

# Three-dimensional barricading of a predatory trap reduces predation and enhances prey capture

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**Abstract** Animal structures come at material, energetic, time, and expression costs. Some orb-web spiders add three-dimensional barrier structures to their webs, but many do not. Predator protection is considered to be the principal benefit of adding these structures. Accordingly, it remains paradoxical why some orb-web spiders might construct the barriers while others do not. Here, we experimentally determined whether the barrier structure added to the horizontal orb web of the spider *Cyrtophora moluccensis* deters predators at the cost of reducing the amount of prey captured in the field. We conducted experiments by day and night to assess whether the effects vary with the time of day. We found that the three-dimensional barriers not only offered protection from predatory wasps by day but also enhanced the amount of prey captured by day and night. Moreover, the barrier structure appears particularly useful at catching moths, the largest and most energetically profitable prey that it encounters. We, therefore, concluded that reducing the energetic and time costs associated with producing and depositing extra silk threads is the principal reason why barrier structures are used intermittently among orb-web spiders.

**Keywords** Costs–benefits · Barrier structure · Three-dimensional orb webs · *Cyrtophora moluccensis*

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## Introduction

Structures are constructed by animals at material, energetic, time, and expression costs (Hansell 2005; Blamires et al. 2010; Tseng et al. 2011). Material costs constitute the limitations of the physical and chemical properties of the materials that the structure is made from. Energetic costs include metabolic energy expended secreting or gathering the materials and building the structure. Time costs include the time diverted from foraging, mating, or avoiding predators. Expression costs are encountered over and above the other costs and may include reduced prey capture success and increased exposure to predators (Hansell 2005).

Aerial web building was a key evolutionary innovation that enabled spiders to capture and consume flying insects (Nentwig and Heimer 1987; Craig 2003; Blackledge et al. 2009). It, nonetheless, came at various costs including the energetic cost of producing more and a wider range of silk, a loss of time that could be devoted to foraging or reproduction and increased exposure to predators (Craig 2003; Hansell 2005). Some araneid and nephilid orb-web spiders add three-dimensional barrier structures, made principally from stiff major ampullate silk, to their two-dimensional webs, while many other orb-web spiders do not (Blackledge et al. 2009, 2011; Blamires et al. 2012a). In some taxa (e.g., members of the genera *Cyrtophora* and *Mecynogea*; Levi 1997), the structures are always present, suggesting it is an obligate component of their web-building behavior. However, in other taxa (e.g., members of the genus *Nephila*), the webs are vertical and contain sticky silk, and the building of a barrier structure depends on the species and/or ontogenetic stage (Higgins 1990, 1992; Blamires et al. 2010). Barrier structures, henceforth, do not seem to be of homologous origin among orb-web spiders. The mechanical properties of the silk threads from which the

barrier structures are made, however, are homologous across the different users (Blamires et al. 2012a, b).

The barrier structures consist of non-sticky inelastic silk, so barricading the web to protect the spider against wasp and bird predators seems to be the primary advantage of adding them to orb webs (Blackledge et al. 2003; Manicom et al. 2008; Blamires et al. 2010; Tseng et al. 2011). This, however, suggests that orb-web spiders that do not add the structures build and occupy webs under greater predation risk. It accordingly seems perplexing why spiders might do this, unless there are considerable, as yet unmeasured, costs associated with adding the structures.

The genera *Cyrtophora* and *Mecynogea* are permanent users of barrier structures, with their orb webs reduced to a horizontally aligned prey-catching orb that lacks the sticky silk characteristic of most other orb webs (Eberhard 1990; Blackledge et al. 2009, 2011; Blamires et al. 2012a). These spiders position themselves on the underside of the horizontal orb and catch prey that ricochet off the barrier structure and fall into the orb. Since the architecture of the webs of these spiders fundamentally differs from those of other orb-web spiders which generally build vertically aligned two-dimensional orb webs (Eberhard 1990; Blackledge et al. 2011), it might be supposed that the barrier structure is used to support the horizontal orb, or the orb, for some reason, cannot function without the barrier structure present, or the presence of barrier silk induces prey to behave differently (Craig 1986; Rypstra and Buddle 2013) and become predisposed to capture. Some spiders, e.g., members of the genera *Leucauge* and *Gertschanapis* (Eberhard 1990; Blackledge et al. 2009, 2011), nevertheless, build horizontal orb webs without barrier structures. Furthermore, other orb-web spiders, e.g., members of the genera *Nephila* and *Thelacantha*, add barrier structures to their vertical two-dimensional webs (Blamires et al. 2010; Tseng et al. 2011). Subsequently, the above proposition seems untenable, although it remains to be determined whether barrier structures predispose insects to alter their behavior.

