Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speed in *Cyclosa*

Kensuke Nakata^{1,*} and Samuel Zschokke²

¹Faculty of Human Environment, Nagasaki Institute of Applied Science, Nagasaki, Japan

²Section of Conservation Biology (NLU), Department of Integrative Biology, University of Basel, Basel, Switzerland

Almost all spiders building vertical orb webs face downwards when sitting on the hubs of their webs, and their webs exhibit an up–down size asymmetry, with the lower part of the capture area being larger than the upper. However, spiders of the genus *Cyclosa*, which all build vertical orb webs, exhibit inter- and intraspecific variation in orientation. In particular, *Cyclosa ginnaga* and *C. argenteoalba* always face upwards, and *C. octotuberculata* always face downwards, whereas some *C. confusa* face upwards and others face downwards or even sideways. These spiders provide a unique opportunity to examine why most spiders face downwards and have asymmetrical webs. We found that upward-facing spiders had upside-down webs with larger upper parts, downward-facing spiders had normal webs with larger lower parts and sideways-facing spiders had more symmetrical webs. Downward-facing *C. confusa* spiders were larger than upward- and sideways-facing individuals. We also found that during prey attacks, downward-facing spiders ran significantly faster downwards than upwards, which was not the case in upward-facing spiders. These results suggest that the spider's orientation at the hub and web asymmetry enhance its foraging efficiency by minimizing the time to reach prey trapped in the web.

Keywords: foraging efficiency; biomechanics; orientation; web asymmetry; gravity; hub displacement

1. INTRODUCTION

Animals in various taxa build some kind of nest. Nests are built to protect the owner from predators, moderate harsh environmental conditions, trap food for consumption or attract females to mate (Hansell 2005). Ecological factors, together with the way the owner animal uses the nest, affect the design and the structure of animal-built structures. Among them, the spider's vertical orb web is a network of silken threads used as a trap.

The orb web is a foraging territory in which the spider can be regarded as a central-place forager. Most orb web spiders wait for prey at the hub (the place where the web's radial threads converge; Witt *et al.* 1968; Zschokke 1999), which is usually located in the central part of the web. Web building can be regarded as a foraging investment (Sherman 1994), and spiders adjust web size, web shape and sticky spiral density according to environmental and internal conditions, presumably to enhance return from the investment (e.g. Sherman 1994; Schneider & Vollrath 1998; Venner *et al.* 2000; Nakata & Ushimaru 2004; Nakata 2007), resulting in a large inter- and intraspecific variability in web morphology (Eberhard 1990; Heiling & Herberstein 2000). On the other hand, most vertical orb webs have a common design feature: their up–down size asymmetry (Witt & Reed 1965; Heiling & Herberstein 1998). With very few exceptions, the lower part is larger than the upper part; that is, the distance from the centre of the hub to the outermost spiral is

larger below the hub than above it. Another common feature is the spider's orientation when it sits at the hub waiting for the prey: orb web spiders nearly always face downwards.

Why do vertical orb webs exhibit this up–down asymmetry, and why do spiders sit at the hub facing downwards? To answer these questions, we have previously developed an analytical model, and simulated the spider's prey-attack behaviour, assuming that web asymmetry and spider orientation were optimized to maximize prey-capture success (Zschokke & Nakata 2010). Because orb webs hold prey in most cases only temporarily (e.g. Eberhard 1986; Zschokke *et al.* 2006), predation success will be lower if the spider takes more time to reach prey. This implies that the spider should shape its web and orient itself in such a way that the average time to reach the prey trapped anywhere in the web is minimized. Three factors are considered to influence travel time according to the position of prey interception. (i) Some spiders are known to run faster when they move down the web than when they climb up, probably owing to gravity (Masters & Moffat 1983; ap Rhisiart & Vollrath 1994). (ii) The spiders' orientation at the hub affects the time to reach prey. They have to turn at the hub before approaching prey trapped behind them, which may cost them extra time. They can probably also locate prey in front of them more precisely than prey behind (Klärner & Barth 1982). (iii) Prey often struggle to escape from the web. Struggling sometimes causes the prey to tumble down the web (Eberhard 1989), altering the distance from the spider to the prey and hence the spider's travelling time. We concluded that when prey does not tumble

* Author for correspondence (ken@tku.ac.jp).

