Web asymmetry in the tetragnathid orb spider *Metellina mengei* (Blackwell 1869) is determined by web inclination and web size

Tew, Nicholas[1,2] and Hesselberg, Thomas[1*]

Affiliation

1. Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom

2. Department of Life Sciences, Imperial College London, Buckhurst Road, Ascot, SL5 7PY, United Kingdom

* Corresponding author: thomas.hesselberg@zoo.ox.ac.uk

Abstract:

Vertical asymmetry is a widespread feature of orb webs, with the lower part larger than the upper, although its adaptive value is not fully understood. Gravity is thought to play a major role in the generation of asymmetry through increased running speed downwards from the hub. The relationship between spider orientation and gravity has been relatively well studied. However, webs' inclination from vertical has been less studied. Here we conducted a field study on the tetragnathid orb spider *Metellina mengei* Blackwall 1869, which constructs webs that show a marked variation in inclination. Our findings revealed a significant influence of the degree of web inclination and web area on the level of vertical asymmetry, while environmental variables did not have any effect. Thus, our results support the hypothesis that the asymmetry in upwards and downwards running speeds due to gravity is an important determinant of web asymmetry.

Keywords:

vertical web asymmetry, spider running speeds, effects of gravity, optimal foraging theory

The majority of webs from all major orb spider families (Araneidae, Tetragnathidae and Nephilidae) are asymmetric with the area below the hub being larger than the area above (Masters & Moffat 1983; ap Rhiziart & Vollrath 1994; Kuntner et al. 2010b). This vertical web asymmetry is primarily thought to arise from an asymmetry in running speed caused by gravity, which allows for faster downwards running speeds than upwards against gravity, as has been observed in a number of araneids in the laboratory (Masters and Moffat 1983; ap Rhiziart & Vollrath 1994; Nakata & Zschokke 2010). Given this asymmetry in running speed, it follows from optimal foraging theory that spiders optimise their prey capture rate by investing more time and silk resources in web construction below the hub compared to above (Maciejewski 2010; Gregoric et al. 2013). Another hypothesis relating to gravity that has been proposed to explain web asymmetry is that web-building costs should be higher in the upper part of the web (Herberstein & Heiling 1999), although this has not been supported by empirical data (Coslovsky & Zschokke 2009).

A number of predictions arise from the gravity-determined running speed asymmetry hypothesis: *i)* Spiders should be orientated downwards to gain full advantage of the faster downward gravity-assisted running speeds. This prediction is supported by a range of studies that demonstrate a link between vertical asymmetry and spider orientation, including studies that show that the few spider species facing upwards in the hub often have reversed asymmetries with the area above the hub being larger than below (Nakata & Zschokke 2010; Zschokke & Nakata 2010), although this is not always the case (Rao et al. 2011). *ii)* Larger and heavier spiders should build more asymmetric webs as heavier spiders should experience a larger asymmetry in running speeds due to gravity's impact on mass. Studies comparing different sized adults and different ontogenetic stages confirm that larger spiders build more asymmetric webs (Herberstein & Heiling 1999; Hesselberg 2010; Kuntner et al. 2010a). Spiders that build webs with reversed asymmetry build more symmetric webs with increasing size (Nakata 2010), further supporting the notion that upwards running speed is slower in heavier spiders. Alternatively, it has been suggested that web asymmetry is an evolutionary derived trait and that spiders recapitulate this during individual development (the biogenetic law) such that young spiders build symmetric webs and older spiders asymmetric webs even in the absence of any adaptive advantage (Eberhard et al. 2008), but a number of studies specifically tested this hypothesis without finding any support (Hesselberg 2010; Kuntner et al. 2010a; Nakata 2010; Gregoric et al. 2013). *iii)* Since gravity acts vertically in the direction of the center of the Earth, spiders building webs that are not completely vertical should experience less of a difference in upwards and downwards running speed and therefore should build more symmetric webs. This is supported by experimental studies on horizontal web building in the araneid *Araneus diadematus* Clerck 1757, which normally builds vertical webs (Zschokke 2011) and by observational studies of the tetragnathid *Leucauge venusta* Walckenaer 1842 webs classified into three inclination groups (Gregoric et al. 2013). The importance of gravity is further supported by observations of two *A. diadematus* building symmetric webs in space on board Skylab (Witt et al. 1977). *iv)* Web vertical asymmetry should only depend on the gravity-determined differences in running speed (predictions i to *iii* above), suggesting that the majority of other variables known to affect overall orb web geometry, but not expected to affect the asymmetry in running speeds, should not affect web asymmetry. This is the case for spatial constraints (Hesselberg 2013), but has not been specifically studied for other variables such as climatic factors (Vollrath et al. 1997), leg loss (Pasquet et al. 2011) and exposure to neurotoxins (Hesselberg & Vollrath 2004). However, some factors may affect web asymmetry without directly affecting running speed asymmetry including factors such as experiences of prey capture success in different parts of the web (Heiling & Herberstein 1999), inter- and intra-individual variability in web-building behaviour (Heiling and Herberstein 2000), possibly related to differences in behavioural syndromes (Kralj-Fiser & Schneider 2012) and perceived predation risk (Nakata & Mori 2016).

