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ESTIMATION OF CAPTURE AREAS OF SPIDER ORB WEBS IN RELATION TO ASYMMETRY

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ABSTRACT. We examined the utility of several popular formulae used to estimate the capture areas of orb webs across a large sample of *Cyclosa* Menge 1866 and *Tetragnatha* Latreille 1804 webs. All formulae evaluated contained at least some bias in estimation of the capture areas of webs. We identified two types of asymmetry in orb webs that affect capture area estimation differently. Web asymmetry measures the ratio of the horizontal and vertical diameters of orb webs while hub asymmetry measures the displacement of the hub from the geometric center of a web. An analysis of model webs that varied in web and hub asymmetry showed that most formulae overestimated capture area as web asymmetry increased and that some formulae also overestimated capture area as hub asymmetry increased. Only the ''Ellipse−Hub'' formula was unaffected by web and hub asymmetry. Although the ''Adjusted Radii−Hub'' formula provided a slightly more accurate overall estimate of capture area, we recommend that the ''Ellipse−Hub'' formula be used when comparisons of capture area are made between taxa or individuals that vary in web and hub asymmetry.

Keywords: Web architecture, asymmetry, sticky silk, capture spiral, spider web

Orb-weaving spiders provide excellent models for the study of a variety of questions in behavior and ecology because measurement of the architectural features of webs allows us to quantify and compare many aspects of spider behavior. The sizes and shapes of webs can directly influence both the foraging success and predation risk of spiders (Rypstra 1982; Eberhard 1986; Higgins 1992; Blackledge & Wenzel 1999, 2001). Spiders also actively modify the architectures of webs in response to predators and prey (Higgins & Buskirk 1992; Pasquet et al. 1994; Sherman 1994; Vollrath et al. 1997; Blackledge 1998). Thus, studying architectures of spider webs can give us insight into how spiders confront selective pressures in their environment.

Some aspects of webs can be difficult to measure accurately in the field so that formulaic estimators are instead employed (Heiling et al. 1998; Herberstein & Tso 2000; Venner et al. 2001). For instance, the total area of a web, as delimited by the outermost sticky spiral, or the capture area of a web (total area−the central non-sticky free zone and hub) are often used as indicators of the foraging effort of a spider but cannot be measured directly in the field (Sherman 1994; Tso 1996; Blackledge 1998; Herberstein et al. 2000). Some studies have used single radial measurements or circular approximations to estimate web or capture area from field measurements (McReynolds & Polis 1987; Higgins & Buskirk 1992). But, most orb webs have an elliptical shape and an asymmetric placement of the central hub so that capture areas are estimated poorly by simple circular approximations (ap Rhisiart & Vollrath 1994; Herberstein & Heiling 1999; Herberstein & Tso 2000).

Herberstein & Tso (2000) recently examined the accuracy of several formulae used to estimate the capture areas of webs. They used linear regression to compare the capture areas estimated by four formulae and the actual capture areas of 11 *Argiope keyserlingi* Karsch 1878 webs. Herberstein & Tso found that estimates from the ''Adjusted Radii−Hub'' formula were most correlated with the actual capture areas of webs, and they argued that the ''Adjusted Radii−Hub'' formula provided the best estimator of capture area in part because it accounted for web asymmetry. However, to date there has been no assessment of

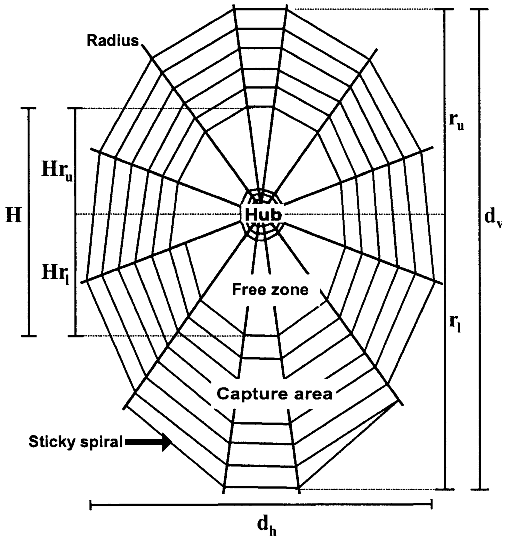

Figure 1.—Orb web illustrating the parameters measured for each of the capture area estimation formulae in Table 1. The outermost spiral of sticky silk delimits total web area. The hub is the innermost portion of the web, where the spider rests, and has a non-sticky hub spiral. The free zone is devoid of a spiral. Capture area is the portion of the web delimited by the innermost and outermost sticky spirals of capture silk. Web asymmetry is a measure of the ratio of the horizontal and vertical diameters of the web $[1 - (d_h/d_v)]$. Hub asymmetry is a measure of the vertical displacement of the hub from the geometric center of the web $[1 - (r_u/r_l)]$. This web has a web asymmetry of 0.27 and a hub asymmetry of 0.26.

the utility of any of these formulae across multiple taxa of spiders even though different species of spiders vary greatly in web architecture. Nor has there been any systematic study of the effects of web or hub asymmetry on the performance of these formulae.