† Present address: Tokyo Keizai University, Minami-chou 1-7-34, Kokubunji, Tokyo 185-8502, Japan.

down, spiders can maximize prey-capture success by facing downwards and building webs with larger lower parts (Zschokke & Nakata 2010). Our model thus successfully explains what can usually be observed in nature. However, the generally uniform up–down size asymmetry of orb webs and the head-down orientation of spiders do not provide any variation that would allow testing our model and simulation. In addition, the assumption that prey does not tumble may not always be valid.

Under the assumption that prey sometimes tumbles down the web, our theoretical study made additional predictions (Zschokke & Nakata 2010). (i) The difference in speed between running upwards and running downwards affects the optimal spider orientation; when the difference is small, sitting head-down is no longer optimal and spiders should face upwards. (ii) The optimal location of the hub to maximize prey-capture success of a head-up spider is always lower than that of a similar head-down spider. In other words, head-up spiders should build webs that have larger upper parts than head-down spiders. Examining these predictions will test the hypothesis from our model that web asymmetry and the spider's orientation are optimized to maximize prey-capture success.

Cyclosa spiders are useful in this context because they exhibit unusual inter- and intraspecific variation in spider orientation at the hub (Wiehle 1928; Nakahira 1961; Yoshikura 1987; Tanikawa 1992). In particular, *Cyclosa ginnaga* and *C. argenteoalba* face upwards, and *C. octotuberculata* faces downwards, whereas some *C. confusa* face upwards and others face downwards or even sideways. During field observations of *Cyclosa octotuberculata*'s prey-capture behaviour, prey tumbling was observed in 27 cases among 204 cases of natural prey hitting the web (K. Nakata 2003–2008, personal observation). For the other *Cyclosa* spiders, no quantitative data on prey tumbling are available, but in the laboratory, we occasionally observed prey tumbling down the web before spiders captured the prey in all species examined. The purpose of the present study is to test our model under the assumption that prey sometimes tumble down the web, by assessing (i) whether webs of spiders facing upwards have larger upper parts, and (ii) whether the upward–downward difference in running speed is less in spiders that face upwards than in spiders facing downwards.

2. MATERIAL AND METHODS

(a) Field investigation of web asymmetry

Cyclosa ginnaga, *C. argenteoalba*, *C. octotuberculata* and *C. confusa* are all common *Cyclosa* species in the western part of Japan. Their webs are all diurnal; spiders construct their webs at dawn and consume them the following night. *Cyclosa argenteoalba* (adult female body length of 4–7 mm and weight of 5–20 mg) and *C. confusa* (about 5–8 mm and 10–20 mg) are the smallest among them, *C. ginnaga* is intermediate in size (about 5–10 mm and 10–20 mg), while *C. octotuberculata* is the largest (about 10–14 mm and 50–250 mg; body lengths are from Tanikawa 1992; and weights are from K. Nakata 2006–2007, personal observation). Study sites were Mt Inasa Park in Nagasaki City, Japan, where *C. ginnaga*, *C. octotuberculata* and *C. confusa* occur,