Most of the above-mentioned studies focus on the effect of only one variable in a highly controlled laboratory study (but see Kuntner et al. 2010a) and use araneids or nephilids with predominantly vertical webs (but see Gregoric et al. 2013). Here we investigate the asymmetry of webs of the tetragnathid *Metellina mengei* in the field measuring a range of different web and climatic variables with the specific aim of testing the third and fourth prediction of the gravity-determined running speed asymmetry hypothesis (see above). To our knowledge, this is the first study to compare the effect of inclination on web asymmetry with both measured as continuous variables.

Metellina mengei is a medium sized orb spider common in woodland understorey in Western and Central Europe in the early spring (in summer and autumn, it is replaced by the very similar *M. segmentata* Clerck 1757). It builds relatively small webs that show a large variation in inclination. In this study, we observed webs ranging from 5° to 85° (but with 85% of 430 measured webs between 40° and 60°). *Metellina* spiders always (when present in the hub) face downwards (Tew, N. & Hesselberg, T. Pers. Obs.). The data used come from a larger study by Tew and Hesselberg (2017), but here we focus on webs from the edge of the forest, where climatic conditions were more variable than in the forest interior. We recorded 430 webs of adult and subadult *M. mengei* on three 200-m transects in Wytham Woods, Oxfordshire, UK (51° 78′ N, 01° 34′ W) during 10 days in May and June 2015 and measured the following variables: the inclination of the web to horizontal (0° - horizontal, 90° - vertical) measured to the nearest 5° with a protractor kept level by placing it on a clipboard, web height above ground level, the vertical and horizontal diameters of web, the upper radius of the web, horizontal diameter of web, the vertical diameter of the free zone. From the latter variables, we calculated vertical web asymmetry with the formula: $(R_U - R_L)/(R_U + R_L)$, where R_U is the upper and R_L the lower radius of the web (Zschokke 1993; Hesselberg 2010), and the area of the capture spiral (web area), with the Ellipse-Hub equation (Herberstein & Tso 2000). In addition, we measured the following climatic variables at the start of each study day: temperature, humidity, pressure and wind speed. See Tew and Hesselberg (2017) for a more detailed description of the methodology.

In order to determine the influence of web and climatic variables on web asymmetry, we used the statistical programming language R (R Core Team 2016) to build a general linear mixed model with web asymmetry as response variable and inclination, web area, web height, wind speed, temperature, pressure and humidity as predictor variables. First order interactions between the first four variables were also included in the model. The study day and transect number were included as random factors. The model was validated following Thomas et al. (2013). Non-significant terms were removed from the full model following the marginal rule until the final model with the lowest AIC score was found. P-values were determined with Type II Wald F tests with Kenward-Roger degrees of freedom. The conditional (R_c^2 fixed and random effects) and marginal (R_m^2, fixed effects only) coefficients of determination were estimated based on the method by Nakagawa and Schielzeth (2013).

We found a clear negative relationship between the degree of inclination and vertical asymmetry (F = 17.76, df = 1, N = 430, P < 0.001), which support prediction *III* above. The less inclined (more horizontally orientated) a *M. mengei* web was, the more symmetric it was (Fig 1A). We furthermore found a significant effect of web area (F = 8.54, df = 1, N = 430, P = 0.004) in that larger webs were significantly more asymmetric (Fig 1B). This lend support to prediction *ii*, since larger webs are usually built by larger and heavier spiders (Heiling & Herberstein 1998). We furthermore found support for prediction *iv* in that none of the climatic variables tested (wind speed, temperature, humidity and pressure) or height of web above the ground were found to have a significant effect on web asymmetry (Wind speed: F = 1.02, df = 1, N = 430, P = 0.340; Temperature: F = 0.88, df = 1, N = 430, P = 0.371; Humidity: F = 1.33, df = 1, N = 430, P = 0.289; Pressure: F = 0.20, df = 1, N = 430, P = 0.672; Height: F = 0.64, df = 1, N = 413, P = 0.423). However, height did have an indirect effect on web asymmetry in that its interaction with inclination was significant (F = 9.89, df = 1, N = 413, P = 0.002) such that webs build lower in the vegetation did not show a clear relationship between inclination and web asymmetry. Similarly, we found a significant interaction between inclination and web area (F = 6.24, df = 1, N = 413, P = 0.013) such that only larger webs showed a clear relationship between inclination and web asymmetry. None of the first order interactions including wind speed, were significant and neither was the interaction between height and web area (results not shown). The full model with fixed and random factors explained 12% of the variance (R_c^2 = 0.124), while the fixed factors alone explained 9% (R_m^2 = 0.089). Thus, the model developed in this study only explained about 12% of the variation in the observed web asymmetry. This suggest that although inclination and web area significantly influence web asymmetry, it is also influenced by a range of other factors not measured in this study such as spider size (although this is partly taken into account by the use of web-size (Heiling & Herberstein 1998), intra- and inter-individual variation in web-building (Heiling & Herberstein 2000), spider age, ontogeny and reproductive status (Hesselberg 2010; Anotaux et al. 2012).

