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Negative allometry of orb web size in spiders and the implications for the evolution of giant webs

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Abstract. Spider webs, and in particular orb webs, are among the most iconic characteristics of spider biology. The evolution of, and developmental changes in, orb webs have been well studied, but we still have a limited understanding of allometric relations between the size of orb webs and spider body size. In this study, we investigate this relationship using measurements from 55 individuals of two common orb-weaving spider (Araneidae) species in South Wales, UK. We recorded body size using two methods: direct measurements with calipers, and estimations from photographs using ImageJ software. We found that these two methods give almost identical measurements, supporting the use of image-based size measurement in many situations where this is advantageous. We also found evidence for negative allometry of orb web size (relative to spider body length), such that larger spiders build proportionately smaller webs. This implies that the 'giant webs' in some orb-weaver species must be the result of a fundamental shift in the constraints or advantages which result in the allometric relationships described here.

Keywords: Body size, orb web construction, measurement techniques, Araneidae
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Allometric scaling of biological traits refers to the way these traits change as the body size of the organism increases (Schmidt-Nielsen 1984). Since body size has a major impact on biological diversity at all levels by placing constraints and limits on biomechanics, physiology, and ecology (Gould 1971; Schmidt-Nielsen 1984; Peters 1986; West et al. 1997), studies of allometry are key to understanding the evolution of many important traits. Furthermore, the shape of the allometric relationship can provide important insights into the plausible physiological constraints behind a trait and the effects of gigantism or dwarfism on the traits in question.

Despite allometric growth being evident in all taxonomic groups, research has focused mainly on scaling of growth within higher vertebrates (Sebens 1987), and this reflects a broad taxonomic bias against invertebrates (even more so if insects are excluded) in animal behavior (Rosenthal et al. 2017). Here we contribute towards reducing this knowledge gap of scaling and growth amongst terrestrial invertebrates by focusing on spiders. Specifically, we investigate the relationship between the body size of orb-weaving spiders (Araneidae) and the size of the webs they build.

Orb-weaver spiders are found on all continents except Antarctica and make up ~25% of the 51,000 known extant species of spiders (Hormiga & Griswold 2014). The evolutionary history of the orb web remains debated (Hormiga & Griswold 2014), particularly whether there was a single origin of orb webs or multiple independent origins, with most but not all studies favouring a single origin and multiple subsequent losses (Dimitrov et al. 2012; Bond et al. 2014; Garrison et al. 2016; Fernández et al. 2018; Coddington et al. 2019). Araneoidea is a large superfamily of orb-weaving (and other) spiders and contains some of the most intensively studied spider genera (Hormiga & Griswold 2014). It includes Araneidae, the third largest family of spiders (Scharff 1997), to which both species considered herein belong.

Previous studies comparing different orb-weaver species living in the same local areas have predictably found that species with larger body sizes have larger capture areas within their webs (LeGuelte 1966; Carrel & Deyrup 2019; Hesselberg & Simonsen 2019). Many studies have found that larger individuals of a species tend to build larger webs, using either age categories (Kuntner et al. 2008) or direct measurements of size of the spiders (Alam & Butt 2016). Similarly, larger individuals of *Larinioides sclopetarius* (Clerck, 1757) build larger webs, though this relationship is far stronger for juveniles than adults (Heiling & Herberstein 1998). However, Dahirel et al. (2019) found that the relationship between body size and web size in *Araneus diadematus* Clerck, 1757 was dependent on spatial scale. Specifically, they found no relationship across different landscapes or populations, but a weak-moderate (though statistically significant) positive correlation within populations. This suggests that although orb web size is likely to vary with spider body size, there is behavioral flexibility in web size that can allow spiders to optimise web size for their current microhabitat. Beyond web size, spider body size has been found to be associated with structural properties of webs (e.g., LeGuelte 1966; Craig 1987; Kuntner et al. 2008; Sensenig et al. 2010; Alam & Butt 2016; Eberhard 2020), and so there is good reason to think that spider body sizes have important ecological implications for the construction of their webs. Nevertheless, investigations of *how* web size or other structural attributes increase with spider body size, their allometric scaling, are lacking (but see Anderson (1987) for an example showing negative allometry in a purse-web spider, Atypidae, and Eberhard (2020) for data suggesting the same in *Nephilingis cruentata* (Fabricius, 1775)).

