella* from southern Cameroon (Breitwisch 1989) have also been observed to use communal retreats.

Aggression was not dependent on colony web size.—Our analysis of colony web size also revealed interesting colony dynamics in *P. republicana*. While we hypothesized that large colony webs would reduce competition for prey, the total number of aggressive interactions per colony did not co-vary with colony web size, even though colony web size and colony size varied independently. This result could be explained by environmental factors. For instance, high prey availability in the wet season might mask differences in prey capture efficiency between colony web sizes. Moreover, if larger colony webs have more access to prey, spiders in large colony webs could have more energy to expend on aggression to retain captured prey, negating our prediction that larger colony webs would have less competition. Alternatively, aggression related to prey might be expressed more gradually over time; the number of immature spiders that eventually remain in a colony as subadults and adults might be dependent on food resources. Colony populations might grow in size until they reach the limit that local food supplies can support (e.g., Smith 1983). In that case the amount of prey per capita and level of aggression over prey might stay relatively constant across a range of colony sizes.

Colonies with more large and medium females had more aggression.—Female-female aggression positively correlated with the number of large females and medium females in the colony (Table 2). Medium and large females participated the most in prey snatching and fighting over captured insects. This finding is consistent with the widespread pattern that larger individuals have an advantage in aggressive interactions because they are more likely to win contests (Potter et al. 1976; Riechert 1978; Christensen & Goist 1979; O'Neill 1983). The increased aggression observed in larger females could make colonies more resilient. Previous studies in both colonial and social spiders have found that dominant, large individuals consistently have greater access to prey (Hodge & Uetz 1995; Ulbrich & Henschel 1999). Ulbrich & Henschel (1999) suggest that in conditions of low prey density, large, dominant individuals may still be able to acquire enough food, which ensures the survival of the colony. In contrast, if individuals in a colony had equal access to prey, no single spider would be able to eat enough to reproduce, and the entire colony would die out.

Colonies with more female-biased sex ratios had lower aggression.—Lubin (1980) reported finding a primary 1:1 sex ratio in *P. republicana*. However, the secondary sex ratios we measured in *P. republicana* were female-biased. A potential explanation for this is that males are more susceptible to predation or there is male-biased dispersal in this species

(Lubin & Bilde 2007). Nevertheless, the levels of both male-male and female-male aggression decreased as the secondary sex ratio became more female-biased, which could be explained by reduced mating competition (Binford & Rypstra 1992). Secondary sex ratio did not affect female-female aggression, suggesting that this type of aggression arises from factors other than mating competition.

Colonies did not exhibit group closure.—Regardless of the translocation treatment, colony members did not display elevated levels of aggression towards translocated females compared to the same-colony controls, meaning *P. republicana* did not exhibit group closure. These results are similar to those found in the social spider *Anelosimus eximius* (Keyserling, 1884) (Pasquet et al. 1997). This does not support our hypothesis that aggressive behaviors would be more frequent towards outsiders than towards members of the same colony. A previous study suggests *P. republicana* disperses in sibling groups and thus within-group relatedness should be higher than between-group relatedness (Lubin 1980). Yet, colony members still responded similarly to all translocated females. Shared natal sites among individuals from different colonies may explain this result, since spatial or genetic relatedness decreases aggression. However, because of the relatively large distances between colonies in the distal treatment of our study, this explanation seems unlikely. Pasquet et al. (1997) hypothesized that the social spider species they studied (*A. eximius*) does not exhibit group closure because (a) it is not part of the spiders' natural behavior to move into existing colonies, so there was no selection on the spiders to evolve a discriminatory response to invaders; (b) spiders lack the variation in chemical compounds between colonies needed to recognize that individuals are invaders or not; and (c) group closure is required in social insects that compete with other colonies for resources and since all of the spiders' feeding is limited to their own colonies, there is no competition with other colonies. These hypotheses may also apply to *P. republicana*. This experiment was limited in that we did not examine how spiders respond to intruders in varying conditions. While group-living spiders have not been found to exhibit group closure under normal conditions, other studies have demonstrated that extenuating circumstances can cause colonies to preferentially discriminate against outsiders (Yip & Rayor 2014). For example, the social spider *Australomisidia ergandros* (Evans, 1995) (Thomisidae) was more likely to cannibalize unfamiliar conspecifics, but only under conditions of starvation (Evans 1995, 1999). Future research on *P. republicana* should focus on the chemical compounds expressed by individuals from different colonies, dispersal distances, dispersal group composition, genetic relatedness between colony mates, and behaviors towards immigrants in varied circumstances and extended periods of time to better understand the apparent lack of group closure in this species.

