



Articles

Multiple structures interactively influence prey capture efficiency in spider orb webs

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Building structures and aggregating can increase an animal's fitness, but the benefits come at a cost. Some orb web spiders build multiple structures or build in aggregations, which may have the same effect on prey capture success as the addition of a structure. As these structures often appear together, they may bestow interactive benefits not realized if the structures were added alone. We performed field experiments to investigate whether the multiple structures associated with the orb webs of two spider species provide interactive benefits. The orb web spider *Nephila clavata* adds barrier webs and prey carcass decorations to its webs. We manipulated their webs in the field by removing either, both or neither the barrier webs or the carcass decorations. We found that prey interception rate was greatest when neither barrier webs nor carcasses were present but, for the prey caught, the prey retention rate was greatest with both structures present. Another orb web spider, *Cyclosa mulmeinensis*, adds prey carcass decorations and forms aggregations. We manipulated the decorations and aggregations of *C. mulmeinensis* in the field to determine their interactive influences. In solitary webs and webs with decorations, prey capture rates were lower than those without structures. These negative foraging effects, however, did not exist in decorated webs that were in aggregations. Our results thus show that multiple structures, individually, are costly, but interactively they provide substantial benefits.

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Animals build a diversity of structures, such as nests, burrows, traps and retreats, from biological or inert materials, secretions or wastes (Hansell 2005). A structure provides benefits such as improved reproductive output, shelter, thermoregulation, protection from predators or foraging gain, but these benefits come at a cost (Korb 2003; Hansell 2005; Manicom et al. 2008; Brown & Funk 2010). This cost includes the energy expended gathering and/or synthesizing the materials, time taken away from foraging, reproduction or social activities, exposure to predation and physiological stress (Korb 2003; Hansell 2005; Mainwaring & Hartley 2009). Secondary structures added to a construction may provide additional benefits that counteract the cost. For example, aromatic or toxic plant material or protective turrets may be added to preconstructed retreats of birds, spiders or beetles as extra protection from predators (Lafuma et al. 2001; Hansell 2005; Williams et al. 2006; Brown & Funk 2010). Despite the benefits, the building of multiple structures by animals is rare, suggesting that the overall cost of construction is usually greater than the

accumulated benefits (Lens et al. 1994; Korb 2003; Hansell 2005; Manicom et al. 2008). Multiple structures, however, may together provide benefits that are not realized when each acts alone. To our knowledge, however, no study aiming to understand the evolutionary significance of coexisting structures has accounted for combined or interacting effects. This failure to account for interactions may have led to unrealistic conclusions (e.g. the benefit of one structure depends upon the presence of a second structure, so studying each structural component in isolation is problematic).

Spider webs are structures for which many of the costs and benefits of their construction can be estimated (Craig 2003). The principal cost for a spider building a web is the energetic cost of silk synthesis and web-building activity (Prestwich 1977; Tanaka 1989; Craig 2003). Building webs additionally consumes and diverts resources such as energy, nutrients, amino acids and time away from somatic maintenance (Craig 2003). The spider web is, thus, a delicate balance between maximizing prey capture efficiency and minimizing the cost. Additionally, spiders often add conspicuous secondary or tertiary structures to their webs (Eberhard 1990; Herberstein et al. 2000; Manicom et al. 2008) and some species aggregate (Whitehouse & Lubin 2005), which may serve to avoid predators or improve foraging gain in a similar way to a secondary

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or tertiary web structure (Uetz 1989, 1996; Aviles & Bukowski 2006). Thus, web-building spiders are excellent model organisms for testing hypotheses regarding the interactive benefits of multiple components in animal structures.

When multiple webs are found in close proximity, insects that bounce off or fly through any one web are likely to have their velocity reduced, thereby rendering them easily caught by another web (Uetz 1988, 1989; Henaut et al. 2001; Yip et al. 2008). The more webs in the vicinity, the more likely it is that an insect will eventually be caught. This phenomenon is described as the 'ricochet effect' (Uetz 1989) and has been proposed as having an evolutionary benefit associated with spider web aggregations (Uetz 1989, 1992, 1996). Aggregated webs may, additionally, allow spiders to share silk with their neighbours and reduce the synthesis costs of web building, improve web mechanics and amplify the signal of any decorations (Craig 1991; Fernandez Campon 2007; Yip et al. 2008). Aggregations, none the less, are rare in spiders, owing to substantial associated costs (Uetz 1996). These costs include

competition for profitable food, increased kleptoparasitic load and inbreeding depression (Elgar 1989; Uetz 1996; Whitehouse & Lubin 2005; Aviles & Bukowski 2006; Bilde et al. 2007).

Decorating the web with prey carcasses and other materials is a peculiar example of a secondary structure added to the webs of *Nephila* spp. and *Cyclosa* spp. (Herberstein et al. 2000; Eberhard 2003; Griffiths et al. 2003; Bjorkman-Chiswell et al. 2004; Chou et al. 2005; Tan et al. 2010). Prey attraction via odour emission has been described as the principal function of prey carcass decorations in *Nephila* (Bjorkman-Chiswell et al. 2004). Many *Nephila* spp. construct barrier webs onto which the prey carcass decorations are added (Fig. 1). Barrier webs may function to protect and/or shelter the spider, provide mechanical support to the web or aid moisture gathering (Lubin 1975; Higgins 1992). Additionally, they increase prey capture efficiency via 'ricochet effects' (Higgins 1992). The interactive fitness benefits afforded *Nephila* spiders by building barrier webs and adding prey carcass decorations are, however, unknown. *Cyclosa* spp. use prey carcasses, detritus or eggsacs to

