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ORIGINAL PAPER

Spider orientation and hub position in orb webs

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Abstract Orb-web building spiders (Araneae: Araneoidea, Uloboridae) can be considered as territorial central place foragers. In territorial central place foragers, the optimal foraging arena is circular, with the forager sitting in its centre. In orb webs, the spider's orientation (head up or head down) whilst waiting for prey on the hub of its web and the downwards–upwards asymmetry of its running speeds are the probable causes for the observed deviation of the hub from the web's centre. Here, we present an analytical model and a more refined simulation model to analyse the relationships amongst the spider's running speeds, its orientation whilst waiting for prey and the vertical asymmetry of orb webs. The results of our models suggest that (a) waiting for prey head down is generally favourable because it allows the spider to reach the prey in its web on average quicker than spiders waiting head up, (b) the downwards–upwards running speed asymmetry, together with the head-down orientation of most spiders, are likely causes for the observed vertical asymmetry of orb webs, (c) waiting head up can be advantageous for spiders whose downwards–upwards running speed asymmetry is small and who experience high prey tumbling rates and (d) spiders waiting head up should place their hub lower than similar spiders waiting head down.

Keywords Biomechanics · Central place foraging · Spider web · Gravity · Up-down asymmetry · Web design

Introduction

Orb-web building spiders (Uloboroidea: Uloboridae; Araneoidea: Anapidae, Araneidae, Nephilidae, Symphytognathidae, Tetragnathidae, Theridiosomatidae) can be considered as strictly territorial hunters. They can capture prey only in their territory, i.e. on their web, and they have largely exclusive access to prey on their web. In contrast to other territorial hunters, size and quality of their territory is not primarily restricted by competing neighbours, but by their own limitations and decisions during web building. Orb-web spiders of the superfamily Araneoidea re-build their web usually every night or every other night (Wiehle 1927; Breed et al. 1964), and with each web-rebuilding, they can re-define the size and shape of their web and thus adapt it to their present requirements (Sherman 1994; Nakata and Ushimaru 1999; Herberstein et al. 2000; Nakata and Ushimaru 2004).

Orb-web building spiders, especially those always waiting for prey on the hub of their web (the hub is the place where the web's radii converge; Zschokke 1999), also face constraints similar to those of central place foragers (Endo 1988; Vollrath 1992; de Crespigny et al. 2001). Central place foraging theory presumes that organisms increase their fitness by maximising the energy delivery rate to a central place like a nest or a burrow, or in the case of orb-web spiders, to the hub of their web (Orians and

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Pearson 1979). Central place foraging theory predicts the value of foraging patches to decrease with their distance from the central place, since in patches requiring a long travelling time, only large prey should be captured (Schoener 1979). In orb webs, the value of a particular part of the web similarly decreases with its distance from the hub, albeit because of the time the spider requires to reach prey intercepted by the web increases with the distance from the hub (ap Rhisiart and Vollrath 1994), thus giving prey in more remote web parts a larger probability to escape before the spider can reach it. In contrast to other central place foragers, spiders do not seem to discriminate differently between large and small prey in different parts of their web (de Crespigny et al. 2001), and spiders have to decide on and make the majority of their foraging investment, i.e. web building, before any prey is actually encountered and not as a reaction to the presence of prey (Peakall and Witt 1976; Venner et al. 2003).

When prey are evenly distributed, the time required to reach the prey is critical and the forager's speed is the same in all directions, central place foraging theory predicts the optimal foraging arena to be circular, with the forager sitting in its centre (Horn 1968). Under these circumstances, the forager can reach the edge of the entire foraging arena within the same amount of time, i.e. there is no area outside the arena that the forager could reach in a shorter time than it takes to reach the most remote part within the arena. For orb webs, the basic shape of the capture area is indeed circular with the spider sitting in its centre (e.g. Zschokke 2002). However, most vertical orb webs show some deviation from the perfectly circular shape; they are vertically asymmetric with the hub positioned above the geometric centre (Fig. 1; Mayer 1952; ap Rhisiart and Vollrath 1994; Heiling and Herberstein 1998). The vertical asymmetry of the capture area is established during the building of the auxiliary spiral (Zschokke 1993). Spiders lacking gravity as orientation when building the auxiliary spiral build circular webs with the hub in their geometric centre (Mayer 1952; Witt et al. 1977; Zschokke 1993). Furthermore, the hub position differs between species, and within species, larger individuals generally build more asymmetrical webs than smaller ones (Mayer 1952; Witt and Reed 1965; Risch 1977; Zschokke and Vollrath 1995; Heiling and Herberstein 1998; Bleher 2000; Kuntner et al. 2008).