Building larger webs appears to come at an energetic cost, though this may be offset by improved foraging success compared to building a smaller web (Venner et al. 2003). This trade-off presumably arises because larger webs, with greater capture areas, are more effective at capturing prey than smaller webs (Watanabe 2001; Blackledge & Eliason 2007). However, evidence for increased prey capture with web size is ambiguous, with some studies finding no relationship (e.g., da Silva et al. 2021) and others finding relatively weak increases in prey capture rate with orb web size, though bigger webs can catch bigger prey items (Venner & Casas 2005; but see Harmer et al. 2015). Given these costs and the limited evidence for benefits of building large webs, it is surprising that some species have evolved 'web gigantism': building disproportionately large orb webs, in some cases well in excess of the range of sizes found in other orb-weavers (Gregorič et al. 2015a). In particular, bark spiders of the genus *Caerostris* Thorell, 1868 build large orb webs that can be >1m in diameter with a $>2\text{m}^2$ capture area, despite having a body size of only 17.9–22 mm (Kuntner & Agnarsson 2010; Gregorič et al. 2015a, b).

The relationships between biological traits and body size are frequently non-linear and can be described by the generalised power law of the form $x = aS^b$, where x is the trait in question, S is size (typically body mass), a is an empirical constant, and b is the allometric exponent. Three types of allometric scaling can be distinguished based on the value of the allometric exponent (Schmidt-Nielsen 1984). Negative allometry, when $b<1$, is when the value of the trait increases at a slower rate than body size, such that large organisms have proportionally smaller traits. Positive allometry, when $b>1$, is when the value of the trait increases at a faster rate than body size, such that large organisms have proportionally larger traits. Isometry, when $b = 1$, represents a trait whose rate of increase is proportionally equal to that of body size, such that the trait is a constant size relative to body size.

There are several common allometric exponent values that apply to many morphological, physiological, and ecological traits due to their relationships with fundamental attributes such as the surface:volume ratio ($b = 0.67$) and nutrient/physiological distribution networks ($b = 0.75$). These specific exponent predictions apply when the measure of body size is body mass (as is typical in allometry studies), but in the current study we only have data on body length. Hence, we refrain from comparing our estimated values for the allometric exponent to these theoretical predictions, and instead concentrate on evaluating the rate of increase of orb web size as body length increases. We note that the use of length as the body size measure in allometric equations is not novel here (Martin 1980; McNab 1988; Heymsfield et al. 2007) and enables future predictions to be made for a wide range of spider species which have length but not (live) mass data available (e.g., from museum or fossil samples).

Measuring body mass of very small specimens in the field, museum specimens, and extinct species can be difficult or impossible, so using body length (such as in our allometric models) is beneficial in many cases. Direct measurement using tools such as ocular reticules or calipers is the standard method of measuring length, however, an alternative method is the use of image analysis of photographs containing a size standard (an object of known size) for calibration. Free software such as ImageJ (Schneider et al. 2012) allows photographs to be easily processed by individual researchers (perhaps including citizen scientists). Nevertheless, despite being a non-invasive and accessible method, photograph-based techniques may suffer from inaccuracies that hamper their use. For instance, if the subject and/or size standard is photographed at an oblique angle the method may systematically underestimate the size, so quantitative evaluation of these methods is needed.

Here, we investigate the allometric relationships of orb web size and present results addressing two aims. First, we examine how orb web size changes with body length, predicting a positive relationship but negative allometry due to the increased costs of building larger webs. Second, we evaluate the accuracy of photographic methods for collecting data on body length of spiders in the field, expecting reasonable performance but slight underestimation of body size.

METHODS

Data were collected in two recreational parks in Swansea, Wales: Singleton Park (Ordnance Survey National Grid SS 63090 92296; 51.612797°N, 3.977549°W) and Brynmill Park (SS 63398 92574, or 51.615370°N, 3.974380°W). Swansea is a coastal city located near the Gower Peninsula, a designated Area of Outstanding Natural Beauty (AONB). The two parks are situated within the urban town area, and land use is primarily residential. The area has a mild, temperate, oceanic climate.

Data were collected over five days between 15 October 2017 and 10 November 2017. On each day, at least ten samples were collected over a 3-hour period from 11 am to 2 pm. We located orb webs attached to vegetation and/or metal railings, and identified spiders using Bee et al. (2017), collecting 55 spiders in total consisting of 12 *Araneus diadematus* and 43 *Zygiella x-notata* (Clerck, 1757). In addition to our main variables of interest (body length and web size), we also recorded species from each observation.