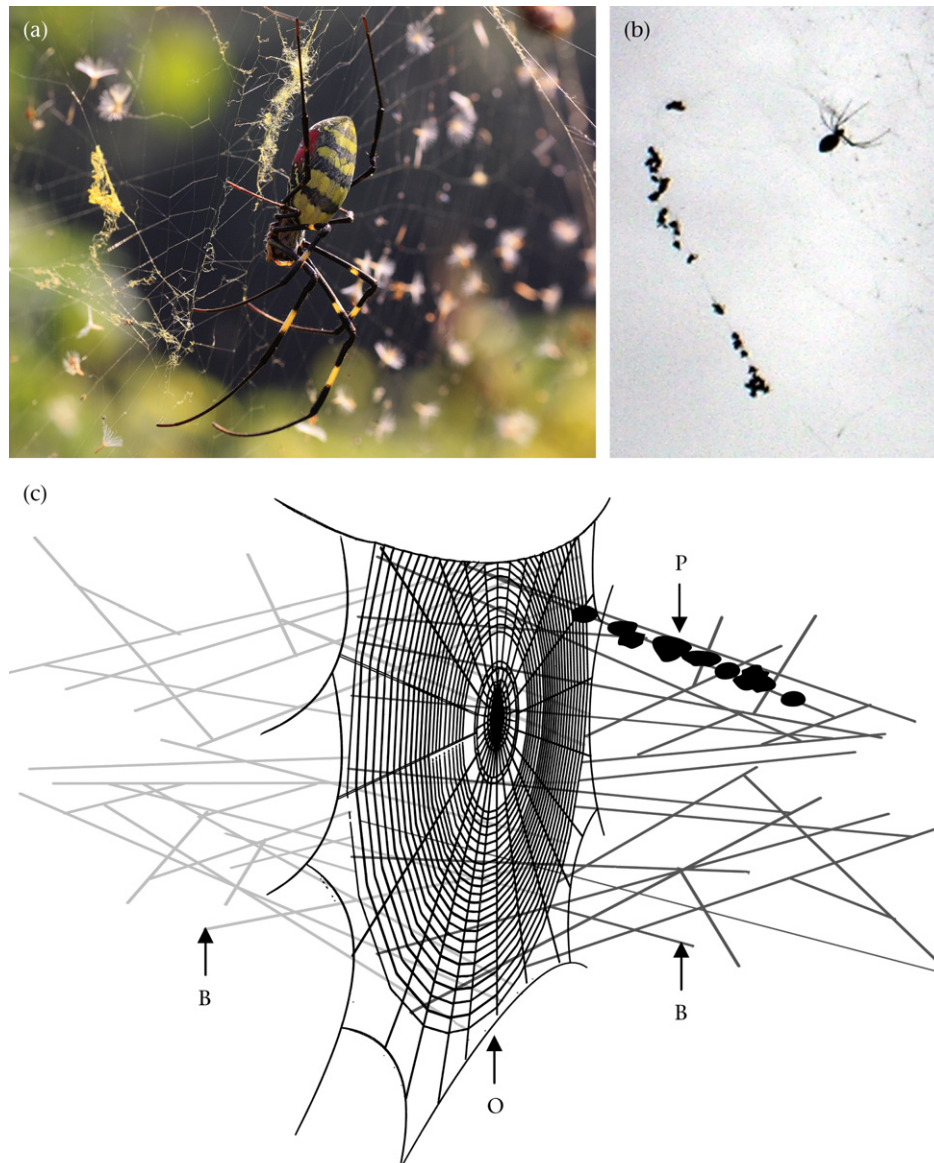


Figure 1. (a) Female *Nephila clavata* and (b) prey carcass decorations in a web of *N. clavata*. (c) Schematic drawing of a typical web complex constructed by female *N. clavata*. O: orb web; B: barrier web; P: prey carcass decorations.

build web decorations, which principally serve as camouflage or act as decoys to predators (Herberstein et al. 2000; Eberhard 2003; Chou et al. 2005; Tseng & Tso 2009). The principal costs of decorating are associated with silk production and decreased prey attraction (Chou et al. 2005; Nakata 2009; Tan & Li 2009). Most *Cyclosa* are solitary; however, *C. mulmeinensis* often forms aggregations of 10–30 individuals, presumably to increase prey capture. The interactive effects of building prey carcass decorations and aggregating have never been quantified in *C. mulmeinensis*. *Argiope* spp. may build decorations in aggregations, but there is conflicting evidence about the importance of this. Some research suggests that the signal function of the decoration is amplified in aggregations (Craig 1991), but other research suggests that it is not (Justice et al. 2005; Rao et al. 2009). *Nephila* and *Cyclosa* rebuild their orb web daily, but do not dismantle the decorations or the barrier webs. Hence it appears that substantial costs render it unprofitable to build these structures repeatedly (Tanaka 1989).

To investigate whether multiple components interactively influence orb web prey capture efficiency, we performed field experiments to examine the interactions between prey carcass decorations and barrier webs in *Nephila clavata*, and between aggregations and prey carcass decorations in *C. mulmeinensis*. As we hypothesized that the barrier webs of *N. clavata* and the aggregations of *C. mulmeinensis* serve similar functions, that is, to increase prey capture efficiency of the web via 'ricochet effects', we treated aggregations as a form of barrier web. We assessed prey interception and retention rates in *N. clavata* and *C. mulmeinensis* webs by removing either, both or neither the barrier web or the carcass decorations. We predicted that if barrier webs/aggregations and decorations interact to facilitate foraging success, then their combined effect should be greater than each of their effects in isolation. If barrier webs and decorations do not interact to facilitate foraging success, then their combined effect should be no more than the sum of their effects in isolation. We consider no effect on foraging success or a reduction in foraging success as equally detrimental.