Flying insects that strike the barrier threads of *Cyrtophora* spp. webs bounce off them and are directed toward the prey-capturing orb (Lubin 1974). This is analogous to the prey capture enhancing “ricochet” or “shadow” effects that result from web aggregations (Uetz 1989; Rao 2009). Accordingly, by enhancing the amount of prey-deflecting silk, and/or the area over which prey are captured, the barrier may be implicit in the capture of significantly more prey compared to the orb alone. Nevertheless, if the preys can see or detect the barrier from a distance and identify it as a threat, they may be able to avoid interacting with it (Craig 1986). If this occurs, the barrier would actually come at an expression cost of significantly reducing the amount of prey captured.

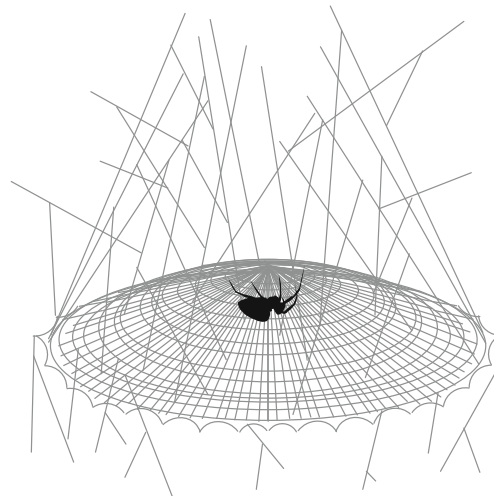
To test the hypothesis that barrier structures deter predators at the expense of a reduction in the amount of prey

captured, we experimentally removed the barrier structures from the webs of wild *Cyrtophora moluccensis*, a large-bodied (adult female body length  $\approx 20$  mm) orb-web spider that forages by both day and night (Lubin 1974; Baba et al. 2007; Blamires et al. 2012a). It adds a three-dimensional silk barrier structure to its web that extends up to 1 m above its approximately 0.3 m-wide horizontal orb (Fig. 1). Since *C. moluccensis* forages diurnally and nocturnally, we conducted the experiments during the day and night to ascertain whether foraging at either time affects the barrier structure’s influence on predator avoidance or prey capture. If the barrier structure does not come at a cost of a reduction in prey capture, it implies that the material, energetic, or time costs associated with producing and depositing the barrier silks deters many orb-web spiders from building barrier structures.

## Materials and methods

### Field experiments

Our experiments were performed over eight consecutive days in 2007 and 2008 in a secondary forest dominated by mulberry and elephant’s ear shrubs at Ape Hill (22°38’19” N, 120°15’54” E), near National Sun Yat-Sen University, Kaohsiung City, Taiwan. At 0800 hours each morning, we randomly selected 18 adult female *C. moluccensis* webs and either removed the web barrier structures using a stick of hot incense (BW– treatment) or retained them (BW+ treatment). Individual spiders generally live for less than a year, so it was unlikely that individuals were repeatedly measured each year as we only used adults. As the orb is anchored to vegetation by frame threads that are distinct from the barrier threads, removing the barrier structure did not affect web



**Fig. 1** Barrier structure and horizontal capture orb of the three-dimensional orb web built by *C. moluccensis*

ension or damage the web. The experiments ran for 14 h and the smell of the incense dissipated within 5–10 s, so it had no effect on the experimental outcomes.

Prior to the manipulations, we measured the body length of each spider using calipers and estimated web volume by measuring with a tape measure ( $\pm 1$  mm) the orb diameter and length of the barrier structure from orb to tip and measured the surface area using a formula (Tso and Severinghaus 2000; Peng et al. 2013). We, subsequently, ensured that we used webs of similar surface area across the different treatments, days, and years (Kruskal–Wallis tests;  $P > 0.05$ ). As the treatments were assigned to haphazardly encountered webs, the distribution of the BW+ and BW– treatments were haphazardly scattered throughout the site.

We monitored the webs between 0800 and 2200 hours using video cameras with infrared scopes that were placed approximately 1 m from each web. Footage from 0800–1700 hours was considered “daytime,” while footage from 1700–2200 hours was considered “nighttime.” All footage was clear enough to identify insects to order (Tseng et al. 2011). Where there were predators and prey from the same order, e.g., Hymenoptera, we distinguished them according to morphology and behavior; all prey flew passively within the vicinity of the webs, while predators flew at, and often attacked, the spider.