Orb webs are vertically asymmetric, probably because the assumption of the central place foraging theory is violated that the forager's speed is equal in all directions. Gravity allows spiders to run downwards faster than upwards (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994; Coslovsky 2007), with the asymmetry between downwards and upwards speeds varying greatly between spiders. Additionally, spiders are able to reach the area lying ahead more quickly than the area behind their back, because they can reach the area ahead without first turning around and because they can probably locate an insect trapped in front of them more accurately than one trapped behind them (Klärner and Barth 1982). In vertical orb webs, these two factors (downwards–upwards running speed asymmetry and orientation of the spider) are therefore likely to influence the optimal position on the web for the spider to wait for prey, i.e. the hub position.

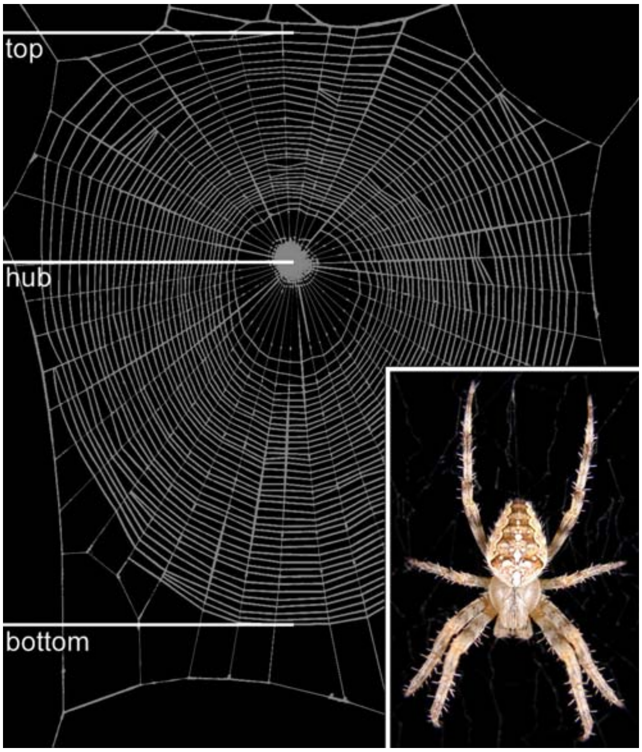

Fig. 1 Orb web of the garden cross spider *Araneus diadematus*. *Inset*: a garden cross spider *A. diadematus* waiting for prey on the hub of its web

Almost all araneoid orb-web spider species building non-horizontal webs and waiting for prey on the hub of their web do so with their head (prosoma) facing down (inset of Fig. 1), even though this orientation has been shown to be disadvantageous for defaecation (Curtis and Carrel 2000). Only few orb-web spiders have been described to not or not always face down whilst waiting for prey on the hub, amongst them several smaller (body length <10 mm) *Cyclosa* species (Wiehle 1928; Nakahira 1961; Yoshikura 1987; Tanikawa 1992) and *Verrucosa arenata* (Levi 1976; Zschokke et al. 2006). A few explanations have been put forward to explain the preference of most araneoid orb-web spider to face down: It has been suggested that the head-down orientation is favourable, because it allows the spider to drop down quickly without first turning around (M. Nyffeler, personal communication) or because it aids thermoregulation or camouflage of diurnal spiders. Until now, however, none of these explanations have been scrutinised, nor has a quantitative test been suggested to explain the preference of most araneoid orb-web spider to wait head down on the hub and to explain why some do so with their head facing up.

The present study aimed to explore the reasons for the head-down orientation of most araneoid orb-web spiders in conjunction with the above-centre hub position in their webs by developing an analytical prey capture model and a more refined prey capture simulation model. In particular, we asked the following questions: (a) why do most—but not all—araneid orb-web spiders face down when waiting for prey on the hub of their vertical web and (b) how do the characteristics of the spider and of the prey in its web influence the optimal spider orientation and hub position?

Analytical model

The analytical model was used to determine the optimal orientation (head up vs. head down) and position for a spider to wait for prey in its orb web. To keep the model simple, only prey captures directly above and below the hub were considered, and prey were assumed to be motionless after being trapped on the web. The spider was assumed to wait for prey on the hub, and as soon as the web had intercepted a prey item, the spider turned around when necessary (requiring t_{rot} time, with t_{rot} independent of the spider's orientation prior to turning around) and then started running towards the prey. We assumed the spider's running speed to be faster running downwards (v_{d}) than running upwards (v_{u}) and the optimal hub position (y^*) to be the position with the shortest average running time to reach any point below and above the hub.

The analytical model was used to determine the optimal position in the web for spiders facing down whilst waiting for prey (y^*_{d}) as well as for spiders facing up whilst waiting for prey (y^*_{u}). In addition, it was used to determine whether there is an inherent advantage for either orientation (facing up or down) whilst waiting for prey. The analytical model is an extension of earlier, implicit models on vertical asymmetry of orb webs by Masters and Moffat (1983) and ap Rhisiart and Vollrath (1994), which however—unlike our model—ignored the time the spider requires to turn around and could therefore not analyse the spider's orientation whilst waiting for prey.