METHODS

Nephila clavata Web Manipulations

We determined the foraging success for *N. clavata* webs when a spider was present on the web by collecting 15 days of data on individual spiders in the forest around Sun Moon Lake, Chi-Tou Recreational Area, Taiwan (23°36'N, 120°48'E) in October 2005 and January 2006. *Nephila clavata* (Fig. 1a) webs are usually composed of vertical orb webs with barrier webs on both sides of the orb and partially consumed prey carcasses assembled in a line on the barrier web (Fig. 1b, c). Each set of field experiments were conducted for 15 days. We randomly selected webs to generate four treatment groups: (1) barrier webs and prey carcasses left intact (the BP treatment group); (2) both the carcasses and barrier webs removed (the O treatment group); (3) barrier webs removed but carcasses left intact (the P treatment group); and (4) carcasses removed but barrier webs left intact (the B treatment group). We used forceps and burning incense to remove barrier webs and carcasses, leaving the orb web unaffected. Spiders were removed from their webs and their cephalothorax length was measured using callipers (to the nearest 0.01 mm) to ensure similar-sized spiders were used in all tests. As we were interested in the influence of barrier webs and prey carcass decorations on prey capture in *N. clavata* webs when *N. clavata* was occupying the web, all spiders were returned to their webs to forage after being measured. *Nephila clavata* are brightly coloured (Fig. 1a) with coloration varying slightly among individuals. We, therefore, repeatedly used the same individuals for the same manipulations over the entire study period to avoid the potential for body

coloration (Tso et al. 2002, 2004) and site-specific prey availabilities to influence prey attraction rates. The spiders were not individually marked to avoid altering the coloration of the spider's body; instead, web location was marked with coloured flagging tape. When we were forced to find a replacement spider because a particular spider had moved or died, we replaced it with a spider of similar size and colour, based on measurements, from a similar location. As the webs (not the spiders) were the subject of our manipulations and each web was built anew each day, all manipulated webs were considered independent samples.

Cyclosa mulmeinensis Web Manipulations

The site for this research was a coastal rock platform near Yu-Ren Village on the north coast of Orchid Island (22°03'N, 121°32'E), southeast of Taiwan, in September 2006. All age classes build vertically oriented prey carcass decorations, although adult females may add eggsacs to the upper half of the web and prey carcasses to the lower half (Fig. 2a). The study area experiences constant strong offshore winds and many *C. mulmeinensis* there build their webs in aggregations (Fig. 2b). We created the following treatment groups ($N = 31$ for each): (1) aggregated webs with decorations left intact (the BP treatment group); (2) solitary webs with decorations removed (the O treatment group); (3) solitary webs with decorations left intact (the P treatment group); and (4) aggregated webs with decorations removed (the B treatment group). To create solitary webs in the study site, we removed all the neighbouring spiders and webs from a focal spider in an aggregation. The removal of web components and spider body measurements were done as described for '*N. clavata* webs' with the same spider used repeatedly unless the spider had moved or died.

Web Area Calculation

We measured (using a tape measure) the radius of *N. clavata* and *C. mulmeinensis* orb webs in four cardinal directions (up, down, left and right) to calculate the orb web catching area using the formula (Herberstein & Tso 2000):

$$\left[\frac{1}{2} \pi r_{\text{au}}^2 - \frac{1}{2} \pi (Hr_{\text{u}})^2 \right] + \left[\frac{1}{2} \pi r_{\text{al}}^2 - \frac{1}{2} \pi (Hr_{\text{l}})^2 \right]$$

$$\text{where } r_{\text{au}} = \frac{r_{\text{u}} + \frac{d_{\text{h}}}{2}}{2} \text{ and } r_{\text{al}} = \frac{r_{\text{l}} + \frac{d_{\text{h}}}{2}}{2}$$

where r_{au} is the adjusted radius of the upper orb half, r_{al} is the adjusted radius of the lower orb half, r_{u} is the radius of the upper orb half, r_{l} is the radius of the lower orb half, d_{h} is the horizontal orb diameter, Hr_{u} is the radius of the upper hub half and Hr_{l} is the radius of the lower hub half.

Video Processing and Statistical Analyses

We placed Sony TRV 118 Hi-8 video cameras 1–2 m away from all webs. Video cameras were set up at angles to the web to maximize the focus on the spider and web area within the constraints of the surrounding habitat, with most of the cameras set up approximately perpendicular to the web. The cameras recorded all insect prey intercepted by webs and consumed by spiders between 0900 and 1700 hours. We ceased recording if it rained or other adverse conditions occurred. Video footage was viewed in the laboratory at Tunghai University on a computer or television. The area of web visible within the field of view on the monitor/television was estimated using spider size as a reference for all footage. All prey interception and capture events were

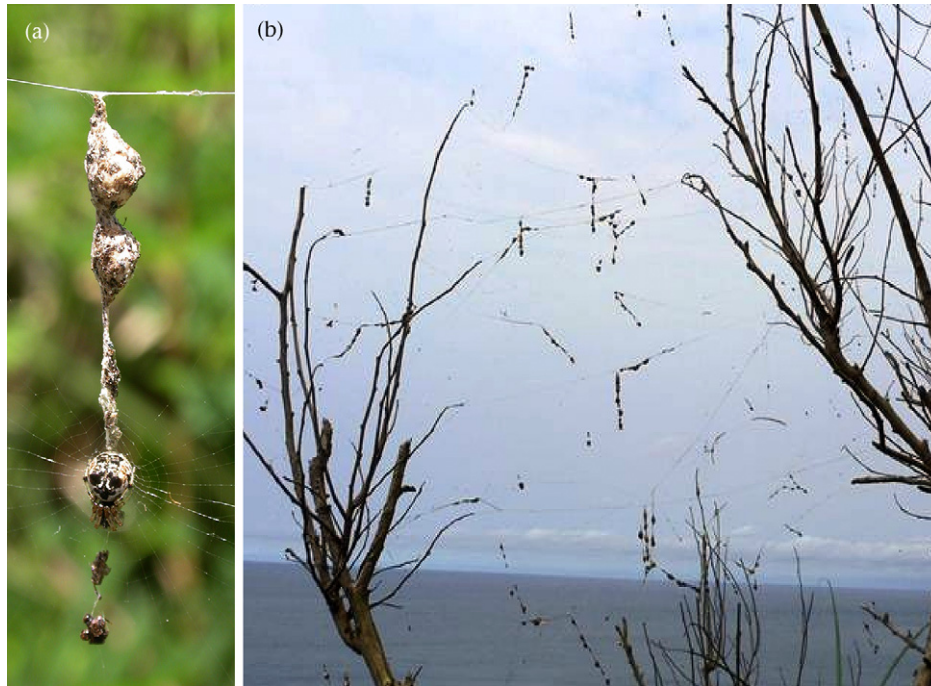


Figure 2. (a) Female *Cyclosa mulmeinensis* with eggsac and prey carcass decorations on web. (b) *Cyclosa mulmeinensis* in an aggregation with decorations on the webs in a typical habitat on Orchard Island, Taiwan.