The web size was measured as the maximum width of the web on a horizontal axis across the capture area, i.e., web diameter, and was recorded to the nearest millimeter using a tape measure. Our choice of web measurement was based on Vincent & Lailvaux (2006), who found that this diameter was the strongest correlate of spider body size of several web measures they used. We note that the two species considered here do not have dramatically asymmetrical capture areas, being roughly circular, and so our linear measurement of web size should be representative (perhaps explaining the results of Vincent & Lailvaux (2006) as their study species also has roughly circular capture areas).

To measure the spider's body length, we first removed it from its web and placed it into a small box to enable manipulation for accurate measurement. Body length was measured directly from the most anterior point of the cephalothorax to the most posterior point of the abdomen using a pair of calipers with a precision of 0.01 mm. We then photographed the dorsum of the spider from directly above using the (8 megapixel) camera of an iPhone 6, alongside a coin as a size standard for calibration, which enabled subsequent body length measurement using ImageJ (Schneider et al. 2012). The spider was immediately returned to the web following these procedures.

Prior to analyses of allometric relationships we $\log_{10}$ transformed both web size and body size (for which we used our caliper measurements), since it is typically proportional rather than absolute size change that is biologically important. For the same reasons, this is standard practice in studies of allometry where, for instance, a doubling of web size with a doubling of body size is the pattern expected for isometry. Additionally, log-transforming these variable means the coefficients in our Generalised Linear Models (GLM) represent the allometric exponents in the equations above. We examined the relationship between orb web size (response variable) and body size (explanatory variable) using a GLM with a Gaussian distribution. Because we had two different species in our dataset, we also checked whether these species had different web sizes for a given body size by fitting another two GLMs, identical to the first but including species with or without an interaction with body size. However, neither of these models provided any improvement in fit over one without species included nor was species (with or without an interaction with body size) a significant predictor of orb web size. Hence, we find that the same allometric relationship applies to both species and only present results of the first model, although for illustrative purposes we distinguish species in our figures where appropriate.

Finally, we compared body length measurements obtained directly via calipers and indirectly via photographs analysed in ImageJ using a one sample t-test. We subtracted the ImageJ measurements from the caliper ones and tested for systematic deviations from a difference of 0 (which would indicate identical measurements from both methods).

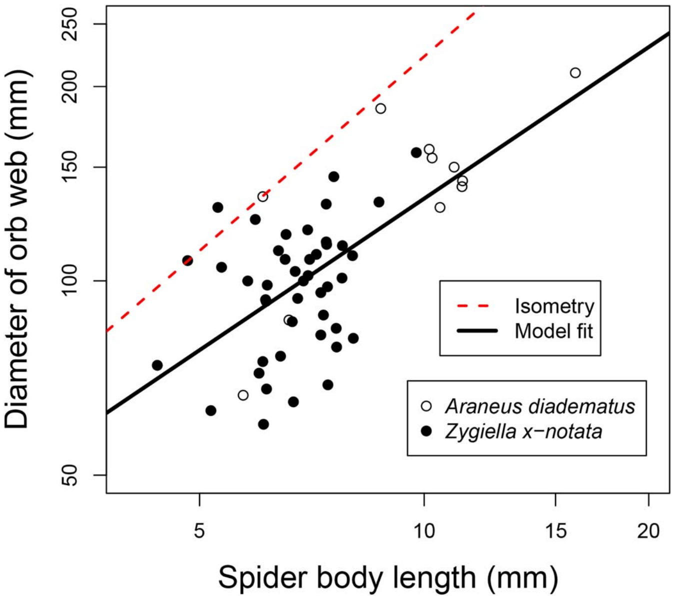

Figure 1.—Allometric relationship between orb web diameter and spider body length. Note that both axes are on log scales. Solid black line shows model fit and is compared to the predicted (dashed red) line based on isometry. The two species included in the analyses are distinguished in the plot for visualisation purposes (open circles, *A. diadematus*; closed circles, *Z. x-notata*) but were analysed together as no evidence was found for different allometric relationships.

All statistical analyses were carried out in RStudio version 3.3.2 or R version 3.4.1 (R Core Team 2016).