We examine the performance of four capture area estimation formulae, used in the current literature and examined by Herberstein & Tso (2000), for a large sample of *Cyclosa* (Araneidae) and *Tetragnatha* (Tetragnathidae) webs. The webs built by these two genera can be quite different from one another and represent a fairly broad range of the interspecific variation to be found in architectural features of orb webs. *Cyclosa* tend to build webs that are under high tension, have large numbers of radii and long sticky spirals, and are relatively asymmetric, while *Tetragnatha* webs tend to be under lower tension, have fewer radii and shorter sticky spirals, and are more symmetric (see Fig.1 and Zschokke 1999 for definitions of orb-web nomenclature).

METHODS

We photographed webs in the field during a 2 mo study of the diversity of Hawaiian orb-weaving spiders, represented exclusively by *Cyclosa* and *Tetragnatha*. Spiders were collected from webs. Webs were then dusted with cornstarch to improve visibility of silk and photographed using a Nikon SLR camera. Only a single web was photographed per spider. Our sample includes multiple individuals for each species and approximately a dozen species for each genus. But our comparison in this study is restricted to that between *Cyclosa* and *Tetragnatha*. We measured the vertical and horizontal diameters of webs in the field to provide scaling factors (d_v and d_h in Fig. 1). Photographs were digitized and analyzed on a Microsoft Windows computer using the Scion Image program (ported from NIH Image for the Macintosh by Scion Corporation and available on the Internet at http://www.scioncorp.com). Using the digital image, we measured the actual capture areas of webs as delimited by the innermost and outermost sticky spirals and all of the parameters necessary to calculate each of the capture area estimation formulae examined by Herberstein & Tso (see Fig.1 and Table 1). All measurements were scaled using the field measurements of web diameters.

We also calculated two types of asymmetry in the architectures of webs. The term web

Table 1.—Capture area estimation formulae examined in Herberstein & Tso (2000).

Vertical Radii - Hub	$(d_v/2)^2\pi - (H/2)^2\pi$
Tso - Hub	$[\frac{1}{2}\pi r_u^2 - \frac{1}{2}\pi(H/2)^2] + [\frac{1}{2}\pi r_l^2 - \frac{1}{2}\pi(H/2)^2]$
Ellipse - Hub	$(d_v/2)(d_h/2)\pi - (H/2)^2\pi$
Adjusted Radii - Hub	$[\frac{1}{2}\pi r_{au}^2 - \frac{1}{2}\pi(Hr_u)^2] + [\frac{1}{2}\pi r_{al}^2 - \frac{1}{2}\pi(Hr_l)^2]$*

* $r_{au} = (r_u + d_h/2)/2$ and $r_{al} = (r_l + d_h/2)/2$.

asymmetry has been used by previous investigators to refer to a disparity in the amount of silk or area of a web above the hub compared to that below the hub (e.g. ap Rhisiart & Vollrath 1994; Herberstein & Heiling 1999). Increase in web asymmetry is often assumed to be synonymous with an increase in the elliptical shape of webs. But the overall shape of a web and placement of the hub can vary independently, so that there are two separate types of asymmetry in orb webs. Here, we define ''web asymmetry'' as the departure of the outermost spiral of sticky silk of an orb-web from a circular shape, calculated as:

$$\text{web asymmetry} = 1 - d_h / d_v$$

Thus, a perfectly circular web has a web asymmetry of 0 while most webs have asymmetry values slightly > 0. Occasionally, webs will have negative web asymmetries. ''Hub asymmetry'' measures displacement of the hub from the geometric center of the web, regardless of the overall shape of the web. It is calculated as:

$$\text{hub asymmetry} = 1 - r_u / r_l$$

Most webs have hub asymmetry values slightly > 0, while the hub asymmetry of a web with the hub in the geometric center $= 0$.