recorded. We defined an interception event as prey briefly interacting with the web and prey capture as prey being entangled in the web for >5 s. We did not distinguish between prey interception and prey capture in *C. mulmeinensis* webs because it was not possible to ascertain whether a captured prey had first interacted with another web when in an aggregation. Prey length was estimated using spider body length as a reference in both studies. Prey interception and capture rates were determined as the number of prey intercepted or captured/h per 100 cm² of web capture area. Prey capture efficiency was defined as the proportion of insects intercepted that were retained in the web. Too few predators were observed interacting with webs or spiders in either study ($N = 4$ for *N. clavata* and $N = 5$ for *C. mulmeinensis*) to incorporate them into our analyses.

To compare the prey interception and capture rates of *N. clavata* BP, P and B webs with those of O webs, because parametric tests were not appropriate (data were not normally or Poisson distributed, even after log and probit transformations), we used Kruskal–Wallis nonparametric tests and Dunn's post hoc comparisons. In Dunn's tests, calculations of observed Q and critical Q' values and statistical significance followed Zar (1999). We used one-tailed tests to perform multiple post hoc comparisons for the following reason. In this study, we tested the hypothesis that barrier webs and decorations combine to increase foraging. Adding these structures uses time, energy and silk (material) so the spider experiences a cost or debt when building them. We wanted to know if that debt is paid back or exceeded (i.e. the spiders gain foraging benefits) when two structures are built. Should we find no foraging benefit, a debt is incurred by the spider, so building the construction is detrimental. Should there be a negative effect on foraging, a debt is still encountered by the spider and building the construction is still detrimental. Since no effects or negative effects are both detrimental to the spider, they can be regarded as equivalently negative outcomes (Ruxton & Neuhauser 2010). Therefore, the one-tailed Dunn's test is biologically relevant to perform to test the interactive benefit of a spider adding multiple structures to its web.

To compare the prey capture rates of *C. mulmeinensis* BP, P and B webs with those of O webs, we used two-way analysis of variance (ANOVA) with pairwise least significant difference (LSD) post hoc comparisons. One-way ANOVA and LSD post hoc comparisons were also used to compare the size of prey intercepted and caught by *N. clavata* webs across the four treatments. Kolmogorov–Smirnov tests and Levene's tests were used to test for a normal distribution and homogeneity of variances, respectively. A chi-square test of homogeneity was used to compare prey capture efficiency between the four *N. clavata* treatments. Too few observations were made of prey retention to calculate and compare prey capture efficiency for the *C. mulmeinensis* web treatments.

RESULTS

Nephila clavata Webs

We viewed a total of 1226 h of video footage: 314 h for the BP treatment ($N = 54$ webs), 276 h for the O treatment ($N = 41$ webs), 292 h for the P treatment ($N = 55$ webs) and 344 h for the B treatment ($N = 51$ webs). We found significant differences between the prey interception (O treatment $>$ all other treatments; Table 1) and prey capture rates (O treatment = BP treatment $>$ all other treatments; Table 1, Fig. 3a). We found a significant difference between the prey capture efficiencies of the four treatments ($\chi^2_{196} = 964.51$, $P < 0.0001$). More than 68% of prey intercepted by the BP webs was captured, but the prey capture efficiency for the other treatments ranged from 35% for the O treatment and P treatment to 25% for the B treatment (Fig. 3a). We found a significant difference in the size of prey intercepted ($F_{3,686} = 4.406$, $P = 0.007$) and captured ($F_{3,450} = 3.674$, $P = 0.012$) among the four treatments (Fig. 3b). Prey intercepted by webs in the BP and P treatments were similar in size, and larger than those in the other two treatments (Table 2). Prey captured in the B treatment were significantly smaller than those captured in webs from the other three treatments, which all caught similar-sized prey (Table 2, Fig. 3b).

Table 1

Results of Kruskal–Wallis (K–W) and post hoc multiple comparisons: one-tailed Dunn's test comparing prey interception and capture rates of *Nephila clavata* webs (number of prey intercepted or captured/h per 100 cm² web area) in four treatment groups

Comparisons	Prey interception rates		Prey capture rates	
	K–W statistic/ Q vs Q' (1)0.05.4	Significant	K–W statistic/ Q vs Q' (1)0.05.4	Significant
	Overall	$\chi^2_3=9.373$	$P=0.025$	$\chi^2_3=18.364$
O vs BP	2.939>2.128	Yes	1.562<2.128	No
O vs P	3.921>2.128	Yes	2.725>2.128	Yes
O vs B	3.149>2.128	Yes	2.395>2.128	Yes

BP: webs containing both barrier webs and prey carcass decorations; O: webs with both the barrier web and prey carcasses removed; P: webs with barrier web removed leaving only prey carcass decorations; B: webs with the prey carcasses removed leaving only barrier webs.

Cyclosa mulmeinensis Webs

A total of 750 h of video footage of *C. mulmeinensis* webs was viewed: 155 h for the BP treatment, 203 h for the O treatment, 194 h for the P treatment and 198 h for the B treatment ($N = 31$ for each). We found that the rate of prey capture differed between the four treatments (one-way ANOVA: $F_{3,117} = 7.11$, $P < 0.001$; Fig. 4). The BP and O treatments had greater prey capture rates than the P and B treatments (Table 3). Even though, as separate treatments, the prey capture rate of all aggregated webs (with or without decorations; BP or B treatments) did not differ significantly from that of solitary webs (O or P treatments), there was a strongly significant effect for the interaction between aggregation/solitary and decorated/undecorated webs (Table 4).