Results of analytical model

Optimal hub position

Under the assumption that insects are intercepted evenly across the web, the optimal hub position is the one where the average time the spider requires to reach any part of the web is minimal. The average time T_{d} for spiders facing down and T_{u} for spiders facing up can be expressed as:

$$T_{\mathrm{d}} = \int_0^y \frac{x}{v_{\mathrm{d}}} dx + \int_0^{1-y} \left(t_{\mathrm{rot}} + \frac{x}{v_{\mathrm{u}}}\right) dx \tag{3.1.1a}$$

resp.

$$T_{\mathrm{u}} = \int_0^y \left(\frac{x}{v_{\mathrm{d}}} + t_{\mathrm{rot}}\right) dx + \int_0^{1-y} \frac{x}{v_{\mathrm{u}}} dx \tag{3.1.1b}$$

where y is the hub position (with 0.0 representing the lower edge of the web's capture area and 1.0 representing its upper edge), v_{d} and v_{u} are the spider's downwards and upwards running speeds and t_{rot} is the time the spider requires to turn around (the first integral in both equations represents the part below the hub and the second integral the part above the hub; cf. area to the left of the bold lines in Fig. 2).

Integrating yields:

$$T_{\mathrm{d}} = \frac{y^2}{2 \times v_{\mathrm{d}}} + t_{\mathrm{rot}} \times (1-y) + \frac{(1-y)^2}{2 \times v_{\mathrm{u}}} \tag{3.1.2a}$$

resp.

$$T_{\mathrm{u}} = \frac{y^2}{2 \times v_{\mathrm{d}}} + t_{\mathrm{rot}} \times y + \frac{(1-y)^2}{2 \times v_{\mathrm{u}}}. \tag{3.1.2b}$$

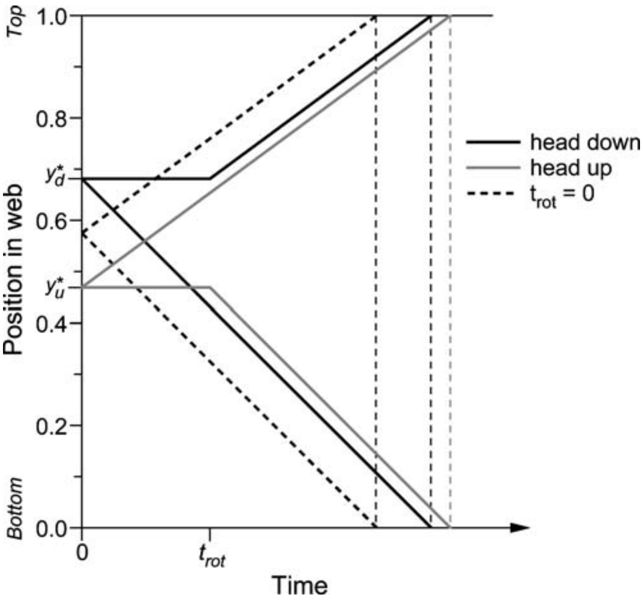

Fig. 2 Graphical representation of the analytical model. *Bold lines* represent the spider's vertical position during prey capture after a prey item has hit the web near the top and bottom edge respectively. *Bold black lines* represent a spider facing down whilst waiting for prey, *bold grey lines* represent a spider facing up whilst waiting for prey and the *bold dashed lines* represent a spider that requires no time to turn around, corresponding to earlier implicit models (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994)

To minimise, the derivative is taken

$$\frac{dT_{\mathrm{d}}}{dy} = \frac{y}{v_{\mathrm{d}}} - t_{\mathrm{rot}} - \frac{1-y}{v_{\mathrm{u}}} \qquad (3.1.3a)$$

resp.

$$\frac{dT_{\mathrm{u}}}{dy} = \frac{y}{v_{\mathrm{d}}} + t_{\mathrm{rot}} - \frac{1-y}{v_{\mathrm{u}}} \qquad (3.1.3b)$$

and set to zero to obtain the optimal hub position for spiders facing down (y_{d}^*) and for spiders facing up (y_{u}^*) respectively:

$$y_{\mathrm{d}}^* = \frac{1 + t_{\mathrm{rot}} \times v_{\mathrm{u}}}{1 + \frac{v_{\mathrm{u}}}{v_{\mathrm{d}}}} \qquad (3.1.4a)$$

resp.

$$y_{\mathrm{u}}^* = \frac{1 - t_{\mathrm{rot}} \times v_{\mathrm{u}}}{1 + \frac{v_{\mathrm{u}}}{v_{\mathrm{d}}}}. \qquad (3.1.4b)$$

For the down facing case (Eq. 3.1.4a), the numerator is larger than 1, since $t_{\mathrm{rot}} \times v_{\mathrm{u}} > 0$, and the denominator is smaller than 2, since $v_{\mathrm{u}} < v_{\mathrm{d}}$. Consequently, y_{d}^* must always be larger than 0.5, which means that the optimal hub position for spiders facing down whilst waiting for prey is always above the web's geometric centre (bold black lines in Fig. 2).