We quantified prey capture as an insect falling or flying into the orb and being attacked and consumed by the spider. Occasional camera positional adjustments, battery failure, or other technical issues resulted in unequal hours of footage for each treatment, so we measured prey capture rate as the number of prey captured per hour of footage. This also accounted for the different number of hours of daytime and nighttime monitoring. We categorized the interactions between the spiders and predators into two types: attack and approach events. Attack events were defined as events where the predator directly attacked the spider. Approach events were defined as events where the predator moved toward the web and hovered but did not launch an attack (Tseng et al. 2011). Predator approach and attack rates were both measured as the number of events per hour of footage.

### Statistical analyses

The prey capture rate data failed tests for normality and homoscedasticity (Kolmogorov–Smirnov and Levene’s tests;  $P < 0.05$ ). As they fitted a negative binomial distribution (Pearson  $\chi^2_{118} = 109.15$ ;  $P = 0.708$ ), negative binomial regressions were used to analyze the effects of treatment (BW+/BW–), time (day/night), year (2007/2008), and their interactions on prey capture rate. Significance was determined by a type III analysis based on a Wald’s test. A  $\chi^2$  test of homogeneity was used to compare the composition of prey captured across treatments during the day and night.

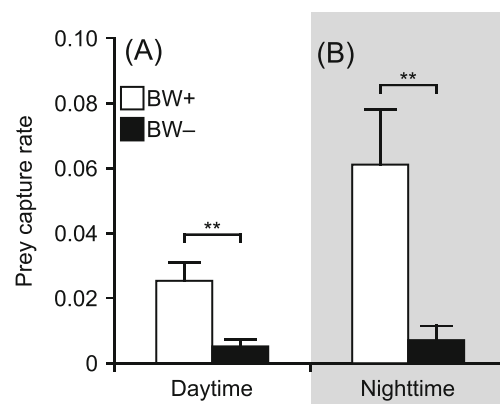
The predator approach and attack data were not normally (Kolmogorov–Smirnov test;  $P < 0.05$ ) or Poisson (binomial test;  $P < 0.05$ ) distributed, so Mann–Whitney  $U$  tests were used to compare predator attack and approach rates between the BW+ and BW– treatments.

### Results

We found that the BW+ treatment captured significantly more prey than the BW– treatment by day and by night (Fig. 2). Year had a significant influence on prey capture rate (Table 1). This effect, however, could not be ascribed to variations in web size or hours of footage, as these factors were accounted for in our procedures. Furthermore, prey types encountered were similar, driven by the predominance of moths, in each year so they were not responsible for the influence of year on prey capture rate. We, accordingly, expected the effect of year to be a product of the likely difference in the number of insects present each year, or an anomaly of signal noise.

The taxonomic composition of prey captured differed by day and night ( $\chi^2_8 = 30.856$ ,  $P < 0.0001$ ). Hemiptera, Hymenoptera, and Diptera were principally captured by day, while Lepidoptera were principally captured by night. Accordingly, the influence of the barrier structure on prey capture did not differ by day and night, but the preys that were caught did, so the energetic return from foraging by night and day probably differed.

All predator approaches and attacks were by wasps and they all interacted with *C. moluccensis* webs during the day, so time of day was not included as a factor in the ensuing analyses. Predator approach rates were not significantly greater for the BW– treatment than they were for the BW+ treatment. Predator attack rates, however, were significantly



**Fig. 2** Between treatment comparisons of prey consumption rates, showing mean ( $\pm$ SE) prey capture rate (number of prey captured per hour of monitoring) recorded during the daytime (A) and nighttime (B). BW+ barrier present, BW– barrier removed; \*\* $P < 0.01$ , significant at this level

**Table 1** Results of type III analyses based on Wald tests after a negative binomial regression comparing prey capture rates of *C. moluccensis* webs across treatments (BW+ or BW-)

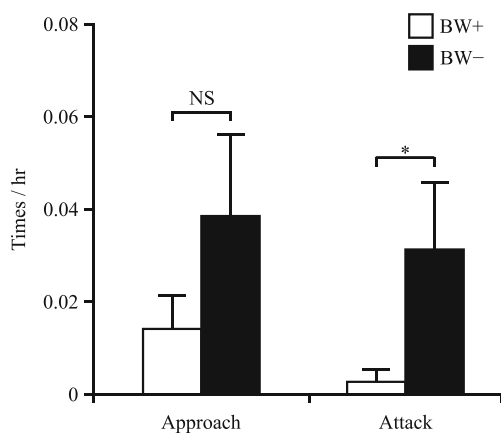
| Source                   | $\chi^2$ | df | P value |
|--------------------------|----------|----|---------|
| Intercept                | 335.0637 | 1  | <0.0001 |
| Treatments               | 26.4745  | 1  | <0.0001 |
| Time                     | 1.2175   | 1  | 0.2699  |
| Year                     | 5.1191   | 1  | 0.0237  |
| Treatments $\times$ time | 0.1759   | 1  | 0.6749  |