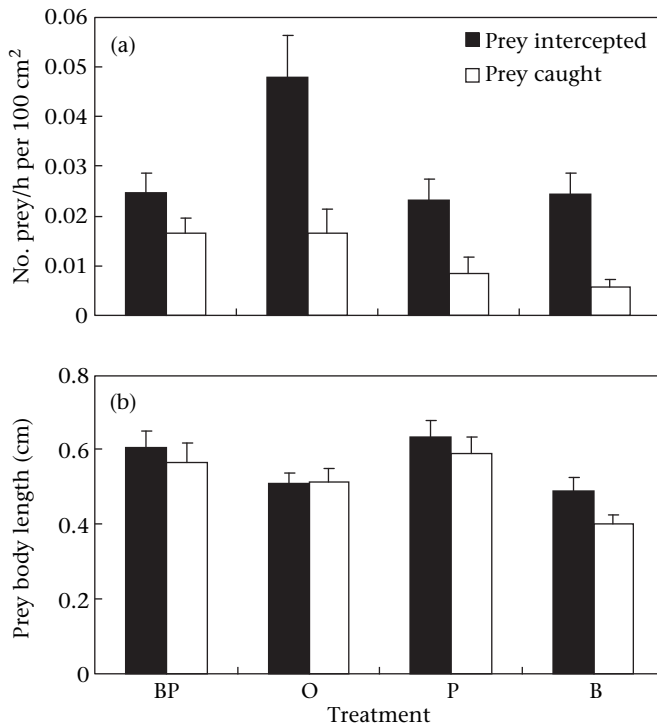


Figure 3. (a) Mean + SE prey interception and capture rates (number of prey intercepted or caught/h per 100 cm² of web capture area) in *N. clavata* webs. (b) Mean + SE body length of prey (cm) intercepted or captured in *N. clavata* webs. BP: webs containing both barrier webs and prey carcass decorations; O: webs with both the barrier web and prey carcasses removed; P: webs with barrier web removed leaving only prey carcass decorations; B: webs with the prey carcasses removed leaving only barrier webs.

Table 2

Results of least significant difference (LSD) pairwise tests comparing the size of prey intercepted and captured by *Nephila clavata* in four treatment groups

Treatment	Prey intercepted				Prey captured			
	BP	O	P	B	BP	O	P	B
BP	—	1.833	0.481	2.024	—	0.071	0.800	2.371
O	0.067	—	2.270	0.346	0.484	—	1.568	1.882
P	0.631	0.023	—	2.432	0.424	0.118	—	3.169
B	0.043	0.730	0.015	—	0.018	0.061	0.002	—

BP: webs containing both barrier webs and prey carcass decorations; O: webs with both the barrier web and prey carcasses removed; P: webs with barrier web removed leaving only prey carcass decorations; B: webs with the prey carcasses removed leaving only barrier webs; upper diagonal: LSD, t statistics; lower diagonal: P values.

DISCUSSION

This study is the first to demonstrate experimentally that multiple structures interactively enhance the performance of an animal's structure. We showed that the orb web spiders *N. clavata* and *C. mulmeinensis* enhance the prey capture efficiency of their webs when they add both prey carcass decorations and barrier webs/aggregations to them. Individually these structures have a negative effect on prey capture efficiency. As prey carcass decorations almost always co-occur with barrier webs/aggregations (for *N. clavata* and *C. mulmeinensis*, respectively) in our study populations, the selection pressure for co-construction of these web components appears to be considerable.

We found that prey interception rate was greatest when we removed both barrier webs and prey carcass decorations from *N. clavata* webs (O treatment). This may have occurred because both the barrier webs and prey carcass decorations are highly visible to insects (Chou et al. 2005; Tan & Li 2009) and were, consequently, avoided. A previous study found that the prey carcass decorations of *Nephila edulis* attract flies (Bjorkman-Chiswell et al. 2004). The majority of the insects encountering the webs in this treatment group were small (<5 mm body length) insects. While flies were well represented among the larger prey encountered by the P treatment webs, they were not encountered frequently enough by these webs to enhance the overall prey interception rate significantly. The webs with both barrier webs and prey carcass decorations intact caught significantly larger insects than those without prey carcass decorations and we frequently witnessed large insects (mostly flies >5 mm body length) hovering around and landing on the prey carcasses, suggesting agile scavengers are attracted to

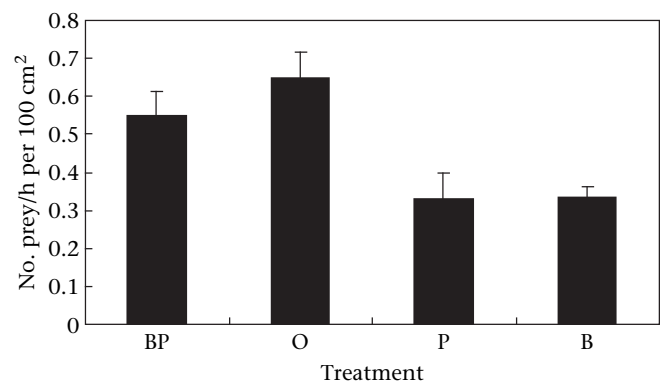


Figure 4. Mean + SE prey capture rates (number of prey caught/h per 100 cm² of web capture area) of *C. mulmeinensis* webs. BP: webs in aggregations with prey carcass decorations; O: solitary webs with prey carcasses removed; P: solitary webs with prey carcass decorations; B: aggregated webs without the prey carcasses.