For the up facing case (Eq. 3.1.4b), y_{u}^* may be larger or smaller than 0.5, depending on the values of t_{rot}, v_{u} and v_{d}, which means that the optimal hub position for spiders facing up whilst waiting for prey may be below or above the web's centre. However, since $t_{\mathrm{rot}} \times v_{\mathrm{u}} > 0$, it follows that the nominator of Eq. 3.1.4a is always larger than the nominator of Eq. 3.1.4b, implying—because the denominators of the two equations are identical—that $y_{\mathrm{u}}^* < y_{\mathrm{d}}^*$. This means that the optimal hub position for a spider facing up whilst waiting for prey is always lower than the optimal hub position for a spider with the same running speeds but facing down whilst waiting for prey.

When $t_{\mathrm{rot}}=0$, i.e. when the time the spider requires to turn around is neglected, then $y_{\mathrm{u}}^* = y_{\mathrm{d}}^*$, which means that under this circumstances, it does not matter whether the spider faces down or up whilst waiting for prey (bold dashed lines in Fig. 2). This situation is the one assumed by the earlier implicit models on orb-web asymmetry (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994). In these models, the optimal hub position was assumed to be the one, from which the spider could reach the web's top and the bottom edge within the same amount of time. It can be shown that this criterion is equivalent to the one used in our model.

Note that the formulas for y_{d}^* and y_{u}^* are only correct for values between 0 and 1, i.e. for hub positions within the web. If the calculated y^* would be smaller than 0 or larger than 1, the optimal hub position is at the edge of the web.

Optimal orientation of spider

To determine whether there is an inherent advantage for the spider to face down or up whilst waiting for prey, we calculated the difference in the average time the spider requires to reach any part of the web between up facing and down facing spiders ($\mathrm{hda_a} = T_{\mathrm{u}} - T_{\mathrm{d}}$). We termed this difference head-down advantage ($\mathrm{hda_a}$—the subscript denotes that it is based on the analytical model), since positive values indicate that spiders facing down require on average less time to reach their prey than spiders facing up. To calculate $\mathrm{hda_a}$, we inserted the formulae for the optimal hub positions (Eqs. 3.1.4a resp. 3.1.4b) into the formulae for the average times the spiders require to reach any part of the web (Eqs. 3.1.2a resp. 3.1.2b). Simplifying yields:

$$\mathrm{hda_a} = t_{\mathrm{rot}} \times \frac{v_{\mathrm{d}} - v_{\mathrm{u}}}{v_{\mathrm{d}} + v_{\mathrm{u}}}. \qquad (3.2.1)$$

Since $v_{\mathrm{u}} < v_{\mathrm{d}}$, it follows that $\mathrm{hda_a}$ is larger than zero, which means that spiders facing down whilst waiting for prey are always on average quicker to reach prey than spiders facing up (cf. the area to the left of the bold black and grey lines in Fig. 2). In addition, the results of our analytical model suggest that the advantage of waiting for prey head down increases with the asymmetry between v_{d} and v_{u} and with the time the spider requires to turn around (t_{rot}).

Simulation model

Whilst the analytical model yields clear results, it falls short of reality in two points: (1) only prey trapped directly above or below the hub was considered and (2) prey was considered to be motionless. In reality, prey is also trapped in positions lateral of the hub, and prey struggles to escape from the web, which sometimes causes it to tumble down within the web (Eberhard 1989; Zschokke et al. 2006). In order to incorporate these aspects, we developed a more refined simulation model, in which the entire prey capture process from prey impact to capture was modelled with a computer simulation. This model allowed us to determine the optimal spider orientation and hub position with a more realistic approach.

In the simulation model, the spider web was circular with a radius of 100 unit (U); the exact web structure (radii, sticky spiral) was not modelled. Nevertheless, we use the term hub to denote the place on the web where the spider is waiting for prey, facing either up or down. The hub position was horizontally centred and—to determine its optimal vertical position—was varied vertically in increments of one unit U to find the position with the highest capture rate. At the start of each simulation run, an insect hit the web at a random location (uniformly distributed across the entire web). Upon impact, the spider started turning towards the prey with an angular speed of A degrees per time step (Table 1). As soon as the spider faced the prey, it advanced towards the prey with a speed that depended on its basic linear speed S, on the downwards–upwards running speed asymmetry R and on the angle δ of the spider's path towards the vertical (vertically up=0°):

$$\text{speed} = S \times (1 - R \times \cos(\delta)).$$

In each time step, the prey had a probability E to escape (i.e. to leave the web immediately) and a probability T to start tumbling (move downwards within the web). When the prey was tumbling, it moved vertically down with the speed P and stopped tumbling again with a probability of 0.2 per time step. When the prey had changed the position on the web due to tumbling, the spider stopped moving and started again turning towards the prey before it resumed advancing towards the prey. Prey that tumbled across the web's lower edge was considered as having left the web.