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SUPPLEMENTAL MATERIALS

Table S1.—Effects of inter-colony translocation treatment on responses of *Philoponella republican*a. Online at https://doi.org/10.1636/JoA-S-20-093.s1

Table S2.—Results of inter-colony translocation experiment. Online at https://doi.org/10.1636/JoA-S-20-093.s2

LITERATURE CITED

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

Alexander RD. 1974. The evolution of social behaviour. *Annual Review of Ecology and Systematics* 5:323–383.

Alves-Costa CP, Gonzaga MO. 2001. Prey capture and spatial distribution of *Philoponella vittata* (Araneae Uloboridae) in host webs. *Ethology Ecology & Evolution* 13:239–246.

Avilés L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498. *In* Evolution of Social Behaviour in Insects and Arachnids. (J. Choe & B. Crespi, eds.). Cambridge University Press, Cambridge.

Avilés L, Guevara J. 2017. Sociality in Spiders. Pp. 188–222. *In* Comparative Social Evolution. (DR Rubenstein, P Abbot, eds.). Cambridge University Press, Cambridge.

Avilés L, Purcell J. 2012. The evolution of inbred social systems in spiders and other organisms: from short-term gains to long-term evolutionary dead ends? *Advances in the Study of Behavior* 44:99–133.

Binford GJ, Rypstra AL. 1992. Foraging behavior of the communal spider, *Philoponella republicana* (Araneae: Uloboridae). *Journal of Insect Behavior* 5:321–335.

Breitwisch R. 1989. Prey capture by a west African social spider (Uloboridae: *Philoponella sp.*). *Biotropica* 21:359–363.

Buskirk RE. 1975a. Coloniality, activity patterns, and feeding in a tropical orb-weaving spider. *Ecology* 56:1314–1328.

Buskirk RE. 1975b. Aggressive display and orb defence in a colonial spider, *Metabus gravidus*. *Animal Behaviour* 23:560–567.

Christensen TE, Goist KC Jr. 1979. Costs and benefits of male-male competition in the orb weaving spider, *Nephila clavipes*. *Behavioral Ecology and Sociobiology* 5:87–92.

Clutton-Brock TH, Parker GA. 1995. Sexual coercion in animal societies. *Animal Behavior* 49:1345–1365.

Evans TA. 1995. Two new species of social crab spiders of the genus *Diaea* from eastern Australia, their natural history and distribution. *Records of the Western Australian Museum, Supplement* 52:151–158.

Evans TA. 1999. Kin recognition in a social spider. *Proceedings of the Royal Society of London* 266:287–292.

Fisher RA. 1930. The Genetic Theory of Natural Selection. Clarendon Press, Oxford.

Gardner A, Grafen A. 2009. Capturing the superorganism: a formal theory of group adaptation. *Journal of Evolutionary Biology* 22:659–671.

Hochberg Y, Benjamini Y. 1990. More powerful procedures for multiple significance testing. *Statistics in Medicine* 9:811–818.

Hodge MA, Uetz GW. 1995. A comparison of agonistic behaviour of colonial web-building spiders from desert and tropical habitats. *Animal Behaviour* 50:963–972.

Holm S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.

Kader GD, Perry M. 2007. Variability for categorical variables. *Journal of Statistics Education* 15:2, DOI: 10.1080/10691898.2007.11889465

Kassambara A. 2020. ggpubr: ′ggplot2′ Based Publication Ready Plots. R package version 0.4.0. https://CRAN.R-project.org/package=ggpubr

Krause J, Ruxton GD. 2002. Living in Groups. Oxford, Oxford University Press.

Kvarnemo C, Ahnesjö I. 1996. The dynamics of operational sex ratios in competition for mates. *Trends in Ecology and Evolution* 11:404–408.

Lehmann L, Keller L, West S, Rose D. 2007. Group selection and kin selection: Two concepts but one process. *Proceedings of the National Academy of Sciences of the United States of America* 104:6736–6739.

Lion S, Jansen VAA, Day T. 2011. Evolution in structured populations: beyond the kin versus group debate. *Trends in Ecology and Evolution* 26:193–201.

Lubin YD. 1980. Population studies of two colonial orb-weaving spiders. *Zoological Journal of the Linnean Society* 70:265–287.

Lubin YD, Bilde T. 2007. The evolution of sociality in spiders. *Advances in the Study of Behavior* 37:83–145.

Marshall JAR. 2011. Group selection and kin selection: formally equivalent approaches. *Trends in Ecology and Evolution* 26:325–332.