Table 3

Results of least significant difference (LSD) pairwise tests comparing the prey capture rates (number of prey captured/h per 100 cm² web area) of *C. mulmeinensis* webs in four treatment groups

	BP	O	P	B
BP	—	0.228	0.011	2.554
O	1.212	—	<0.001	3.736
P	2.584	3.766	—	0.030
B	0.012	<0.001	0.976	—

BP: webs in aggregations with prey carcass decorations; O: solitary webs with prey carcasses removed; P: solitary webs with prey carcass decorations; B: aggregated webs without the prey carcasses; upper diagonal: LSD, *t* statistics; lower diagonal: *P* values.

them. These insects often collided with the barrier web and, as a consequence, altered their flight path towards the web, resembling 'ricochet effects' (Uetz 1989). These prey sometimes escaped from the barrier web, but enough were retained to affect the prey capture efficiency of the webs when both barrier webs and prey carcass decorations were intact. Smaller prey were unaffected by the presence of the barrier webs or prey carcass decorations, with most of them flying past the decorations and through the barrier webs. The prey carcass decorations of *N. clavata* thus lure large prey, as described by Bjorkman-Chiswell et al. (2004) to the barrier webs, causing them to alter their flight behaviour and increasing the probability of their capture.

Barrier webs are complex three-dimensional structures requiring a complex construction behaviour (Higgins 1992), which may explain why *N. clavata* does not repeatedly dismantle and reconstruct them. We found that prey interception and retention were significantly reduced when just a barrier web was added to an orb web. Even if prey carcass decorations are incorporated onto the barrier web, prey capture efficiency is enhanced only to an extent that the prey retention is similar to that of webs with neither structure present. Barrier webs and prey carcass decorations, accordingly, appear to be unprofitable structures for the spiders to build. Nevertheless, barrier webs have other benefits, for example protecting the spiders from wasp attack and moisture gathering (Lubin 1975; Higgins 1992). Prey carcasses also have functions other than prey attraction, such as caching of food (Champion de Crespigny et al. 2001; Griffiths et al. 2003). These benefits, along with the combined benefit of enhancing prey capture efficiency, may make adding barrier webs with prey carcass decorations to orb webs profitable. Additionally, the majority of the prey caught in webs with barrier webs and prey carcass decorations present are large, and when spiders consume large prey growth rates and fecundity are enhanced (Venner & Casas 2005). Thus, adding both barrier webs and prey carcass decorations to their orb webs may bestow fitness benefits on *N. clavata*, providing selection pressure for the construction of barrier webs with prey carcass decorations.

Only small prey were caught in *C. mulmeinensis* webs. Solitary *C. mulmeinensis* webs with prey carcass decorations caught fewer prey than solitary spiders on undecorated webs, suggesting that the prey carcass decorations on solitary *C. mulmeinensis* webs were not

Table 4

Results of two-way ANOVA evaluating the individual and interacting effects of aggregation and decoration on prey capture rates of *Cyclosa mulmeinensis*

Source	Type III sum of squares	<i>df</i>	Mean square	<i>F</i>	<i>P</i>
Total	41.195	121			
Intercept	26.263	1	26.263	244.691	<0.001
Decoration	0.074	1	0.074	0.693	0.407
Aggregation	0.082	1	0.082	0.765	0.383
Interaction	2.147	1	2.147	19.999	<0.001
Error	12.558	117	0.107		

attractive to insects, agreeing with field and laboratory observations for other species of *Cyclosa* (Eberhard 2003; Chou et al. 2005; Tan & Li 2009; Tseng & Tso 2009). None the less, we found that when *C. mulmeinensis* built webs with prey carcasses in aggregations, prey capture rates were enhanced. Aggregating the decorations thus appears to amplify their visual and/or aromatic properties, enhancing their attractiveness to insects. This supports the hypothesis tested in *Argiope* that aggregating enhances the signal intensity of individual web decorations (Craig 1991). Recent studies have nevertheless refuted this hypothesis (Justice et al. 2005; Rao et al. 2009). Perhaps the signal amplification is stronger for *C. mulmeinensis* decorations in aggregation than for *Argiope* decorations in aggregation because: (1) *C. mulmeinensis* aggregates more closely than any *Argiope* spp., and (2) *C. mulmeinensis* webs emit both olfactory and visual signals.

As decorated *C. mulmeinensis* webs had greater prey capture success when aggregated than when solitary, the question remains: why do *Cyclosa* spp. often build solitary webs with decorations? Aggregating has both benefits (e.g. silk sharing, enhanced web mechanical strength; Fernandez Campon 2007; Yip et al. 2008) and costs (e.g. increased competition, kleptoparasitism, disease and inbreeding depression; Elgar 1989; Aviles & Bukowski 2006; McCrate & Uetz 2010) for spiders. In most instances, the benefits appear not to outweigh the costs, so most spiders remain solitary (Uetz 1996). *Cyclosa* probably build decorations even when solitary because the decorations bestow protection from predators (Eberhard 2003; Chou et al. 2005; Tseng & Tso 2009; Tan et al. 2010). As solitary *C. mulmeinensis* webs without decorations caught as many prey as decorated *C. mulmeinensis* webs in aggregations, it does not seem optimal for *C. mulmeinensis* either to aggregate or to build decorations. Yet, at our study site, they almost always (>90% of cases; I.-M. Tso, unpublished data) do both. At other locations, for example at the forest edges on Orchard Island, *C. mulmeinensis* aggregates less frequently (S. J. Blamires, personal observations). The most saliently differing factor at our site compared to the forest edge is wind speed, with constantly strong offshore winds blowing at our site. *Cyclosa mulmeinensis* adjusts its web architecture in response to wind exposure (Liao et al. 2009). Our study suggests spider aggregations function similarly to web structures, so may be considered a component of the web architecture. Aggregating thus seems to be a web architectural response of *C. mulmeinensis* to cope with strong winds. Exactly how aggregating in strong winds is advantageous for *C. mulmeinensis* is unknown, but we speculate that aggregating may be a web architectural response providing some kind of barrier to physiological stress, as, for example, aggregating on a rocky shore helps periwinkles, *Littorina unifasciata*, avoid desiccation (Chapman 1995). We suggest more studies should assess the role of extreme environments on the formation of spider aggregations.

