

Experimental Evidence for the Amelioration of Shadow Competition in an Orb-Web Spider Through the 'Ricochet' Effect

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Abstract

Stationary predators such as spiders can face competition from conspecifics simply by virtue of the spatial positioning of their webs. Shadow competition, wherein a predator 'upstream' restricts access to prey for another individual further 'downstream', can affect the foraging success of stationary predators. However, in spiders that build orb-webs in proximity to each other, insect prey often 'ricochet' off the outer web and land on the inner web. In this study, I asked whether the negative effect of shadow competition could be compensated for by the ricochet effect. I experimentally show that despite a strong spatial advantage to a spider on the outer side in terms of prey interceptions, the likelihood of prey intercepting the inner web is increased through the ricochet effect. I also show that the degree of overlap between the webs significantly influences both the number of prey intercepted as well as the number of ricochets. This study shows experimentally that a spider that builds its web close to a conspecific's web suffers very little cost in terms of lost prey interception.

Introduction

Trap building stationary predators are rare in nature. Less than 1% of all terrestrial animals are known to build traps; some examples of trap building predators are ant-lion larvae, fungus gnats, caddis fly larvae and spiders (Ruxton & Hansell 2009). Building a trap to catch prey has both benefits and costs. By building traps, the predators do not have to invest energy in finding prey. Instead, stationary predators wait for prey to come to them. However, the presence of a visible structure, the trap, may attract predators as well as repel prey (Bruce 2006). Furthermore, there is considerable initial investment into building traps, and once built, predators are reluctant to move again to minimize further costs such as lost opportunity costs and increase in predation risk during relocation (Ruxton & Hansell 2009). A further cost to stationary trap builders is indirect competition from conspecifics. For example, ant-lion larvae dig pits in the soil, and once the pit has been dug and is occupied, the individual antlion faces competition

from other antlions that dig pits in the vicinity (Linton et al. 1991). An ant is more likely to fall prey to ant-lion pits at the periphery of an aggregation rather than pits in the center. This type of competition is termed shadow competition, wherein stationary predators restrict the foraging success of other conspecifics that are further away from the food source (Lubin et al. 2001). Shadow competition has been described in a variety of stationary predators (Linton et al. 1991; Lubin et al. 2001), and even in some non-stationary predators such as blackfly larvae (Hart 1986) and sea trout (Elliott 2002). In these examples, there is a strong effect of shadow competition, because a prey that encounters the first predator is generally unavailable to the subsequent one. In antlions, the effect of shadow competition leads to the peculiar hyperdispersed ('doughnut' shaped) distribution patterns of antlion pits, with more individuals in the periphery and fewer in the centre (Linton et al. 1991).

Shadow competition can occur in spiders as well. As the characteristics of the surrounding vegetation

can constrain web site selection (Uetz & Burgess 1979; McNett & Rypstra 2000; Rao & Poyyamoli 2001), spiders can cluster together in aggregations in areas where there is a dearth of suitable habitats. Aggregating spiders can face shadow competition in cases where a spider's web is located in between two others. Studies have shown that there is competition within the aggregation for a suitable web site, and there is trade-off between protection from predators and the likelihood of prey encounter (Rypstra 1979). Another advantage for spiders living in aggregations is from prey that escape from an outer web can become entangled in a subsequent web. This phenomenon has been termed the 'ricochet effect' (Uetz 1989). The ricochet effect is a consequence of the lack of retention of insects by spider webs. The time of prey retention in a web depends on how actively the prey struggles, its body weight (Nentwig 1982), the mesh width of the web and the taxa of the prey (Blackledge & Zevenbergen 2006).

Both the ricochet effect and shadow competition have traditionally been applied to high density aggregations of spiders, specifically colonial spiders, with the assumption that these factors come into play at only a certain density of individuals (Uetz 1989; Lubin et al. 2001). However, the mechanics of either effect can operate at a small scale even in low densities of spiders. Orb-web spiders sometimes occur in proximity to each other. Species such as *Nephila clavipes* (Rypstra 1985), *Austracantha minax* (previously *Gasteracantha minax*; Lloyd & Elgar 1997) and *Argiope radon* (Robinson & Robinson 1980; Rao et al. 2007) often connect their frame threads and are found in clusters ranging from a few individuals to many. In such spiders, it is likely that the position of an individual spider's web significantly affects the number of prey intercepted. Furthermore, the decision to break site fidelity and search for another suitable web site may be triggered by the indirect influence of other orb-web spiders. Costs of relocation include lost foraging opportunities, increased predation risk and energy expenditure during web building (Jakob et al. 2001).