and the Botanical Garden of Kyoto University, Kyoto, Japan, where *C. argenteoalba* lives. We surveyed the study sites to observe adult females of *C. ginnaga* (late July), *C. argenteoalba* (September) and *C. octotuberculata* (June and July), and adult and subadult (we were not able to distinguish adults and subadults with certainty in the field) females of *C. confusa* (September and October). When we found a spider sitting on the hub of the web, spider orientation was recorded from the dorsal side. When it was within $\pm 45^\circ$ from facing directly upwards, the spider was categorized as facing up, and downward, rightward and leftward orientations were defined in the same way. *C. ginnaga* ($n = 28$) and *C. argenteoalba* ($n = 19$) all faced upwards, whereas all 28 *C. octotuberculata* faced downwards. We observed 24, 8, 13 and 20 *C. confusa* to face up-, right-, left- and downwards, respectively. Because the same individual sometimes changed orientation from right to left and *vice versa* on the same web during the same day, we grouped these spiders as sideways sitter. We never observed upward- and downward-facing spiders to change their orientation within the same day, but sideways sitters sometimes did; when sideways sitters turned to the direction of prey impact and the prey escaped before the spider initiated to move towards the prey, they were sometimes observed to keep their facing direction for a while (from 10 min to an hour). In the laboratory, we observed that *C. confusa* sometimes changed its orientation from one day to the next, having built a new web. For each spider we assessed the asymmetry of its web by measuring the distance from the hub to the outermost spiral in all four directions (vertical up, vertical down, horizontal right and horizontal left). Measured *C. ginnaga* and *C. octotuberculata* spiders were marked with enamel lacquer to avoid measuring the same individual's web more than once. We did not mark *C. argenteoalba* and *C. confusa*, but kept the spiders whose webs had been observed in the laboratory until the survey was terminated. For *C. confusa*, we measured the carapace width of individual spiders with digital callipers.

The asymmetry index of the web was calculated as the difference in radius between up and down direction divided by the sum of the two. Positive and negative values indicated that webs had larger upper and lower parts, respectively. Differences in the asymmetry index were examined by ANOVA both interspecifically among *C. ginnaga*, *C. argenteoalba* and *C. octotuberculata*, and intraspecifically among upward-, sideways- and downward-facing *C. confusa*. One-sample *t*-tests were conducted for each species and group of individuals to examine whether web asymmetry indexes were different from zero. To examine the relationship between spider size and orientation in *C. confusa*, we conducted an ordered logistic regression, with carapace width as an explanatory variable and orientation as a dependent variable, by considering orientation as an ordered variable (i.e. facing upwards = 0, sideways = 1 and downwards = 2).

(b) Laboratory observation of running speed difference

Apart from the field survey, we collected 13 *C. ginnaga*, 13 *C. argenteoalba*, 12 *C. octotuberculata*, 12 upward-facing *C. confusa* and 16 downward-facing *C. confusa* from our study sites (all were adult females). They were installed individually in acrylic frames (45 × 45 × 5 cm), each of which was put between two transparent cover sheets (Zschokke & Herberstein 2005). The frames were placed in the laboratory

in Nagasaki city under a natural D:L cycle, and the spiders constructed a new web at dawn several days after collection.

Predation behaviour was observed for each spider twice on the same day: once for prey in the upper and once for prey in the lower part of web. Each time, one prey (fruitfly for *C. ginnaga*, *C. argenteoalba* and *C. confusa*, and syrphid fly for *C. octotuberculata*, collected from a nearby field) was cooled in the refrigerator and picked up by its wing using tweezers. After the prey restored its activity, it was put quietly into the web, either above or below the hub. Care was taken not to damage the wings or the body of prey. We did not throw prey into the web, since throwing is not possible with a constant impact of the prey into the web, which might produce unnecessary variation in spider's response. Spiders soon turned to face the prey and initiated predation behaviour, which was recorded in a digital movie (30 frames s⁻¹). The part of the web (i.e. upper or lower) that received the first fly was randomly assigned. The first and the second video recordings were conducted with an interval of 3–5 h, during which the focal spider finished feeding on the first prey. Each individual was used for only two running speed measurements (up and down).