In conclusion, we have demonstrated that multiple structures and/or aggregations act interactively to enhance foraging gain for the spiders *N. clavata* and *C. mulmeinensis*. We therefore suggest that studies aiming to understand the evolutionary significance of animal structures should account for interactive effects of the structures. Unaccounted for interactive effects may, for example, be a reason why conflicting explanatory results have been found for web decoration functions in *Argiope* spiders (but see Cheng et al. 2010 for other explanations). For both *N. clavata* and *C. mulmeinensis*, prey carcass decorations perform specific functions that alone may be detrimental to foraging. However, the addition of a barrier web (in *N. clavata*) or aggregation (in *C. mulmeinensis*) acts to retain more of the prey intercepted or enhance the prey attraction function of the prey carcass decorations (Tietjen et al. 1987; Bjorkman-Chiswell et al. 2004; Henaut et al. 2010), offsetting the costs of building each structure. Enhanced survivorship, through

consumption of more large and profitable prey, protection from predators and protection from the environment are potential benefits afforded *N. clavata* and *C. mulmeinensis* when they build multiple structures. None the less, a dilemma remains: if utilizing multiple web structures or aggregations effectively offsets the costs encountered and provides fitness benefits, why are similar construction strategies so rare? It has been suggested that architectural complexity is rare in nature because the fitness benefits rarely extend beyond the accumulated building and other associated costs (Hansell 2005). A more thorough understanding of the evolutionary costs and limitations of building multiple structures provides a resolution to the dilemma. For spiders, this means better quantification of the costs of silk synthesis, the energetics of web building, the predators encountered during web building, and the time and energy diverted from somatic maintenance, reproduction and other activities. Our current knowledge of these costs is limited, or based on estimates (Craig 2003). We therefore suggest future research aims to quantify these costs individually and interactively.