For the simulations, the parameters were varied systematically over a large range to encompass the variability of real orb-web spiders. Three different values were used for each parameter (Table 1). However, parameter combinations where the escape probability and the tumbling probability were both 0 were omitted, because under these circumstances, prey would always be caught. For each of the remaining 648 parameter combinations, 500,000 simulations runs were performed. In each simulation run, 402 virtual spiders (201 tested starting positions for the spiders and for each starting position one spider facing down and one spider facing up) were tested simultaneously to reduce the variability caused by the randomness of the prey's behaviour. When the prey hit the web, all virtual spiders simultaneously started moving (i.e. turning and walking) towards the prey and the simulation run was ended, when either the prey had left the web or when all 402 virtual spiders had captured it. Prey capture rate was calculated by dividing the number of prey captures for each virtual spider by the number of simulation runs. For each parameter combination, the hub position with the highest capture rate was then determined separately for both orientations (head up and head down) to an accuracy of 0.25 U after smoothing the capture rates across the starting positions with triangular smoothing over 16 U (Huffman and Brown 2005). Finally, it was evaluated and recorded for each parameter combination, whether a spider facing up or a spider facing down fared better, along with its capture rate (termed maximum capture rate) and its optimal hub position. The entire simulation was performed with a program written using the Pascal programming language and compiled with the GNU Pascal compiler version 3.3.2. The program source code is available on request.

Data analysis

Differences between prey capture rates were assessed by calculating the relative difference, i.e. by dividing the absolute difference between two values by their average.

The relative benefits of spiders waiting for prey head down compared to those waiting for prey head up was evaluated for each parameter combination by comparing the highest capture rate of spiders facing down with that of spiders facing up. Since this difference indicates the advantage for a spider waiting for prey head down compared to waiting for prey head up, we also used the term head-down advantage (hda_s—the subscript denotes that it is based on the simulation model). Note that whilst hda_a and hda_s are both measures for the advantage of spiders facing down, they cannot be directly compared, since they use different metrics.

We used Kruskal–Wallis tests to evaluate the strength of the influence of each parameter on maximum capture rate, on hda_s and on the optimal position of a spider facing down. We used the H value to classify the relationship as very strong (H>300), strong (H>100), moderate (H>30) or weak (H>10, which is roughly equivalent to P<0.01).

Results of simulation model

Maximum capture rate

The median of the maximum capture rates of the 648 parameter combinations was 68.50%. The maximum capture rate, which assumed for each parameter combina-

Table 1 Parameter summary of the simulation model

Abbreviation	Description
A	Angular speed of spider (10/30/90° per time step)
S	Basic linear speed of spider (2/6/18 U per time step)
R	Downwards–upwards asymmetry of spider running speeds (see text; 0.0/0.1/0.3)
E	Escape probability of prey per time step (0/0.0167/0.05)
T	Probability per time step for prey to start tumbling (0/0.033/0.1)
P	Tumbling speed of prey (3/10/30 U per time step)

Parameter values were varied over a large range to encompass the variability of real orb-web spiders tion the optimal hub position, increased very strongly with the spider's basic linear speed and decreased strongly with the prey's escape probability (Fig. 3a). In addition, it decreased with the prey's tumbling speed, tended to increase with the spider's angular speed and tended to be higher for small tumbling probabilities than for no tumbling or high tumbling probability. However, the spider's downwards–upwards speed asymmetry had no influence on the maximum capture rate.

Spider orientation

hda$_s$ (head-down advantage, see above) increased very strongly with the spider's downwards–upwards speed asymmetry (Fig. 3b). In addition, hda$_s$ decreased with the prey's tumbling probabilities, increased with the prey's escape probability and tended to decrease with the spider's angular speed.

hda$_s$ was positive, i.e. indicating that a spider facing down achieved a higher capture rate than a spider facing up, in 392 (60.5%) of the 648 tested parameter combinations. hda$_s$ was positive for all parameter combinations without prey tumbling and for almost all (97%) of the parameter combinations with a large downwards–upwards speed asymmetry of the spider (Table 2).

The largest hda$_s$s were found for parameter combinations with slow angular speed, slow or medium spider speed and a large downwards–upwards speed asymmetry. In contrast, the lowest hda$_s$s (i.e. most strongly suggesting that the spider should face up whilst waiting for prey) were found in parameter combinations with slow angular speed, no or small downwards–upwards speed asymmetry and with a large tumbling probability.