As orb-web spiders generally build webs low in the vegetation, potential prey approach the webs from the direction that is relatively open. If a spider builds its web just behind another web, there is a significant chance that approaching prey are more likely to intercept the outer web rather than the inner web. However, the ricochet effect may compensate for the potentially disadvantageous position of being the spider that is further away from a prey source (Uetz 1989).

The ricochet effect has been recorded only under field conditions with a colonial spider, i.e. spiders that live in obligate large semi-permanent clusters (Uetz 1989). While field studies are useful, there is substantial variation in prey approach, prey type, number of webs in the colony and even the degree of overlap between two webs. This highlights the need for an experimental approach to determine the effect of web proximity on prey interception.

In this study, I determined the effect of shadow competition in an orb-web spider under semi-natural experimental conditions. In particular, I test the following hypotheses: (1) shadow competition can occur even in low densities of orb-web spiders, (2) the degree of overlap of webs affects prey interception and (3) the ricochet effect can compensate for shadow competition. Accordingly, I predicted that Outer webs would receive more prey interceptions than Inner webs, and that as the degree of overlap increases, so does the proportion of prey intercepting the outer web, and there would be a number of prey items that ricochet off from the Outer web to the Inner web, such that the costs of being the inner web decreases.

Materials and Methods

Study Species

Argiope keyserlingi Karsch, 1878 (Araneae: Araneidae), the St. Andrew's Cross Spider, is an orb-web spider with distributions recorded along the eastern coast of Australia (Levi 1983; Platnick 2009) in a wide variety of habitats, ranging from rainforest margins to urban gardens. It is locally abundant and typically found on long-leaved bushes such as *Lomandra longifolia* and *Pandanus* sp. (Rao et al. 2007). *Argiope keyserlingi* builds silk decorations in the form of zigzag deposits of silk, stretching outwards from the centre of the web (Herberstein et al. 2000). These spiders are solitary but can often be found in proximity to each other (Rao et al. 2007). Stingless bees of the Genus *Trigona* are known to be a common prey of *Argiope* spiders (Craig et al. 2001). *Trigona carbonaria* Smith (Hymenoptera: Apidae) are stingless bees native to Australia. *T. carbonaria* is found all along the eastern coast of Australia, and extends as far north as the tropics, and typically nest in hollow logs (Michener 1961). The bees are quite small (body length of worker bees: 3.9–4.3 mm; Dollin et al. 1997) and typical colonies contain a single queen and hundreds of workers.

Experimental Setup

In a semi-enclosed greenhouse, a commercially available hive box (Russell and Janine Zabel Pty Ltd, Hatton Vale, Queensland, Australia) was set up on a table. Bees were trained to approach a feeder with sugar water (ratio of sugar to water 1:3) that was placed 1 m away from the hive. One hive was used for all experiments.

Subsequently, I trained stingless bees to fly through two empty hoops (28 cm diameter each) with different degrees of overlap en route to the feeder. The empty hoops were considered as the control and as a measure of bee activity because stingless bee activity is correlated with environmental variations (Heard & Hendrikz 1993). For the experiments, I then swapped the empty hoops with hoops with webs from adult female *A. keyserlingi*. For the experiment, webs were collected from *A. keyserlingi* individuals that were previously housed in a greenhouse. The hoops used for control and the treatments were of similar dimensions. Approaching bees always encountered the web against a background of *Lomandra* photographs, which have similar colour properties to that of actual plants (Hoese et al. 2006). Using *Lomandra* photographs rather than real plants as background has the advantage that the background can be held as a constant for all experiments, thereby eliminating any effect of plant variation and motion on bee behaviour.