Masumoto T. 1998. Cooperative prey capture in the communal web spider, *Philoponella raffayi* (Araneae, Uloboridae). *Journal of Arachnology* 26:392–396.

McCook HC. 1889: American Spiders and their Spinning Work. A Natural History of the Orbweaving Spiders of the United States, with Special Regard to their Industry and Habits.

Nentwig W. 1985. Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). *Behavioral Ecology and Sociobiology* 17:79–85.

O'Neill KM. 1983. The significance of body size in territorial interactions of male beewolves (Hymenoptera: Sphecidae, *Philanthus*). *Animal Behaviour* 31:404–411.

Opell B. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. *Bulletin of the Museum of Comparative Zoology* 148:443–549.

Pasquet A, Trabalon M, Bagnères AG, Leborgne R. 1997. Does group closure exist in the social spider *Anelosimus eximius*? Behavioural and chemical approach. *Insectes Sociaux* 44:159–169.

Potter DA, Wrensch DL, Johnston DE. 1976. Aggression and mating success in male spider mites. *Science* 193:160–161.

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rayor LS. 1996. Attack strategies of predatory wasps (Hymenoptera: Pompilidae; Sphecidae) on colonial orb web-building spiders (Araneidae: *Metepeira incrassata*). *Journal of the Kansas Entomological Society* 69:67–75.

Rayor LS, Uetz GW. 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. *Behavioral Ecology and Sociobiology* 27:77–85.

Rayor LS, Uetz GW. 1993. Ontogenetic shifts within the selfish herd: predation risk and foraging trade-offs change with age in colonial web-building spiders. *Oecologia* 95:1–8.

Rayor LS, Uetz GW. 2000. Age-related sequential web building in the colonial spider *Metepeira incrassata* (Araneidae): an adaptive spacing strategy. *Animal Behaviour* 59:1251–1259.

Redd R. 2021. ragree: Rater agreement. R package version 0.0.4.https://github.com/raredd/ragree

Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.

Riechert SE. 1978. Games spiders play: behavioral variability in territorial disputes. *Behavioral Ecology and Sociobiology* 3:135–162.

Rypstra AL. 1979. Foraging flocks of spiders: a study of aggregate behavior in *Cyrtophora citricola* Forskål (Araneae; Araneidae) in West Africa. *Behavioral Ecology and Sociobiology* 5:291–300.

Schneider JM. 1995. Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). *Insectes Sociaux* 42:237–248.

Smith DRR. 1983. Ecological costs and benefits of communal behavior in a presocial spider. *Behavioral Ecology and Sociobiology* 13:107–114.

Sprent P, Smeeton NC. 2007 Applied Nonparametric Statistical Methods, 4th edition, Chapman & Hall/CRC, New York.

Uetz GW. 1988. Group forating in colonial web-building spiders. *Behavioral Ecology and Sociobiology* 22:265–270.

Uetz GW. 1989. The "ricochet effect" and prey capture in colonial spiders. *Oecologia* 81:154–159.

Uetz GW, Hieber CS. 1997. Colonial web-building spiders: balancing the costs and benefits of group-living. Pp. 458–475. *In* The Evolution of Social Behavior in Insects and Arachnids. (JC Choe, BE Crespi, eds.). Cambridge University Press, Cambridge.

Ulbrich K, Henschel JR. 1999. Intraspecific competition in a social spider. *Ecological Modeling* 115:243–251.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. 4th edition. Springer, New York. ISBN 0-387-95457-0

Verhoeven KJ, Simonsen KL, McIntyre LM. 2005. Implementing false discovery rate control: increasing your power. *Oikos* 108:643–647.

Wickham, H. 2007. Reshaping data with the reshape Package. *Journal of Statistical Software* 21(12), 1–20. URL http://www.jstatsoft.org/v21/i12/.

Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wilke CO. 2019. cowplot: Streamlined Plot Theme and Plot Annotations for ′ggplot2′. R package version 1.0.0. https://CRAN.R-project.org/package=cowplot

World Spider Catalog. 2022. World Spider Catalog. Version 23.5. Natural History Museum, Bern. http://wsc.nmbe.ch/, accessed on 24 July, 2022. doi: 10.24436/2

Ydenberg RC, Giraldeau LA, Falls JB. 1988. Neighbours, strangers, and the asymmetric war of attrition. *Animal Behaviour* 36:343–347.

Yip EC, Rayor LS. 2014. Maternal care and subsocial behaviour in spiders. *Biological Reviews* 89:427–449.

Yip EC, Levy T, Lubin Y. 2017. Bad neighbors: hunger and dominance spacing and position in an orb-weaving spider colony. *Behavioral Ecology and Sociobiology* 71:1–11.

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