Despite the relatively large number of studies on web asymmetry in orb spiders, there is still much we do not know, especially in relation to webs in the wild. In this study, we focussed on some of the mechanistic factors influencing the asymmetry, but there is also a need to look at the functional aspects. In particular it would be interesting to study prey capture success and the resulting growth rate and reproductive success in spiders that build webs of different inclination (and hence asymmetry) in greater detail as our previous study suggests that inclination is a significant determinant of prey capture success in the webs of this species (Tew & Hesselberg 2017). The webs of *M. mengei* that were measured in this study varied quite significantly in both inclination and asymmetry (with 3% of webs even having larger upper parts than lower parts – see figure 1). If a given inclination and web asymmetry provides the largest return in terms of prey capture, why do webs in the wild show such a large variation? One intriguing possibility is that predation risk may affect the degree of web asymmetry in that asymmetric webs are posited to be more complex and take longer time to build than symmetric webs causing spiders to build more symmetric webs when they perceive a risk of predation (Nakata & Mori 2016). However, our previous study did not show any differences in the asymmetry of webs between the more exposed forest edge with presumably higher predation risk and the more sheltered interior of the forest (Tew & Hesselberg 2017).

References

Anotaux, M., Marchal, J., Chaline, N., Desquilbet, L., Leborgne, R., Gilbert, C., & A. Pasquet. 2012. Ageing alters spider orb-web construction. Animal Behaviour 84: 1113–1121.

ap Rhiziart, A. & F. Vollrath. 1994. Design features of the orb web of the spider, *Araneus diadematus*. Behavioral Ecology 5: 280-287.

Coslovsky, M. & S. Zschokke. 2009. Asymmetry in orb-webs: an adaptation to web building costs? Journal of Insect Behavior 22: 29–38.

Eberhard, W. G., Barrantes, G. & Madrigal-Brenes, R. 2008. Vestiges of an orb-weaving ancestor? The “biogenetic law” and ontogenetic changes in the webs and building behavior of the black widow spider *Lactodectus geometricus* (Araneae Theridiidae) Etholology Ecolology & Evolution 20: 211-244.

Gregoric, M., Kiesbuy, H. C., Quiñones Lebron, S. G., Rozmann, A., Agnarsson, I. & M. Kuntner. 2013. Optimal foraging, not biogenetic law, predicts spider orb web allometry. Naturwissenschaften 100: 263-268.

Heiling, A. M. & M. E. Herberstein. 1998. The web of *Nuctenea sclopetaria* (Araneae, Araneidae): relationship between body size and web design. Journal of Arachnology 26: 91-96.

Heiling, A. M. & M. E. Herberstein. 1999. The role of experience in web-building spiders (Araneidae). Animal Cognition 2: 171-177.

Heiling, A. M. & M. E. Herberstein. 2000. Interpretations of orb-web variability: a review of past and current ideas. Ekológia 19: 97-106.

Herberstein, M.E. & A. M. Heiling. 1999. Asymmetry in spider orb webs: a result of physical constraints? Animal Behaviour 58: 1241–1246.

Hesselberg, T. 2010. Ontogenetic changes in web design in two orb-web spiders. Ethology 116: 535-

545.

Hesselberg, T. 2013. Web-building flexibility differs in two spatially constrained orb spiders. Journal of Insect Behavior 26: 283-303.

Hesselberg, T. & Vollrath, F. 2004. The effects of neurotoxins on web-geometry and web-building behaviour in *Araneus diadematus* Cl. Physiology & Behavior 82: 519-529.

Kralj-Fiser, S. & J. Schneider. 2012. Individual behavioural consistency and plasticity in an urban spider. Animal Behaviour 84: 197-204.

Kuntner, M., Gregoric, M. & D. Li. 2010a. Mass predicts web asymmetry in *Nephila* spiders. Naturwissenschaften 97: 1097-1105.