I set up five experimental treatments based on the degree of overlap (Fig. 1): (1) webs with no overlap (0 overlap), (2) webs with slight overlap (0.25), (3) webs with moderate overlap (0.5), (4) webs with large overlap (0.75) and (5) webs with full overlap (1). The webs were positioned such that at any given trial, one web was behind the other by 5 cm, and both webs were in the flight path of the bees. This arrangement is not uncommon in field conditions (Rao et al. 2007; D. Rao, pers. obs.). Control hoops

were also similarly positioned. All treatments included spiders on their webs [without silk decorations; spiders of this species frequently build webs without decorations (Rao et al. 2007)], and spiders chosen for the experiment were matched for size. The order (left or right) and position (Outer or Inner) of the treatments and control hoops were randomized, and there was a delay of at least 10 min between two treatments. The control and the treatments were run one after the other and each treatment with 15 trials was run consecutively. In all treatments, I ensured that the stingless bees flew in a northerly direction and were on their foraging flight, because previous experiments had revealed that bees were most responsive in this context (Rao et al. 2008). Approaching bees were monitored in 15 1-min trials for each treatment and all bees that intercepted the webs per minute were counted. The bees that intercepted the web directly were termed as 'direct interceptions', and the bees that bounced off the first web and then intercepted the second (i.e. bees that intercepted both webs) were counted separately and termed as 'ricochets'. Ricocheting bees are due to a lack of retention of the Outer web. Retention is defined as the proportion of bees that remain entangled in the web after interception (Nentwig 1982). In this study, I focused on interception rates and did not measure retention rates, except in the case of bees that intercepted both webs. Not all bees that escape from the Outer web intercepted the Inner web.

As the data were normally distributed, I conducted ANOVAS with Tukey's HSD *post hoc* tests, with an alpha of 0.05 using the statistical package JMP version 5 (SAS Institute, Cary, NC, USA). I used bee activity (i.e. number of bees that went through the empty hoop) as a covariate because there was a correlation between bee activity and interception in previous experiments (Rao et al. 2008).

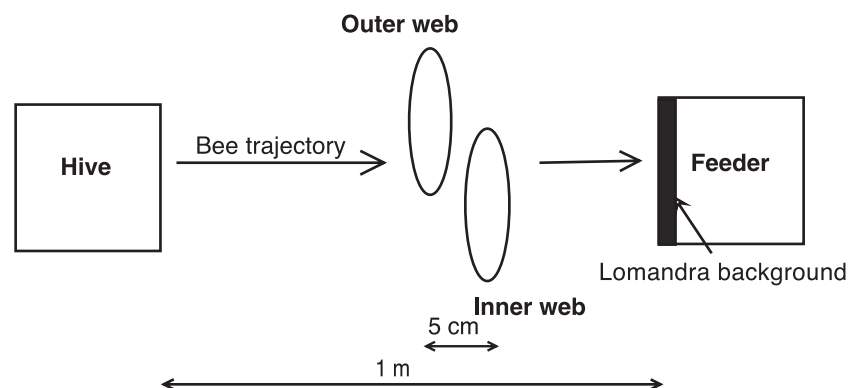


Fig. 1: Schematic representation of the experimental setup (top view) showing a 50% degree of overlap. Bees flew from the hive to the feeder and encountered two hoops with webs (separated by 5 cm). See text for details.

Ricochet Analysis

The number of bees that intercepted the webs can be termed as 'i', bees intercepting the outer web as 'Oi' and the bees intercepting the Inner web as 'Ii'. The number of bees ricocheting off the Outer web and subsequently intercepting the Inner web can be termed 'R', where R is a subset of Oi. Therefore, the total number of direct interceptions to the Outer web is Oi; the number of direct interceptions to the Inner web is Ii; and the total number of interceptions (including ricochets) to the Inner web is Ii + R.

Accordingly, I did the following analyses. First, to test whether there was a difference in direct interception between Outer webs and Inner webs (i.e. between Oi and Ii), I conducted an ANOVA with the number of bees that intercepted the web as the dependent variable and as the degree of overlap treatments and the position of the webs as independent variables. Second, for the analysis of ricochets, I conducted an ANOVA with the number of ricochets as the dependent variable and the degree of overlap as the independent variable. Third, to test the effect of ricochets on the interception rates of the inner web, I conducted an ANOVA, where the number of bees that intercepted the web was the dependent variable and the independent variables were the degree of overlap treatments and the Inner web with ricochets and without ricochets; i.e. Ii and Ii + R. Finally, I compared the total interception of bees to the Outer web (Oi) with the total interception of bees to the Inner web (Ii + R) with an ANOVA, with the number of interceptions as the dependent variable and the degree of overlap treatments and the position of the web as independent variables.