In most cases, spiders being aware of the prey did not rush to the prey immediately. They usually jerked radial threads several times to locate the prey before they initiated their approach. We started running speed measurements when the spider left the hub. Even after that, they sometimes paused on the way to the prey to jerk radial threads again. To assess the running speed, such pauses were excluded from the time needed for spiders to reach the prey, because we wanted to exclude the possible effect of directional difference in the efficiency for spiders to locate the prey (Nakata 2010). To do this, we determined the vertical position of the spider's head in every frame of the video and calculated its distance between two consecutive frames from the start of running to the first touch on the prey. Then, we calculated a three-frame-interval moving average of the distance and regarded a spider as pausing when the moving average was less than 0.33 mm. In other words, we summed up the duration when spiders moved more than 10 mm s⁻¹ at the resolution of 1/30 s, and the total time was regarded as the time the spiders needed to reach the prey. We also measured the distance between prey and the hub, and running speed was calculated by dividing the distance by the time. We pooled the data for each species and group irrespective of which part of the web (i.e. upper or lower) received the fly first, since preliminary analysis revealed no significant effect of prey presentation order. We compared the running speed between upward and downward directions for each of *C. ginnaga*, *C. argenteoalba*, *C. octotuberculata*, upward-facing *C. confusa* and downward-facing *C. confusa* by paired *t*-tests. Additionally, we compared running speeds among *C. ginnaga*, *C. argenteoalba*, *C. octotuberculata*, upward-facing *C. confusa* and downward-facing *C. confusa* separately in upward and downward directions by one-way ANOVA.

3. RESULTS

(a) Web asymmetry

Web asymmetry differed between *C. ginnaga*, *C. argenteoalba* and *C. octotuberculata* ($F_{2,72} = 29.55$, $p < 0.001$; figures 1 and 2), as well as between *C. confusa* spiders with different orientations (upwards, sideways and downwards; $F_{2,62} = 15.44$, $p < 0.001$; figure 2). The average

web asymmetry indexes for *C. ginnaga*, *C. argenteoalba* and upward-facing *C. confusa* were significantly greater than zero ($t = 7.665$, d.f. = 27, $p < 0.001$; $t = 4.610$, d.f. = 18, $p < 0.001$; $t = 2.209$, d.f. = 23, $p < 0.05$, respectively), indicating that their webs had a larger upper part. On the other hand, the average web asymmetry indexes for *C. octotuberculata* and downward-facing *C. confusa* were significantly less than zero ($t = -2.806$, d.f. = 27, $p < 0.01$; $t = -5.360$, d.f. = 19, $p < 0.001$, respectively), indicating that these webs had a larger lower part. The web asymmetry indexes for sideways-facing *C. confusa* were negative, but the result was only marginally significant ($t = -2.064$, d.f. = 20, $p = 0.052$), indicating that these webs were less asymmetrical in the vertical direction. The result of the ordered logistic regression indicated a significant effect of carapace width on spider orientation in *C. confusa* (model: log likelihood = -56.02, $\chi^2 = 19.50$, $p < 0.001$; coefficient of carapace width: $\chi^2 = 15.29$, d.f. = 1, $p < 0.001$), with small spiders tending to face upwards, medium-sized spiders facing sideways and large spiders tending to face downwards (figure 3).

(b) Running speed

Figure 4 shows the mean running speed in upward and downward directions for each species and the two types of *C. confusa*. In spiders facing upwards (i.e. *C. ginnaga*, *C. argenteoalba* and upward-facing *C. confusa*), running speed did not differ between upward and downward directions ($t = -1.630$, d.f. = 12, $p = 0.129$; $t = -1.663$, d.f. = 12, $p = 0.122$; $t = -0.273$, d.f. = 11, $p = 0.790$, respectively). In contrast, spiders facing downwards (i.e. *C. octotuberculata* and downward-facing *C. confusa*) ran downwards significantly faster than upwards ($t = -6.275$, d.f. = 11, $p < 0.001$; $t = -3.321$, d.f. = 15, $p = 0.005$, respectively).

There was a significant interspecific and intraspecific difference in downward running speed (ANOVA: $F_{4,61} = 13.10$, $p < 0.001$). Scheffe *post hoc* comparison revealed that downward running speed was significantly faster in *C. octotuberculata* than in the upward-facing spiders *C. ginnaga*, *C. argenteoalba* and upward-facing *C. confusa* ($p < 0.001$ for all comparisons). Similarly, downward running speed was significantly faster in downward-facing *C. confusa* than in *C. argenteoalba* ($p < 0.037$) and upward-facing *C. confusa* ($p = 0.004$), and tended to be faster than *C. ginnaga* ($p = 0.069$). On the other hand, there was no significant difference in upward running speed (ANOVA: $F_{4,61} = 0.79$, $p = 0.533$) among the spiders, although *C. octotuberculata* ran slightly faster upwards than *C. ginnaga* and *C. argenteoalba*, and downward-facing *C. confusa* also ran slightly faster upwards than upward-facing *C. confusa*.