All four capture area estimation formulae that we consider calculate an estimate of the total area of a web, measured from the outermost spiral of sticky silk, and then subtract a circular approximation of the area of the free zone and hub to calculate the remaining area of the web, which is covered by capture silk (see Fig. 1 and Table 1). The ''Vertical Radii−Hub'' formula provides a simple circular approximation for total web area, using only a single vertical diameter distance each for the total web (d_v) and hub (H) areas respectively (Brown 1981; McReynolds & Polis 1987; Higgins & Buskirk 1992 all use single geometric radial measurements as indices of web area). The ''Tso−Hub'' formula treats the upper and lower halves of a web as separate semi-circles, estimating areas of each semi-circle based upon a single measurement of a geometric radius each (r_u and r_l; Tso 1996). These radii (r_u and r_l) are measured from the hub of the web and will therefore vary with changes in hub asymmetry even when web asymmetry remains constant. The ''Ellipse−Hub'' formula is the only formula that uses an elliptical, rather than circular, approximation of total web area, based upon both horizontal and vertical geometric radial distances (Miyashita 1997; Blackledge 1998; Watanabe 1999). The ''Adjusted Radii−Hub'' formula is a modification of the ''Tso−Hub'' formula that computes geometric radial distances from the average of both the horizontal and vertical geometric radial distances, for both the lower and upper half of the web (Table 1; Herberstein & Tso 2000). The ''Vertical Radii−Hub'' and ''Ellipse−Hub'' formulae calculate geometric radial distances from the geometric center of the web by halving the diameter of the web, which does not vary with hub asymmetry. The ''Tso−Hub'' and ''Adjusted Radii−Hub'' formulae measure geometric radial distances from the hub of the web so that these measurements will vary with changes in hub asymmetry.

After estimating capture areas of webs using each formula, we followed the example of Herberstein & Tso (2000) and used linear regression to examine the relationship between the actual and estimated capture areas of webs. Herberstein & Tso (2000) found that, for *Argiope keyserlingi*, the accuracy of formulae varied by up to 60%. They suggested that some of the differences in accuracies of capture area estimations were due to differences in the abilities of each formula to account for the elliptical shapes of webs. But, Herberstein & Tso (2000) did not specifically examine how accuracy of those formulae was affected by web asymmetry. They also did not examine the impact of hub asymmetry on performance of the ''Tso−Hub'' and ''Adjusted Radii−Hub'' estimators. Therefore we performed a second set of regression analyses examining the correlation between error generated by each estimator and web and hub asymmetry. We calculated the % error generated by each estimate as:

$$(\text{estimated capture area} - \text{measured capture area}) * 100/\text{measured capture area}$$

Finally, we used each formula to estimate the areas of a series of model webs. We generated ellipses that varied in shape from a perfect circle to model webs that had 10 and 20% greater vertical diameters than horizontal diameters (web asymmetry values of 0, 0.09, and 0.17 respectively). For each of these web asymmetry values we also varied hub asym-

Table 2.—Mean estimated capture area and regression of measured capture area versus estimated capture area for each of four different formulae. $n = 226$.

Estimator	Mean ± SE (cm^2)	Functional relationship	$F_{1,225}$	P	Adjusted R^2
Measured area	164.0 ± 7.4				
Vertical Radii - Hub	214.3 ± 11.3	$y = -14.2 + 0.91x$	1090.8	<0.00001	0.829
Tso - Hub	222.2 ± 12.6	$y = -26.4 + 0.89x$	810.9	<0.00001	0.783
Ellipse - Hub	151.6 ± 6.8	$y = 3.2 + 0.99x$	7251.0	<0.00001	0.970
Adjusted Radii - Hub	159.8 ± 7.4	$y = -1.42 + 0.95x$	4499.9	<0.00001	0.952

metry from model webs where the hub was at the geometric center to model webs where hubs were 10 and 20% closer to the tops (hub asymmetry values of 0, 0.18, and 0.23 respectively). This analysis controlled for error generated when real spider webs are not perfectly elliptical in shape as well as any effects of measurement error with the experimental webs. Therefore, any error in estimation of capture area of these model webs is due solely to the effects of web and hub asymmetry.