Results

There was a significant effect of both position of the web (i.e. Outer or Inner) and the degree of overlap on the interception of prey (Table 1). Overall, significantly more bees directly intercepted the Outer web

Table 1: The likelihood of bee interception was influenced by the degree of overlap between the webs and the position (Outer or Inner) of the web (ANOVA, $F_{10,139} = 8.18$, $p < 0.0001$)

Parameters	df	Sum of squares	F ratio	p
Activity	1	0.41	0.07	0.79
Degree of overlap	4	22.44	0.93	0.45
Position	1	81.37	13.50	0.0003
Degree of overlap × position	4	230.78	9.57	<0.0001

than the Inner web (Tukey's HSD, $Q = 1.98$, $p < 0.05$). However, the mean number of bee interceptions to both Inner and Outer webs was significantly influenced by the interaction between the degree of overlap between the webs and the position of the web (Table 1). The number of bee interceptions to the Outer web increased with degree of overlap, whereas the number of bee interceptions to the Inner web decreased with degree of overlap (Fig. 2). In the no-overlap treatment, the Inner web intercepted more prey than the Outer web, but this difference was not statistically significant (Tukey's HSD, $Q = 3.21$, $p < 0.05$).

The number of ricochets significantly increased with the degree of overlap (ANOVA; $F_{4,70} = 19.67$, $p < 0.0001$; Fig. 3). The number of ricochets was highest at an overlap of 0.75.

With an increase in the degree of overlap, there was a significant difference in the number of interceptions to the Inner web as a result of the ricochet effect (ANOVA; $F_{1,139} = 21.20$, $p < 0.0001$; Fig. 4). When total interception rates were compared, there was no significant difference between the interception rates of Outer webs and Inner webs with ricochets (ANOVA; $F_{1,139} = 0.026$, $p = 0.872$; Fig. 5).

Discussion

Overall, stingless bees were more likely to directly intercept the Outer web than the Inner web. Interception was influenced by the degree of overlap

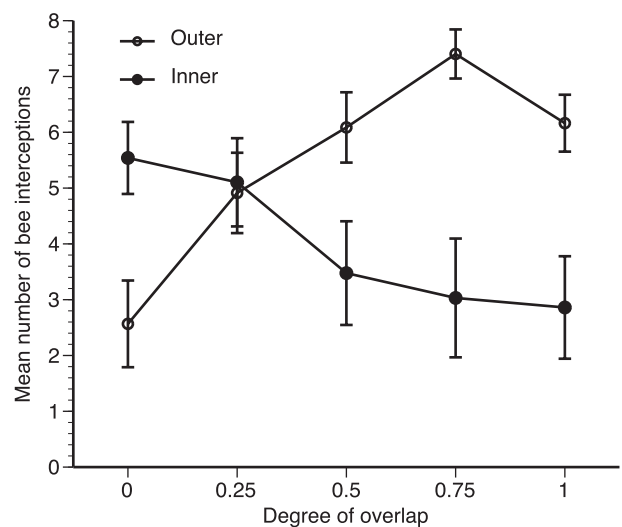


Fig. 2: The number of direct interceptions ($\bar{x} \pm SE$) of stingless bees increased with the degree of overlap for the outer web (Oi) and decreased for the inner web (Ii) ($n = 15$ trials per treatment).

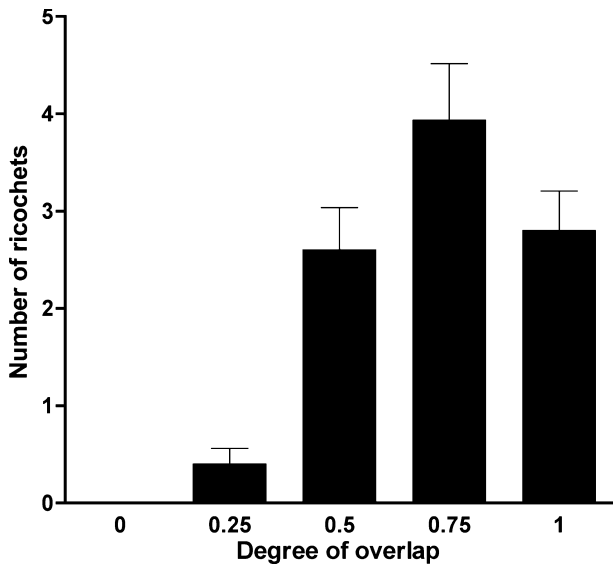


Fig. 3: The number ($\bar{x} \pm SE$) of ricochets (R), i.e. bouncing off the outer web and intercepting the inner web, increased with the degree of overlap between the outer and inner webs ($n = 15$ trials per treatment).