Kuntner, M., Krajl-Fiser, S. & Gregoric, M. 2010b. Ladder webs in orb-web spiders: ontogenetic and evolutionary patterns in Nephilidae. Biological Journal of the Linnean Society 99: 849-866.

Maciejewski, W. 2010. An analysis of the orientation of an orb-web spider. Journal of Theoretical Biology 265: 604-608.

Masters, M. & A. Moffat. 1983. A functional explanation of top-bottom asymmetry in vertical orb webs. Animal Behaviour 31: 1043-1046.

Nakagawa, S. & H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4: 133-142.

Nakata, K. 2010. Does ontogenetic change in orb web asymmetry reflect biogenetic law? Naturwissenschaften 97: 1029-1032.

Nakata, K. & Y. Mori. 2016. Cost of complex behaviour and its implications in antipredator defence in orb-web spiders. Animal Behaviour 120: 115-121.

Nakata, K. & S. Zschokke. 2010. Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speeds in *Cyclosa*. Proceeding of the Royal Society of London. Series B. 277: 3019-3025.

Pasquet, A., Anotaux, M. & R. Leborgne. 2011. Loss of legs: is it or not a handicap for an orb-weaving spider? Naturwissenschaften 98: 557-564.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rao, D., Fernandez, O. C., Casteñedo-Barbosa, E. & F. Diaz-Fleischer. 2011. Reverse positional orientation in a neotropical orb-web spider, *Verrucosa arenata*. Naturwissenschaften 98: 699-703.

Tew, N. & T. Hesselberg. 2017. The effect of wind exposure on the web characteristics of a tetragnathid orb spider. Journal of Insect Behavior 30: 273-286.

Thomas, R., Vaughan, I. & J. Lello. 2013. Data Analysis with R statistical Software: A Guidebook for Scientists. – Eco-Explore, Newport.

Vollrath, F., Downes, M. & S. Krackow. 1997. Design variability in web geometry of an orb-weaving spider. Physiology & Behavior 62: 735-743.

Witt, P. N., Scarboro, M. B., Daniels, R., Peakall, D. B., & R. L. Gause. 1977. Spider web-building in outer space: evaluation of records from the Skylab experiment. Journal of Arachnology 4: 115-124.

Zschokke, S. 1993. The influence of the auxiliary spiral on the capture spiral in *Araneus diadematus* Clerk (Araneidae). Bulletin of the British Arachnological Society 9: 169-173.

Zschokke, S. 2011. Spiral and web asymmetry in the orb webs of *Araneus diadematus* (Araneae: Araneidae). Journal of Arachnology, 39, 358-362.

Zschokke, S. & K. Nakata. 2010. Spider orientation and hub position in orb web. Naturwissenschaften 97: 43-52.

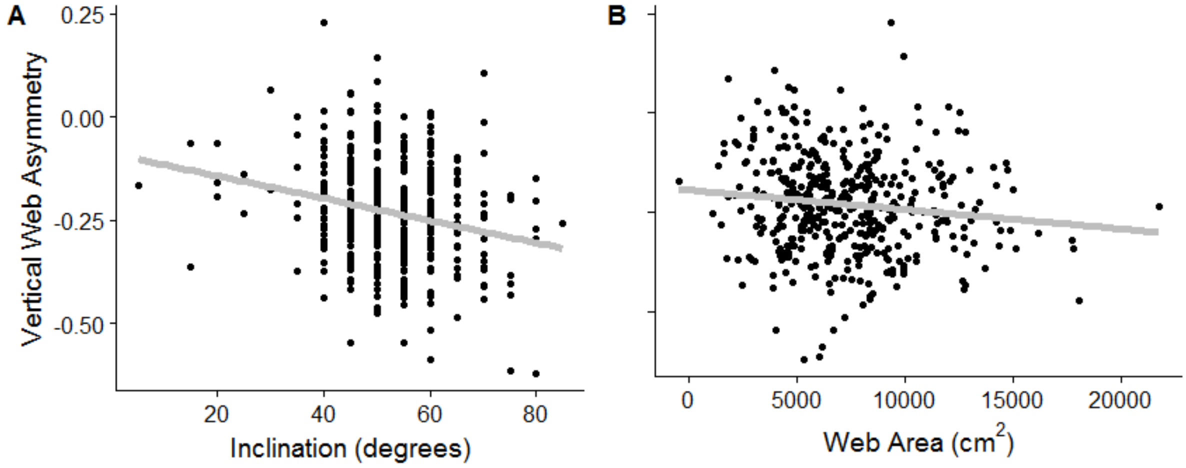

Figure 1. The vertical asymmetry of field webs of the tetragnathid *Metellina mengei* as a function of (A) The inclination of the webs to horizontal (n = 430) and (B) The area of the capture spiral (n = 430). The grey regression lines were calculated from a simple linear regression between the two variables.