Times were day or night and year was 2007 and 2008. A Pearson's goodness-of-fit test indicates that the negative binomial regression fit the data reasonably.  $\chi^2=133.5968$ ,  $df=118$ ,  $P=0.1547$

greater for the BW- treatment (Mann-Whitney's *U* test:  $U=728.501$ ,  $P=0.039$ ; Fig. 3), so the barrier structure significantly reduces the frequency of predatory attacks.

## Discussion

We found that when the three-dimensional barrier structures were removed from *C. moluccensis*' webs, the rate of prey captured by the spider was compromised. Hence, the barrier structure does not come at a cost of reducing the amount of prey captured. Conversely, the structure seems to serve to both protect the spider against wasp predators and increase the amount of prey captured. A reduction in prey capture success therefore does not explain why many orb-web spiders do not add three-dimensional structures to their webs. It seems that many orb-web spiders do not build the structures to avoid the costs associated with extra silk production and deposition of the threads. As recent research has revealed that the material performance costs of major ampullate silks



**Fig. 3** Between treatment comparisons of predator approach and attack rates, showing mean ( $\pm$ SE) predator approaches and attacks on the various treatment groups, recorded during the daytime. BW+ barrier present, BW- barrier removed; \* $P<0.05$ , significant at this level; NS nonsignificant at  $P>0.05$

in spiders that build three-dimensional webs do not differ from those of spiders that build two-dimensional webs (Blamires et al. 2012a, b), we expect it to be the time and energetic costs that the spiders are avoiding.

A potential confounding factor in our experiment was that the BW+ and BW- treatment groups not only differ in presence/absence of barrier structure but also in quantity of silk. Since webs in the BW- treatment contained less silk, it was possible that the observed variations in prey interception rates between these two groups were due to inherent properties of the silk, such as presence of chemical attractants. Although there is currently no literature reporting the presence of chemicals in barrier silks, we suggest that follow-up experiments control for the difference in silk quantity while manipulating the presence of the barrier structures. Judging from the responses of the prey, however, we conclude that it was the presence/absence of the barrier structure rather than differences in silk quantity that generated the results. In all instances of prey capture that we observed, the insects collided with the barrier structure and were directed towards the orb, in a similar way that insects that interact with the barrier structure of *Nephila clavata* are redirected toward the web (Blamires et al. 2010). However, unlike in *N. clavata* where the addition of prey carcasses to the barrier structures induces insects to move toward the web and adopt a “hovering” behavior, we could not ascribe any behavioral variation from normal flight for any of the insects observed. The presence of the barrier silk in *C. moluccensis* webs thus seems unlikely to elicit insects to adopt behaviors that predispose them to being captured.

Our findings support the proposition that the barrier structure functions to reduce the kinetic energy of fast-moving prey and increase the likelihood of their capture (Blamires et al. 2010; Blackledge et al. 2011), an effect analogous to the “ricochet” or “shadow” effects found in spider web aggregations (Uetz 1989; Roa 2009; Blamires et al. 2010). In some instances, barrier structures may reduce the amount of prey captured or only serve to increase the number of prey captured when other structures, such as decorations, are added to the web (Blamires et al. 2010; Tseng et al. 2011). However, we found that the barrier structures added to *C. moluccensis* webs enhance the number of prey captured while deterring predators without interacting with other structures.

The time of day did not affect the influence of the barrier on prey capture rate, but there was a difference in the types of prey caught with lepidopterans (moths) principally caught by night. As moths were the largest and most predominant prey captured, nighttime foraging is probably more energetically advantageous for *C. moluccensis*. We did not observe any predator interactions with webs or spiders at night, so foraging by night also seems to afford *C. moluccensis* a reduction in predatory exposure. Indeed,

the advantages of foraging by night seem so profound that it is inexplicable why *C. moluccensis* forages by day at all. It may be that there are physiological, e.g., thermoregulatory or reproductive, requirements necessitating their activity by day, particularly among the larger individuals used in our experiments. Perhaps, the protection afforded by the barrier structure facilitates daytime activity. We could not clearly ascertain why there was a significant effect of year on the prey capture rate, but we expect it was owing to uncontrolled variations in environmental factors or the amount of prey experienced between years.