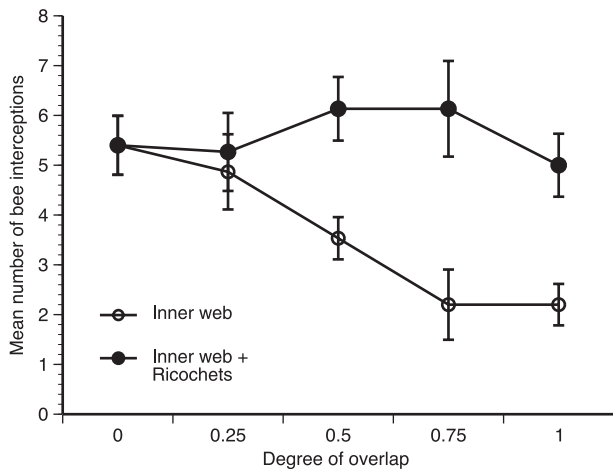


Fig. 4: When corrected for ricochets, there was a significant difference in the number of interceptions ($\bar{x} \pm SE$) between the inner web with ricochets ($li + R$) and the inner web without ricochets (li) ($n = 15$ trials per treatment).

between the webs, with more bees directly intercepting the Outer web as the degree of overlap increased. There were also a substantial number of bees that ricocheted off the outer web and intercepted the inner web, and the number of ricochets increased with the degree of overlap. The rate of direct interceptions to the Inner web decreased with increase in overlap, but this decrease was diminished by the bees that ricocheted to the inner web. When

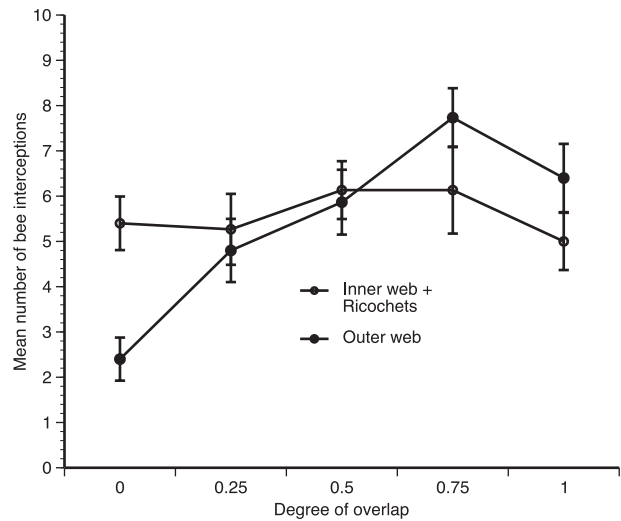


Fig. 5: When corrected for ricochets, there was no difference in interception ($\bar{x} \pm SE$) between the outer web (O_i) and the inner web ($li + R$) ($n = 15$ trials per treatment).

the number of interceptions for the Inner web was corrected for ricochets, the Inner web with ricochets performed better than an Inner web without ricochets. Furthermore, there was no difference in total interception between Outer webs and Inner webs when corrected for ricochets.

Shadow competition is thought to influence the distribution of stationary predators. Typically, when sedentary predators occur in high density, the effect of shadow competition is seen by the eventual redistribution of the predators in a ‘doughnut’ shaped pattern (Linton et al. 1991). However, although there is limited evidence of such dispersion pattern in spiders (Riechert et al. 1973), there are a few differences between typical stationary predators such as ant-lion larvae and spiders. Spiders that build webs can relocate, and establish new webs in other areas. In aggregating spiders, the benefits of staying in proximity to other conspecifics, such as ease of access to males, silk sharing and protection from predators through the ‘selfish herd’ effect may outweigh the potential costs of shadow competition (Rypstra 1979). Furthermore, there is an increased likelihood of capturing prey that have bounced off a conspecific’s web (Uetz 1989 and present study).