Hub position

For spiders waiting with their head facing down (the usual position), hub positions above the web's geometrical centre were optimal for 377 (58.2%) of the 648 parameter combinations.

Positions above the centre were in particular favourable for parameter combinations with a slow angular speed, a fast spider speed, a large downwards–upwards speed asymmetry, non-zero escape probabilities and a low tumbling probability (Fig. 3c). In contrast, the lowest hub positions were optimal for parameter combinations with a fast angular and a slow linear speed of the spider without downwards–upwards speed asymmetry and prey tumbling, but not directly escaping from the web.

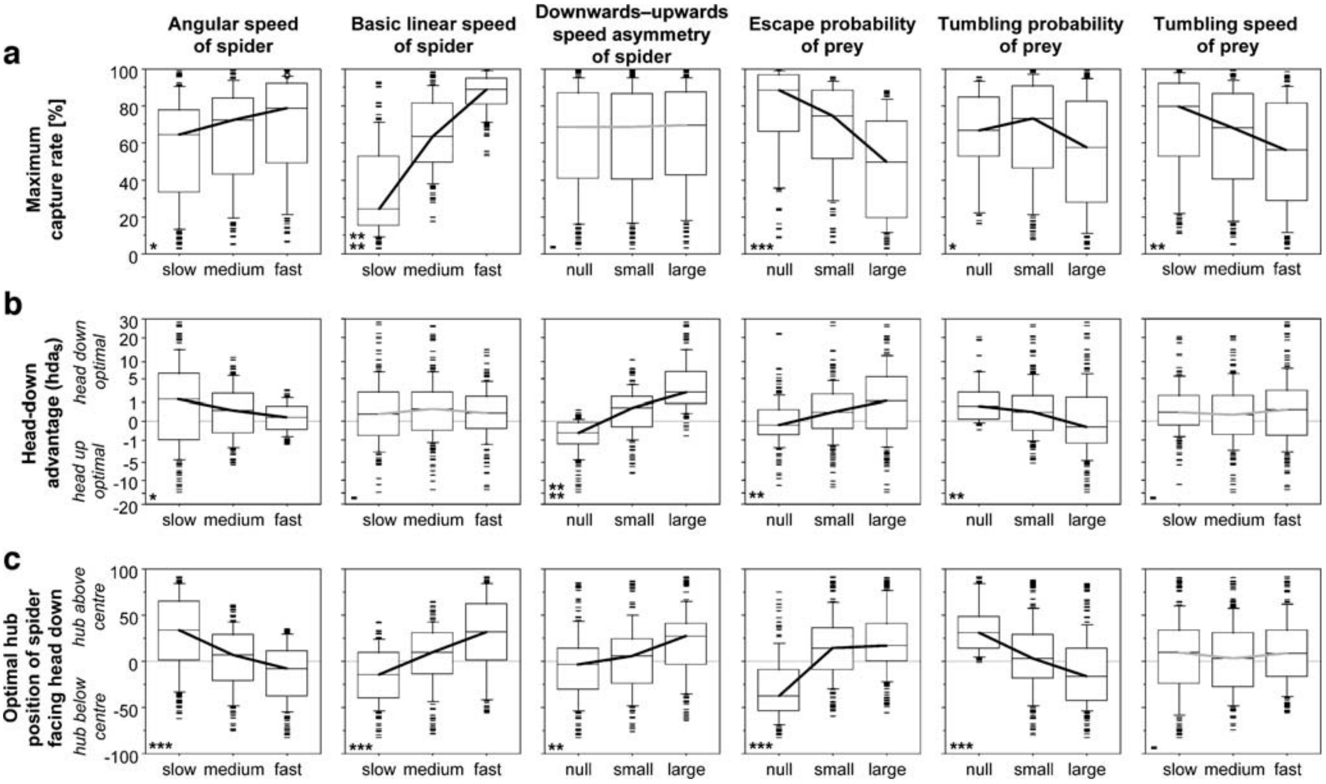

Fig. 3 Influence of angular speed of spider, basic linear speed of spider, downwards–upwards asymmetry of spider running speeds, escape probability of prey, tumbling probability of prey and tumbling speed of prey on **a** maximum capture rate, **b** relative difference in capture rate between head-up and head-down spiders (hda$_s$) and **c** optimal hub position when spider is facing down. ****H>300; ***H>100; **H>30; *H>10; –H<10 (Kruskal–Wallis test, n=648)

Table 2 Number of parameter combinations in which a spider facing down had a higher capture rate than the spiders facing up (i.e. hda_s was positive)

	No tumbling	Small tumbling probability	Large tumbling probability	Total
R=0	Horizontal web	4 (4.9%) n=81	4 (4.9%) n=81	8 (4.9%) n=162
R small	54 (100%) n=54	61 (75.3%) n=81	33 (40.7%) n=81	148 (68.5%) n=216
R large	54 (100%) n=54	79 (97.5%) n=81	76 (93.8%) n=81	209 (96.8%) n=216
Total	108 (100%) n=108	144 (59.3%) n=243	113 (46.5%) n=243	365 (61.4%) n=594

Parameter combinations corresponding to a horizontal web (upwards speed=downwards speed, no tumbling) were omitted

R = downwards–upwards asymmetry of spider speed

For all parameter combinations without tumbling, the optimal hub position for spiders facing down was on or above the web's centre (n=162). For every parameter combination, the optimal hub position was lower for a spider facing up than for a spider facing down.