RESULTS

Araneus diadematus were larger on average than *Zygiella x-notata* (9.47 ± 2.99 vs 6.81 ± 1.02 mm) and also had correspondingly larger webs (137.88 ± 40.62 vs 99.37 ± 22.55 mm). Body size ranged from 4.39–15.95 mm across species (5.72–15.95 mm for *A. diadematus* and 4.39–9.76 mm for *Z. x-notata*), and the orb web size ranged from 60–210 mm across species (66.5–210 mm for *A. diadematus* and 60–158 mm for *Z. x-notata*).

We found evidence of negative allometry (Fig. 1; Table 1) such that, although bigger spiders produce bigger webs (GLM: $t_{1,53} = 6.119$, $P = 1.2 \times 10^{-7}$), web size increases at a slower rate than body size. In other words, web size gets *proportionally* smaller as orb-weaving spiders get bigger. The allometric exponent was estimated as 0.78 (Table 1), with the full allometric equation estimated as $D = 22.28L^{0.78}$, where D is orb web diameter (mm) and L is body length (mm).

Our comparisons of caliper *vs.* photograph-based image analysis as methods for measuring body size found no difference in body size based on measurement method (one-sample t-test: $t_{54} = -0.472$, $P = 0.639$; Fig. 2). In addition to the statistical support for similarity of the measurements, the absolute magnitude of the differences amounted to a mean body size measurement 0.06 mm larger using ImageJ on photographs. This is only ~0.8% of the mean body size in our sample, strongly demonstrating that measurements made using the two methods were indistinguishable and of negligible magnitude.

Table 1.—Allometric relationship of $\log_{10}$ orb web diameter based on GLM analysis. SE = standard error of the estimated coefficient.

	Coefficient	SE	t	P-value
Intercept	1.348	0.110	12.266	$<2 \times 10^{-16}$
$\log_{10}$(body length)	0.780	0.127	6.119	1.2×10^{-7}

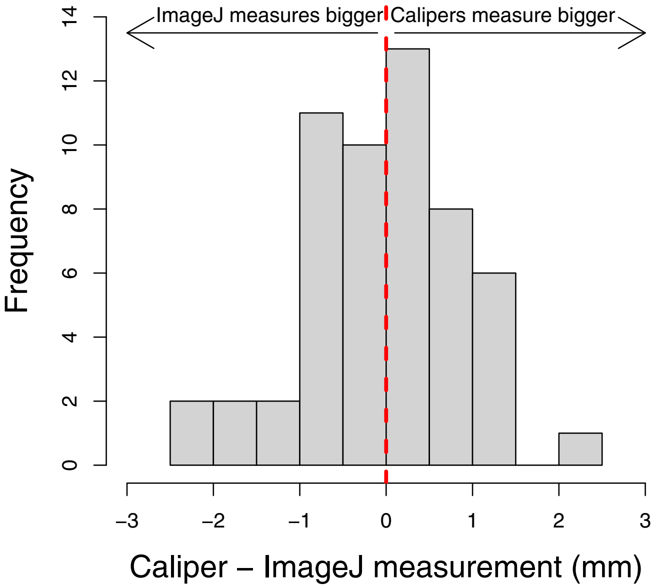

Figure 2.—Histogram of differences in body length measurements between calipers and photographic analysis in ImageJ. Dashed red line shows identical measurements between the two methods.

DISCUSSION

We investigated two species of orb-weaving spider to understand the allometric relationship of web size and methods for measuring size. We found that larger spiders built larger webs (with indistinguishable relationships for the two species) but that web size showed negative allometry, such that larger spiders had *proportionately* smaller webs. Comparing direct measurements of body size using calipers with those using image analysis of photographs, we find that the latter method performed better than expectations and appears to be a highly accurate alternative to direct measures.

Allometry of web size.—Our finding that web size increases with body size is consistent with previous literature on many different species, in which the same pattern was found (LeGuelte 1966; Benforado & Kistler 1973; Heiling & Herberstein 1998; Venner et al. 2003; Gregorič et al. 2015b; Dahirel et al. 2019; Eberhard, 2020). However, our study adds to previous work by estimating *how* web size increases with body size in terms of allometric relationships, rather than simply demonstrating that it does. Specifically, orb web size increases with negative allometry as larger spiders appear to build relatively smaller webs. This is perhaps due to costs of silk production. Gregorič et al. (2015b) found that investment in silk produced by orb-weavers showed similar negative allometric relationships, although web structure and silk investment can both be altered to manage these body size-dependent costs to some extent. Although costs of producing silk increase proportionally to body size (Venner et al. 2003), the effectiveness of the web produced may not continue to increase, leading to lower investment in web size in larger spiders (Gregorič et al. 2015b). Hence, the trade-off between building a larger web (which presumably conveys some benefit) with limited material due to scaling of energetic costs of construction and silk production (Venner et al. 2003; Gregorič et al. 2015b) are one plausible explanation of our results. In essence, web size is constrained such that altering structural or chemical attributes of the web that convey biomechanical benefits to interception or retention of prey is a better strategy than simply increasing web size. We note that the generality of our analyses may be limited by our inclusion of only two species in our sample. However, the fact that our allometric equation is indistinguishable between the two species (despite differences in body size between them) suggests that may it be a general rule, at least amongst Araneidae.