The retention rate in orb-web spiders is quite low even after interception because flying prey can escape from the web before the spider can capture it (Eberhard 1990). Consequently, the ricochet effect phenomenon allows for the amelioration of the negative effect of shadowing even in low densities of aggregation. In this study, when corrected for

ricochets, the Inner web received more interceptions than it would have without the ricochets. As the velocity of the bee would have decreased subsequent to the impact on the outer web, the inner web has a greater likelihood of prey capture, although this was not measured in this study. Therefore, there is a decrease in the cost of being on the inside. When there was no overlap, the Inner web received more interceptions than the Outer web (Fig. 2), suggesting that bees responded to the Outer web by changing their trajectory and subsequently intercepting the Inner web, but the reason for this difference is not clear. The optimum degree of overlap for spiders to benefit from the ricochets is likely to be between 50 and 75% overlap. This implies that aggregations with individuals showing this level of overlap can still receive enough prey per individual.

The ricochet effect is a consequence of the lack of retention of insects by spider webs. In this study, I did not measure the retention rates of the webs in either position. Not all bees that escaped from the outer webs subsequently intercepted the inner web, and there is no data on the number of bees that escaped from the inner web. The ricochet effect predicts that the rate of retention would be higher in the inner web, but since this study was aimed towards characterizing the difference in interception rates, there is no data available on the retention rates of the two webs. Nevertheless, in terms of interception, there are differences in the rates of impact based on the spatial positioning of the webs.

Shadow competition has been studied in spiders only once before, but with a spider that builds webs on the ground (Lubin et al. 2001). Using a combination of field study and modeling, they found a distinct effect of spatial positioning on the growth and survival of members of the colony of spiders. However, the model did not take into account the possible benefits of the ricochet effect, in the sense that ants (the most common prey) that are not captured by one web may subsequently hit another web. Until now, the ricochet effect has been studied only in colonial spiders. In *Metepeira spinipes* and *Metepeira incrassata*, over half the prey that hit the first web ricocheted off (Uetz 1989). However, because of the density of these aggregations, there is a greater chance of subsequent prey capture. In facultative aggregations such as those found in *Argiope* or *Nephila*, we would expect a smaller ricochet success. Nevertheless, under the right circumstances, I show that despite the low density of overlapping webs, i.e. even with just two webs, there is no substantial

disadvantage in being in proximity to another orb-web spider in terms of prey interception. In field conditions, *A. keyserlingi* are often found in proximity to each other (Rao et al. 2007). As they prefer to build webs on plants with particular architectures such as *Lomandra*, there is a limitation on suitable websites. In such a situation, building webs in proximity would not negatively impact the spiders in terms of prey interception. While aggregations in *A. keyserlingi* are not large (D. Rao, pers. obs.), the results from this study can be extrapolated to any orb-web spider that builds webs in proximity to conspecifics.

In this study, I presented spiders with a unidirectional steady stream of prey. In nature, however, spiders catch prey that are infrequent and highly stochastic, as well as arriving from all directions. Furthermore, orb-webs are thought to target large and infrequent prey, because a single large prey item may be sufficient to sustain the spider through to the next instar (Venner & Casas 2005). However, with large prey comes the chance of web damage because of a greater insect velocity on impact as well as an increased likelihood of the prey escaping before capture. Therefore, another advantage of building close to a conspecific is that much of the momentum of the flying insect is absorbed by the first web, allowing the second web to capture the prey easily.

This study shows that the potentially costly effect of shadow competition can be compensated for by the ricochet effect even at a small scale. This study also shows that the degree of overlap significantly influences prey interception rates and that the benefits of being close to a conspecific outweighs the disadvantages.

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Literature Cited

Blackledge, T. A. & Zevenbergen, J. M. 2006: Mesh width influences prey retention in spider orb webs. *Ethology* **112**, 1194–1201.