Moths were the largest prey item captured, and they were exclusively captured at night; hence, there are likely to be fitness advantages associated with their consumption. Indeed, moths, owing to their large mass and high energy content, are desirable prey for many insectivorous animals, and capturing them drives much of their behavior (Nentwig 1987; Barclay 1991; Pavey et al. 2009). Moths are, nevertheless, difficult to capture in two-dimensional orb webs, as their wing scales do not stick to the spirals and they readily fall out under gravity (Nentwig 1987). Moth specialization has accordingly been hypothesized to drive the evolution of many variations in spider web forms, including the evolution of “ladder webs” and “bolases” (Eberhard 1990; Yeagen 1994; Kuntner et al. 2010). Henceforth, it may be plausible that, in addition to avoiding predators, more efficient moth capture may drive the use of three-dimensional structures among orb-web spiders. Webs built by *Cyrtophora* spp. have a horizontal non-sticky orb rather than a vertical orb with sticky spiral threads (Lubin 1974; Eberhard 1990; Blamires et al. 2012a), meaning the moth escape mechanism of tumbling out of the web under gravity is rendered ineffective. In addition to redirecting moths to the orb, the silks of the barrier structures added to *Cyrtophora* webs may also absorb the impacts of moth strikes, reducing the velocity of their flight and rendering them less likely to break the orb when they fall into it. Further observations coupled with mechanical tests of the silk threads are, nonetheless, required to verify this proposition.

Advantages other than predator protection or enhanced prey capture have been proposed for the use of barrier structures among orb-web spiders and include: (1) a means of prey capture that alleviates the need to produce sticky silks and (2) a means to deter ants from invading the orb webs of spiders that do not, or cannot, add chemical deterrents to their frame silks (Blackledge et al. 2011; Zhang et al. 2012). The sticky silks are comprised of numerous compounds that are not readily synthesizable (Townley et al. 2006; Sahni et al. 2011); hence, they may be expensive to produce. Nonetheless, the widespread use of sticky silks among orb-web spiders, including many that add barrier structures (Peters 1987; Blackledge et al. 2011), and their

use in three-dimensional cob webs, albeit in small amounts (Peters 1987; Sahni et al. 2011), render the former proposition unlikely as a major advantage for using barrier structures, although it cannot be entirely ruled out. There is currently not enough information on the use of chemical deterrents on silk in different orb-web spiders, and whether or not it corresponds with barrier structure use, to confirm or refute the latter proposition.

Orb webs with barrier structures generally remain in service longer (several weeks compared to a few days) than those without (Blackledge et al. 2011; Blamires et al. 2012a). It might therefore be supposed that the material or energetic costs of barrier threads are only worth paying when a spider receives more than a few days of service from them (i.e., when one large construction effort is better than a series of successive small construction efforts). This might be the case if the major ampullate silks of *Cyrtophora* spp. retain their properties over several weeks while those of spiders that build two-dimensional orb webs do not. On the contrary, the major ampullate silks of *Cyrtophora* spp. do not appear to retain their performance any longer than those of other orb-web spiders when left exposed to natural conditions for weeks at a time (Blamires et al. 2012a). Accordingly, we conclude that it is avoidance of the energetic and time costs, and not material costs, associated with building barrier structures that limits their use among orb-web spiders.

Despite demonstrable benefits, the permanent use of barrier structures is restricted among araneids to members of the genera *Cyrtophora* and *Mecynogea* (Blackledge et al. 2009, 2011). Given that web three-dimensionality seems to be a successful web-building strategy among the immensely diverse theridiids and linyphiids (Blackledge et al. 2009; Platnick 2012), the paradox remains: If three-dimensional webs are barriers to predators and effective prey traps, why has there not been similar diversification in web three-dimensionality among araneids? No studies manipulating linyphiid or theridiid web structures in the field have been performed. Nor has there been any determination of predator or prey interactions or any quantification of the material, energetic, or time costs involved in building linyphiid or theridiid webs, so we do not know whether the web components perform similar functions and come at similar costs to those of *Cyrtophora* spp. and *Mecynogea* spp. Perhaps, owing to their larger bodies, three-dimensional structures are associated with greater material, energy, time, or expression costs in orb-web spiders than they are in linyphiids or theridiids. Alternatively, orb-web spiders may have devised other means for reducing the predation costs associated with building two-dimensional structures, e.g., by using retreats and/or decoys (Manicom et al. 2008; Tseng and Tso 2009; Blamires et al. 2010; Tseng et al. 2011). To resolve the above paradox, we suggest that experiments be combined

with comparative analyses to determine the costs and benefits of different web components in a wider array of spiders.

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