RESULTS

The ‘‘Adjusted Radii−Hub’’ formula gave the closest mean estimate of capture area to that of the actual capture area, but its mean estimate did not differ significantly from that of the ‘‘Ellipse−Hub’’ formula (Table 2). The ‘‘Ellipse−Hub’’ formula was slightly more correlated with variation in the actual capture areas of webs (see R^2 in Table 2). Both of these formulae tended to underestimate capture areas of webs (Table 2). In contrast, the ‘‘Vertical Radii−Hub’’ and ‘‘Tso−Hub’’ formulae both greatly overestimated sizes of webs and were about 20–25% less correlated with actual capture areas (see R^2 in Table 2). For larger webs, all formulae, except the ‘‘Ellipse−Hub’’ formula, tended to give higher estimates for the capture areas of *Cyclosa* webs than for *Tetragnatha* webs (Fig. 2).

Web asymmetry was greater for *Cyclosa* (mean ± SE = 0.24 ± 0.02) than for *Tetragnatha* (mean ± SE = 0.13 ± 0.02). Hub asymmetry of webs was also higher for *Cyclosa* (mean ± SE = 0.28 ± 0.02) than *Tetragnatha* (mean ± SE = 0.09 ± 0.02). Web and hub asymmetry were largely uncorrelated with one another ($R^2 = 0.02$; Fig. 3).

Over 90% of the error in estimation of capture areas could be explained by variation in web and hub asymmetry when using the ‘‘Vertical Radii−Hub’’ and ‘‘Tso−Hub’’ formulae (Table 3). Web and hub asymmetry also explained 20% of the variation in estimation error generated by the ‘‘Adjusted Radii−Hub’’ formula. But web asymmetry and hub asymmetry was uncorrelated with error from the ‘‘Ellipse−Hub’’ formula and hub asymmetry explained only 5% of the variation of the total error generated by the ‘‘Ellipse−Hub’’ formula.

Analysis of model webs showed that all formulae gave perfect estimates when there was no web or hub asymmetry (i.e. when web shape was a perfect circle; Fig. 4). Error increased with increasing web asymmetry for all formulae except the ‘‘Ellipse−Hub’’ formula. Error also increased as hub asymmetry increased for the ‘‘Tso−Hub’’ and ‘‘Adjusted Radii−Hub’’ formulae. Overall, the ‘‘Vertical Radii−Hub’’ and ‘‘Tso−Hub’’ formulae generated much larger errors, an order of magnitude larger than the ‘‘Adjusted Radii−Hub’’ formula. The ‘‘Ellipse−Hub’’ generated no error in the estimation of capture areas of model webs as web or hub asymmetry changed.

DISCUSSION

We found that the ‘‘Adjusted Radii−Hub’’ formula of Herberstein & Tso (2000) produced a mean estimate of capture area of webs that was closest to the mean of the actual measured values, but that capture area estimates from the ‘‘Ellipse−Hub’’ formula were more correlated with measured capture areas of individual webs (Table 2). Both the ‘‘Vertical Radii−Hub’’ and ‘‘Tso−Hub’’ formulae performed much worse, giving mean estimates of capture area that were approximately 30% greater than the mean of the measured capture area. Estimates from the ‘‘Vertical Radii−Hub’’ and ‘‘Tso−Hub’’ formulae were also about 20% less correlated with measured

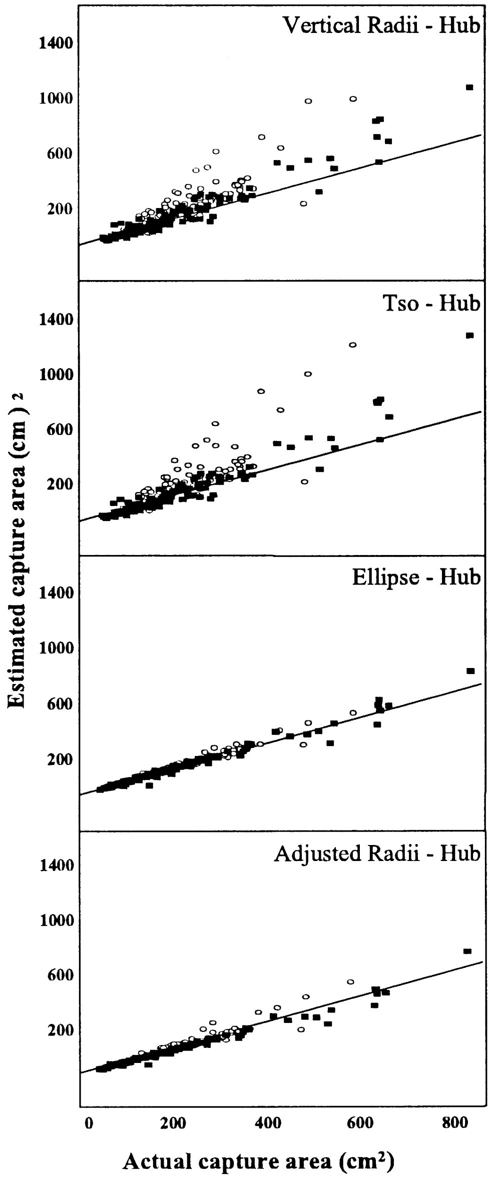

Figure 2.—Relationships between capture area estimates and actual capture areas of webs for each of four formulae. Lines denote perfect correlations. ■ = *Tetragnatha,* ◦ = *Cyclosa.*