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References

- Aviles, L. & Bukowski, T. C. 2006. Group living and inbreeding depression in a subsocial spider. *Proceedings of the Royal Society B*, **273**, 157–163.
- Bilde, T., Coates, K. S., Birkhofer, K., Bird, T., Maklakov, A. A., Lubin, Y. & Aviles, L. 2007. Survival benefits select for group living in a social spider despite reproductive costs. *Journal of Evolutionary Biology*, **20**, 2412–2426.
- Bjorkman-Chiswell, B. T., Kulinski, M. M., Muscat, R. L., Nguyen, K. A., Norton, B. A., Symonds, M. R. E., Westhorpe, G. E. & Elgar, M. A. 2004. Web-building spiders attract prey by storing decaying matter. *Naturwissenschaften*, **91**, 245–248.
- Brown, C. G. & Funk, D. J. 2010. Antipredator properties of an animal architecture: how complex faecal cases thwart arthropod attack. *Animal Behaviour*, **79**, 127–136.
- Champion de Crespigny, F. E., Herberstein, M. E. & Elgar, M. A. 2001. Food caching in orb-web spiders (Araneae: Araneidae). *Naturwissenschaften*, **88**, 42–45.
- Chapman, M. G. 1995. Aggregation of the littorinid snail *Littorina unifasciata* in New South Wales, Australia. *Marine Ecology Progress Series*, **126**, 191–202.
- Cheng, R. C., Yang, E. C., Lin, C. P., Herberstein, M. E. & Tso, I. M. 2010. Insect form vision as one potential shaping force of spider web decoration design. *Journal of Experimental Biology*, **213**, 759–768.
- Chou, I. C., Wang, P. H., Shen, P. S. & Tso, I. M. 2005. A test of prey-attracting and predator defence functions of prey carcass decorations built by *Cyclosa* spiders. *Animal Behaviour*, **69**, 1055–1061.
- Craig, C. L. 1991. Physical constraints on group foraging and social evolution: observations on web spinning spiders. *Functional Ecology*, **5**, 649–654.
- Craig, C. L. 2003. *Spiderwebs and Silk: Tracing Evolution from Molecules to Genes to Phenotypes*. Oxford: Oxford University Press.
- Eberhard, W. G. 1990. Function and phylogeny of spider webs. *Annual Review of Ecology and Systematics*, **21**, 341–372.
- Eberhard, W. G. 2003. Substitution of silk stabilimenta for egg sacs by *Allocclosa bifurca* (Araneae: Araneidae) suggests that silk stabilimenta function as camouflage devices. *Behaviour*, **140**, 847–868.
- Elgar, M. A. 1989. Kleptoparasitism: a cost of aggregating for an orb weaving spider. *Animal Behaviour*, **37**, 1052–1055.
- Fernandez Campon, F. 2007. Group foraging in the colonial spider *Parawixia bistriata* (Araneidae): effect of resource levels and prey size. *Animal Behaviour*, **74**, 1551–1562.
- Griffiths, B. V., Holwell, G. I., Herberstein, M. E. & Elgar, M. A. 2003. Frequency, composition and variation in external food stores constructed by orb-web spiders: *Nephila edulis* and *Nephila plumipes* (Araneae: Araneidae). *Australian Journal of Zoology*, **51**, 119–128.
- Hansell, M. 2005. *Animal Architectures*. Oxford: Oxford University Press.
- Henaut, Y., Pablo, J., Ibarra-Nunez, G. & Williams, T. 2001. Retention, capture and consumption of experimental prey by orb-web weaving spiders in coffee plantations of Southern Mexico. *Entomologia Experimentalis et Applicata*, **98**, 1–8.
- Henaut, Y., Machkour-M'Rabet, S., Winterton, P. & Calme, S. 2010. Insect attraction by webs of *Nephila clavipes* (Araneae: Nephilidae). *Journal of Arachnology*, **38**, 135–138.
- Herberstein, M. E. & Tso, I. M. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneidae, Araneae). *Journal of Arachnology*, **28**, 180–184.
- Herberstein, M. E., Craig, C. L., Coddington, J. A. & Elgar, M. A. 2000. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biological Reviews*, **75**, 649–669.
- Higgins, L. E. 1992. Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae: Tetragnathidae). *Journal of Insect Behavior*, **5**, 635–655.
- Justice, M. J., Justice, T. C. & Vesce, R. L. 2005. Web orientation, stabilimentum structure and predatory behavior of *Argiope florida* Chamberlin & Ivie 1944 (Araneae, Araneidae, Argiopinae). *Journal of Arachnology*, **33**, 82–92.
- Korb, J. 2003. Thermoregulation and ventilation of termite mounds. *Naturwissenschaften*, **90**, 212–219.
- Lafuma, L., Lambrechts, M. M. & Raymond, M. 2001. Aromatic plants in bird nests as protection against blood-sucking flying insects. *Behavioural Processes*, **56**, 113–120.
- Lens, L., Wauters, L. A. & Dhondt, A. A. 1994. Nest building by crested tit *Parus cristatus* males: an analysis of the costs and benefits. *Behavioral Ecology and Sociobiology*, **35**, 431–436.
- Liao, C. P., Chi, K. J. & Tso, I. M. 2009. The effect of wind on trap structural and material properties of a sit-and-wait predator. *Behavioral Ecology*, **20**, 1194–1203.
- Lubin, Y. D. 1975. Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae, Araneidae) on Daphne and Santa Cruz Islands, Galapagos. *Journal of Arachnology*, **2**, 119–126.
- McCrate, A. T. & Uetz, G. W. 2010. Kleptoparasites: a twofold cost of group living for the colonial spider, *Metepeira incassata* (Araneae, Araneidae). *Behavioral Ecology and Sociobiology*, **64**, 389–399.
- Mainwaring, M. C. & Hartley, I. R. 2009. Experimental evidence for state-dependent nest weight in the blue tit, *Cyanistes caeruleus*. *Behavioural Processes*, **81**, 144–146.
- Manicom, C., Schwarzkopf, L., Alford, R. A. & Schoener, T. W. 2008. Self-made shelters protect spiders from predation. *Proceedings of the National Academy of Sciences U.S.A.*, **105**, 14903–14907.
- Nakata, K. 2009. To be or not to be conspicuous: the effects of prey availability and predator risk on spider's web decoration building. *Animal Behaviour*, **78**, 1255–1260.
- Prestwich, K. N. 1977. The energetics of web-building in spiders. *Comparative Biochemistry and Physiology*, **57A**, 321–326.
- Rao, D., Webster, M., Heiling, A. M., Bruce, M. J. & Herberstein, M. E. 2009. The aggregating behaviour of *Argiope radon*, with special reference to web decorations. *Journal of Ethology*, **27**, 35–42.
- Ruxton, G. D. & Neuhauser, M. 2010. When should we use one-tailed hypothesis testing? *Methods in Ecology & Evolution*, **1**, 114–117.
- Tan, E. J. & Li, D. 2009. Detritus decorations of an orb-weaving spider, *Cyclosa mulmeinensis* (Thorell): for food or camouflage? *Journal of Experimental Biology*, **212**, 1832–1839.
- Tan, E. J., Seah, S. W. J., Yap, L. Y. L., Goh, P. M., Gan, W., Liu, F. & Li, D. 2010. Why do orb weaving spiders (*Cyclosa ginnaga*) decorate their webs with silk spirals and plant detritus? *Animal Behaviour*, **79**, 179–186.
- Tanaka, K. 1989. Energetic costs of web construction and its effects on web relocation in the web building spider *Agelena limbatia*. *Oecologia*, **81**, 459–464.
- Tietjen, W. J., Rao Ayyagari, L. & Uetz, G. W. 1987. Symbiosis between social spiders and yeast: the role in prey attraction. *Psyche*, **94**, 151–158.
- Tseng, L. & Tso, I. M. 2009. A risky defense by a spider using conspicuous decoys resembling itself in appearance. *Animal Behaviour*, **78**, 425–431.
- Tso, I. M., Tai, P. L., Ku, P. H., Kuo, H. C. & Yang, E. C. 2002. Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Animal Behaviour*, **63**, 175–182.
- Tso, I. M., Lin, C. W. & Yang, E. C. 2004. Colourful orb-weaving spiders, *Nephila pilipes*, through a bee's eyes. *Journal of Experimental Biology*, **207**, 2631–2637.
- Uetz, G. W. 1988. Group foraging in colonial web building spiders: evidence for risk sensitivity. *Behavioral Ecology and Sociobiology*, **22**, 265–270.
- Uetz, G. W. 1989. The 'ricochet effect' and prey capture in colonial spiders. *Oecologia*, **81**, 154–159.
- Uetz, G. W. 1992. Foraging strategies of spiders. *Trends in Ecology & Evolution*, **7**, 155–159.
- Uetz, G. W. 1996. Risk sensitivity and the paradox of colonial web-building in spiders. *American Zoologist*, **36**, 459–470.
- Venner, S. & Casas, J. 2005. Spider webs designed for rare but life-saving catches. *Proceedings of the Royal Society B*, **272**, 1587–1592.
- Whitehouse, M. E. A. & Lubin, Y. 2005. The functions of societies and the evolution of group living: spider societies as a test case. *Biological Reviews*, **80**, 347–361.
- Williams, J. L., Moya-Lorano, J. & Wise, D. H. 2006. Burrow decorations as anti-predator devices. *Behavioral Ecology*, **17**, 586–590.
- Yip, E. C., Powers, K. S. & Aviles, L. 2008. Cooperative capture of large prey solved scaling challenge faced by spider colonies. *Proceedings of the National Academy of Sciences U.S.A.*, **105**, 11818–11822.
- Zar, J. H. 1999. *Biostatistical Analysis*. 4th edn. Upper Saddle River, New Jersey: Prentice Hall.