4. DISCUSSION

The field survey revealed a clear relationship between spider orientation at the hub and up-down asymmetry (i.e. hub displacement) of orb webs in *Cyclosa* spiders. Webs of *C. ginnaga* and *C. argenteoalba*, which consistently faced upwards, had larger upper parts, whereas the downward-facing *C. octotuberculata* built webs with larger lower parts, as most other araneid spiders do. *Cyclosa confusa* exhibited individual variability in

Figure 1. Orb webs of (a) *C. ginnaga*, (b) *C. argenteoalba*, (c) *C. octotuberculata*, (d) *C. confusa* facing upwards and (e) *C. confusa* facing downwards. Webs of *C. ginnaga*, *C. octotuberculata* and *C. confusa* facing downwards have debris decorations (Tan *et al.* 2010) and the web of *C. ginnaga* additionally has silk decoration. Pictures were resized for each web to have the same vertical diameter. Broken lines indicate the top and the bottom of the webs. Arrows indicate the height of hub and dotted lines indicate the height of the geometric centre of the web. Scale bars, 10 mm.

Figure 2. Up–down asymmetry in orb webs of *Cyclosa* spiders. The asymmetry index was calculated as the difference between the upper and lower radius of the outermost spiral divided by the sum of these two. Positive and negative values indicate that the webs have larger upper and lower parts, respectively. Asterisks indicate that the asymmetry index differed significantly from zero (* < 0.05, ** < 0.01, *** < 0.001). Error bars indicate s.e. White, facing upward; grey, facing sideways; black, facing downwards.

Figure 3. Relationship between spider's size (measured as carapace width) and spider orientation in *C. confusa*.

Figure 4. Upward and downward running speeds during prey capture of *Cyclosa* spiders. Asterisks indicate significant differences between upward (black triangles) and downward (white triangles) running speeds within species or group (** < 0.01, *** < 0.001), and letters denote significant differences in downward running speeds between species and groups (same letter denotes no difference, different letters indicate significant difference with $p < 0.05$). Upward running speeds did not differ between species and groups. Error bars indicate s.d.

orientation: those facing upwards had larger upper parts, those facing downwards had larger lower parts and those facing sideways had more symmetrical webs. These results support the prediction of our model (Zschokke & Nakata 2010) that webs of spiders facing upwards should have larger upper parts than webs of spiders facing downwards. To our knowledge, very few spiders systematically build vertical orb webs with larger upper parts; only some ladder-web building *Scoloderus* (Eberhard 1975) and spiders of the genera *Deliochus* (Kuntner *et al.* 2008a) and *Cyclosa* (this study) have been reported to do so.

Laboratory observation of prey-attack behaviour revealed that running speeds did not differ between upward and downward direction in the upward-facing *C. ginnaga*, *C. argenteoalba* and *C. confusa* facing upwards. On the other hand, the downward-facing *C. octotuberculata* ran faster downwards than upwards, as did

C. confusa facing downwards. Small sample size and large variation may be the reason for the lack of significant directional difference in running speed in upward-facing spiders. Nevertheless, speed differences between the two directions were larger in spiders facing downwards than in spiders facing upwards, and the trend was consistent both in interspecific and intraspecific comparisons. These results support another prediction from the theoretical study assuming that prey sometimes tumble down the web: spiders should face upwards when the difference in running speed between upward and downward direction is small (Zschokke & Nakata 2010).