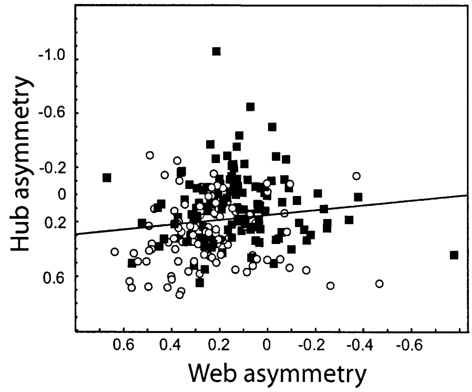

Figure 3.—Hub and web asymmetry can vary independently of one another in webs (R^2 = 0.02). ■ = *Tetragnatha,* ◦ = *Cyclosa.*

capture area compared to estimates from the ‘‘Ellipse−Hub’’ and ‘‘Adjusted Radii−Hub’’ formulae (Table 2).

Our analysis of model webs gives an explanation for much of the error generated by capture area estimation formulae. The analysis demonstrates that all formulae except for the ‘‘Ellipse−Hub’’ formula give biased estimates as web asymmetry increases (Fig. 4). The ‘‘Vertical Radii−Hub’’ and ‘‘Tso−Hub’’ formulae give gross over-estimates of the capture areas of elliptical webs because their circular approximations of web area use only vertical measurements when calculating area. The ‘‘Adjusted Radii−Hub’’ formula performs better because it calculates an average distance based upon both vertical and horizontal measurements. Yet, the ‘‘Adjusted Radii−Hub’’ formula still generates some error with increasing web asymmetry because its estimation is based upon approximating capture area as two semi-circles, rather than a single ellipse, even when a web has an elliptical shape. The ‘‘Tso−Hub’’ and ‘‘Adjusted Radii−Hub’’ formulae have a second source of bias. The error of both estimators also increases with hub asymmetry, even when capture area is constant (Fig. 4). This error occurs because both of these formulae calculate radial measures from the center of the hub of the web rather than the geometric center of the web. As hub asymmetry increases the semicircular estimate of the capture area of the lower halves of webs greatly overestimates capture area, while capture area of the upper halves of webs is underestimated. Because most of the capture areas of webs with high hub asymmetry is in the lower half, the overestimation of area in the lower halves of webs overshadows the underestimation of areas in the upper halves of webs resulting in a net overestimation of web capture area.

These findings from model webs largely agree with our data from real webs. Error was

Table 3.—Regression of the error of capture area estimates on web (x) and hub (z) asymmetry. Web and hub asymmetry were significant predictors of error for all formulae, except the "Ellipse − Hub" estimator for which only hub asymmetry was significant.

Estimator	Functional relationship	$F_{2,224}$	P	Adjusted R^2
Vertical Radii − Hub	y = 1.1 − 0.94x	970.6	<0.00001	0.90
Tso − Hub	y = 1.3 − 0.87x − 0.23z	1120.6	<0.00001	0.91
Ellipse − Hub	—	2.6	N.S.	0.02
Adjusted Radii − Hub	y = 0.2 − 0.31x − 0.33z	37.4	<0.00001	0.25