Perhaps because of the costs and trade-offs inherent in web construction, the size of the webs is reasonably tightly linked to body size across species (Gregorič et al. 2015a). However, a small proportion of species have web sizes >1 standard deviation above that expected from body size, with the most extreme cases having web sizes >2 standard deviations greater than expected (Gregorič et al. 2015a). All of the latter cases belong to the genus *Caerostris*, such as the recently described *C. darwini* Kuntner & Agnarsson, 2010, which therefore represent a fairly clear example of 'orb web gigantism' (Kuntner & Agnarsson 2010; Gregorič et al. 2011, 2015a). The mean web diameter for female *C. darwini* is 636 mm while the body size of the spiders was 17.9–22 mm (Kuntner & Agnarsson 2010). Using our allometric equation, an orb-weaving spider of that size would be expected to build webs with a diameter of 211–248 mm (2.5–3 times smaller), or alternatively a spider building a web that large would be expected to be 73 mm in length (3–4 times larger). Hence, the evolution of web gigantism in this *Caerostris* sp. must have been enabled by changes in silk investment (quantity or quality), web architecture, a shift in energetic consequences (greater intake or reduced output via behavioral or metabolic changes), or similar adaptations.

The implied constraints of our finding of allometric growth, and the fact they have been overcome in cases of web gigantism, therefore suggest that substantial changes in the biology of these species must have occurred to free them to evolve such large webs. A fruitful aim for future studies of web gigantism would be to investigate what these changes might be. As a first step, and to confirm this is the case, studies of allometric relationships of web size in *C. darwini* (or among *Caerostris* species) would be useful in understanding how these spiders are able to build such large webs.

If a spider invests in building a bigger web, we would expect greater effectiveness in capturing prey, since greater capture areas should lead to an increased chance of intercepting prey (Waldorf 1976; Eberhard 1986, 1990), though this could be moderated by other factors such as mesh size (ap Rhisiart & Vollrath 1994). Indeed, we would expect this to create a positive feedback loop where larger webs lead to higher prey availability which then leads to larger body size, which in turn will allow a larger energy investment in web building in the future. However, there is variation among studies in their support for more efficient prey capture in larger webs, with some studies finding little or no increase in prey capture rate with increased web size (Venner & Casas 2005; da Silva et al. 2021). The breakdown of the expected relationship between web size and prey capture effectiveness is likely a consequence of the fact that as web size changes, a range of other structural changes occur that may impact subjugation or retention of prey in the web beyond a simple interception function (LeGuelte 1966; Craig 1987; Kuntner et al. 2008; Sensenig et al. 2010; Alam & Butt 2016; Eberhard 2020).

The lack of relationship between prey capture and web size in some previous work is perhaps surprising, but Venner & Casas (2005) suggest that the major benefit of large webs is not number of prey items, but size of prey items. They find that larger individual prey items are found in larger webs, and that these contribute a substantial proportion of the energy available to the spiders. However, Harmer et al. (2015) dispute the importance of 'rare, large prey' to the design of spider webs and instead find that such items comprise a relatively small proportion of energy capture. Nevertheless, the proportion of large *versus* small prey is likely to be highly variable based on location, season, and the baseline species composition of prey communities. In addition to the issues with the 'rare, large prey' hypothesis already mentioned, Eberhard (2013) also shows that the estimates of the biomass of large prey used to support the idea are problematic. Hence, although not entirely discounting the importance of rare, large prey as an important selection pressure for spider web design, current evidence suggests that it is unlikely to explain the limited evidence of a positive relationship between web size and rate of prey capture.