Our results on running speeds in *C. ginnaga*, *C. argenteoalba* and upward-facing *C. confusa* contrast with those in the orb web spiders *Araneus diadematus* and *Larinioides sclopetarius* (= *Nuctenea sclopetaria*), who run downwards faster than upwards (Masters & Moffat 1983; ap Rhiart & Vollrath 1994), as did the downward-facing *C. octotuberculata* and downward-facing *C. confusa* in the present study. We consider that the size of the spiders through its influence on running speed is largely responsible for this difference: gravity may help large spiders to run faster downwards. In addition, Moya-Laraño *et al.* (2009) suggested that the optimal body length to maximize climbing-up speed was 7.4 mm. Above that, their biomechanical model predicted that relative upward climbing speed decreases with spider size. This optimal body length for climbing thus lies within or near the size ranges of *C. ginnaga*, *C. confusa* and *C. argenteoalba*, but is clearly smaller than the size range of *C. octotuberculata*. The results from our study do not support this hypothesis, probably because Moya-Laraño *et al.* (2009) model assumed that the proportion of leg length to whole body is constant irrespective of spider's size, which was not the case in the spiders used in our study. Contrary to expectations, *C. octotuberculata*, which has a smaller leg-length-to-body-length ratio than other two species (Tanikawa 1992), ran fastest. Interspecific differences in web morphology may also influence running speed: *C. ginnaga* and *C. argenteoalba* build webs with denser sticky spirals than does *C. octotuberculata* (figure 1), and dense sticky spirals may inhibit spiders from running fast. However, the effect of sticky spiral density should occur irrespective of running direction and can thus not explain why downward-facing spiders ran significantly faster only in the downward direction. Moreover, it also cannot explain why the results of the intraspecific comparison of upward and downward running speed using *C. confusa* were similar to the results of the interspecific comparison.

We suggest that spider size is an important factor to explain the pattern in directional difference in running speed observed in this study: larger spiders tend to have larger differences between their upward and downward running speeds. Furthermore, we suggest that the difference in running speeds affects spider orientation and up-down web asymmetry (Zschokke & Nakata 2010). Consequently, it can be expected that smaller spiders may face upwards, and that larger spiders always face downwards and build asymmetrical webs with larger lower parts. The results of the present study fulfil this expectation; the relatively small *C. ginnaga* and *C. argenteoalba* (body length less than 10 mm) face upwards and built webs with larger upper parts, whereas the larger

C. octotuberculata (body length greater than 10 mm) faced downwards and built webs with larger lower parts. Similarly, within *C. confusa*, smaller individuals generally faced upwards and built webs with larger upper parts and larger individuals faced downwards and built webs with larger lower parts. However, a few large *C. confusa* faced upwards and a few small *C. confusa* faced downwards (figure 3), suggesting that spider size is not the sole determinant of *C. confusa*'s (nor perhaps of other spiders') running speed and orientation; we cannot exclude that developmental changes or the spider's reproductive state also influence spider orientation. Nevertheless, there is some evidence also from other *Cyclosa* species that smaller individuals are more likely to face upwards than larger ones. For example, Nakahira (1961) described juvenile *C. sedeculata* to face upwards, sideways or downwards, whereas the larger adults always faced downwards. In addition, many earlier studies have revealed that up-down web asymmetry is interspecifically and intraspecifically related to spider size: while smaller individuals spin more symmetrical webs, the webs of larger individuals show typical web asymmetry with larger lower parts (e.g. interspecific comparison: Zschokke & Vollrath 1995; *L. scolopetarius*: Heiling & Herberstein 1998; *Nephilengys cruentata*: Japyassú & Ades 1998; *Eriophora fuliginea*: Graf & Nentwig 2001; *Clitaetra irenae*: Kuntner *et al.* 2008b).

To summarize, we suggest that smaller spiders tend to have smaller upward-downward differences in running speed, and that such small running speed differences lead to an increase in the size of the upper part of the web (thus making the web more symmetrical), and can even lead to the spider facing upwards. Facing upwards leads to an additional increase in the size of the upper part of the web, which can then become larger than the lower part. Larger spiders generally face downwards, and only the relationship between spider size and web asymmetry is observed, as reported in previous studies.