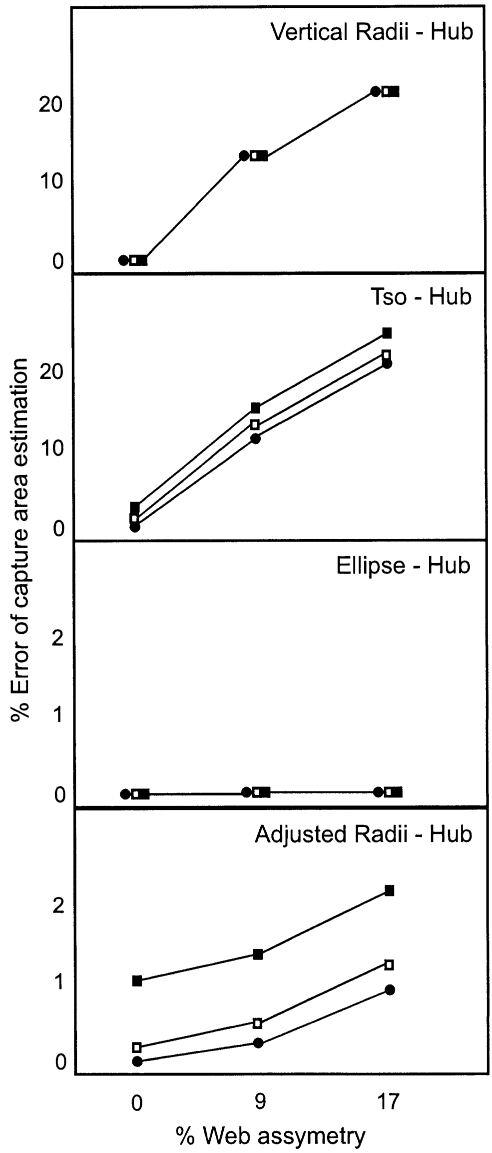

Figure 4.—Error generated by formulae when estimating capture area of model webs of perfect elliptical shape that vary in web and hub asymmetry. Hub asymmetry: ● = 0%, □ = 18%, and ■ = 23%.

strongly related to both web and hub asymmetry for the "Tso−Hub" formula (R^2 = 0.99, Table 3). Web asymmetry also explained much of the variation in error from the "Vertical Radii−Hub" formula (R^2 = 0.90, Table 3). Unexpectedly, hub asymmetry was also a significant predictor, although its slope in the regression analysis was much smaller than for web asymmetry indicating that hub asymmetry accounted for much less of the variability in error (β = 0.86 and 0.12 respectively). Both web and hub asymmetry were also correlated with the error generated by the "Adjusted Radii−Hub" formula, but explained relatively less of the error generated by this formula (R^2 = 0.19, Table 3). An additional source of error for all formulae can be explained by the extreme reduction in sticky silk in the upper portions of some webs. Especially for spiders such as *Cyclosa* (pers. obs.) or *Nephilengys* (Edmunds 1993) that sometimes build webs with little or no sticky silk above the hub, webs with extreme hub asymmetry can assume a semi-circular, rather than elliptical, shape that cannot be accurately estimated by any of the formulae. Thus, departure from an elliptical shape by some orb webs is a third important source of error when estimating capture area, although our study gives no evidence to suggest whether formulae differ in their ability to account for oddly shaped webs. A final source of error is that introduced by researchers when making the measurements of parameters necessary to use each formula. Although we did not examine how this varies between formulae, we expect this source of error to be greater for formulae that require more parameters.

Overall, the performance of the "Vertical Radii−Hub" and "Tso−Hub" formulae were so poor that we recommend they not be used. The "Adjusted Radii−Hub" gave a slightly more accurate estimation of capture area than the ‘‘Ellipse−Hub’’ formula when averaged across all webs, but its precision was slightly worse (Tables 2 & 4, total range of errors was −39 to +56% and −21 to +58% respectively). The ‘‘Adjusted Radii−Hub’’ formula had a lower mean error because it tended to underestimate areas of symmetric webs but overestimated capture area when web and hub asymmetry were high resulting in a low net error, while the ‘‘Ellipse−Hub’’ formula consistently underestimated capture areas of all webs slightly. Because the error generated by the ‘‘Adjusted Radii−Hub’’ formula changes systematically with variation in web and hub asymmetry, we recommend that investigators use this formula only in studies in which web and hub asymmetry are known to be relatively similar between webs to prevent *a priori* biases when comparing capture areas. The ‘‘Ellipse−Hub’’ formula may be the most efficient formula to use. It has a small overall error and relative independence from changes in web and hub asymmetry. Furthermore, the small number of measurements necessary to use the ‘‘Ellipse−Hub’’ formula not only reduces measurement errors, it may also allow the formula to be used on damaged webs in the field when all of the measurements necessary to use a more parameter rich formula might not be possible (e.g. if the hub of a web is damaged). Finally, all formulae use a circular approximation to calculate the area of the free zone. Using an elliptical approximation such as that used to calculate the total area of the web in the ‘‘Ellipse−Hub’’ formula would further improve estimation of capture areas of orb webs.

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