As a study on allometry, we have focused on how web size per se (measured as horizontal diameter of the capture area), but it is important to recognise that such a measurement is not the only functional attribute of spider webs. Larger webs have a larger total capture area, and therefore can reasonably be expected to intercept more prey, however interception is only the first step of prey capture in orb-weaving spiders. Once the prey hits the web, it must be retained long enough for the spider to effectively and safely subdue it before it escapes (Eberhard 2020). Attributes of webs may combine and interact with web size in complex ways to influence the likelihood of intercepting prey or retaining it sufficiently long, and these interactions may vary with body size in ways that can either mask or exaggerate the costs or benefits of larger web size as spider size increases. For instance, Kuntner et al. (2008) found that larger *Clitaetra irenae* Kuntner, 2006 spiders tended to build webs that were more vertically elongated and with the hub nearer the top, which has been suggested to be an adaptation to trapping more moths (Eberhard 2020). Similarly, spiders' webs vary in the number of spirals and radial threads in their webs—a pattern which often changes with size (LeGuelte 1966)—and in structural and biomechanical attributes of the silk used in web construction (e.g., elasticity and adhesiveness) (Craig 1987; Sensenig et al. 2010). Since these are all likely to have an impact on the effectiveness of the web in prey capture, influencing either or both interception and retention of prey, changes in such diverse attributes could explain the pattern of negative allometry seen in the current study. This might be particularly the case if other attributes of webs can change with less cost in energy or resources than web size, as functional effectiveness can then be maintained (or even increased to support the greater demands of a larger spider) by altering structural or chemical aspects of the webs instead of increasing their size.

In an example of structural changes to spider webs that vary with size, LeGuelte (1966) documented that as young *Z. x-notata* grew, the spacing between their spiral threads in their webs became increasingly wide due to the spiders using their legs as a 'measuring tool' to maintain even spacing throughout the web. However, as the growth in spacing and web area increased linearly (related to leg length), this results in relatively smaller webs compared to body mass and hence the spider starts to impose a suboptimal degree of tension in the web. Consequently, to maintain effective function the spiders can weave thicker threads to cope with greater tension and increase the number of these thicker threads. This can potentially lead to maintenance or improvement of web function without necessarily increasing web size (LeGuelte 1966), and these changes may then lead to reduced selection pressure for larger (potentially more costly) webs that would maintain isometric increases in web size.

Image analysis for size measurement.—Our validation of non-invasive body size measurements using photographs taken in the field followed by image analysis using ImageJ is encouraging. Indeed, we found better performance than we expected and demonstrate that this method is highly consistent with direct measurement using calipers. Given equivalent performance, we would encourage the use of photographic measurements of spiders in many scenarios.

First, it breaks down some barriers to productive public engagement with science via citizen science programmes, such as the necessity of resource provision and/or skill requirements. Citizen science can be a highly useful strategy to involve the public in collecting vast amounts of scientific data on larger geographic scales than is often feasible when restricting data collection to a small number of professional researchers (Bonney et al. 2009). Using submitted photographs (with a size standard) for data collection would enable a centralised curator of such records to obtain measurements (and check identifications etc.). Alternatively, such a strategy could enable citizen scientists to collect data using freely accessible software that requires minimum training and no provision of measurement equipment, improving participation (Bonney et al. 2009).

Secondly collection of size measurements from photographs may improve the ease of obtaining such measurements remotely. For instance, appropriate measurements could be made from specimens distributed in collections across the world, and perhaps with less time and effort needed for museum curators, who need only get photographs of all specimens with a size standard. Increased availability of data from specimens while minimising use of the limited resources of collection managers is another potential benefit of image measurements.

Finally, photographic measurements eliminate the need to remove the spider from the web, therefore minimising potential disturbance to the spider. Although short-term and harmless removal from webs (or other habitats) is perhaps unlikely to have severe welfare implications, as field biologists we should aim to minimise disturbance to our study species wherever possible (Soulsbury et al. 2020). Where feasible, photograph-based data collection provides a way to minimise interventions with no loss of accuracy. Other studies have used a similar technique for obtaining web measurements, using stills from a video recording containing a scale for calibration, emphasising the potential versatility of this approach (Rao et al. 2019). Although we were unable to get clear photos of webs with our available camera even when webs were misted with water (Solano-Brenes et al. 2018), other researchers may have more luck with their equipment and be able to use photography for scientific measurement of web size. Nevertheless, estimates of the accuracy of non-invasive web and other biological measurements would help contribute to the ethical practice of our field.

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