However, it remains unclear why other small spiders do not face upwards, and why the relatively large *Verrucosa arenata* (body length 13 mm, body mass 230 mg; Zschokke *et al.* 2006) always face upwards (Levi 1976; Zschokke *et al.* 2006). It is possible that the running speeds do not relate to body size in the same way in all spiders—clearly more research is needed on that aspect.

To conclude, the results of the present study support the hypothesis that up-down web asymmetry and spider orientation are adaptations to maximize prey-capture success by minimizing the average time to reach prey trapped anywhere in the web (Zschokke & Nakata 2010).

We thank Dr William Eberhard and two anonymous reviewers for constructive comments on this manuscript. This study was partly supported by the MEXT Grant-in-Aid for Young Scientists (B), 15770017, 2003–2004 and Grant-in-Aid from the Japan Society of Promotion of Science for Scientific Research (C) (20570025), 2008–2010 to K.N. and by the Treubelfonds, Basel, to S.Z.

REFERENCES

- ap Rhiart, A. & Vollrath, F. 1994 Design features of the orb web of the spider, *Araneus diadematus*. *Behav. Ecol.* **5**, 280–287. (doi:10.1093/beheco/5.3.280)
- Eberhard, W. G. 1975 The 'inverted ladder' orb web of *Scoloderus* sp. and the intermediate orb of *Eustala*(?) sp. *Araneae: Araneidae*. *J. Nat. Hist.* **9**, 93–106. (doi:10.1080/00222937500770071)
- Eberhard, W. G. 1986 Effects of orb-web geometry on prey interception and retention. In *Spiders: webs, behavior and evolution* (ed. W. A. Shear), pp. 70–100. Stanford, CA: Stanford University Press.
- Eberhard, W. G. 1989 Effects of orb web orientation and spider size on prey retention. *Bull. Brit. Arachnol. Soc.* **8**, 45–48.
- Eberhard, W. G. 1990 Function and phylogeny of spider webs. *Annu. Rev. Ecol. Syst.* **21**, 341–372. (doi:10.1146/annurev.es.21.110190.002013)
- Graf, B. & Nentwig, W. 2001 Ontogenetic change in coloration and web-building behavior in the tropical spider *Eriophora fuliginea* (Araneae, Araneidae). *J. Arachnol.* **29**, 101–110. (doi:10.1636/0161-8202(2001)029[0104:OCI CAW]2.0.CO;2)
- Hansell, M. 2005 *Animal architecture*. Oxford, UK: Oxford University Press.
- Heiling, A. M. & Herberstein, M. E. 1998 The web of *Nuctenea scolopetaria* (Araneae, Araneidae): relationship between body size and web design. *J. Arachnol.* **26**, 91–96.
- Heiling, A. M. & Herberstein, M. E. 2000 Interpretations of orb-web variability: a review of past and current ideas. *Ekologia (Bratisl)* **19**(Suppl. 3), 97–106.
- Japyassú, H. F. & Ades, C. 1998 From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). *Behaviour* **135**, 931–956.
- Klärner, D. & Barth, F. G. 1982 Vibratory signals and prey capture in orb-weaving spiders (*Zygiella x-notata*, *Nephila clavipes*; Araneidae). *J. Comp. Physiol. A* **148**, 445–455. (doi:10.1007/BF00619783)
- Kuntner, M., Coddington, J. A. & Hormiga, G. 2008a Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. *Cladistics* **24**, 142–217. (doi:10.1111/j.1096-0031.2007.00176.x)
- Kuntner, M., Haddad, C. R., Aljančić, G. & Blejec, A. 2008b Ecology and web allometry of *Clitaetra irenae*, an arboricolous African orb-weaving spider (Araneae, Araneidae, Nephilidae). *J. Arachnol.* **36**, 583–594. (doi:10.1636/T07-54.1)
- Levi, H. W. 1976 The orb-weaver genera *Verrucosa*, *Acanthepeira*, *Wagneriana*, *Acacesia*, *Wixia*, *Scoloderus* and *Alpaida* North of Mexico (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* **147**, 351–391.
- Masters, W. M. & Moffat, A. J. M. 1983 A functional explanation of top-bottom asymmetry in vertical orb webs. *Anim. Behav.* **31**, 1043–1046. (doi:10.1016/S0003-3472(83)80010-4)
- Moya-Laraño, J., Vinković, D., Allard, C. M. & Foellmer, M. W. 2009 Optimal climbing speed explains the evolution of extreme sexual size dimorphism in spiders. *J. Evol. Biol.* **22**, 954–963. (doi:10.1111/j.1420-9101.2009.01707.x)
- Nakahira, K. 1961 Spiders in Kochi Prefecture (in Japanese). *Atypus* **23/24**, 27–60.
- Nakata, K. 2007 Prey detection without successful capture affects spider's orb-web building behaviour. *Naturwiss.* **94**, 853–857. (doi:10.1007/s00114-007-0264-9)
- Nakata, K. 2010 Attention focusing in a sit-and-wait forager: a spider controls its prey-detection ability in different web sectors by adjusting thread tension. *Proc. R. Soc. B* **277**, 29–33. (doi:10.1098/rspb.2009.1583)
- Nakata, K. & Ushimaru, A. 2004 Difference in web construction behavior at newly occupied web sites between two *Cyclosa* species. *Ethology* **110**, 397–411. (doi:10.1111/j.1439-0310.2004.00983.x)