- Bruce, M. J. 2006: Silk decorations: controversy and consensus. *J. Zool.* **269**, 89–97.
- Craig, C. L., Wolf, S. G., Davis, J. L. D., Hauber, M. E. & Maas, J. L. 2001: Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. *Evolution* **55**, 986–993.
- Dollin, A. E., Dollin, L. J. & Sakagami, S. F. 1997: Australian stingless bees of the genus *Trigona* (Hymenoptera: Apidae). *Invert. Taxon.* **11**, 861–896.
- Eberhard, W. G. 1990: Function and phylogeny of spider webs. *Ann. Rev. Ecol. Sys.* **21**, 341–372.
- Elliott, J. M. 2002: Shadow competition in wild juvenile sea-trout. *J. Fish Biol.* **61**, 1268–1281.
- Hart, D. 1986: The adaptive significance of territoriality in filter-feeding larval blackflies (Diptera: Simuliidae). *Oikos* **46**, 88–92.
- Heard, T. A. & Hendrikz, J. A. 1993: Factors influencing flight activity of colonies of the stingless bee *Trigona carbonaria* (Hymenoptera: Apidae). *Aus. J. Zool.* **41**, 343–353.
- 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. *Biol. Rev.* **75**, 649–669.
- Hoese, F. J., Law, E. A. J., Rao, D. & Herberstein, M. E. 2006: Distinctive yellow bands on a sit-and-wait predator: prey attractant or camouflage? *Behaviour* **143**, 763–781.
- Jakob, E. M., Porter, A. H. & Uetz, G. W. 2001: Site fidelity and the costs of movement among territories: an example from colonial web-building spiders. *Can. J. Zool.* **79**, 2094–2100.
- Levi, H. W. 1983: The orb-weaver genera *Argiope*, *Gea* and *Neogea* from the Western Pacific region (Araneae:Araneidae: Argiopinae). *Bull. Mus. Comp. Zool.* **150**, 247–338.
- Linton, M. C., Crowley, P. H., Williams, J. T., Dillon, P. M., Aral, H., Strohmeier, K. L. & Wood, C. 1991: Pit relocation by antlion larvae: a simple model and laboratory test. *Evol. Ecol.* **5**, 93–104.
- Lloyd, N. J. & Elgar, M. A. 1997: Costs and benefits of facultative aggregating behaviour in the orb-spinning spider *Gasteracantha minax* Thorell (Araneae: Araneidae). *Aust. J. Ecol.* **22**, 256–261.
- Lubin, Y., Henschel, J. R. & Baker, M. B. 2001: Costs of aggregation: shadow competition in a sit-and-wait predator. *Oikos* **95**, 59–68.
- McNett, B. J. & Rypstra, A. L. 2000: Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. *Ecol. Entomol.* **25**, 423–432.
- Michener, C. D. 1961: Observations on the nests and behavior of *Trigona* in Australia and New Guinea (Hymenoptera, Apidae). *Am. Mus. Nov.* **2026**, 1–46.
- Nentwig, W. 1982: Why do only certain insects escape from a spider's web? *Oecologia* **53**, 412–417.
- Platnick, N. 2009: The World Spider Catalog, version 9.5. American Museum of Natural History. Available at: <http://research.amnh.org/entomology/spiders/catalog/index.html>.
- Rao, D. & Poyyamoli, G. 2001: Role of structural requirements in web-site selection in *Cyrtophora cicatrosa* Stoliczka (Araneae: Araneidae). *Curr. Sci. India* **81**, 678–680.
- Rao, D., Cheng, K. & Herberstein, M. E. 2007: A natural history of web decorations in the St Andrew's Cross spider (*Argiope keyserlingi*). *Aus. J. Zool.* **55**, 9–14.
- Rao, D., Cheng, K. & Herberstein, M. E. 2008: Stingless bee response to spider webs is dependent on the context of encounter. *Behav. Ecol. Sociobiol.* **64**, 209–216.
- Riechert, S., Reeder, W. & Allen, T. 1973: Patterns of spider distribution (*Agelenopsis aperta* (Gertsch)) in desert grassland and recent lava bed habitats, south-central New-Mexico. *J. Anim. Ecol.* **42**, 19–35.
- Robinson, M. H. & Robinson, B. 1980: Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pac. Insects Monogr.* **36**, 1–218.
- Ruxton, G. D. & Hansell, M. H. 2009: Why are pitfall traps so rare in the natural world? *Evol. Ecol.* **23**, 181–186.
- Rypstra, A. L. 1979: Foraging flocks of spiders. *Behav. Ecol. Sociobiol.* **5**, 291–300.
- Rypstra, A. L. 1985: Aggregations of *Nephila clavipes* (L.) (Araneae, Araneidae) in relation to prey availability. *J. Arachnol.* **13**, 71–78.
- Uetz, G. W. 1989: The 'ricochet effect' and prey capture in colonial spiders. *Oecologia* **81**, 154–159.
- Uetz, G. W. & Burgess, J. W. 1979: Habitat structure and colonial behavior in *Metepeira spinipes* F.P. Cambridge (Araneae: Araneidae), an orb-weaving spider from Mexico. *Psyche* **86**, 79–89.
- Venner, S. & Casas, J. 2005: Spider webs designed for rare but life-saving catches. *Proc. R. Soc. Lond. B Biol. Sci.* **272**, 1587–1592.