Comparison between models

The main differences between our models were web shape (analytical model: vertically linear; simulation model: circular) and the inclusion of tumbling in the simulation model but not in the analytical model. To check the consistency between the two models, we compared the results for the optimal hub position across 2 (head up, head down)×27 different parameter combinations (all parameter combinations without tumbling and with a low escape probability) by inserting the parameter values into the equations of the analytical model and comparing the resulting y^*_d and y^*_u with the corresponding values from the simulation model.

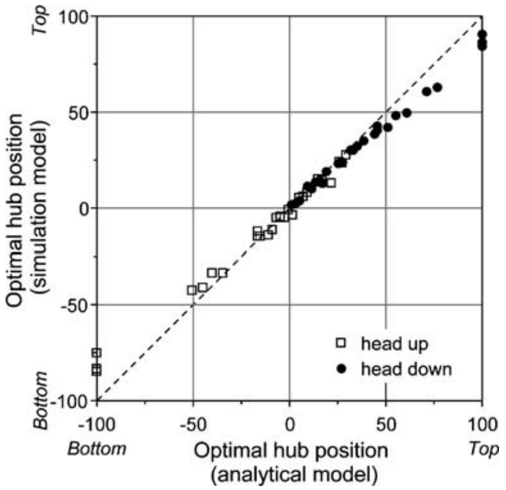

Fig. 4 Comparison between the analytical model and the simulation model (without tumbling). For most parameter combinations, there is a good agreement between the two models (*dashed line*=identity). The largest deviation was found for the three parameter combinations with a slow angular and a fast linear speed, where the analytical model predicts a hub position at the web's edge

We found a close match between the two models for most parameter combinations (Fig. 4). Substantial differences were only found for hub positions away from the web centre, notably those positions based on parameter combinations with a slow angular speed and a fast linear speed, where the analytical model suggested optimal hub positions at the web's edge. In addition, both models predicted the head-down advantage (hda) to be large with large downwards–upwards speed asymmetry and a slow angular speed of the spider. We conclude that the simulation model *without tumbling* is very similar to the analytical model. Consequently, differences between the simulation model *with tumbling* and the analytical model are likely to be related to prey tumbling.

Discussion

Analytical model

The results of the analytical model support the earlier hypothesis that the vertical asymmetry of orb webs is an adaptation to the spider's downwards–upwards running speed asymmetry and that therefore the vertical asymmetry of orb webs increases with the spider's running speed asymmetry. In addition, the model demonstrated that facing head down whilst waiting for prey allows the spider to reach all parts of its web on average quicker than when facing head up. We suggest this to be the explanation why almost all orb-web spiders face down whilst waiting on the hub of their web. Furthermore, the model predicts that—should a spider face up whilst waiting for prey—the hub should be in a lower position than the position for a similar spider facing down whilst waiting for prey. Finally, the model showed that the hub can be expected to be higher in the web than predicted by the earlier implicit models by Masters and Moffat (1983) and ap Rhisiart and Vollrath (1994), which did not consider the time needed by the spider to turn around.

This is the first time that a well-founded explanation has been put forward to explain the preference of almost all orb-web spider to face down whilst waiting for prey. However, our explanation does not exclude the possibility that alternative explanations, e.g. that spiders wait head down to allow easier escape by dropping down without the need to turn around, also play a role in explaining this behaviour.

Simulation model

Not unexpectedly, fast spiders in webs with low escape rates and slow tumbling achieved the highest capture rates in the simulation model, which was based on a circular web. Interestingly, however, the spider's downwards–upwards speed asymmetry did not affect the maximum capture rate at all, suggesting that spiders with similar downwards and upwards running speeds and spiders with a large downwards–upwards speed asymmetry can be expected to be equally successful, as long as their average running speeds are the same.

The spider's downwards–upwards speed asymmetry did, however, affect the hub position, with larger speed asymmetries leading to hubs placed further up. The speed asymmetry can be expected to increase with spider size—even when we assume that the downwards speed does not increase with spider size—since the upwards running speed of spiders is expected to decrease with spider size (Moya-Laraño et al. 2002, 2007). Consequently, we suggest that our models explain why web asymmetry increases with spider size (Mayer 1952; Witt and Reed 1965; Risch 1977; Zschokke and Vollrath 1995; Heiling and Herberstein 1998; Bleher 2000; Kuntner et al. 2008).