- Schneider, J. M. & Vollrath, F. 1998 The effect of prey type on the geometry of the capture web of *Araneus diadematus*. *Naturwiss.* **85**, 391–394. (doi:10.1007/s001140050521)
- Sherman, P. M. 1994 The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Anim. Behav.* **48**, 19–34. (doi:10.1006/anbe.1994.1208)
- Tan, E. J., Seah, S. W. H., Yap, L.-M. 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? *Anim. Behav.* **79**, 179–186. (doi:10.1016/j.anbehav.2009.10.025)
- Tanikawa, A. 1992 A revisional study of the Japanese spiders of the genus *Cyclosa* MENGE (Araneae: Araneidae). *Acta Arachnol.* **41**, 11–85. (doi:10.2476/asjaa.41.11)
- Venner, S., Pasquet, A. & Leborgne, R. 2000 Web-building behaviour in the orb-weaving spider *Zygiella x-notata*: influence of experience. *Anim. Behav.* **59**, 603–611. (doi:10.1006/anbe.1999.1327)
- Wiehle, H. 1928 Beiträge zur Biologie der Araneen, insbesondere zur Kenntnis des Radnetzbaues. *Z. Morphol. Ökol. Tiere* **11**, 115–151. (doi:10.1007/BF02425772)
- Witt, P. N. & Reed, C. F. 1965 Spider-web building: measurement of web geometry identifies components in a complex invertebrate behavior pattern. *Science* **149**, 1190–1197. (doi:10.1126/science.149.3689.1190)
- Witt, P. N., Reed, C. F. & Peakall, D. B. 1968 *A spider's web*. New York, NY: Springer.
- Yoshikura, M. 1987 *The biology of spiders (in Japanese)*. Tokyo, Japan: Japan Scientific Societies Press.
- Zschokke, S. 1999 Nomenclature of the orb-web. *J. Arachnol.* **27**, 542–546.
- Zschokke, S. & Herberstein, M. E. 2005 Laboratory methods for maintaining and studying web-building spiders. *J. Arachnol.* **33**, 205–213. (doi:10.1636/CT04-72.1)
- Zschokke, S. & Nakata, K. 2010 Spider orientation and hub position in orb webs. *Naturwiss.* **97**, 43–52. (doi:10.1007/s00114-009-0609-7)
- Zschokke, S. & Vollrath, F. 1995 Web construction patterns in a range of orb-weaving spiders (Araneae). *Eur. J. Entomol.* **92**, 523–541.
- Zschokke, S., Hénaut, Y., Benjamin, S. P. & García-Ballinas, J. A. 2006 Prey-capture strategies in sympatric web-building spiders. *Can. J. Zool.* **84**, 964–973. (doi:10.1139/z06-074)