In previous analyses of the vertical asymmetry of orb webs, prey tumbling had been ignored, even though it had been shown to be a common phenomenon in vertical orb webs (Eberhard 1989). Our simulation model showed that tumbling is an important factor in orb-web design and is likely to influence both the hub position as well as the spider's orientation whilst waiting for prey. In particular, our model predicts that spiders experiencing large tumbling rates should move their hub downwards. If prey never escape directly but only through tumbling, even spiders facing down can be expected to build the hub below the web centre.

An extreme example for this is the tropical spiders of the genus *Scoloderus*, which build highly elongated orb webs ("ladder webs") with the hub far below the centre of the web (Eberhard 1975), specialised for capturing moths. When a moth flies into this web, it tumbles down along the web, thereby losing its scales, until it has lost enough scales to adhere to the sticky threads (Stowe 1978).

In addition, our model suggests that high tumbling rates will induce spiders with similar downwards and upwards running speeds to face up whilst waiting for prey. We infer that our model thus explains the preference of some *Cyclosa* species to face up whilst waiting for prey, since these *Cyclosa* spiders are generally relatively small species (body mass<0.02 g; Miyashita 1999) and smaller spiders can be expected to have more similar downwards and upwards running speeds than larger species (see above). In contrast, *V. arenata*, which also faces up whilst waiting for prey, is considerably larger (13 mm long, 0.23 g; Zschokke et al. 2006) and can therefore be expected to have a relatively large downwards–upwards running speed asymmetry. Our model can thus not explain why *V. arenata* waits for prey facing up in its web. However, prey capture in *V. arenata* often differs somewhat from that of most other orb-web spiders and from that assumed in our models. When a prey has been intercepted by a *V. arenata* web, the spider turns and starts walking towards it like other orb-web spiders, but when it has walked a part of the distance, *V. arenata* often stops walking and starts pulling the web with the prey towards itself until it can grab the prey (observed in eight of 13 prey captures recorded during the field study of Zschokke et al. 2006). It is possible that pulling prey trapped above the hub downwards is faster than pulling prey trapped below the hub upwards, which could compensate the spider's slower upwards running speed compared to its downwards speed. Consequently, the resulting net speed for the spider to reach the prey might be similar below and above the hub.

A particular orientation of a spider may be—depending on the coloration of its prosoma and abdomen—advantageous for camouflage or thermoregulation. Whilst it is indeed likely that body colouration and spider orientation are linked, we suggest that—due to the fundamental reasons why most spiders should face downwards given in the present study—it is more likely that body colouration is adapted to spider orientation, rather than vice versa.

Limitations of our models

In orb webs in which the spider sometimes or always waits for prey in a retreat at the web's edge, the spiders move the hub towards the retreat, most probably to reduce the travelling time between retreat and hub (Le Guelte 1967). The resulting additional vertical (and horizontal) shift of the hub position is not addressed in the present study.

Capturing prey at the web periphery is more costly for the spider than at the web's centre, because the spider requires more time to reach the prey, thus requiring more energy and invoking a greater danger of being detected by visual predators. In addition, because webs are damaged along the spider's path, a longer distance between hub and prey implies more web damage. A strategy of the spider might therefore be to focus on larger, more profitable prey at the web's periphery by using a larger mesh there (Uetz et al. 1978). In addition, there may be other reasons why some web parts are more valuable than other parts, and the spider could be expected to adjust the mesh size within the web accordingly (Blackledge and Zevenbergen 2006). Finally, most orb webs are vertically elongated to some degree and not circular as assumed in our simulation model. We are addressing these points in a future study.

The exact building costs of different orb-web parts are unknown and may differ between upper and lower web parts (Herberstein and Heiling 1999). Whilst the results of a recent study suggest that web-building costs are higher in the upper part than in the lower part (Coslovsky and Zschokke 2009), its relationship to web asymmetry is still poorly understood and is not considered in our models.

Lastly, physicists have suggested that a circular web with the hub in its centre would be the most advantageous shape from a structural perspective (Denny 1976). Again, the disadvantage that may arise from deviations from this structurally optimal web cannot easily be quantified, and we therefore ignored it in our models.

Conclusions

Our models suggest for spiders waiting for prey on the hub of their non-horizontal orb web that:

- Waiting head down is generally favourable because it allows the spider to reach the prey in its web on average quicker than spiders waiting head up
- The downwards–upwards running speed asymmetry, together with the head-down orientation of most spiders, are likely causes for the observed vertical asymmetry of orb webs
- Waiting head up can be advantageous for spiders whose downwards–upwards running speed asymmetry is small and who experience a high prey tumbling rate
- Spiders waiting head up should place their hub lower than similar spiders waiting head down
- Prey tumbling influences web design more than hitherto supposed

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